

Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.



United States Department of Agriculture

Forest Service

Pacific Northwest Forest and Range Experiment Station

Research Note PNW-362 1980

9.9
254
ERUE

Population Response of the Northern Red-Backed Vole (*Clethrionomys rutilus*) to Differentially Cut White Spruce Forest

Stephen D. West, R. Glenn Ford, and John C. Zasada

COR/STA

2.3
CURRENT SERIAL RECORDS
PERMANENT SECTION

DEC 18 '80

U.S.D.A. NAT'L AGRIC LIBRARY RECEIVED

520

Abstract

The population response of the northern red-backed vole (*Clethrionomys rutilus*) to a differentially cut white spruce (*Picea glauca*) forest 30 km southwest of Fairbanks, Alaska, was monitored by simultaneous livetrapping in a clearcut, in a partially cut or shelterwood area, and in an area of uncut forest. During the first summer after logging, vole density was similar in the shelterwood and uncut forest, but lower in the clearcut. Breeding occurred in all areas, and only overwintering females had litters. Movement between areas was minimal. Populations in all areas were similar in age and sex composition, per capita female reproduction, subadult survival, and the size of average home range. It is hypothesized that an unequal distribution of overwintering females produced the differences in density between areas, and that this difference resulted from variation in ground cover produced by the logging treatments. Population responses of *C. rutilus* to habitat alteration in interior Alaska are compared with responses of *Clethrionomys* populations at lower latitudes.

KEYWORDS: Population dynamics, [wildlife habitat management], animal populations, voles, logging (-wildlife, white spruce, [*Picea glauca*], [Alaska](interior)).

STEPHEN D. WEST is a research assistant professor for forest zoology, College of Forest Resources, University of Washington, Seattle.

R. GLENN FORD is with the Department of Biology, University of New Mexico, Albuquerque.

JOHN C. ZASADA is silviculturist at the Institute of Northern Forestry, Pacific Northwest Forest and Range Experiment Station, Fairbanks, Alaska.

Introduction

The northern red-backed vole, *Clethrionomys rutilus*, occurs in virtually all developmental stages of aspen (*Populus tremuloides*), birch (*Betula papyrifera*), black spruce (*Picea mariana*), and white spruce (*Picea glauca*) forests in interior Alaska. It is an abundant microtine rodent in this region, occasionally reaching fall densities of 80 animals per hectare. Red-backed voles are known predators of white spruce seed (Radvanyi 1966, 1970, 1971; Graber 1969). Tree seed consumption by *Clethrionomys* has been studied in Canada and in the northern United States, and is of increasing interest in Alaska where forests of the interior will be subject to increased harvesting in the future. In the search for data on which to base forest practice recommendations, the Bureau of Land Management and the United States Department of Agriculture, Forest Service in Fairbanks began intensive studies of the consequences of different silvicultural systems in white spruce forests at the Bonanza Creek Experimental Forest southwest of Fairbanks in 1970. During 1972 and 1973, part of this program was devoted to investigating potential differences in numeric response, population structure, long-distance movement, and habitat usage patterns of red-backed vole populations inhabiting differentially cut forest areas.

Study Area and Methods

The study was initiated in summer 1972 on an upland (350-m elevation) white spruce site in the Bonanza Creek Experimental Forest 30 km southwest of Fairbanks, Alaska (lat. 64°51'N, long. 147°44'W). The forest was about 160 years old and had an average density of 494 trees per hectare. Eighty-one percent of the trees were white spruce; and 8 percent were hardwoods, mainly birch and aspen.

Before logging, the areas were surveyed to determine percent cover and frequency of occurrence of all plant taxa. Two cutting methods were used. These produced two 1-hectare and 1.6-hectare clearcut areas and three 2- to 3-hectare shelterwoods (fig. 1). In all harvested areas, full tree logging, a method which removes the entire tree, was used. Each clearcut was bordered by a 30-m or wider zone of uncut forest. The shelterwood areas contained an average of 87 trees per hectare. Site preparation (scarification or the removal of organic matter to expose a mineral soil surface) was uniformly applied in both shelterwoods and clearcuts to evaluate the effect of seedbed preparation on forest regeneration. The centers of each 2- X 4-m scarified plot were spaced in a 5- X 9-m pattern on each area, thus creating a patchwork of scarified and unscarified ground. After logging, vegetation response was observed on each logged area from 20 quadrats with 1-m sides on both scarified and unscarified ground.



Figure 1.--Aerial photograph of Bonanza Creek study area. Snap trapping was conducted on the uncut forest (top left), shelterwood (top center), and clearcut (top right). Live-trapping was conducted on the 1.6-hectare clearcut (bottom center), the uncut forest (bottom left), and the shelterwood (center left).

To assess small mammal populations prior to logging, three areas were snap trapped with McGill mousetraps during the summer and fall of 1972. These areas are shown linearly arrayed at the top of figure 1. The clearcut areas were logged during July and August, and the shelterwood areas were logged in late September 1972. One hundred traps baited with peanut butter and rolled oats were placed in a 10 X 10 grid with 10-m trap spacing on each area and run for 3 consecutive days. Snap trapping was conducted on May 22-25, June 28-30, and September 13-15. Trapping in May and June preceded logging. September trapping was done after the clearcut had been logged, but the shelterwood remained uncut.

The following summer, three untrapped areas, a clearcut, a shelterwood, and a control area of uncut forest were selected for live-trapping. In the study area shown in figure 1, livetrapping was conducted in the left two-thirds of the 1.6-hectare clearcut (bottom center), in the block of uncut forest just to the left of the clearcut (bottom left), and in the shelterwood directly above the uncut forest (center left). One hundred Sherman large size folding aluminum traps were placed in a 10 X 10 grid with 10-m trap spacing, covered with plywood boards to shield traps from the sun, and provided with rolled oats. Livetrapping began on June 10, 1973, and continued for 3 consecutive days, every 2 weeks, until October 26, 1973. Traps were opened at night and closed during the midday hours.

Information taken at each trapping included point of capture, individual identification by means of toe clips, sex, weight, and reproductive condition. Reproductive state was assessed by external morphology, i.e., scrotal testes in males, perforate vagina, lactation, and obvious pregnancy in females. Voles were considered adult if they entered breeding condition at some time during the summer. Subadult voles, including juvenile animals, did not attain reproductive maturity. Home range was estimated with the technique recently presented by Ford and Krumme (1970). The method uses location records of any number of individuals to generate an average home range. Estimates of abundance accounted for the number of voles known to be alive on the trapping grids. Accordingly, voles not captured in a particular trapping period, but caught within two subsequent periods, were included.

Considering the disparate sizes of clearcut and shelterwood, and anticipating different movement patterns among voles inhabiting all three areas, we expected a difference in edge effect between areas. Accordingly, each area was analyzed for edge effects following the procedures of Pelikan (1970). Using a chi-square test, we compared the total number of captures on the five concentric rings of traps on the trapping grid with the total expected if captures occurred on the grid randomly. By progressively testing observed and expected proportions with χ^2 , we eliminated successive concentric rings of traps; both shelterwood and clearcut were found to have edges two-trap-stations wide (20 m), while the control had an edge one-trap-station wide (10 m). Density estimates were derived by excluding voles caught only in traps on lines within the estimated edge. Voles were considered residents only if they had been captured more than once, and further, captured at least once on the interior portion of the trapping grid.

Results

The snap trapping survey in 1972 indicated that the areas shared a common species composition and abundance of small mammals before logging. A total of four C. rutilus and one shrew (Sorex) on the control, three C. rutilus on the clearcut, and six C. rutilus and one Sorex in the shelterwood were captured in May and June. These numbers represent typical population sizes for early summer in spruce forests, because interior Alaskan populations of red-backed voles undergo an annual fluctuation of abundance, with lowest numbers during early summer and peak numbers during late summer and fall (Whitney 1976, West 1979). The September trapping, which occurred after the clearcut was logged, reflects increased density of animals in the fall, with 26 C. rutilus caught in the control, 22 C. rutilus in the clearcut, and 27 C. rutilus in the shelterwood.

Density and partial distributions of maturity and sex for the resident animals from each area during summer livetrapping are given in figure 2. The subadult sex ratio of residents was not significantly different from one to one on any area (χ^2 , $0.9 \geq p \geq 0.1$), and subadult males and females have been pooled in figure 2.

Slightly more animals were captured in the shelterwood than the control. If we had not considered the effects of edge, the density of resident voles between areas would have been misinterpreted. When we allowed for the same edge effect in the 1972 snap trapping and included the animals removed earlier in the summer, the September densities of resident voles in both control and clearcut were very similar between years. Calculated densities were 18 voles per hectare in 1972 versus 19 voles per hectare in 1973 in the control, and 10 and 11 voles per hectare in the clearcut. The shelterwood was not comparable between years, because it was logged after the 1972 snap trapping.

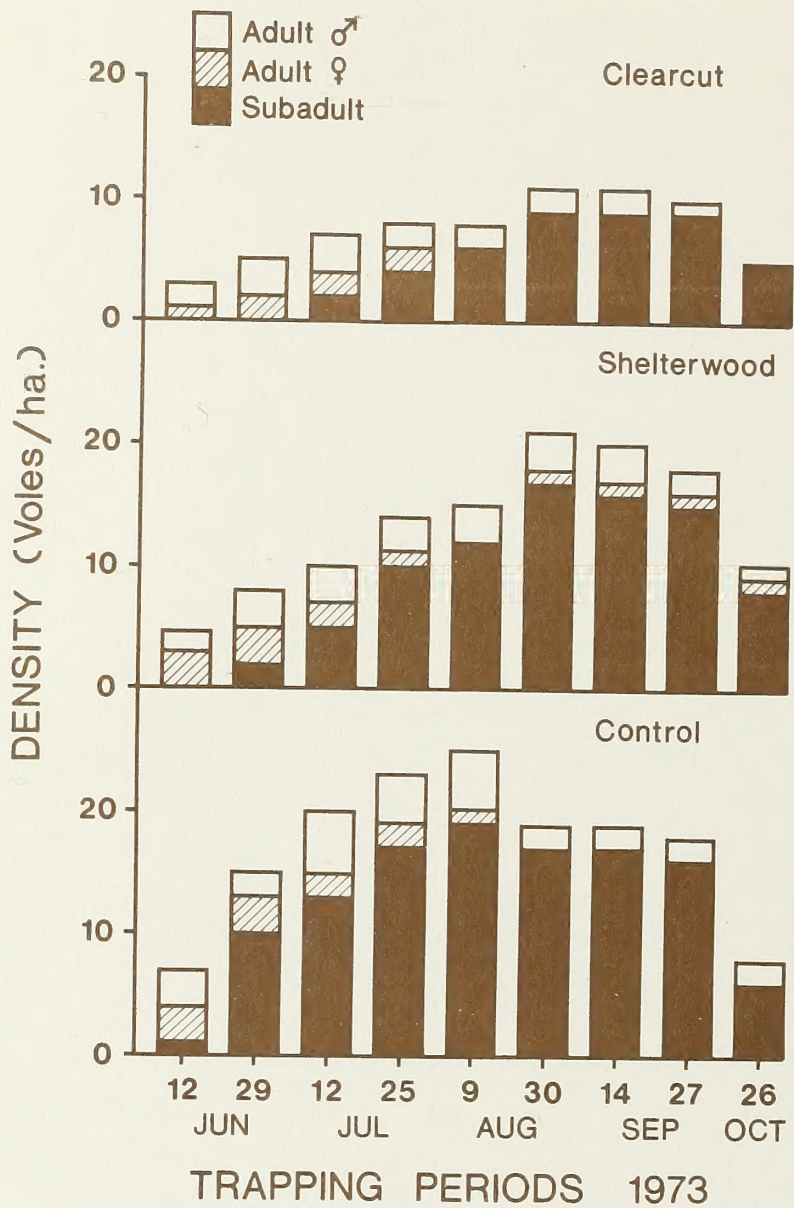


Figure 2.--Density of *C. rutilus* per hectare (ha) on the clearcut, shelterwood, and control livetrapped during summer 1973. Each date represents the 2d day of a 3-day trapping period. For estimation of density see text.

Maximum density of voles in the clearcut was about half that observed in either shelterwood or control. Both shelterwood and control supported very similar maximum densities, although peak density was reached a month earlier on the control than on clearcut or shelterwood. Maximum density occurred in both clearcut and shelterwood in early September. Replicate population measurements, however, were not taken in different areas within the three logging treatments; and the statistical significance of different densities cannot be assessed across treatments.

Between-area movement was not an important factor in producing the apparent density difference. Over the course of the summer, only 13 voles (10 males) were caught on more than one area. There were 27 movements between areas, representing 3.9 percent of all movements. Permanent exchange between areas resulted in adding one vole to the clearcut and two to the shelterwood. These were lost from the control.

The proximal cause of low density in the clearcut was low recruitment of young. The proportions and the sex ratios of mature voles were similar in all populations, except for a slightly greater abundance of adult males in the clearcut. The proportion of the population that was adult male in the clearcut was 0.29, the shelterwood 0.17, and the control 0.19. Similarly, adult and subadult females accounted for 0.10 and 0.62 of the population in the clearcut, 0.10 and 0.73 in the shelterwood, and 0.08 and 0.73 in the control. A critical determinant of recruitment is the total number of breeding females present in each area. From June 12 through August 9, only two different breeding females were captured in the clearcut, while three and four were caught in the shelterwood and control, respectively. In the clearcut, one female was caught in the June 12 trapping period, the other for the first time in the June 29 period. All other overwintering females, except for one female in the control caught in the June 29 period, were caught in the first trapping period.

Total numbers of litters per female were similar in all areas. Overwintering females were responsible for all reproductive output. Three breeding females produced a single litter and six produced two litters, in all cases with postpartum impregnation. One of the two females in the clearcut had two litters, the other just one. As a result, an average of 4.3 young per litter reached trappable age in the clearcut, 4.4 young per litter in the shelterwood, and 5.0 young per litter in the control. Total number of litters per female were similar in all areas in spite of variation in the onset of breeding. Of 36 resident males caught initially as juveniles or subadults, only 7 attained sexual maturity, 1 in the clearcut, 1 in the shelterwood, and 5 in the control. None of the 34 resident subadult females became sexually active.

Recruitment in logged areas was delayed about a month in relation to the control. Young voles were present on June 12 in the control, but not until July 12 in the clearcut. Allowing 20 days to reach trappable age (Morrison et al. 1954) and a 25-day gestation period (Whitney 1976), reproduction began in the control in the 1st week in May. The larger number of males reaching maturity in the control probably reflected the earlier initiation of breeding in that area. Reproduction ceased in all areas in early August.

Subadult survival over the summer was also similar between areas, as indexed by the average number of days subadult voles were present on the trapping grids. In the clearcut, subadult animals were present an average of 47 days, compared with 55 days in the shelterwood, and 50 days in the control.

For most ground-level plant taxa shared among areas, the dispersion and abundance of the plants in the control differed greatly from that in both clearcut and shelterwood.¹ The data for plant dispersion (frequency of occurrence) indicate some differences between the clearcut and shelterwood, but plant dispersion is probably an unimportant determinant of small mammal density in these areas. This is the case, as will be shown below, because average home range size of red-backed voles easily encompasses the small scale plant dispersion pattern. In terms of abundance (percent cover) of shared plant taxa, the clearcut and shelterwood were virtually identical, with the exception of moss cover, which was two times greater in the shelterwood. Pre-logging analyses of vegetation showed that these areas contained similar moss coverage. The greater abundance of moss cover in the shelterwood was a result of the logging operation which left some ground undisturbed at the base of unharvested trees.

Since an edge effect was present in each area, which would cause underestimation of home range, home ranges were calculated for resident voles only. Further, given similar population structure in all populations, location data for all residents were pooled and an average home range estimate calculated to compare population movement patterns between areas. This procedure admittedly obscures different sex and age-related movement patterns.

¹Vegetation data on file at Institute of Northern Forestry, USDA Forest Service, Fairbanks, Alaska 99701.

The question we ask, however, is not whether different movement patterns exist among sex and age classes, as they surely do, but whether similarly structured populations show different space-use patterns on extensively altered habitat. The probability of capture (P) as a function of the minimum area which will contain P is shown in figure 3. The use of space by resident animals was very similar in all areas. The curve for the shelterwood lies consistently above the other curves, but this difference is not statistically significant. Because replicate measurements were not taken in different areas within the three logging treatments, this test is inferentially ambiguous since the home range response might have been due either to a priori differences in movement tendencies of voles inhabiting each area or to their response to habitat alteration caused by the logging treatment. That voles residing on the three areas would have different inherent movement tendencies seems unlikely because these populations were all derived from the larger population which inhabited the very uniform white spruce forest before logging. The most likely expectation would be that voles colonizing the clearcut would have a tendency toward longer range movement.

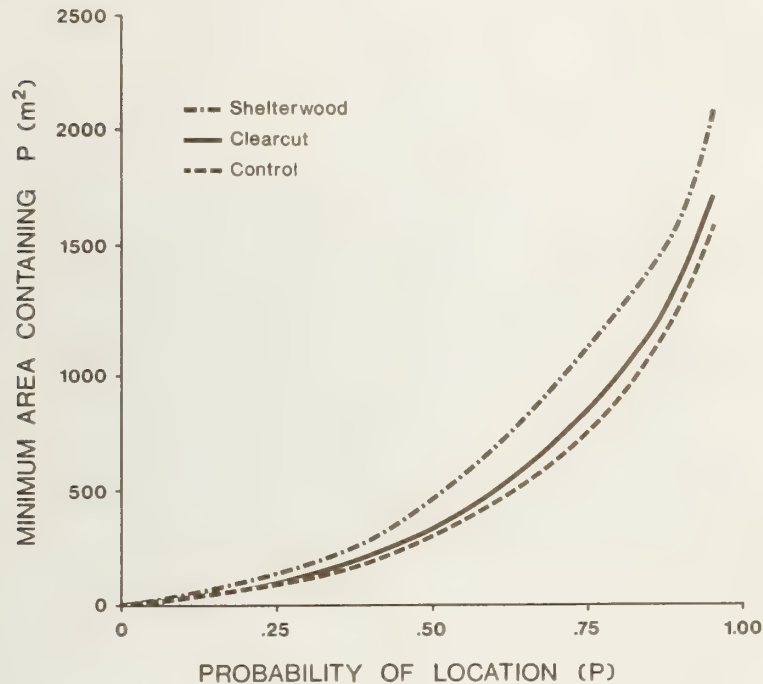


Figure 3.--Home range size computed for resident voles on the clearcut, shelterwood, and control. The abscissa is the probability of locating a vole (P) and the ordinate is the minimum area (m^2) which will contain P . Differences between the three curves are not significant.

Thus, in this study, as was the case in severely burned and unburned forest (West 1979), there was no support for the hypothesis that C. rutilus might increase the size of home range in response to extensive habitat alteration. If this were the case, the curve for the clearcut would have been highest, followed by the curves for shelterwood and control. In fact, the curves for clearcut and control were nearly identical. In terms of the general shape of the curves and home range configuration, there is better than a 0.50 probability of locating C. rutilus in less than 500 m². Beyond this core area, successive increments of area yield proportionally smaller increases in probability of location. An area roughly 2 000 m² is required to enclose 0.95 of all locations.

Discussion

This study has demonstrated substantial similarity between the populations in each treatment area. The most apparent population response was an alteration of density, decreasing with increasing removal of white spruce forest habitat. Resident, reproductively active females were present on both logged areas. Net movements by resident voles between areas were few, and most use of logged areas by nonresident voles was made by voles residing just off the trapping grids.

The edge effect varied between areas. Several methods have been proposed for estimating the area actually sampled during trapping (Smith et al. 1975, O'Farrell et al. 1977). In this study, the primary factor determining the larger edge effect in the logged areas was an unequal distribution of voles, i.e., higher density just beyond the border of the trapping grid. In the logged areas, many of the edge-caught animals were from the nearby uncut forest (fig. 1), a phenomenon which could explain the surprisingly high number of voles caught in the clearcut during the September 1972 snap trapping.

Despite density corrections for edge-caught animals, 1-hectare areas may be too small to fully analyze numeric response of C. rutilus, since males may have home ranges exceeding this area. This is supported by the fact that 10 of the 13 voles making interarea movements were males. Consequently, density of males may be inflated in all areas to an unknown degree. The problem is less severe for females and subadults which have small home ranges. Ideally, future investigations should be conducted on larger grids (perhaps 5 hectares) and replicated within treatments.

The density reduction observed in the clearcut might have been the result of factors operative prior to the breeding season, which resulted in the unequal distribution of overwintering females, or of factors active during the breeding season which resulted in net movement from the clearcut or hindered recruitment of young. There was little indication that differential movement occurred among areas. Since per capita litter production and subadult survival were similar between areas, and since plant abundance in the clearcut was virtually identical to the shelterwood, low recruitment of young was simply due to the smaller number of breeding females. Therefore, the likely explanation lies with factors responsible for the distribution of overwintering females at the initiation of the breeding season. Trapping was not conducted at Bonanza Creek prior to snowmelt, and direct assessment of prebreeding season factors was not possible; however, information from prior studies may provide a working hypothesis.

While the colonization of an area of burned black spruce (*Picea mariana*) taiga 60 km north of Fairbanks was being monitored (West 1974), red-backed voles were observed to vacate the 1-year-old burn during early winter (November) in favor of nearby unburned forest. The burned area was not repopulated until the following summer. In fact, this pattern was observed for the first 2 years after burning, and overwintering on the burned area did not occur until the third winter. Livetrapping through the first winter revealed that not only did voles vacate the burned area, but they also avoided areas lacking a thick moss cover within the unburned forest. This resulted in an aggregation of voles in midwinter (as described in West 1977).

The critical point is that there is a great selective premium on the ability of red-backed voles to discriminate between suitable and unsuitable overwintering sites. One major determinant of suitability appears to be thick ground cover, a quantity conspicuously absent from the burned area and the clearcut at Bonanza Creek. The lower number of adult females and the month-long reproductive delay may be the result of the clearcut having been abandoned during the previous winter and repopulated following snowmelt in early June. The larger population observed on the shelterwood might be attributed to successful overwintering since some undisturbed ground cover was present.

If the pattern of midwinter abandonment is a general phenomenon of C. rutilus in areas where ground cover has been extensively removed, this study implies that continuous habitat occupancy was more strongly constrained by winter conditions than by conditions during the breeding season. Further, if colonization of severely disturbed areas is a function of both suitable overwintering sites and the range of movement realized by individual voles, areas lying at some distance from source areas should lack reproducing populations until vegetation has developed sufficiently to provide suitable overwintering sites.

The continued presence of C. rutilus on the logged areas is in marked contrast to the response of Gapper's red-backed vole, C. gapperi, and western red-backed vole, C. occidentalis at lower latitudes. Both C. occidentalis (Tevis 1956, Gashwiler 1959 and 1970) and C. gapperi (Miller and Getz 1972, 1973 and 1977, Sims and Buckner 1973, Lovejoy 1975, Martell and Radvanyi 1977; but see Kirkland 1977) are considered inhabitants of mature forest. Following logging or forest fire, the density of C. occidentalis and C. gapperi usually drops precipitously within 1 or 2 years. An extensive survey of microtine habitat occupancy in interior Alaska (West 1979) corroborates the general pattern found in this study. Clethrionomys rutilus persists on all early successional sites and is usually the most abundant microtine. Whereas reduced cover on disturbed areas has been presumed responsible for the absence of Clethrionomys in southern regions, this is not the case in Alaska, nor on islands (Cameron 1964) where Clethrionomys occupies grassland areas if other competing small mammal species are absent.

The small mammal competitive environment in interior Alaska favors C. rutilus. At lower latitude, Microtus is capable of reducing and perhaps excluding Clethrionomys from well-developed grassland (Grant 1978). In the interior, Microtus rarely reaches densities high enough to severely depress Clethrionomys abundance and does not exclude it from grassland (West 1979). Aside from the northern jumping mouse, Zapus hudsonius, northern populations of C. rutilus have nearly exclusive claim to the frugivorous and granivorous small mammal niche (Whitney 1976). Peromyscus, a genus trophically similar to Clethrionomys and potentially a strong competitor, is not present in the interior. Although not investigated to the extent of the Microtus-Clethrionomys interaction, Peromyscus might play an important role in decreasing Clethrionomys abundance on disturbed areas. During the year-long period prior to colonization of a clearcut by P. maniculatus in northern Ontario, C. gapperi was common (Martell and Radvanyi 1977) then declined to rare status with the concomitant rise in P. maniculatus density. Dyke (1971) suggested the occurrence of habitat displacement between P. maniculatus and C. rutilus in forests of the Northwest Territories, Canada, where midsummer

increases of P. maniculatus and simultaneous decreases in C. rutilus density were followed in autumn by decreases in P. maniculatus and increases in C. rutilus density. Field experimentation is needed to clarify the competitive relationship between Clethrionomys and Peromyscus (Grant 1972).

Radvanyi (1970, 1971) has shown that conifer seed depredation is a function of both density of small mammals and seed vulnerability. Snow cover promotes seed survival by concealment, though density of small mammals may be rather high, whereas in snow-free seasons seed loss is much higher, though densities of small mammals may be low. Fall, the season of peak annual density for C. rutilus and peak white spruce seedfall (Zasada and Viereck 1970), probably has the highest rate of seed depredation (Graber 1969). Given the probability of a temporary reduction of C. rutilus density in large clearcut areas and the absence of deermice (Peromyscus), notorious consumers of spruce seed, reforestation by direct seeding might prove more successful in interior Alaska than has been the case in Canada.

Acknowledgments

We gratefully acknowledge the financial support provided by the United States Department of the Interior, Bureau of Land Management, and the United States Department of Agriculture, Forest Service, Institute of Northern Forestry. The University of California Computer Center provided subsidized computer time. This paper was improved by the helpful criticisms of Drs. William A. Fuller, Frank A. Pitelka, and Paul Whitney. We thank Patrick Mulligan, Douglas Pengilly, and Jerry Wolff for trapping assistance.

Literature Cited

- Cameron, A. W.
1964. Competitive exclusion between the rodent genera Microtus and Clethrionomys. *Evolution* 18:630-634.
- Dyke, G. R.
1971. Food and cover of fluctuating populations of northern cricetids. Ph.D. dissertation, University of Alberta, Edmonton. 245 p.
- Ford, R. G., and D. K. Krumme.
1979. The analysis of space use patterns. *J. Theor. Biol.* 76:125-155.
- Gashwiler, J. S.
1959. Small mammal study in west-central Oregon. *J. Mammal.* 42:128-139.
- Gashwiler, J. S.
1970. Further study of conifer seed survival in a western Oregon clearcut. *Ecol.* 51:849-854.
- Getz, L. L.
1969. Laboratory studies of interactions between the white-footed mouse and red-backed vole. *Can. Field Nat.* 83:141-146.

- Graber, R. E.
1969. Seed losses to small mammals after fall sowing of pine seed. USDA For. Serv. Res. Pap. NE-135. Northeastern For. Exp. Stn., Upper Darby, Pa.
- Grant, P. R.
1972. Interspecific competition among rodents. *Annu. Rev. Ecol. Syst.* 3:79-106.
- Grant, P. R.
1978. Competition between species of small mammals. p. 38-51. *In* Populations of small mammals under natural conditions. D. P. Snyder, ed. Special Publ. Ser. No. 5. Pymatuning Laboratory of Ecology. Univ. Pittsburgh, Penn.
- Kirkland, G. L., Jr.
1977. Responses of small mammals to the clearcutting of northern Appalachian forests. *J. Mammal.* 58:600-609.
- Lovejoy, D. H.
1975. The effect of logging on small mammal populations in New England northern hardwoods. Univ. of Connecticut Occas. Pap. (Biol. Sci. Ser.) 2:269-291.
- Martell, A. M., and A. Radvanyi.
1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. *Can. Field-Nat.* 91:41-46.
- Miller, D. H., and L. L. Getz.
1972. Factors influencing the local distribution of the redback vole, *Clethrionomys gapperi*, in New England. Univ. of Connecticut Occas. Pap. (Biol. Sci. Ser.) 2:115-138.
- Miller, D. H., and L. L. Getz.
1973. Factors influencing the local distribution of the redback vole, *Clethrionomys gapperi*, in New England. II. Vegetation cover, soil moisture, and debris cover. Univ. of Connecticut Occas. Pap. (Biol. Sci. Ser.) 2:159-180.
- Miller, D. H., and L. L. Getz.
1977. Factors influencing local distribution and species diversity of forest small mammals in New England. *Can. J. Zool.* 55:805-814.
- Morrison, P. R., R. A. Ryser, and R. L. Strecker.
1954. Growth and the development of temperature regulation in the tundra red-backed vole. *J. Mammal.* 35:376-386.
- O'Farrell, M. J., D. W. Kaufman, and D. W. Lundahl.
1977. Use of livetrapping with the assessment line method for density estimation. *J. Mammal.* 58:575-582.
- Pelikan, J.
1970. Testing and elimination of the edge effect in trapping small mammals, p. 57-61. *In* Energy flow through small mammal populations. K. Petruszewicz and L. Ryszkowski, eds. Polish Scientific Publishers. Warsaw.
- Radvanyi, A.
1966. Destruction of radio-tagged seeds of white spruce by small mammals during summer months. *For. Sci.* 12:307-315.

- Radvanyi, A.
1970. Small mammals and regeneration of white spruce forests in western Alberta. *Ecology* 51:1102-1105.
- Radvanyi, A.
1971. Lodgepole pine seed depredation by small mammals in western Alberta. *For. Sci.* 17:213-217.
- Sims, H. P., and C. H. Buckner.
1973. The effect of clearcutting and burning of Pinus banksiana forests on the populations of small mammals in southeastern Manitoba. *Am. Midl. Nat.* 90:228-231.
- Smith, M. H., R. H. Gardner, J. B. Gentry, D. W. Kaufman, and M. J. O'Farrel.
1975. Density estimations of small mammal populations, p. 25-53. *In* Small mammals: their productivity and population dynamics. F. B. Golley, K. Petruszewicz, and L. Ryszkowski, eds. Cambridge Univ. Press. New York.
- Tevis, L., Jr.
1956. Responses of small mammal populations to logging of Douglas-fir. *J. Mammal.* 37:189-196.
- West, S. D.
1974. Post-burn population response of the northern redbacked vole, Clethrionomys rutilus, in interior Alaska. Unpublished Master's Thesis. Univ. of Alaska, Fairbanks.
- West, S. D.
1977. Midwinter aggregation in the northern red-backed vole, Clethrionomys rutilus. *Can. J. Zool.* 55:1404-1409.
- West, S. D.
1979. Habitat responses of microtine rodents to central Alaskan forest succession. Ph.D. dissertation. Univ. California. Berkeley.
- Whitney, P.
1976. Population ecology of two sympatric species of subarctic microtine rodents. *Ecol. Monogr.* 46:85-104.
- Zasada, J. C., and L. A. Viereck.
1970. White spruce cone and seed production in interior Alaska, 1957-68. USDA For. Serv. Res. Note PNW-129. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

The Forest Service of the U.S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives — as directed by Congress — to provide increasingly greater service to a growing Nation.

The U.S. Department of Agriculture is an Equal Opportunity Employer. Applicants for all Department programs will be given equal consideration without regard to age, race, color, sex, religion, or national origin.