
Edge Effects and Isolation: Red-Backed Voles on Forest Remnants

L. SCOTT MILLS*

Department of Biology, University of California, Santa Cruz, Santa Cruz, CA 95064, U.S.A.

Abstract: Negative effects of habitat edge have been advanced as an important proximate cause of extinction, and a growing literature calls attention to the matrix surrounding habitat remnants as a critical factor determining population persistence. I examined spatial distribution of California red-backed voles (*Clethrionomys californicus*) on 13 forest remnants and five control sites in southwestern Oregon. The species was virtually isolated on remnants, making little use of the regenerating clearcuts surrounding the remnants. The effects of the clearcut also impinged on the remnants as edge effects: six times more voles were captured per trap in the interior of remnants than on the edge. Consequently, the density of voles per unit area on remnants increased with remnant size, despite the potential buildup of population density in small isolates due to limited emigration. I explored potential mechanisms of the negative edge effect on voles and found that the biomass of coarse woody debris, per se, did not explain the vole distribution because both number and volume of logs increased from the interior to the edge of remnants. However, the distribution of the vole's primary food item, hypogeous sporocarps of mycorrhizal fungi, did correspond to the vole edge effect.

El efecto de los bordes y el aislamiento: el ratón campestre (*Clethrionomys californicus*) en remanentes de bosque

Resumen: Los efectos negativos del borde de los hábitats ha sido propuesto como una importante causa inmediata de extinción, y una literatura creciente está poniendo énfasis en la matriz que rodea los remanentes como un factor crítico en la determinación de la persistencia poblacional. Examiné la distribución espacial de los ratones de campo californianos (*Clethrionomys californicus*) en 13 remanentes de bosque y 5 sitios de control en el suroeste de Oregon. La especie estaba virtualmente aislada en los remanentes y hacía poco uso de los claros que se regeneran alrededor de los remanentes del bosque. Los efectos de los claros también afectaron a los remanentes en forma semejante al efecto de los bordes: se capturaron 6 veces más ratones por trampa en el interior de los remanentes que en los bordes. Consecuentemente, la densidad de los ratones por unidad de área en los remanentes se incrementó con el tamaño del remanente, a pesar del crecimiento potencial en la densidad de la población en pequeñas áreas aisladas debido a una limitada emigración. Exploré los mecanismos potenciales de los efectos negativos sobre los ratones y encontré que la biomasa de los restos de madera no explican por sí mismos la distribución de los ratones, debido a que tanto el número como el volumen de los troncos se incrementa del interior de los remanentes hacia sus bordes. Sin embargo, la distribución del alimento primario de los ratones, esporocarpos de micorrizas, sí se correspondió con el efecto de los bordes sobre los ratones

* Current address: Wildlife Biology Program, School of Forestry, University of Montana, Missoula, MT 59812, U.S.A.
Paper submitted March 24, 1994; revised manuscript accepted May 23, 1994.

Introduction

Vertebrate populations in forest remnants face probabilities of extinction that depend largely on the remnant's

size and degree of isolation. Fragmenting a large population into small, isolated populations increases the probability of extinction due to factors including stochastic demographic and environmental variation (see Lande 1993) and inbreeding depression (Frankel & Soulé 1981; Mills & Smouse 1994). Exacerbating these risks are negative edge effects, which may shrink the functional size of the remnants by reducing habitat quality at the interface of the remnant and surrounding habitat (see Yahner 1988).

Mechanisms driving negative edge effects include both biotic and abiotic factors. A rapidly growing literature documents changes in the susceptibility of birds to edge-induced predation and nest parasitism (review by Andrén & Angelstam 1988; Reese & Ratti 1988). Furthermore, abiotic conditions and associated vegetation structure and composition differ between the edge and interior of forest remnants (review by Saunders et al. 1991; see also Williams-Linera 1990; Laurance 1991). These phenomena have been assumed to affect mammals negatively as well, prompting general concern that edge effects will decrease the densities of certain species on forest remnants surrounded by a human-altered landscape (Harris 1984; Franklin & Forman 1987).

To date, however, data documenting negative edge effects for mammals are sparse, and an explicit connection of these effects to mechanisms is virtually nonexistent. In addition, the literature examining small mammals on islands (or strongly isolated habitat remnants) predicts that small islands will actually contain higher densities than larger ones due to limited emigration (review in Glicwicz 1980); this prediction is exactly opposite to expectation if negative edge effects drive population dynamics (Bierregaard et al. 1992).

The forests of the Pacific Northwest have received little attention with respect to edge effects on vertebrates (see review in Paton 1994). These forests should be a model system for examining issues related to edge effects and fragmentation on small mammals, due to the extensive clearcutting and wide range of small-mammal responses to forest fragmentation (Tevis 1956; Gashwiler 1970; Hooven & Black 1976; Mills 1993). California red-backed voles (*Clethrionomys californicus*) respond negatively to clearcutting of forests; their abundance is lower for at least 10 years (and up to 30–60 years) following forest harvest (Hooven & Black 1976; Taylor et al. 1988; Raphael 1988; Rosenberg et al. 1994). The avoidance of clearcuts by red-backed voles has been linked to the scarcity of coarse woody debris and/or their primary food: the belowground sporocarps of mycorrhizal fungi (Tevis 1956; Ure & Maser 1982; Hayes et al. 1986).

I tested whether edge effects influenced the distribution of red-backed voles on a collection of unharvested forest remnants in southwestern Oregon and compared

the space use on remnants to that in unfragmented control sites and in the matrix of regenerating forest surrounding the remnants. I also explored mechanisms underlying the edge effect for red-backed voles, including the biomass of woody debris and the distribution of belowground fungal sporocarps.

Methods

Study Area

All sites were located in the Klamath Mountains physiographic province of (Franklin & Dyrness 1973) of southwestern Oregon (Fig. 1, Table 1) and were under federal or state ownership. The 13 forest remnants were unlogged mature-to-old-growth forest (more than 80 years old) surrounded entirely by land clearcut one to 30 years previously. The remnants were primarily *Pseudotsuga menziesii*/*Abies* spp. communities, while clearcuts included *Rubus*, *Ribes*, *Ceanothus*, and *Epilobium* associations (Dyrness 1973). Virtually no trees were retained in the clearcuts, although saplings were established in some sites.

Remnants analyzed in this study were small (0.6–2.5 ha; Table 1), which allowed for accurate on-the-ground measurement of remnant size and edge characteristics. The remnants varied in elevation, slope, aspect, and the width of the clearcut matrix surrounding them (Table 1).

I also sampled five control sites, with at least one control within 13 km of each remnant (Fig. 1, Table 1). For this study, “control” was defined as unlogged mature-to-old-growth forests more than 250 ha in size. The inclusion of more or larger control sites, or sites closer to remnants, was precluded by the extensive forest fragmentation in the region.

Vole Trapping

Trapping was conducted from June 25 to September 14, 1990, and from June 7 to September 6, 1991. Both medium (9 × 8 × 23 cm) and small (6.5 × 5.5 × 16.5) Sherman live traps were used, with a ratio of 3:1 medium to small traps held constant with respect to both distance from edge and across remnant, control, and clearcut sites. In each summer, up to 85 live traps were set for four nights in a measured, regularly-spaced trapping grid on both remnants and controls. Although smaller remnants were not able to hold all 85 traps (Table 1), trapping effort per unit area was constant among sites due to standardized trap spacing: 15 meters apart, with adjustment of up to 4 meters in either direction tolerated if traps could be placed under or near fallen logs. All traps were baited with 1:1 oat groats to sunflower seeds, and an approximately 1-cm³ chunk of fresh apple. Upon capture, voles were individually marked by toe clipping.

The group of remnants (and associated clearcuts)

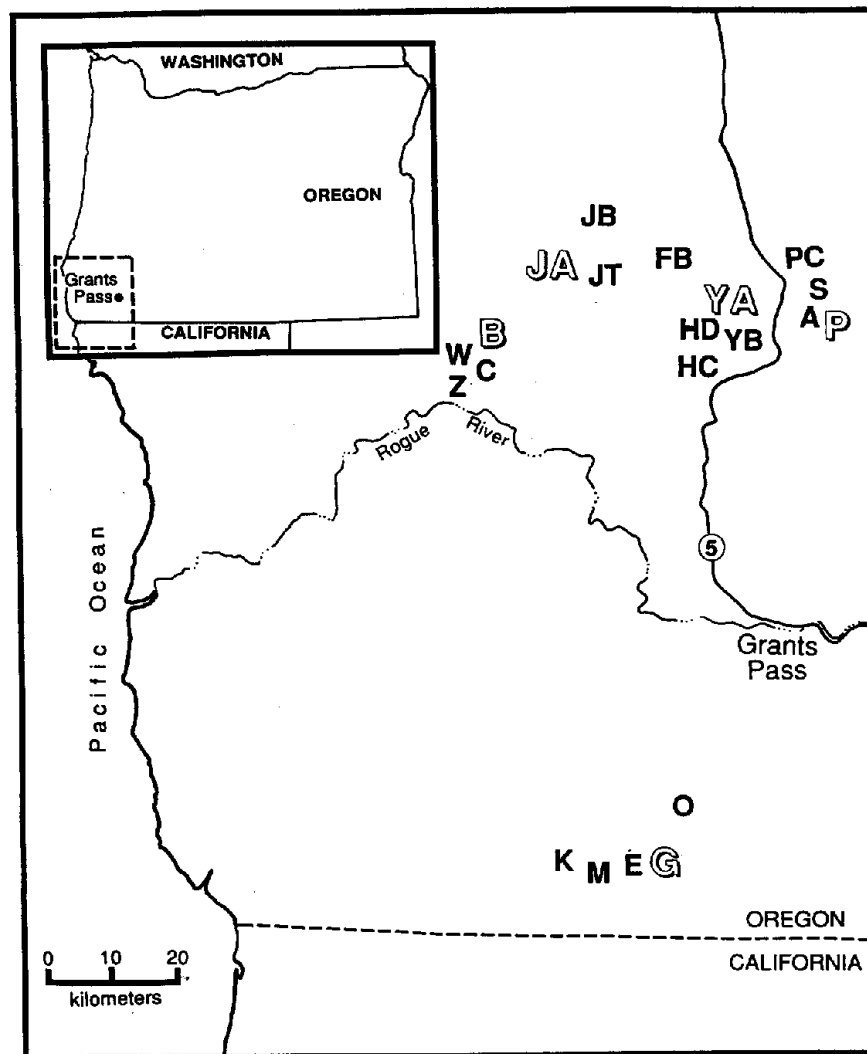


Figure 1. Locations of remnant and control sites analyzed for red-backed vole space use in southwestern Oregon, 1990 and 1991. Control sites (>250 ha) are indicated by open type, remnants by solid type.

nearest each control was trapped within a month of when the control was trapped. Simultaneous with sampling a remnant, the surrounding clearcuts were sampled with 16 Sherman traps placed in four lines of four traps each. Each line was placed roughly at a cardinal compass direction from the remnant, in the middle of and perpendicular to the likely line of travel of an animal crossing the regenerating clearcut between the nearest forest and the remnant. As in the forest, traps were set for four nights, located under logs whenever possible, and spaced 15 meters apart within lines.

Analysis

The edge, or clearcut/forest interface, was generally obvious. To ensure that measurements were repeatable

across remnants, however, the edge was operationally defined as the minimum convex polygon comprised of the outermost conifer trees that were at least two-thirds the mean diameter of conifers in the remnant center. The edge was allowed to be concave if the distance from one edge tree to the next was more than 30 meters. To eliminate the influence of occasional unharvested trees outside the remnant, a conifer was not considered an edge tree if the line of travel along the remnant perimeter and out to the tree formed an angle of less than 135 degrees, and the tree was farther than 20 meters from any two trees inside the edge.

By measuring the distance from each trap to the marked edge, I could assign traps to one of four edge classes: 0–15 meters, 16–30 meters, 31–45 meters, and 46–90 meters into the forest from the edge. Estimates of

Table 1. Biogeographic characteristics of forest remnants and controls (>250 ha) used to study red-backed vole responses to forest fragmentation.

Site ^a	Size (ha)	Number Traps ^b	Distance to Forest ^c (m)	Aspect	Slope (degrees)	Elev ^d (m)
Remnants						
O	3.6	85	150	W	31	1403
HC	2.5	84	95	W	24	976
E	2.5	85	100	W	32	1342
JB	2.5	69	140	SE	13	686
FB	2.0	81	120	W	25	671
W	1.4	67	60	SE	14	732
S	1.3	63	150	E	33	991
YB	1.3	68	75	N	35	915
HD	1.1	42	110	S	22	976
Z	1.0	52	60	S	22	732
PC	0.9	52	170	N	35	640
JT	0.6	30	50	E	2	991
M	0.3	20	100	W	10	1220
Controls						
G	N/A	85	N/A	S	19	1586
B	N/A	85	N/A	SE	9	1083
P	N/A	85	N/A	E	31	884
YA	N/A	85	N/A	E	37	817
JA	N/A	85	N/A	—	2	991

^a Sites with single letter designations were sampled in both 1990 and 1991; all others were sampled only in 1991.

^b Number of traps set for four nights each on measured grid with 15-meter spacing. Lack of perfect concordance between trap number and remnant size reflects the influence of remnant shape on trapping grid layout.

^c Distance to nearest forest more than 7 ha in size, the area of the largest remnant studied by Mills (1993).

^d Elevation at approximate center of site.

actual vole density in each edge class would have required considerably longer trapping periods than the four nights I used due to the relatively small number of animals and potential trap responses (Menkens & Anderson 1988; Pollock et al. 1990); increasing the trapping period would have forced me to reduce the number of replicate remnants examined. Because I was simply interested in relative changes in space use by voles and felt that the number of different animals captured per unit effort should not change in a biased fashion across edge classes, I relied on a simple index of space use: the number of different animals captured weighted by number of traps, or the number of different animals per trap over the four days of trapping.

Six of the 13 remnants and three of the controls were trapped in the spring/summer of both 1990 and 1991 using identical methodology (Table 1). For these sites, the trapping index values were averaged across years to give site values. The other sites were trapped only in 1991.

Based on natural history responses (see Tevis 1956; Gashwiler 1970; Hooven & Black 1976; Raphael 1988), we would predict an edge effect to be negative for California red-backed voles. Thus, the preferred statistical technique should test whether space use ranked as 0–15 meters $\leq$ 16–30 meters $\leq$ 31–45 meters $\leq$ 46–90 meters. In order to test for both heterogeneity and directionality using categorical (edge class) data, I used an ordered-heterogeneity test (Rice & Gaines 1994a,b).

Specifically, heterogeneity among density index values (number of different voles per trap) across edge classes was determined by an ANOVA that is robust to unequal group variances (Rice & Gaines 1989). The ANOVA *P*-value was combined with the order component, assessed by a Spearman's rank correlation. From the product of these two ($r_s P_c$), a *P* value was obtained for the ordered heterogeneity test (Rice & Gaines 1994b).

To compare vole use of remnants to that of surrounding clearcuts and nearby controls, I determined number of voles per trap for each remnant by dividing the total number of different voles captured by number of traps on the remnant. I then used a Behrens-Fisher *T*-test allowing for inequality of treatment variances to compare the average vole number per trap on remnants to that on surrounding clearcuts, as well as to that on nearby controls.

I used line intercept sampling (DeVries 1974) to estimate log volume (m^3/ha) and log number (number/ha) on each of two 20-meter line transects randomly located in each edge class of each remnant. For the purposes of this study, a "log" was defined as any dead woody material less than 45 degrees to the ground and greater than 10 cm diameter at the large end. Data for logs were analyzed with an ordered heterogeneity test as described above for data on vole captures.

The distribution of hypogeous sporocarps of mycorrhizal fungi (truffles) was sampled on several of the rem-

nants and regenerating clearcuts to examine the relationship between voles and truffles and between truffles and coarse woody debris (Clarkson & Mills 1994). From mid-June through mid-August 1991, four remnants (sites O, HC, E, S) and the regenerating clearcuts surrounding two of them (O, E) were sampled. Truffle plots were one square meter in size and were placed by raking down to the organic-mineral soil interface. Each of the four remnants had at least eight plots in each edge class (described above). The regenerating clearcuts surrounding the two sites had 40 plots each. Because distance between truffle plots and the edge is known, we can relate truffle distribution to edge effects. However, the small number of replicate sites for truffle sampling limits analysis to a qualitative approach.

Results

California red-backed voles on forest remnants in southwestern Oregon are strongly and negatively affected by clearcutting of forest (Fig. 2). They were exceptionally rare in clearcuts, with only three voles captured in 1404 trap nights (351 traps out for four nights) over the 1990 and 1991 seasons (vole density index = 0.014 different voles/trap). In contrast, a total of 135 different voles were captured during 7332 trap nights on remnants (index = 0.086) and 85 were captured in 2792 trap nights on controls (index = 0.15). Voles were captured on all 5 controls, on 10 of 13 remnants, and on 3 of 13 regenerating clearcuts surrounding remnants. The average number of different voles per trap in remnants was sig-

nificantly greater ($p = 0.003$) than the average number in clearcuts. Although there was a trend toward fewer voles per trap in remnants, on average, than in controls, the difference was only marginally significant ($p = 0.1$).

Voles also exhibited a significant negative edge effect ($p = 0.003$), with six times as many voles per trap in the interior of the remnants as on the edges (Fig. 2). Furthermore, the regression of the vole density index (number of different voles/trap/remnant) against remnant area is significantly positive (Fig. 3).

The significant increase in vole density with remnant area may result from the fact that small remnants have a higher ratio of edge to interior, so that they have lower vole densities per unit area. Alternatively, the density/area relationship may arise from area-related phenomenon that are independent of edge, such as the effects of remnant size on probabilities of extinction, predation, and/or immigration. If area-related phenomena do, in fact, drive the density of voles on remnants, the possibility arises that my observed edge effects within remnants arise simply as an artifact of interior edge classes being found solely on remnants that have higher density due to large size. To consider this possibility, I re-analyzed the vole edge-effect data using only the eight remnants that were large enough to have all edge classes represented, without the possible confounding factor of stand size. The results were unchanged: vole density decreased significantly from the interior to edges of remnants ($p = 0.005$), indicating that the edge effect is not merely a function of area relationships on remnants.

The biomass of coarse woody debris showed a trend opposite to that of voles (Fig. 4), with numbers increasing from the interior to the edge of the remnant for both

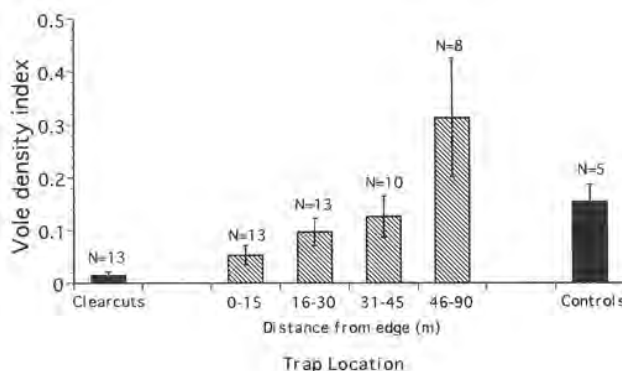


Figure 2. Mean and standard errors of the California red-backed vole density index and the number of different voles captured per trap for four nights of trapping in southwestern Oregon, 1990 and 1991. Forest-edge classes (striped bars) represent number of meters from trap to the nearest forest-clearcut interface. The N refers to the number of sites trapped. Small remnants often did not have any area further than 30 meters from an edge.

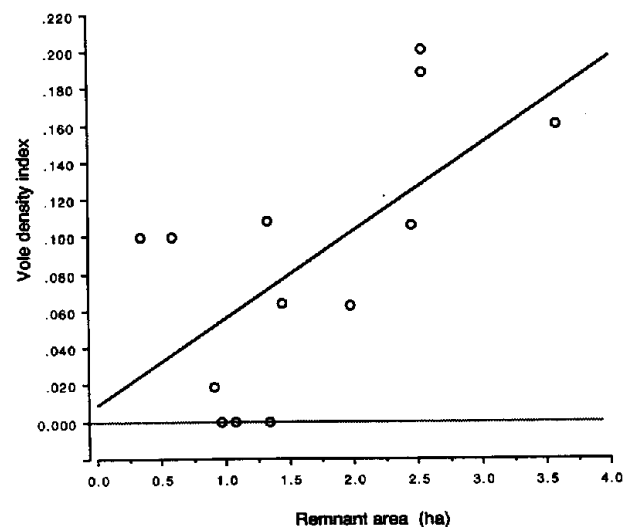


Figure 3. Relationship between size of remnants (ha) and average vole density index for that remnant in southwestern Oregon, 1990 and 1991 (regression $p = 0.02$; $r^2 = 0.40$).

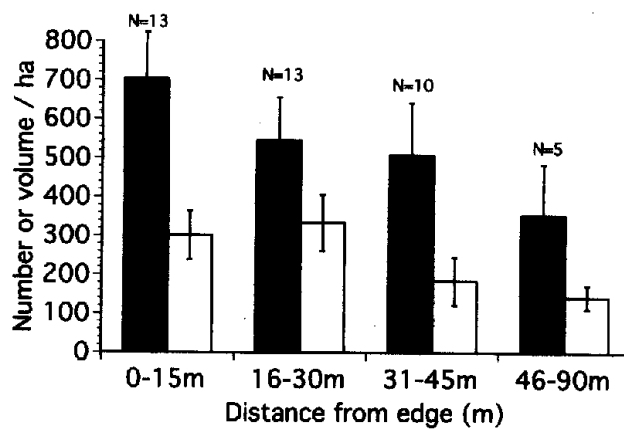


Figure 4. Mean and standard errors of downed log biomass values relative to distance from edge for all remnants trapped for red-backed voles in southwest Oregon. Solid bars show number of logs per hectare, white bars represent the volume of log per hectare (m^3/ha). The N refers to the number of remnants analyzed. For the most-interior edge class (46–90 meters), three sites (W, S, and PC) that had traps in that edge class did not have enough area to sample logs, so $N = 5$ compared with $N = 8$ in Fig. 2.

log volume ($p = 0.04$) and number of logs ($p = 0.05$). A sequential Bonferroni correction of P -values (Rice 1989) to account for inflated Type I error due to two tests of the same hypothesis (edge effects on log volume and number) changes significance levels to $p = 0.07$ for both volume and number of logs.

We sampled a total of 136 truffle plots on four forest remnants and 40 plots in the clearcuts surrounding each of two remnants. On the four remnants, 29 of 136 plots (21.3%) had at least one truffle, with sporocarps coming from 12 genera (Clarkson & Mills 1994).

Only one plot out of 80 had any truffles in the clearcuts, despite a sampling regime that was intentionally biased toward finding truffles in the clearcuts (Clarkson & Mills 1994). Furthermore, no truffles were found in the 32 plots in the first edge class (0–15 meters) of the four remnants. Truffles were found, however, in 11 of the 32 plots from 16–30 meters from the edge, 11 of the 32 plots from 31–45 meters, and 7 of the 40 plots from 46–90 meters. Fresh-weight biomass followed the same trends.

Discussion

Although forest remnants in southwest Oregon cannot be considered analogous to true islands for all small-mammal species (Mills 1993; Doak & Mills 1994), they do appear to be operating as islands for California red-backed voles. Voles were captured in most remnants but rarely in clearcuts surrounding remnants. Within the

remnants, a negative edge effect decreased vole density from the interior to the edge of the remnants (also see Walters 1991). These trends hold across a wide range of clearcut ages; thus, isolation and edge effects on voles appear to be general phenomena for varying conditions in the matrix of regenerating clearcuts in southwest Oregon.

Edge effects may be more severe on remnants than in continuous forest because the edge effect at any point is a function not only of the nearest edge but also of the rest of the circumference of the remnant (Bierregaard et al. 1992). Because small remnants have a larger proportion of their area close to an edge, negative edge effects would be expected to translate into proportionately lower densities on smaller remnants (Temple 1986). The prediction that negative edge effects decrease the functional size of a remnant, so that density of a species increases with increasing remnant size, forms the core of several landscape-level approaches to quantifying the effects of forest fragmentation (see Harris 1984; Franklin & Forman 1987; Groom & Schumaker 1993).

On the other hand, small-mammal studies have long documented that limited dispersal can lead to higher densities in enclosures or islands (Lidicker 1975; Gaines & Johnson 1987). The demographic consequences of this “fence effect” has led to the counterintuitive prediction that population densities per unit area should decrease as island size increases (Gliwicz 1980). Studies of presumed habitat islands have demonstrated that the relationship between small-mammal density and remnant size is mediated by the demographic effects of crowding and environmental conditions, and whether isolation is complete enough to prohibit emigration out of the population (Gottfried 1979; Kozakiewicz 1985, 1993; Szacki 1987).

I found that the index of vole density (per unit area) did increase significantly with remnant size (Fig. 3), implying population-level consequences of the negative edge effects. The increase in vole densities in control sites versus remnants overall, however, was only marginally significant. In particular, the most interior portions of remnants had higher densities than controls, while densities near the edge were substantially lower (Fig. 2). Collectively, these results may indicate that although the negative edge effect decreases the functional size of the remnants, the strong degree of isolation also plays a role by limiting dispersal into the surrounding matrix. It may be that the deleterious effects of edge on density are somewhat counteracted by density buildup from lack of dispersal within the isolated remnants. Additional support for the notion of the ecological isolation of voles on remnants comes from preliminary examination of DNA fingerprints from five of the remnants and two of the controls, in which remnant voles have lower genetic variation than control voles (Mills 1993).

Although the value of coarse woody debris to small-mammal space use in forests is well established (Harmon et al. 1986), logs per se do not explain the negative edge effect for red-backed voles. In this study, both volume and number of logs tended to increase toward the remnant edges, trends that are opposite the vole edge effect. This lack of concordance between log and vole distribution may seem surprising given the strong positive association between red-backed voles and logs (Doyle 1987; Hayes & Cross 1987; Tallmon & Mills 1994). Although the number and volume of downed logs in the interior edge classes of my remnants (Fig. 4) were mostly within the range of values obtained previously for Oregon Coast Range forest stands older than 80 years (Spies et al. 1988), the first two edge classes contain up to 1.5 times higher log volume and number. The large amount of woody biomass on the remnant edge probably results from cut trees falling into the forest and from subsequent death and blowdown of trees on the edge (Lovejoy et al. 1986; Williams-Linera 1990; Laurance 1991). Thus there is a rapid accumulation of coarse woody debris on the edge due to clearcutting, but the wood is not of advanced decay class (Williams-Linera 1990; Chen et al. 1992; Bierregaard et al. 1992). Tallmon and Mills (1994) used radiotelemetry to document that voles on one remnant (site E: Table 1) preferentially use logs of advanced decay, which indicates that the high biomass of logs at the forest-clearcut interface of remnants may represent excess coarse woody debris that does not necessarily benefit wildlife, or at least red-backed voles, in the short term.

In contrast to total biomass of woody debris, the distribution of hypogeous sporocarps of mycorrhizal fungi was consistent with the space-use trends shown by voles: truffles were virtually absent from regenerating clearcuts and from near the edges of remnants. Truffles make up over three quarters of the diet of California red-backed voles (Maser et al. 1978; Ure & Maser 1982), and Clarkson and Mills (1994) found that red-backed voles were significantly more likely to be captured in traps with truffles nearby than expected by chance. It appears that food supply may provide a mechanism for the observed decrease in vole numbers in the regenerating clearcuts and in remnants immediately adjacent to edges.

Although microclimatic edge gradients, including changes in light, moisture, and temperature, may extend 50 meters or more into the forest (Lovejoy et al. 1986; Chen et al. 1992; Matlack 1993; Young & Mitchell 1994), I do not have direct evidence relating abiotic factors to the distribution of voles or truffles on these remnants. Soil characteristics may also mediate the vole-truffle relationship (Rosenberg et al. 1994).

These results, indicating effects of both edge and remnant area on the density of red-backed voles, concur with studies of birds in fragmented landscapes. In a re-

cent review, Paton (1994) concluded that predation and parasitism rates on birds are often significantly greater within 50 meters of an edge than in the forest interior. Obviously, not all mammal species will exhibit negative edge effects (Mills 1993), but Paton's (1994) call for rigorous examination of edge effects in forests certainly holds true for mammals, which have received amazingly little attention with respect to potential negative impacts of edge.

This study has several implications for remnants as nature reserves. Whether the ideal shape for reserves is round or not (Diamond 1975; Wilson & Willis 1974) depends on the relative effects of shape on extinction and immigration (Game 1980); the consequences of shape, in turn, will be weighted by edge effects. In my study, edge effects for red-backed voles do not diminish over the 90-meter boundary that I examined, implying that small remnants are dominated by edge for this species and that larger remnants will have decreased functional size. However, the fact that even very small remnants sometimes had voles on them implies that these remnants may serve important functions for species persistence (Fahrig & Merriam 1994).

Acknowledgments

This research was supported by grants from the Pacific Northwest Research Station (U.S. Forest Service) and the National Audubon Society. For unsurpassed field help I thank Team v: Rich Nauman, Chris O'Conner, David Clarkson, David Tallmon, and Tara Reinertson. Michael Soule provided fierce edits, steady wisdom, and the Blue Bruiser. Various drafts of the manuscript were improved by comments from David Tallmon, David Clarkson, Bill Rice, Jim Estes, Bill Lidicker, Dan Doak, Ken Berger, and especially John P. Hayes. Jenn Knauer drew the study-area figure. I thank the many employees of the Forest Service, the Bureau of Land Management and the State of Oregon who helped me throughout the study. Final manuscript preparation occurred while author was a visiting faculty member in the Fisheries and Wildlife Department, University of Idaho.

Literature Cited

- Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69:544-547.
- Bierregaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. Augusto dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments. *Bioscience* 42:859-866.
- Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological applications* 2:387-396.
- Clarkson, D. A., and L. S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. *Northwest Science* 68:259-265.

- Devries, P. G. 1974. Multi-stage line intersect sampling. *Forest Science* 20:129–133.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129–146.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* 75:615–626.
- Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus*, *Microtus oregoni* and *M. richardsoni*. *American Midland Naturalist* 118:258–265.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western cascades of Oregon. *Ecology* 54:57–69.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- Frankel, O. H., and M. E. Souli . 1981. Conservation and evolution. Cambridge University Press, Cambridge, England.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. General Technical Report PNW-8. U.S. Forest Service, Portland, Oregon.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecology* 1:5–18.
- Gaines, M. S., and M. L. Johnson. 1987. Phenotypic and genotypic mechanisms for dispersal in *Microtus* populations and the role of dispersal in population regulation. Pages 162–179 in B. D. Chepko-Sade and Z. T. Halpin, editors. *Mammalian dispersal patterns*. University of Chicago Press, Chicago, Illinois.
- Game, M. 1980. Best shape for nature reserves. *Nature* 287:630–632.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* 51:1018–1026.
- Gliwicz, J. 1980. Island populations of rodents: Their organization and functioning. *Biological Reviews* 55:109–138.
- Gottfried, B. M. 1979. Small mammal populations in woodlot islands. *American Midland Naturalist* 102:105–112.
- Groom, M. J., and N. Schumaker. 1993. Evaluating landscape change: Patterns of worldwide deforestation and local fragmentation. Pages 24–44 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interaction and global climate change*. Sinauer Associates, Sunderland, Massachusetts.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Harris, L. D. 1984. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. The University of Chicago Press, Chicago, Illinois.
- Hayes, J. P., and S. P. Cross. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. *Canadian Field-Naturalist* 101:543–546.
- Hayes, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. *Northwest Science* 60:250–257.
- Hooven, E. F., and H. C. Black. 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. *Northwest Science* 50:189–208.
- Kozakiewicz, M. 1985. The role of habitat isolation in formation of structure and dynamics of the bank vole population. *Acta Theriologica* 30:193–209.
- Kozakiewicz, M. 1993. Habitat isolation and ecological barriers—the effect on small mammal populations and communities. *Acta Theriologica* 38:1–30.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Laurance, W. F. 1991. Edge effects in tropical forest fragments: Application of a model for the design of nature reserves. *Biological Conservation* 57:205–219.
- Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals. Pages 103–128 in F. B. Golley, K. Petrusewicz, and L. Ryszkowski, editors. *Small mammals: Their production and population dynamics*. Cambridge University, London, England.
- Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soul , editor. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799–809.
- Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66:185–194.
- Menkens, G. E., Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. *Ecology* 69:1952–1959.
- Mills, L. S. 1993. Extinctions in habitat remnants: Proximate mechanisms and biogeographic consequences. Ph.D. dissertation. University of California, Santa Cruz, California.
- Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. *American Naturalist* 144:412–431.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17–26.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monograph* 107:1–97.
- Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of Northwestern California. Pages 23–31 in *Proceedings of the symposium: Management of amphibians, reptiles, and small mammals in North America*. General technical report RM-166. U.S. Forest Service, Fort Collins, Colorado.
- Reese, K. P., and J. T. Ratti. 1988. Edge effect: A concept under scrutiny. *Transactions of 53rd North American Wildlife and Natural Resources Conference* 53:127–136.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Rice, W. R., and S. D. Gaines. 1989. One-way analysis of variance with unequal variances. *Proceedings of National Academy of Sciences* 86:8183–8184.
- Rice, W. R., and S. D. Gaines. 1994a. Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypotheses. *Proceedings of the National Academy of Sciences* 91:225–226.
- Rice, W. R., and S. D. Gaines. 1994b. The ordered-heterogeneity family of tests. *Biometrics* 50:746–752.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 1994. Habitat associations of California red-backed voles in young and old-growth forests in Western Oregon. *Northwest Science* 68:266–272.
- Saunders, D. A., R. J. Hobbs, C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18–32.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–1702.
- Szacki, J. 1987. Ecological corridor as a factor determining the structure and organization of a bank vole population. *Acta Theriologica* 32:31–44.

- Tallmon, D. A., and L. S. Mills. 1994. Use of logs within home ranges of California red-backed voles on remnant of forest. *Journal of Mammalogy* 75:97–101.
- Taylor, C. A., C. J. Ralph, and A. T. Doyle. 1988. Differences in the ability of vegetation models to predict small mammal abundance in different aged Douglas-fir forests. Pages 368–374 in *Proceedings of the symposium on management of amphibians, reptiles, and small mammals in North America*. General technical report RM-166. U.S. Forest Service, Fort Collins, Colorado.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: A comparison of two models. Pages 301–304 in J. Verner, M. L. Morrison, C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- Tevis, L., Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. *Journal of Mammalogy* 37:189–196.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. *Canadian Journal of Zoology* 60:3307–3315.
- Walters, B. B. 1991. Small mammals in a subalpine old-growth forest and clearcuts. *Northwest Science* 65:27–30.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78:356–373.
- Wilson, I. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2:333–339.
- Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67:63–72.

