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

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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 raton 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 sudoeste de Oregon. La especie estaba virtualmente aislada en los remanentes y hacía poco uso de los clareos que se regeneran alrededor de los remanentes del bosque. Los efectos de los clareos 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 distribucióm 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*

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Introduction

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

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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 significantly 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 reanalyzed 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

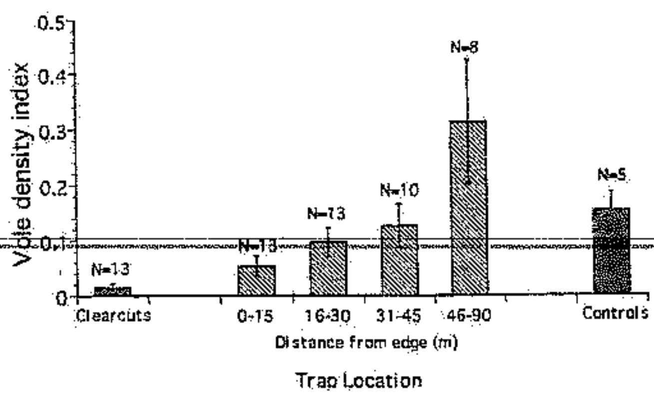

Figure 2. Mean and standard errors of the California red-backed vole density index and the number of different voles captured per trap for four nights of trapping in southwestern Oregon, 1990 and 1991. Forest-edge classes (striped bars) represent number of meters from trap to the nearest forest-clearcut 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.

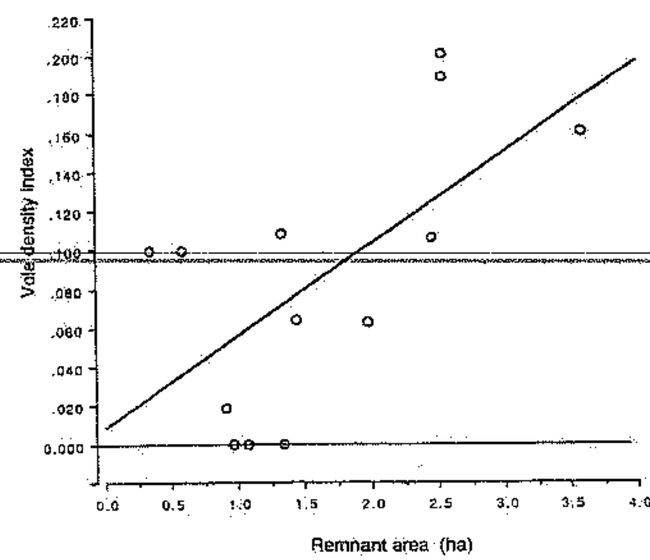

Figure 3. Relationship between size of remnants (ha) and average vole density index for that remnant in southwestern Oregon, 1990 and 1991 (regression $p = 0.02$; $r^2 = 0.40$).

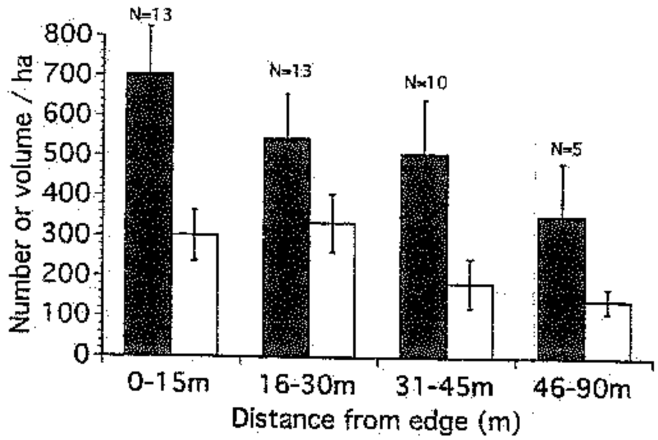

Figure 4. Mean and standard errors of downed log biomass values relative to distance from edge for all remnants trapped for red-backed voles in southwestern Oregon. Solid bars show number of logs per hectare, white bars represent the volume of log per hectare (m^3/ha). The N *refers to the number of 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 Bonferonni 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 emmigration 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).