WILDLIFE USE OF MANAGED FORESTS:
A LANDSCAPE PERSPECTIVE

Volume 3

East-Side Studies
Research Results

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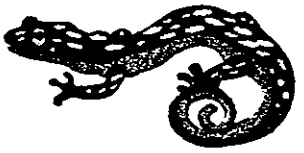

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SAMPLING AND ANALYSIS OF VEGETATION
EAST-SIDE STUDIES

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The forested land of northeastern Washington is managed primarily by the U.S. Forest Service, the WA Department of Natural Resources, private timber companies, and private landowners. Timber management practices during the last 100 years have included high-grading, clearcutting, post-harvest burning with replanting, fire suppression, selective cutting, and uneven-aged management. These management practices, coupled with natural variation in forest structure due to slope, aspect, edaphic characteristics, and fire, have resulted in a mosaic of forest stands of varying structure and spatial configurations. Based on our GIS analysis, the 3 most common forest types (82% of the total area) are mature, closed-canopy forest; regenerating forest; and clearcuts including basal-area retention cuts; we selected these 3 forest types for our examination of wildlife use of managed forests. Although the forest stands in this region vary considerably in size, 2 size classes were both representative and sufficiently different to have biological significance: 12-15 ha and >35 ha.

We examined forest stand structure of the 36 study sites at 2 scales. First, we measured habitat features of plots established on the 300- to 400-m and 1,200-m point-count transects of the 13-ha and >34-ha stands, respectively. This sampling covered about 40% of the total stand area. Second, we measured habitat features at each of the 36 pitfall trapping grids (60 by 60 m). The point-count transects and the pitfall trapping grids never overlapped.

FIELD SAMPLING: POINT-COUNT TRANSECTS

At each of the point-count stations we established a 24-m x 24-m plot with 4 transects extending from the center point in each of the 4 cardinal directions. In each direction, strip transects with widths of 1, 2, and 3 m were established (Fig. 1).

Trees and snags--Within each 576-m^2 plot, all trees were identified and counted by size class and all snags were counted by size, decay, and height class. We used 4 size classes for trees and snags based on diameter at breast height (d.b.h.): 1 (4-10 cm), 2 (11-25 cm), 3 (26-50 cm), and 4 (>50 cm). Snags were categorized as either Condition 1 if all bark was essentially intact and Condition 2 if the bark was peeling off or absent. In addition, snags were assigned to 1 of 2 height classes: 1-5 m or >5 m. This yielded 4 potential snag categories that were counted by size class. Tree heights of 4 representative live trees were estimated using a clinometer and a metric tape.

Canopy cover--Percent canopy cover was measured using a spherical densiometer at the center of the plot and at the 8-m interval along each transect for a total of 5 measurements per 576-m^2 plot.

Shrubs--Along each 1-m strip transect, all shrubs with stems within the strip were identified. The length and width of each shrub was measured to obtain an estimate of area and each shrub was assigned to 1 of 3 height classes: 1 (0.5-1 m), 2 (>1-1.5 m), or 3 (>1.5 m).

Woody debris--The size and decay classes of all logs intersecting or encompassed within the 2-m wide strip transects were recorded. Four size classes were designated: 1 (<15 cm d.b.h., >5 m long), 2 (>15-25 cm d.b.h., >2.5 m long), 3 (>25 cm d.b.h., <5 m long), and 4 (>25 cm d.b.h., >5 m long). Decay classes of logs were as follows: 1 (freshly fallen tree, bark intact, no decomposition), 2 (bark beginning to slough or almost completely gone, decomposition has begun but log still firm), 3 (wood soft and breaks into blocks), and 4 (wood has decomposed to point of soil-like texture, includes

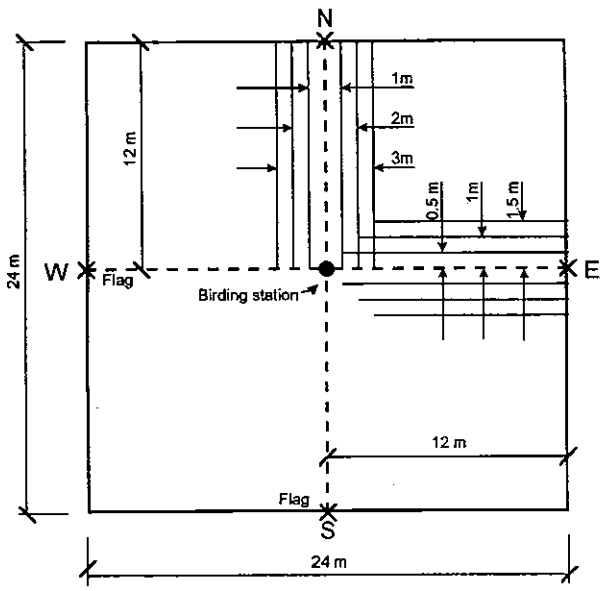

Figure 1. Sampling scheme for vegetation surrounding the bird point-count stations.

hummocks). The type and decay class of all stumps within the 3-m wide transect were recorded. Stumps were divided into 2 types, cut and natural, and into the 4 decay classes described above. If a stump had been burned, it was not assigned to a decay class, but recorded as "burned".

Regenerating trees--Number, type (coniferous or deciduous), and height class (0.5-1.5 m and >1.5 m) of all regenerating trees within the 2-m wide strip transects were recorded. Saplings were included if >0.5 m in height and <4 cm d.b.h.

Ground cover--To measure ground cover, a 20- by 50-cm plot frame was placed at the plot center and along the 4 transects at 4-, 8-, and 12-m intervals. Visual estimates of the cover of vegetative types (herbaceous, grass, fern, shrub, regenerating trees, and moss) and litter types (organic litter, soil, rocks, and logs) were scored between 1 and 6. These scores corresponded to the following percent cover: 1 (>0-5%), 2 (>5-25%), 3 (>25-50%), 4 (>50-75%), 5 (>75-95%), 6 (>95-100%). Only shrubs and regenerating trees <0.5 m were recorded in this measure.

FIELD SAMPLING: PITFALL GRIDS

The methods used to measure habitat components on the pitfall grids and the categories used to describe these components were identical to those outlined above. The sampling configuration for the pitfall grids differed from that for the point-count transects. The pitfall grids consisted of 6 grid lines with 6 stations at 10-m intervals for a total of 36 stations. Four 20- x 20-m (400 m^2) plots were established at the corners of each pitfall grid. Each of these plots was divided into four 10- by 10-m quadrants. Six 1-m strip transects were established on each grid line (Fig. 2).

Trees and snags--Within each 400-m^2 plot all trees were identified and counted by size class, and all snags were counted by size, decay, and height class. Tree heights of 4 representative live trees were measured.

Canopy cover--Canopy cover was measured at the center and corners of each of the 400-m^2 plots for a total of 20 measurements per pitfall grid.

Shrubs--Along each of the 1-m strip transects, all shrubs with stems within the strip were identified. The length and width of each shrub were measured to obtain an estimate of area and each shrub was assigned to 1 of 3 height classes: 1 (0.5-1 m), 2 (>1-1.5 m), or 3 (>1.5 m).

Woody debris--Within 2 of the 10- by 10-m quadrants of each 400-m^2 plot, the size and decay classes of all logs and the type and decay class of all stumps were recorded. Stumps were divided into 2 types, cut and natural, and into the 4 decay classes described above. Burned stumps were not assigned to a decay class, but were recorded as "burned".

Regenerating trees--The number, type (coniferous or deciduous), and height class (0.5-1.5 m and >1.5 m) of all regenerating trees were counted within 2 of the 10- by 10-m quadrants of each 400-m^2 plot. For saplings to be counted they had to be ≥0.5 m in height and <4 cm d.b.h.

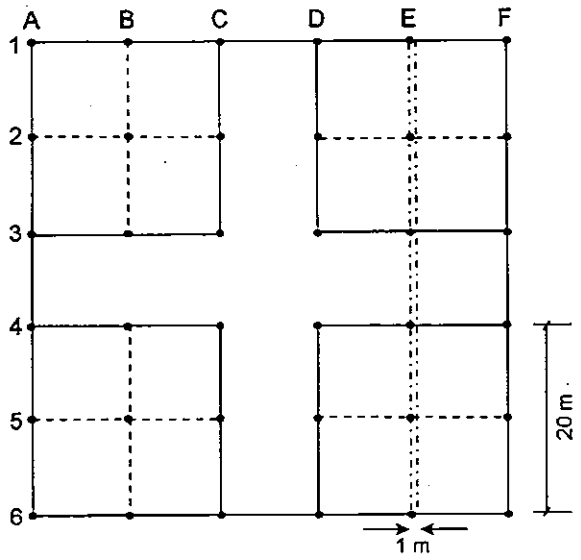

Figure 2. Sampling scheme for vegetation on the small mammal pitfall grids. Each pitfall grid had 36 traps in a 6 x 6 array with 10 m between traps. Solid circles indicate trap stations.

Ground cover--To measure ground cover, a 20- by 50-cm plot frame was placed at each of the 36 grid stations. Visual estimates of the cover of vegetative types (herbaceous, grass, fern, shrub, regenerating trees, and moss) and litter types (organic litter, soil, rocks, and logs) were scored between 1 and 6. Only shrubs and regenerating trees <0.5 m were recorded in this measure.

ANALYSIS OF VEGETATIVE CHARACTERISTICS

Habitat measurements were averaged for each 576-m^2 point-count plot of the bird transect (N = 276) and for each of the four 400-m^2 plots for the pitfall grids (N = 144). Measurements associated with individual trapping stations on the pitfall grids (e.g., percent ground cover, shrub area) were assigned to the plot encompassing those stations. Any variables that had 0 values throughout were not included in the analyses. Given that a primary goal of the habitat analysis was to correlate animal distribution with habitat structure, the manner by which variables were combined differed between the bird transect plots and the pitfall grid plots. For example, all log types and decay classes were combined for the bird transect plots but considered separately for the pitfall grid plots. Consequently, the total number of variables analyzed was 23 for the

bird plots and 56 for the pitfall grid plots. The tree and shrub species composition was examined by calculating the mean frequency of a particular species for those sites at which the species occurred.

Multivariate analysis of variance (MANOVA) was used to compare the means between forest types and stand sizes. Discriminant function analysis (DFA) was then conducted to determine if the variables correctly differentiated the forest stand types and sizes. We then conducted a stepwise DFA to determine the variables that were most significant in describing the forest stand types. All analyses were conducted using the GLM and DISCRIM procedures of the Statistical Analysis System (SAS Institute 1989).

General comparisons

The 3 forest types for the bird point-count plots differed significantly (MANOVA, F = 24.50; df = 46, 496; $P < 0.0001$; Table 1). The mean values for 20 of the 23 habitat variables differed between the 3 forest types (univariate ANOVA). The overall MANOVA for the pitfall grids also indicated significant differences between the 3 forest types (F = 12.43; df = 112,166, $P < 0.0001$; Table 1). The mean values for 43 of the 56 habitat variables differed between the 3 forest stand types. These results indicate that the habitat variables we measured reflect the structural differences between these forest types.

There were also significant differences between the 2 stand sizes for both point count and pitfall grid data sets (MANOVA-point count, $F = 2.57$, df = 23,248, $P < 0.0002$; pitfall grid, $F = 3.333$, df = 56, 83, $P < 0.001$). However, the means for only 3 of 23 and 16 of 56 habitat variables differed between the 2 stand sizes for point count and pitfall grid data sets, respectively, suggesting that the differences are relatively minor.

For the bird point-count plots, DFA correctly classified 97.8% of the closed-canopy plots, 95.7% of regenerating stand plots, and 89.1% of the clearcut plots. Clearcut stand plots were incorrectly classified as regenerating stands in 8.7% of the cases (N = 8) and as closed-canopy stands in 2.2% (N = 2). For the pitfall grid plots, the DFA correctly classified 100% of the 48 closed-canopy plots, 97.9% of the 48 clearcut, and

Table 1. Comparison of mean (± 1 SD) of habitat variables by forest type for measurements from point count stations (N = 276) and from pitfall grids (N = 144) for northeastern Washington.

	Bird Plot			Pitfall Grid		
Habitat variable	Closed-canopy	Regen	Clearcut	Closed-canopy	Regen	Clearcut
Canopy cover %	90 ± 9	36 ± 31	22 ± 20	91 ± 9	36 ± 29	22 ± 19
Tree height (m)	18 ± 5	5 ± 3	12 ± 7	21 ± 6	5 ± 2	9 ± 7
Coniferous trees/plot						
>50 cm	1.3 ± 2.1	0.0	0.1 ± 0.5	1.8 ± 2.9	0.0	0.04 ± 0.2
26 - 50 cm	12.5 ± 6.8	0.2 ± 0.7	1.5 ± 2.5	9.0 ± 4.8	0.1 ± 0.6	0.8 ± 1.5
11-25 cm	30.9 ± 20.4	5.5 ± 6.1	4.3 ± 6.3	26.3 ± 18.3	9.7 ± 15.7	2.7 ± 3.2
4 - 10 cm	36.6 ± 29.7	18.8 ± 16.0	3.6 ± 5.6	18.5 ± 19.9	29.2 ± 35.2	2.1 ± 2.3
Deciduous trees/plot						
>50 cm	0.0	0.0	0.0	0.0	0.0	0.0
26-50 cm	0.1 ± 0.3	0.0	0.0	0.02 ± 0.1	0.0	0.0
11-25 cm	0.4 ± 1.0	0.3 ± 2.2	0.02 ± 0.1	0.3 ± 0.7	0.1 ± 0.3	0.0
4-10 cm	2.0 ± 3.5	1.5 ± 3.5	0.8 ± 3.5	0.6 ± 1.4	1.9 ± 3.7	0.0
Snags/plot						
>50 cm	0.3 ± 0.6	0.0	0.2 ± 0.6	0.1 ± 0.4	0.02 ± 0.1	0.04 ± 0.2
26-50 cm	2.0 ± 2.3	0.01 ± 0.1	0.8 ± 1.0	0.7 ± 1.0	0.06 ± 0.2	0.4 ± 0.7
11-25 cm	5.5 ± 4.1	0.1 ± 0.4	2.2 ± 2.3	6.4 ± 5.0	0.3 ± 1.32	1.9 ± 2.2
4-10 cm	9.1 ± 7.7	0.2 ± 0.5	1.5 ± 2.4	5.9 ± 5.4	0.3 ± 0.8	0.9 ± 1.5
Shrub area/plot						
0.5-1 m^2	5.6 ± 6.8	11.1 ± 10.8	7.2 ± 6.8	5.5 ± 7.7	16.3 ± 20.0	7.6 ± 10.9
>1-1.5 m^2	2.4 ± 5.6	12.1 ± 18.4	4.2 ± 6.6	1.5 ± 2.9	7.7 ± 10.6	2.8 ± 4.3
>1.5 m^2	0.7 ± 2.1	32.6 ± 45.8	5.0 ± 13.6	0.6 ± 2.1	34.7 ± 64.0	1.1 ± 4.2
Logs-All	27.6 ± 18.4	16.7 ± 11.3	32.1 ± 14.1			
Logs-Size 1						
Decay class 1				3.1 ± 3.4	0.6 ± 1.8	1.1 ± 1.2
Decay class 2				5.3 ± 5.2	2.6 ± 3.2	4.0 ± 3.0
Decay class 3				0.5 ± 0.8	0.1 ± 0.3	0.2 ± 0.6
Decay class 4				0.04 ± 0.2	0.02 ± 0.1	0.02 ± 0.1
Burned				0.0	0.8 ± 1.4	0.3 ± 0.9
Logs-Size 2						
Decay class 1				0.8 ± 1.1	0.2 ± 0.7	2.1 ± 2.7
Decay class 2				3.9 ± 2.9	5.0 ± 5.5	10.9 ± 6.9
Decay class 3				2.2 ± 2.0	0.9 ± 1.6	1.2 ± 1.4
Decay class 4				0.9 ± 1.4	0.2 ± 0.9	0.1 ± 0.3
Burned				0.06 ± 0.2	4.0 ± 4.3	1.1 ± 2.6
Logs-Size 3						
Decay class 1				0.0	0.0	0.02 ± 0.1
Decay class 2				0.04 ± 0.2	0.06 ± 0.2	0.5 ± 0.9
Decay class 3				0.3 ± 0.9	0.1 ± 0.4	0.5 ± 1.2
Decay class 4				0.5 ± 0.8	0.2 ± 0.5	0.4 ± 0.7
Burned				0.02 ± 0.1	0.7 ± 1.3	0.2 ± 0.5
Logs-Size 4						
Decay class 1				0.4 ± 0.9	0.02 ± 0.1	0.2 ± 0.4
Decay class 2				0.5 ± 0.8	0.3 ± 0.8	1.6 ± 2.0
Decay class 3				1.1 ± 1.5	0.2 ± 0.5	0.4 ± 0.6
Decay class 4				0.9 ± 1.2	0.2 ± 0.8	0.3 ± 0.7
Burned				0.02 ± 0.1	0.8 ± 1.9	0.2 ± 0.5
Regeneration						
Coniferous	24.7 ± 28.7	24.0 ± 18.2	9.2 ± 13.1	10.7 ± 13.5	15.4 ± 14.4	11.3 ± 13.4
Deciduous	0.4 ± 1.3	12.1 ± 15.3	3.4 ± 7.4	0.3 ± 1.0	11.1 ± 27.4	0.5 ± 1.8
Ground cover: %/plot						
Grasses	0.4 ± 1.9	7.8 ± 13.8	7.8 ± 15.2	2.4 ± 5.3	19.3 ± 16.7	17.0 ± 13.5
Herb. dicot	11.4 ± 16.4	24.4 ± 19.3	20.2 ± 15.9	24.0 ± 19.7	43.4 ± 16.8	27.2 ± 18.1
Shrub <0.5m				20.8 ± 23.7	33.8 ± 19.4	27.2 ± 18.1
Litter				85.7 ± 18.6	80.6 ± 13.4	77.7 ± 12.6
Litter Depth				14.2 ± 5.1	12.6 ± 5.2	13.0 ± 5.4

100% of the 48 regenerating plots. Again, these results indicate that the habitat variables we measured reflect the structural differences between stand types.

Discrimination between the 2 size classes of stands was less accurate. For the point count stations, analysis classified 76.8% of the large stands and 71.7% of the small stands correctly. For the pitfall grids, DFA classified 90.3% of the large stands and 88.9% of the small stands correctly.

For the bird point-count plots, stepwise DFA identified 10 variables with significant *F* statistics ($P < 0.05$) to be included in the selection process and 19 variables for the pitfall grid plots. For both sampling levels, mean canopy cover explained >60% of the partial *r* value (64% for the bird plots, 68% for the pitfall grid plots; Fig. 3). Other habitat variables that were highly significant ($P < 0.00001$) were number of 26- to 50-cm d.b.h. coniferous trees (Fig. 4), area of shrubs >1.5 m tall (Fig. 5), mean tree height (Fig. 6), and number of deciduous saplings <4 cm d.b.h. In all cases, mean values were similar between the bird plots and the pitfall grid plots (Figs. 3-7).

This suggests that habitat variables measured at the smaller scale of the pitfall grid were representative of the habitat conditions of the forest stand measured at the larger scale of the bird plots.

STAND DESCRIPTIONS

Closed-canopy--These stands were dominated by Douglas-fir, grand fir, western larch, western hemlock, western redcedar, and lodgepole pine (Tables 2 and 3; see tables for scientific names). On average, each bird point-count plot and pitfall-grid plot contained 1 tree > 50 cm d.b.h., 10 trees 26-50 cm d.b.h., 28 trees 11-25 cm d.b.h., and 27 trees 4-10 cm d.b.h. Deciduous trees were uncommon and all were in small size classes. Similarly, regenerating coniferous trees were common in the closed-canopy stands whereas regenerating deciduous trees were very uncommon. These closed-canopy stands were characterized by >90% canopy cover and a mean tree height of about 20 m (Table 1). Tall snags (>5 m) of both decay classes were present on all the closed canopy sites and averaged about 5 snags in each plot or grid. Shorter snags were not present at all sites and were less common when present (Tables 2 and 3). Snags of the 4- to 10-cm and 11- to 16-cm d.b.h. size classes were most common, but larger snags were present (Table 1).

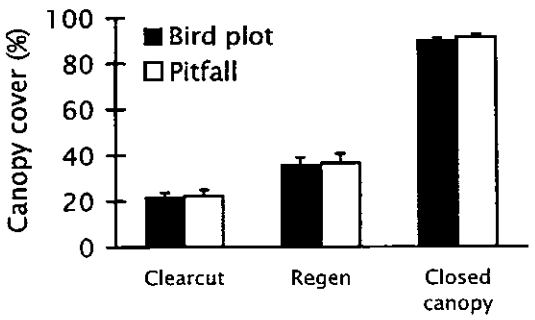

Figure 3. Mean canopy cover in the 3 forest types in northeastern Washington for both point count plots and pitfall trapping grids.

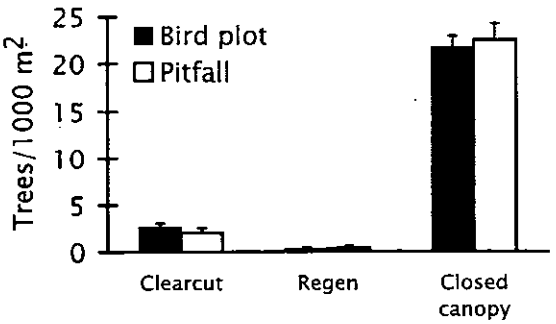

Figure 4. Mean number of coniferous trees on the 3 forest types in northeastern Washington for both point count plots and pitfall trapping grids.

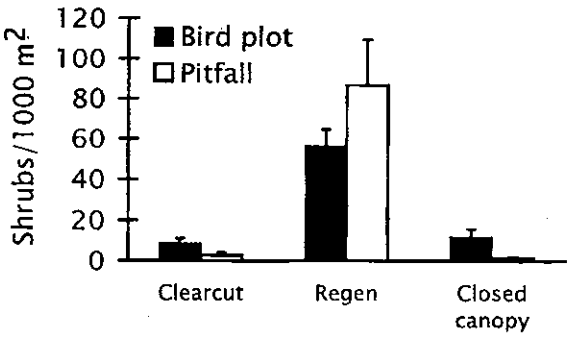

Figure 5. Mean number of shrubs per plot on the 3 forest types in northeastern Washington for both point count plots and pitfall trapping grids.

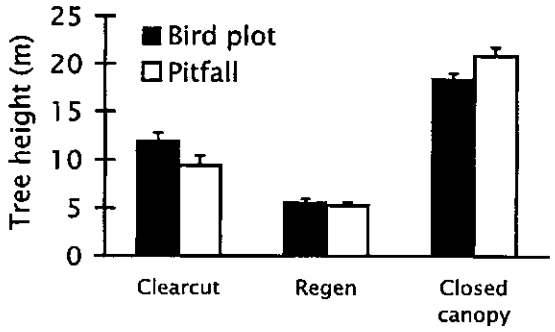

Figure 6. Mean tree height on each of the 3 forest types in northeastern Washington for both point count plots and pitfall trapping grids.

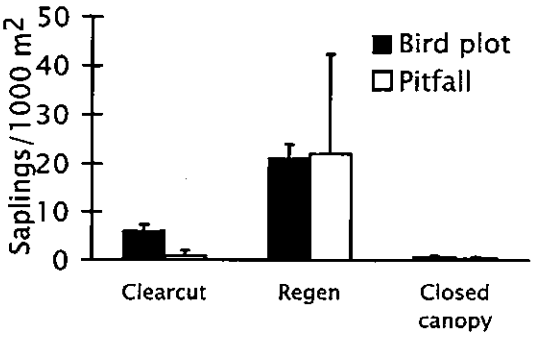

Figure 7. Mean number of deciduous saplings for the 3 forest types in northeastern Washington for both point count plots and pitfall trapping grids.

The main shrubs in the closed-canopy stands were ninebark, rose, and mountain boxwood (Tables 4 and 5; see tables for scientific names). The mean area per plot covered by shorter shrubs (0.5-1.0 m) was greater than by medium-height shrubs (1.0-1.5 m), which in turn was greater than the area covered by the taller shrubs (>1.5 m).

Woody debris was common in the closed-canopy stands. Not surprisingly, the mean numbers of smaller diameter logs of decay classes 1 and 2 per plot were greater than for those of the smaller, older logs or large logs. More larger logs of decay classes 3 and 4 were present in the closed-canopy stands than in either of the other 2 forest stands. The mean number of cut stumps per plot was similar to the mean number of natural stumps for all but the oldest stumps, for which the natural stumps were more common (Table 1).

Table 2. Mean number (± 1 SE) of trees at point count stations calculated for sites where a species was present. Number of sites is in parentheses.

	Closed-canopy		Regenerating		Clearcut	
	Small	Large	Small	Large	Small	Large
Alder, *Alnus* spp.	1.33 ± 0.00 (1)	0.23 ± 0.07 (4)		0.46 ± 0.15 (4)		
Serviceberry, *Amelanchier alnifolia*	0.75 ± 0.00 (1)	0.08 ± 0.00 (1)				
Birch, *Betula* spp.		0.17 ± 0.08 (2)	1.00 ± 0.25 (2)	0.85 ± 0.28 (4)		0.08 ± 0.00 (1)
Black cottonwood, *Populus trichocarpa*		1.08 ± 0.00 (1)	0.25 ± 0.00 (1)	0.08 ± 0.00 (1)		
Douglas fir, *Pseudotsuga menziesii*	7.71 ± 3.15 (6)	16.33 ± 6.91 (6)	6.29 ± 4.81 (6)	6.99 ± 2.34 (6)	0.31 ± 0.03 (3)	2.02 ± 0.68 (5)
Engelmann spruce, *Picea engelmannii*	4.50 ± 0.17 (2)	1.19 ± 0.77 (4)	1.33 ± 1.00 (2)	5.00 ± 4.83 (2)	0.67 ± 0.00 (1)	
Grand fir, *Abies grandis*	15.03 ± 4.91 (6)	23.58 ± 8.37 (6)	2.63 ± 1.88 (2)	4.47 ± 2.17 (5)	2.17 ± 1.83 (2)	3.75 ± 1.03 (6)
Lodgepole pine, *Pinus contorta*	2.82 ± 1.72 (6)	9.72 ± 4.22 (6)	13.49 ± 6.64 (6)	3.33 ± 1.14 (6)	0.25 ± 0.00 (1)	1.06 ± 0.48 (4)
Ponderosa pine, *Pinus ponderosa*	0.75 ± 0.00 (1)	0.61 ± 0.49 (3)	5.19 ± 4.74 (3)	0.29 ± 0.15 (4)		1.75 ± 0.00 (1)
Quaking aspen, *Populus tremuloides*		0.28 ± 0.10 (3)	6.17 ± 5.83 (2)	0.21 ± 0.13 (2)	2.67 ± 0.00 (1)	0.13 ± 0.04 (2)
Subalpine fir, *Abies lasiocarpa*	1.33 ± 0.33 (3)	0.92 ± 0.58 (2)	1.50 ± 0.50 (2)	0.14 ± 0.03 (3)	0.33 ± 0.00 (1)	
Vine maple, *Acer circinatum*	0.25 ± 0.00 (1)	0.40 ± 0.16 (4)		0.33 ± 0.00 (1)		0.86 ± 0.43 (3)
Western hemlock, *Tsuga heterophylla*	12.94 ± 5.96 (4)	9.17 ± 2.54 (6)	1.08 ± 0.64 (3)	0.35 ± 0.16 (4)	0.67 ± 0.19 (3)	2.44 ± 2.03 (3)
Willow, *Salix* spp.	0.29 ± 0.04 (2)	2.72 ± 1.40 (5)		1.46 ± 0.46 (2)		1.50 ± 0.42 (2)
Western larch, *Larix occidentalis*	6.08 ± 2.84 (5)	8.42 ± 1.66 (6)	4.67 ± 2.15 (4)	4.10 ± 1.64 (6)	0.42 ± 0.05 (4)	0.50 ± 0.16 (6)
Western redcedar, *Thuja plicata*	14.39 ± 3.92 (6)	19.33 ± 2.92 (6)	1.27 ± 0.28 (4)	1.63 ± 0.96 (4)	2.40 ± 0.96 (4)	3.18 ± 0.84 (6)
Western white pine, *Pinus monticola*	0.79 ± 0.51 (4)	0.81 ± 0.34 (4)	3.35 ± 1.10 (4)	1.58 ± 0.85 (5)		0.13 ± 0.04 (2)
Snag C1-5 m high; Condition 1	2.90 ± 1.30 (4)	3.39 ± 0.82 (6)	0.83 ± 0.50 (2)	0.15 ± 0.02 (4)	0.63 ± 0.23 (4)	0.79 ± 0.28 (6)
Snag C1-5 m high; Condition 2	1.32 ± 0.35 (5)	2.17 ± 0.30 (6)		0.21 ± 0.13 (2)	0.67 ± 0.33 (2)	0.92 ± 0.23 (6)
Tree C>5 m high; Condition 1	5.40 ± 1.59 (6)	7.03 ± 1.01 (6)		0.14 ± 0.06 (3)	0.98 ± 0.43 (4)	1.72 ± 0.42 (6)
Tree C>5 m high; Condition 2	4.42 ± 0.71 (6)	5.28 ± 1.18 (6)		0.42 ± 0.00 (1)	1.31 ± 0.34 (4)	1.90 ± 0.53 (6)

Table 3. Mean number (± 1 SE) of trees on pitfall trapping grids calculated for sites where a species was present. Number of sites is in parentheses.

	Closed-canopy		Regenerating		Clearcut	
	Small	Large	Small	Large	Small	Large
Alder, *Alnus* spp.	0.38 ± 0.13 (2)	1.88 ± 1.38 (2)	1.50 ± 0.00 (2)	2.58 ± 0.65 (3)		
Serviceberry, *Amelanchier alnifolia*	1.00 ± 0.00 (1)	0.25 ± 0.00 (1)				
Black cottonwood, *Populus trichocarpa*		0.25 ± 0.00 (1)		2.38 ± 1.88 (2)		
Douglas fir, *Pseudotsuga menziesii*	7.29 ± 2.32 (6)	4.71 ± 1.93 (6)	8.60 ± 4.73 (5)	8.50 ± 3.29 (5)	0.25 ± 0.00 (2)	0.88 ± 0.07 (4)
Engelmann spruce, *Picea engelmannii*	2.25 ± 1.75 (2)	2.63 ± 1.63 (2)	2.58 ± 0.85 (3)	0.88 ± 0.63 (2)		0.38 ± 0.13 (2)
Grand fir, *Abies grandis*	17.70 ± 6.07 (5)	13.80 ± 6.87 (5)	3.44 ± 1.55 (4)	7.19 ± 3.83 (4)	0.83 ± 0.30 (3)	2.19 ± 1.04 (4)
Lodgepole pine, *Pinus contorta*	5.42 ± 3.60 (6)	9.60 ± 4.55 (5)	22.15 ± 16.75 (5)	3.46 ± 2.02 (6)	0.25 ± 0.00 (1)	0.25 ± 0.00 (1)
Mountain ash, *Sorbus* spp.			0.75 ± 0.00 (1)			
Ponderosa pine, *Pinus ponderosa*	0.25 ± 0.00 (1)		1.00 ± 0.00 (1)			
Quaking aspen, *Populus tremuloides*		0.25 ± 0.00 (1)	0.50 ± 0.00 (1)			
Subalpine fir, *Abies lasiocarpa*	0.50 ± 0.00 (1)		3.75 ± 0.00 (1)		0.25 ± 0.00 (1)	1.25 ± 0.00 (1)
Vine maple, *Acer circinatum*	1.00 ± 0.25 (2)			1.00 ± 0.00 (1)		
Western hemlock, *Tsuga heterophylla*	2.65 ± 1.07 (5)	19.13 ± 9.28 (6)	1.17 ± 0.51 (3)	0.25 ± 0.00 (1)	0.75 ± 0.00 (1)	2.67 ± 1.62 (3)
Willow, *Salix* spp.	0.00 ± 0.00 (1)	0.67 ± 0.42 (3)		3.00 ± 1.75 (2)		
Western larch, *Larix occidentalis*	2.50 ± 0.80 (5)	11.10 ± 2.96 (5)	36.75 ± 30.44 (4)	3.10 ± 1.18 (5)	0.44 ± 0.06 (4)	0.88 ± 0.33 (4)
Western redcedar, *Thuja plicata*	9.83 ± 1.40 (6)	14.29 ± 3.01 (6)	2.20 ± 0.90 (5)		2.45 ± 0.85 (5)	3.92 ± 1.17 (6)
Western white pine, *Pinus monticola*	0.92 ± 0.67 (3)	0.67 ± 0.08 (3)	3.08 ± 2.24 (3)	2.25 ± 1.06 (4)		
Snag C1-5 m high; Condition 1	1.45 ± 0.74 (5)	2.17 ± 0.42 (6)	0.50 ± 0.25 (2)	0.38 ± 0.13 (2)	0.44 ± 0.12 (4)	1.00 ± 0.37 (6)
Snag C1-5 m high; Condition 2	1.54 ± 0.58 (6)	1.30 ± 0.50 (5)	0.38 ± 0.13 (2)	1.25 ± 0.00 (1)	0.50 ± 0.14 (3)	0.55 ± 0.15 (5)
Tree C>5 m high; Condition 1	3.42 ± 0.71 (6)	11.58 ± 3.28 (6)	2.25 ± 0.00 (1)		1.25 ± 0.38 (3)	2.21 ± 0.79 (6)
Tree C>5 m high; Condition 2	3.33 ± 0.85 (6)	2.00 ± 0.53 (6)	0.75 ± 0.50 (4)		1.42 ± 1.04 (3)	1.00 ± 0.16 (6)

Table 4. Mean number (± 1 SE) of shrubs at point count stations calculated for sites where a species was present. Number of sites is in parentheses.

	Closed-canopy		Regenerating		Clearcut	
	Small	Large	Small	Large	Small	Large
Alder, *Alnus* spp.	2.17 ± 0.83 (2)			10.00 ± 5.82 (5)	0.92 ± 0.58 (2)	0.47 ± 0.35 (3)
Serviceberry, *Amelanchier alnifolia*	0.92 ± 0.58 (2)			0.17 ± 0.08 (2)	0.56 ± 0.09 (4)	0.61 ± 0.18 (6)
Black cottonwood, *Populus trichocarpa*						0.08 ± 0.00 (1)
Oregon grape, *Berberis aquifolium*				3.58 ± 1.67 (2)	2.67 ± 0.00 (1)	
Birch, *Betula* spp.	0.42 ± 0.13 (3)		0.50 ± 0.17 (2)	0.17 ± 0.00 (1)	0.54 ± 0.21 (2)	0.17 ± 0.00 (1)
Red stem ceanothus, *Ceanothus sanguineus*		0.08 ± 0.00 (1)				
Ceanothus sp., *Ceanothus* sp.	0.75 ± 0.00 (1)	0.08 ± 0.00 (1)	2.33 ± 0.00 (1)	4.25 ± 0.92 (2)		2.22 ± 0.81 (5)
Mountain balm, *Ceanothus velutinus*			1.00 ± 0.00 (1)	0.14 ± 0.06 (3)	3.13 ± 2.88 (2)	1.17 ± 0.00 (1)
Red osier dogwood, *Cornus stolonifera*				0.08 ± 0.00 (1)		0.08 ± 0.00 (2)
Bear-brush, *Garrya fremontii*						0.08 ± 0.00 (1)
Ocean-spray, *Holodiscus discolor*	1.29 ± 0.96 (2)	0.69 ± 0.49 (3)	0.58 ± 0.13 (3)	0.17 ± 0.05 (3)		1.79 ± 0.73 (4)
Oregon trailing honeysuckle, *Lonicera ciliosa*				0.08 ± 0.00 (2)		0.33 ± 0.00 (1)
Hairy honeysuckle, *Lonicera hispidula*		0.08 ± 0.00 (1)		0.43 ± 0.21 (5)		0.19 ± 0.03 (3)
Utah honeysuckle, *Lonicera utahensis*	2.35 ± 1.13 (4)	0.49 ± 0.22 (6)	0.52 ± 0.17 (4)			0.65 ± 0.36 (4)
Mountain ash, *Sorbus* spp.	0.75 ± 0.00 (1)				0.25 ± 0.00 (1)	
Mountain boxwood, *Pachistima myrsinites*	0.50 ± 0.00 (1)	11.42 ± 5.92 (4)	4.25 ± 2.75 (2)	5.60 ± 3.64 (5)	0.29 ± 0.04 (2)	2.11 ± 1.45 (3)
Ninebark, *Physocarpus malvaceus*	36.00 ± 0.00 (1)	5.88 ± 5.54 (2)		0.17 ± 0.00 (1)	10.00 ± 0.00 (1)	10.22 ± 4.36 (5)
Chokecherry, *Prunus virginiana*	0.25 ± 0.00 (1)					
Quaking aspen, *Populus tremuloides*				0.58 ± 0.00 (1)		0.08 ± 0.00 (1)
Gooseberry, *Ribes* spp.	0.42 ± 0.13 (3)	0.83 ± 0.00 (1)	14.17 ± 9.35 (3)	6.60 ± 3.38 (5)	3.53 ± 1.34 (5)	7.17 ± 2.02 (6)
Rose, *Rosa* spp.	8.63 ± 5.99 (4)	3.72 ± 1.09 (6)	0.64 ± 0.22 (3)	1.47 ± 0.86 (5)	2.78 ± 0.98 (6)	6.43 ± 2.46 (6)
Raspberry, *Rubus ideaus*			1.53 ± 0.70 (3)	0.19 ± 0.10 (4)	2.86 ± 1.42 (3)	1.35 ± 0.56 (4)
Thimbleberry, *Rubus parviflorus*	3.14 ± 1.82 (3)	0.13 ± 0.04 (2)	21.14 ± 10.35 (3)	50.28 ± 22.21 (5)	3.20 ± 1.71 (5)	9.33 ± 2.15 (6)
Elderberry, *Sambucus cerulea*	0.33 ± 0.00 (1)		0.25 ± 0.00 (1)	0.25 ± 0.08 (2)		0.67 ± 0.25 (5)
Soapberry, *Sheperdia canadensis*	6.67 ± 0.00 (1)	3.54 ± 3.21 (2)	1.25 ± 0.39 (4)	0.96 ± 0.34 (4)		
Shiny-leaf spiraea, *Spiraea betifolia*	3.17 ± 2.83 (2)	0.17 ± 0.05 (3)	0.28 ± 0.03 (3)	0.19 ± 0.04 (4)	1.97 ± 1.14 (3)	1.80 ± 1.02 (5)
Snowberry, *Symphoricarpos albus*	1.06 ± 0.64 (3)	0.48 ± 0.22 (4)	16.33 ± 0.00 (1)	0.21 ± 0.13 (2)	2.50 ± 1.08 (3)	1.13 ± 0.80 (4)
Huckleberry, *Vaccinium* spp.		4.02 ± 1.89 (5)	1.33 ± 0.67 (2)	4.02 ± 2.79 (5)	1.42 ± 0.69 (6)	4.40 ± 3.49 (5)
Vine maple, *Acer circinatum*		0.13 ± 0.04 (2)		0.29 ± 0.21 (2)	0.75 ± 0.25 (2)	0.63 ± 0.27 (4)
Willow, *Salix* spp.			2.50 ± 0.25 (2)	3.71 ± 1.50 (6)	0.94 ± 0.65 (3)	1.21 ± 0.13 (6)

Table 5. Mean number (± 1 SE) of shrubs on pitfall trapping grids calculated only for sites where a species was present. Number of sites is in parentheses.

	Closed-canopy		Regenerating		Clearcut	
	Small	Large	Small	Large	Small	Large
Alder, *Alnus* spp.	1.00 ± 0.00 (1)	1.00 ± 0.00 (1)	32.50 ± 5.50 (2)		2.00 ± 0.00 (1)	6.00 ± 0.00 (1)
Serviceberry, *Amelanchier alnifolia*	5.00 ± 3.00 (2)	5.00 ± 0.00 (1)	16.00 ± 9.07 (3)	2.00 ± 0.00 (1)	2.00 ± 0.00 (3)	
Oregon grape, *Berberis aquifolium*			9.00 ± 0.00 (1)	27.00 ± 24.00 (2)	5.00 ± 0.00 (1)	
Birch, *Betula* spp.				3.00 ± 0.00 (1)	1.50 ± 0.50 (2)	
Ceanothus sp., *Ceanothus* sp.				11.00 ± 0.00 (1)	2.50 ± 1.50 (2)	42.50 ± 12.50 (2)
Mountain balm, *Ceanothus velutinus*			1.67 ± 0.67 (3)	6.00 ± 0.00 (1)	10.67 ± 6.77 (3)	
Red osier dogwood, *Cornus stolonifera*				5.50 ± 4.50 (2)		
Ocean-spray, *Holodiscus discolor*	2.00 ± 0.58 (3)	1.00 ± 0.00 (1)	30.50 ± 21.50 (2)			1.50 ± 0.50 (2)
Utah honeysuckle, *Lonicera utahensis*	4.75 ± 1.65 (4)	2.00 ± 0.00 (1)	9.00 ± 3.54 (5)	10.25 ± 4.87 (4)	8.33 ± 3.76 (3)	12.00 ± 0.00 (1)
Mountain ash, *Sorbus* spp.	1.00 ± 0.00 (1)		2.00 ± 0.00 (1)	94.00 ± 93.00 (2)	1.00 ± 0.00 (1)	
Mountain boxwood, *Pachistima myrsinites*		100.00 ± 47.51 (3)	12.67 ± 11.17 (3)	28.20 ± 14.90 (5)	10.00 ± 6.66 (3)	2.00 ± 0.00 (1)
Ninebark, *Physocarpus malvaceus*	39.50 ± 32.50 (2)	4.00 ± 2.00 (2)			1.00 ± 0.00 (1)	51.50 ± 34.50 (2)
Quaking aspen, *Populus tremuloides*			1.00 ± 0.00 (1)	2.33 ± 0.88 (3)	3.00 ± 0.00 (1)	
Gooseberry, *Ribes* spp.	5.00 ± 4.00 (2)	1.00 ± 0.00 (1)	76.00 ± 38.80 (3)	34.00 ± 11.00 (3)	19.60 ± 11.78 (5)	22.50 ± 12.95 (4)
Rose, *Rosa* spp.	21.00 ± 10.94 (5)	17.33 ± 0.67 (3)	18.75 ± 13.21 (4)	18.75 ± 7.60 (4)	46.60 ± 32.76 (5)	8.50 ± 5.60 (6)
Raspberry, *Rubus ideaus*			16.75 ± 10.22 (4)		22.25 ± 13.97 (4)	1.00 ± 0.00 (2)
Thimbleberry, *Rubus parviflorus*	4.00 ± 0.00 (2)	1.00 ± 0.00 (1)	251.33 ± 105.53 (3)	155.75 ± 63.08 (4)	9.20 ± 2.22 (5)	17.40 ± 6.73 (5)
Elderberry, *Sambucus cerulea*			2.50 ± 0.50 (2)	1.00 ± 0.00 (1)		1.50 ± 0.50 (2)
Soapberry, *Sheperdia canadensis*	42.00 ± 0.00 (1)	41.00 ± 0.00 (1)	9.67 ± 5.55 (3)	1.00 ± 0.00 (1)	1.00 ± 0.00 (3)	
Shiny-leaf spiraea, *Spiraea betifolia*	1.00 ± 0.00 (3)	1.50 ± 0.50 (2)	1.50 ± 0.50 (2)	10.00 ± 6.45 (4)	33.50 ± 23.50 (2)	26.00 ± 0.00 (1)
Snowberry, *Symphoricarpos albus*	1.00 ± 0.00 (1)	1.50 ± 0.50 (2)		4.50 ± 2.50 (2)	10.00 ± 0.00 (1)	7.67 ± 4.06 (3)
Huckleberry, *Vaccinium* spp.	24.40 ± 5.59 (5)	21.67 ± 19.17 (3)	41.75 ± 38.11 (4)	37.50 ± 13.45 (4)	37.50 ± 23.16 (4)	10.00 ± 5.00 (2)
Vine maple, *Acer circinatum*	2.00 ± 0.00 (1)		12.33 ± 5.93 (3)	9.00 ± 0.00 (1)	14.00 ± 0.00 (1)	9.00 ± 4.16 (3)
Willow, *Salix* spp.			7.00 ± 6.00 (2)	37.20 ± 23.57 (5)	15.00 ± 7.78 (5)	10.00 ± 2.65 (3)

Grasses averaged only about 0.5 to 2% of the cover in the 20- x 50-cm plots, whereas herbaceous and woody (shrubs < 0.5 m) dicots were more common. Most of the ground was covered by litter with an average depth of 14 cm (Table 1).

Regeneration--These stands were dominated by Douglas-fir, lodgepole pine, and quaking aspen (Tables 2 and 3). On average, 0.2 trees 26-50 cm d.b.h., 7.6 trees 11-25 cm d.b.h., and 23 trees 4-10 cm d.b.h. were present on each bird count plot or pitfall grid plot. There were no large (>50 cm d.b.h.) coniferous or deciduous trees in these stands. Deciduous trees in the smaller size classes were uncommon. Regenerating coniferous and deciduous trees were common in the regeneration stands. These regeneration stands were characterized by about 30% canopy cover and a mean tree height of about 5.3 m. Snags of any size or decay class averaged <1 snag per plot (Table 1).

The main shrubs in the regenerating stands were alder, mountain boxwood, gooseberry, thimbleberry, and huckleberry (Tables 4 and 5). Taller (>1.5 m) shrubs covered 2-3 times the mean area per plot compared to the mean area covered by shorter shrubs (0.5-1.0 m) or medium-height shrubs (1.0-1.5 m; Table 1).

Burned logs and stumps were more common on the regenerating stands than either of the other 2 forest stand types. There was less unburned woody debris of any size or decay class on these sites than on the other stand types. The mean number of cut stumps per plot was greater than the mean number of natural stumps for all decay classes (Table 1).

Grasses averaged about 7-19% of the cover in the 20- x 50-cm plots, whereas herbaceous and woody (shrubs < 0.5 m) dicots were more common. Most of the ground was covered by litter which had an average depth of 13 cm (Table 1).

Clearcut--The most common trees remaining on these stands were Douglas-fir, grand fir, western redcedar, and quaking aspen (Tables 2 and 3). On average, 1.6 trees 26-50 cm d.b.h., 3.5 trees 11-25 cm d.b.h., and 2.8 trees 4-10 cm d.b.h. were present on each bird count plot or pitfall grid plot. No large (>50 cm d.b.h.) coniferous or deciduous trees occurred in these stands. Deciduous trees in the smaller size classes were uncommon.

Regenerating coniferous trees were common in the clearcut stands compared to regenerating deciduous trees. These clearcut stands were characterized by about 22% canopy cover and a mean tree height of about 10.5 m. Snags of any size or decay class averaged <2 snags per plot (Tables 1-3).

The main shrubs in the clearcut stands were gooseberry, thimbleberry, and serviceberry (Tables 4 and 5). The mean area per plot covered by shorter shrubs (0.5-1.0 m) was greater than by medium-height shrubs (1.0-1.5 m), which in turn was greater than the area covered by the taller shrubs (>1.5 m) (Table 1).

Medium-sized (15-25 cm diameter) logs of decay class 1 and 2 were more common on the clearcut stands as compared to the other 2 forest stand types. The mean number of cut stumps per plot was greater than the mean number of natural stumps for all but the oldest decay classes (Table 1).

Grasses averaged about 9-17% of the cover in the 20- x 50-cm plots, whereas herbaceous and woody (shrubs <0.5 m) dicots were more common. Less of the ground was covered by litter in clearcut than in the other 2 forest types, but mean litter depth of 13 cm was similar to that of the other stands (Table 1).

HABITAT OCCUPANCY AND POPULATION PATTERNS OF SMALL MAMMALS IN MANAGED FORESTS

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INTRODUCTION

Small mammals are important components of forest ecosystems as consumers (e.g., on seeds, insects, and fungi), as dispersers of seeds and mycorrhizal fungi, and as prey for reptilian, avian, and mammalian carnivores. Unmanaged forests represent a mosaic of habitat conditions due to differences in edaphic factors and natural disturbance regimes. Small mammal species exhibit differential adaptations to these different habitat conditions, but populations of most species have the capacity to respond relatively rapidly to changes in habitat conditions. In forests managed for timber harvest both the spatial and temporal scale of this mosaic of habitat conditions is changed. This study examined the distribution and occurrence of small mammal species with respect to both local habitat and landscape level factors in forests managed for timber harvest.

Studies of forest-floor small mammal communities in the Pacific Northwest have focused primarily on comparisons of old-growth forests with naturally regenerated young (e.g., Aubry and others 1991, Corn and Bury 1991, Gilbert and Allwine 1991, West 1991) or managed (e.g., Carey and Johnson 1995) forests west of the Cascade Crest. Studies of small mammals in old-growth and naturally regenerated forests of Washington and Oregon found few consistent patterns in community composition across different age classes of forest stands (Aubry and others 1991) nor were there strong correlations between habitat features and small mammal abundance (e.g., Corn and Bury 1991). West (1991) suggested that the lack of strong community patterns was unsurprising given the focus on old-growth and naturally regenerated forests. The latter retain most of the structural components (especially woody debris) of old-growth forests and thus meet thresholds of critical habitat variables for many small mammal species (West 1991).

Carey and Johnson (1995) compared small mammal community composition and response of small mammal species to woody debris and understory vegetation in old-growth forests (300-400 yrs) and clearcutting regenerated forests (44-67 yrs) on the Olympic Peninsula. They also considered their results relative to the earlier studies in old-growth and naturally regenerated forests. They reported little difference in

community composition between old-growth forests, naturally regenerated forests, and clearcutting regenerated forests although the number of individuals supported by the old-growth forests was greater (Carey and Johnson 1995). In contrast to Corn and Bury (1991), Carey and Johnson (1995) found that variables describing coarse woody debris and understory vegetation were good predictors of small mammal abundance. Clearly, timber management practices that alter these components can impact small mammal abundance in Pacific Northwest forests.

Further understanding of how timber management practices impact small mammal distribution and abundance requires comparisons of small mammal communities across a range of forest conditions resulting from timber management. Additionally, our understanding of small mammals in forests managed for timber harvest requires studies in regions that are ecologically different (e.g., edaphic conditions) and are subject to different timber management regimes. Our study examined the relationship between local habitat and landscape level factors and the distribution and abundance of small mammals in the managed forests of northeastern Washington. We also consider the effects of temporal variability on distribution and abundance.

METHODS

STUDY SITE

Research was conducted in mixed-coniferous forests managed for timber production in the Selkirk Mountains of northeastern Washington (Stevens and Pend Oreille counties). Forest harvest over the past 30 years has created a mosaic of patches of different sizes and ages within a matrix of closed-canopy, second-growth forest. Forest composition is variable and is affected by slope, aspect, edaphic factors, fire history, and timber management practices. Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), and grand fir (*Abies grandis*).

We used Landsat data to classify the forest into 4 predominant patch types—clearcut, regeneration (<30 yrs old), closed-canopy (65-80 yrs old), and disturbed

(areas modified by timber activities and usually with a deciduous component). We mapped the patches in 20 watersheds by using ARC/INFO (ESRI, Redlands, CA) with a minimum mapping unit of 2 ha (J.G. Hallett and others, in litt.). We selected 36 sites for study in 7 watersheds, which were moderately to heavily fragmented for this region (30-50% cutover). Six replicates of each of 2 stand sizes (~12 and ≥36 ha) and the 3 predominant, upland forest types (mature, closed canopy, >60 yrs; regeneration, 12-20 yrs; and recent clearcuts) were sampled for small mammals. The 2 stand sizes reflect those typically produced by forest harvest. The clearcut sites had some standing live and dead trees and we refer to them as basal area retention (BAR) sites to distinguish them from clearcut areas west of the Cascade Crest.

SAMPLING PROCEDURES

At each site we established a 6 by 6 trapping grid with 10-m spacing between trap stations. Grids were placed in areas considered representative of each stand and were ≥50 m from riparian areas and >100 m from the edge of the stand. One pitfall trap was placed at each station. Traps were constructed from 2 #10 cans taped together and fitted with a plastic funnel constructed from a margarine tub to prevent animals from climbing out. A plywood cover was supported above the trap to prevent debris from entering. Trapping was conducted for 2 weeks at each site during late May, June, or early July of 1993, 1994, and 1995. Traps were checked every 2 days. This sampling effort yielded 18,144 trap nights/year for a total of 54,432 trap nights. Captured animals were weighed, measured, numbered, labeled, and frozen.

Specimens were later autopsied to determine reproductive condition; museum study skins and skeletons were prepared and deposited in the Conner Museum of Washington State University. Species identification was based on dental characteristics, relative body measurements, and pelage. Reproductive data collected for females included size of nipples, number and size of embryos, and number of placental scars and corpora lutea. Females were considered reproductive if embryos or placental scars were present. Determination of male reproductive condition was based on size of testes and epididymis.

HABITAT SAMPLING AND LANDSCAPE DESCRIPTION

Habitat features were measured in July 1993. Four 20- x 20-m plots were established at the corners of each pitfall grid. Each plot was divided into four 10- by 10-m quadrants. Within each 400-m^2 plot, we identified and measured diameter at breast height (d.b.h.) for all trees. For standing dead trees (i.e., snags), we recorded d.b.h., height class (1-5 m or >5 m), and condition. Snags were categorized as either condition 1 if all bark was essentially intact or condition 2 if the bark was peeling off or absent. Based on d.b.h., trees and snags were placed into 1 of 4 size classes: 1 (4-10 cm); 2 (11-25 cm); 3 (26-50 cm); 4 (>50 cm). Tree heights of 4 representative live trees were measured using a clinometer. Canopy cover was measured using a spherical densiometer at the center and corners of each 400-m^2 plot for a total of 20 measurements per pitfall grid.

Along six 1-m strip transects that passed over each row of the trapping grid, we identified all shrubs with stems within the strip. Length and width of each shrub were measured to estimate its area and each shrub was assigned to 1 of 3 height classes: 1 (0.5-1 m), 2 (>1-1.5 m), or 3 (>1.5 m). Within two 10- by 10-m quadrants in each 400-m^2 plot, the size and decay classes of all logs, and type and decay class of all stumps were recorded. Stumps were classified as cut or natural and placed into 1 of the 4 decay classes described above. If a stump had been burned, it was not assigned to a decay class, but recorded as "burned". The number, type (coniferous or deciduous), and height class (0.5-1.5 m and >1.5 m) of all regenerating trees were determined within two 10- by 10-m quadrants in the 400-m^2 plots. Saplings were included if $\geq$0.5 m in height and <4 cm d.b.h. To measure ground cover, a 20- by 50-cm plot frame was placed at each trapping station and vegetative (herbaceous, grass, fern, shrub, regenerating trees, and moss) and litter cover (organic litter, soil, rocks, and logs) were scored into 7 classes: 0 (no cover), 1 (>0-5%), 2 (>5-25%), 3 (>25-50%), 4 (>50-75%), 5 (>75-95%), or 6 (>95-100%). We used the midpoint of each percentage class in the analyses. Shrubs and regenerating trees were recorded if <0.5 m.

For each pitfall grid, we characterized the landscape within a 1 km-radius circle. Because our earlier work had revealed that some measures of landscape structure were invariant (e.g., perimeter-area fractals) or were highly intercorrelated (e.g.,

proportion of area in a forest type and pmL-fractals), we examined only the number of patches, total perimeter, and proportion of area in each forest type. In this analysis, we included the disturbed forest category. Variable mnemonics and descriptions are listed in Table 1.

ANALYSIS

Species richness and abundance were compared between years and between forest stand types and sizes by analysis of variance (ANOVA). Demographic patterns were examined by comparing body mass, age structure, sex ratios, and reproductive condition of captured animals between years and between forest stand types and sizes by ANOVA (body mass, age structure, reproductive condition) and by Chi-square (sex ratios).

To examine the relationship between capture frequency and habitat structure at the stand level we used stepwise multiple regression with capture frequency at each pitfall grid as the dependent variable and mean values of the habitat variables for each grid as independent variables. In addition to the specific habitat variables, we incorporated dummy variables representing each forest type and stand size in the model. We conducted this analysis for each year for each species that had >20 captures in that year. Because of the large number of habitat variables used to describe the pitfall grids, we report only the first 3 variables to enter each regression model (df = 3,35 for each model).

We conducted a second set of stepwise multiple regressions to examine the relationship between number of captures of a species on a pitfall grid and the landscape variables. We did not consider variables that were highly intercorrelated as revealed by a principal components analysis.

All analyses were conducted using the Statistical Analysis System (PROC GLM; SAS Institute, 1989). All statistical tests were considered significant at $P < 0.05$ unless otherwise noted.

Table 1. Habitat and landscape variables used in regression analyses.

Variable	Description
	Trees and snags
Cancov	% canopy cover
d.b.h.1	Coniferous and deciduous trees 4-10 cm d.b.h.
d.b.h.2	Coniferous and deciduous trees 11-25 cm d.b.h.
d.b.h.3	Coniferous and deciduous trees 26-50 cm d.b.h.
d.b.h.4	Coniferous and deciduous trees > 50 cm d.b.h.
Snag1	Snags 4-10 cm d.b.h.
Snag2	Snags 11-25 cm d.b.h.
Snag3	Snags 26-50 cm d.b.h.
Snag4	Snags >50 cm d.b.h.
	Shrubs
AreatHt1	Area of shrubs 0.5-1.0 m in height
AreatHt2	Area of shrubs >1.0-1.5 m in height
AreatHt3	Area of shrubs >1.5 m in height
	Regeneration
DR1	Broadleaf regeneration 0.5-1.5 m in height
DR2	Broadleaf regeneration >1.5 m in height
CR1	Coniferous regeneration 0.5-1.5 in height
CR2	Coniferous regeneration >1.5 in height
	Woody debris-type class
LS	Logs >5 m in length & <15 cm diameter
M	Logs >2.5 m in length & 16-25 cm diameter
SF	Logs $\leq$5 m in length & $\geq$25 cm diameter
LF	Logs >5 m in length & >25 cm diameter
NS	Natural stump
CS	Cut stump
	Woody debris-decay class
1	No decomposition, bark intact, wood solid
2	Decomposition has begun, bark beginning to slough to almost completely gone, sapwood partially softened
3	Decomposition has progressed to point that wood is generally soft, breaks into blocks, no integrity to log or stump
4	Wood has decomposed to point of soil-like texture
B	Burned
	Ground cover
Grass	% of 20- x 50-cm plot frame covered by grasses
Herb	% of 20- x 50-cm plot frame covered by herbaceous dicots
Shrub	% of 20- x 50-cm plot frame covered by shrubs <0.5 m high
Litter	% of 20- x 50-cm plot frame covered by litter
Soil	% of 20- x 50-cm plot frame covered by bare ground

Table 1. Continued

Variable	Description
LitDep	Litter depth (cm)
	Landscape metrics
DisN	Number of disturbed habitat patches in 1-km radius of pitfall grid
DisA	Total area of disturbed habitat patches in 1-km radius of pitfall grid
DispP	Total perimeter of disturbed habitat patches in 1-km radius of pitfall grid
CutN	Number of clearcut habitat patches in 1-km radius of pitfall grid
CutA	Total area of clearcut habitat patches in 1-km radius of pitfall grid
CutP	Total perimeter of clearcut habitat patches in 1-km radius of pitfall grid
MatN	Number of closed-canopy habitat patches in 1-km radius of pitfall grid
MatA	Total area of closed-canopy habitat patches in 1-km radius of pitfall grid
MatP	Total perimeter of closed-canopy habitat patches in 1-km radius of pitfall grid
RegN	Number of regenerating habitat patches in 1-km radius of pitfall grid
RegA	Total area of regenerating habitat patches in 1-km radius of pitfall grid
RegP	Total perimeter of regenerating habitat patches in 1-km radius of pitfall grid

RESULTS

General Capture Trends

We captured a total of 3,739 individuals of 18 species. The mean number of species captured per site was greater in 1994 (7.5) than in 1993 (4.5) or 1995 (5.0; $F = 6.06$, df = 2, $P < 0.001$). Clearcuts had the greatest species richness ($\bar{x} = 7.0$) followed by regenerating (5.1) and closed-canopy (4.5) stands ($F = 23.55$, df = 2, $P < 0.001$; Fig. 1A). Species diversity did not differ between large and small stands ($F = 0.64$, df = 1, $P > 0.4$; Fig. 1B).

Seven species were not adequately sampled with pitfall traps (*Spermophilus columbiana* [12 captures], *Lepus americanus* [8], *Tamias amoenus* [6], *Tamias ruficaudus* [2]) or were quite rare at the study sites because they are associated with more mesic habitat (*Microtus pennsylvanicus* [15], *Microtus richardsoni* [1], and *Sorex palustris* [1]) and are not considered further. For the remaining 11 species, number of captures and the distribution among different patch types and sizes varied substantially among years (Table 2). All species were found on $\geq$1 site in all years, and no species

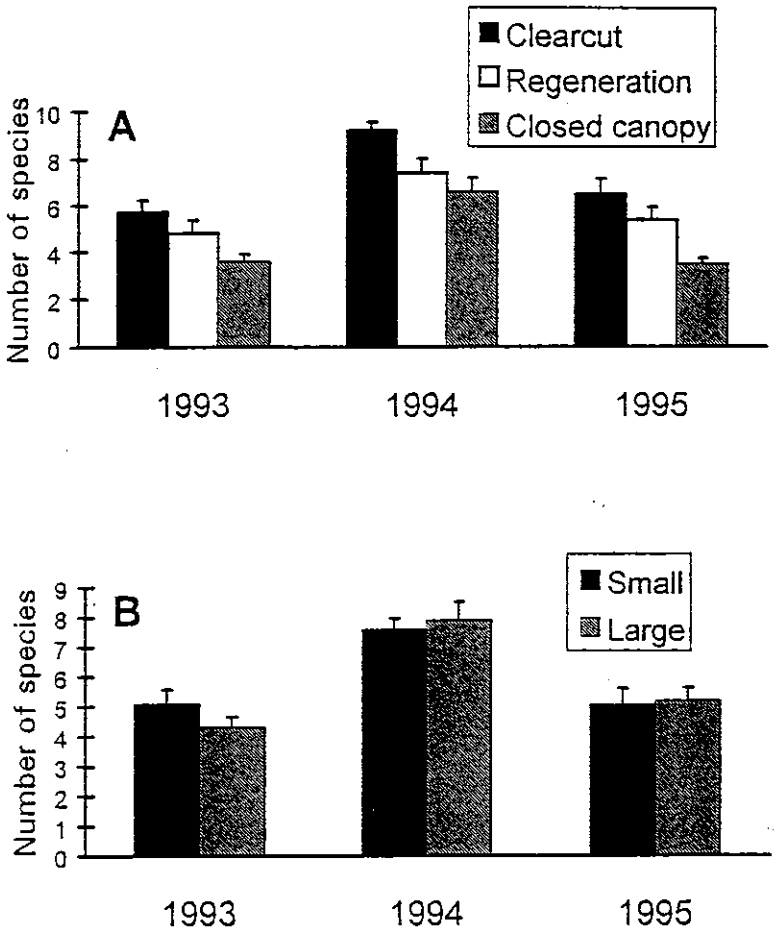

Figure 1. Mean species richness of small mammals for (A) the 3 forest types and (B) the 2 stand sizes for 1993-1995.

was found on all sites during all years (Fig. 2, Table 2). *Sorex vagrans* was present on all sites in 1993 but absent from 2 sites in 1994 and 7 sites in 1995. Six of the 11 species were captured on more sites in 1994 than in either 1993 or 1995. In contrast, *S. vagrans* and *Thomomys talpoides* were captured on more sites in 1993, *S. hoyi* and *Zapus princeps* occurred on more sites in 1995, and *Phenacomys intermedius* was at fewer sites in 1993 but an equal number of sites in 1994 and 1995 (Fig. 2, Table 2).

The total number of captures in 1994 (2,248) was about 3 times that in 1993 (743) or 1995 (718; Fig. 3). *Clethrionomys gapperi*, *Peromyscus maniculatus*, *Microtus longicaudus*, *Microtus montanus*, *Sorex cinereus*, *Sorex monticolus*, and *Sorex vagrans* were captured significantly more frequently in 1994 than in other years (Table 2).

Table 2. Abundance rankings of the small mammal species in each forest type for 1993-1995. The number of captures in each habitat (**N**), the percentage of total captures in each forest type, and the total number of sites in which a species occurred are presented.

	1993				1994				1995			
Rank	Species	N	%	No. of sites	Species	N	%	No. of sites	Species	N	%	No. of sites
					Clearcut							
1	*S. vagrans*	127	49.0	12	*S. vagrans*	374	39.6	12	*S. vagrans*	96	33.3	11
2	*P. maniculatus*	43	16.6	10	*P. maniculatus*	145	15.4	12	*P. intermedius*	38	13.2	10
3	*S. cinereus*	18	6.9	6	*M. longicaudus*	138	14.6	12	*P. maniculatus*	29	10.1	10
4	*Z. princeps*	17	6.6	3	*C. gapperi*	70	7.4	12	*S. cinereus*	27	9.4	8
5	*T. talpoides*	16	6.2	9	*S. cinereus*	62	6.6	10	*Z. princeps*	25	8.7	5
6	*P. intermedius*	11	4.2	6	*P. intermedius*	43	4.6	9	*T. talpoides*	20	6.9	8
7	*C. gapperi*	10	3.9	6	*T. talpoides*	39	4.1	8	*C. gapperi*	17	5.9	8
8	*M. longicaudus*	8	3.1	7	*Z. princeps*	34	3.6	8	*M. longicaudus*	17	5.9	6
9	*S. monticolus*	7	2.7	7	*S. monticolus*	26	2.8	11	*S. monticolus*	11	3.8	3
10	*S. hoyi*	1	0.4	1	*M. montanus*	13	1.4	6	*S. hoyi*	4	1.4	2
11	*M. montanus*	1	0.4	1					*M. montanus*	4	1.4	2
					Regeneration							
1	*S. vagrans*	146	61.3	12	*S. vagrans*	379	55.3	10	*S. vagrans*	113	45.6	9
2	*S. cinereus*	23	9.7	8	*S. cinereus*	76	11.0	11	*P. intermedius*	34	13.7	12
3	*P. maniculatus*	21	8.8	7	*P. intermedius*	60	8.7	12	*S. cinereus*	34	13.7	6
4	*T. talpoides*	13	5.5	5	*C. gapperi*	45	6.6	7	*C. gapperi*	19	7.6	7
5	*Z. princeps*	12	5.0	4	*P. maniculatus*	42	6.1	12	*P. maniculatus*	14	5.7	9
6	*P. intermedius*	8	3.4	6	*Z. princeps*	24	3.5	6	*Z. princeps*	14	5.7	6
7	*C. gapperi*	7	2.9	4	*S. monticolus*	21	3.1	7	*S. hoyi*	7	2.8	5
8	*S. hoyi*	2	2.1	2	*M. longicaudus*	16	2.3	7	*T. talpoides*	3	1.2	2
9	*S. monticolus*	3	1.3	3	*S. hoyi*	12	1.8	4	*M. longicaudus*	3	1.2	2
10					*M. montanus*	7	1.0	5	*M. montanus*	1	0.4	1
11					*T. talpoides*	4	0.6	3				

Table 2. Continued

	1993				1994				1995			
Rank	Species	N	%	No. of sites	Species	N	%	No. of sites	Species	N	%	No. of sites
					Closed-canopy							
1	*S. cinereus*	124	50.4	12	*S. cinereus*	193	31.9	12	*S. cinereus*	65	36.3	11
2	*S. vagrans*	80	32.5	12	*S. vagrans*	159	26.2	12	*C. gapperi*	58	32.4	10
3	*C. gapperi*	27	11	7	*C. gapperi*	126	20.8	12	*S. vagrans*	37	20.7	9
4	*S. monticolus*	8	3.3	6	*P. maniculatus*	64	10.6	11	*S. hoyi*	6	3.3	3
5	*P. maniculatus*	3	1.2	2	*S. monticolus*	37	6.1	11	*P. intermedius*	5	2.8	2
6	*T. talpoides*	1	0.81	2	*S. hoyi*	10	1.6	5	*S. monticolus*	4	2.2	3
7	*S. hoyi*	1	0.4	1	*M. longicaudus*	5	0.83	3	*P. maniculatus*	2	1.1	2
8	*M. montanus*	1	0.4	1	*P. intermedius*	5	0.83	3	*T. talpoides*	2	1.1	1
9					*T. talpoides*	2	0.5	2				
10					*M. montanus*	3	0.33	2				
11					*Z. princeps*	3	0.33	2				

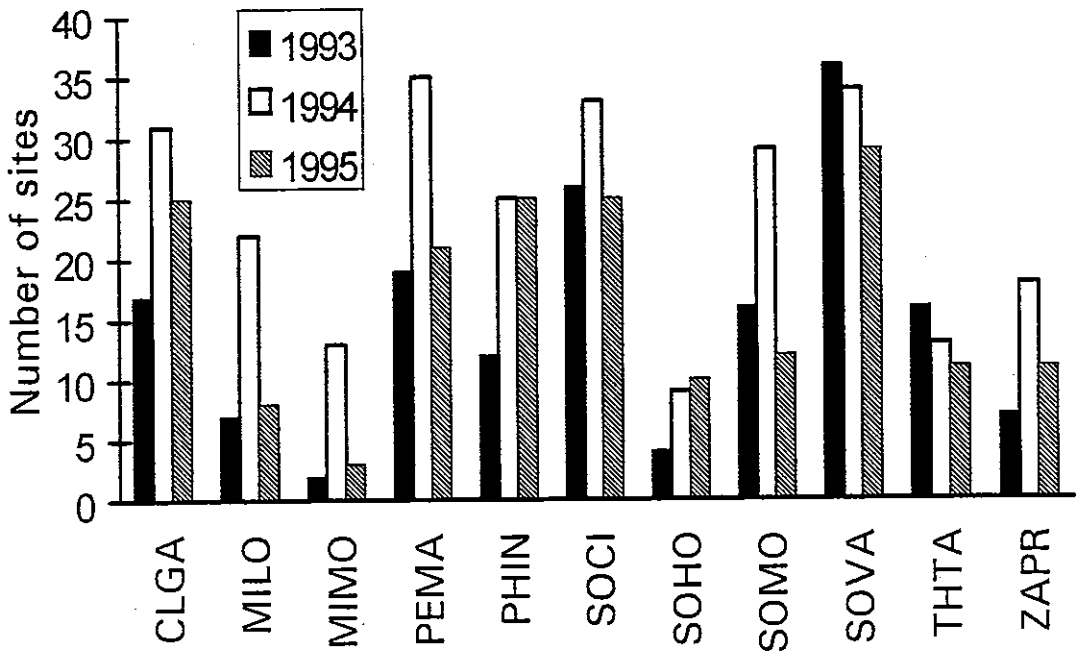

Figure 2. Number of sites at which each species was captured during 1993-1995. CLGA = *Clethrionomys gapperi*, MILO = *Microtus longicaudus*, MIMO = *Microtus montanus*, PEMA = *Peromyscus maniculatus*, PHIN = *Phenacomys intermedius*, SOCI = *Sorex cinereus*, SOHO = *Sorex hoyi*, SOMO = *Sorex monticolus*, SOVA = *Sorex vagrans*, THTA = *Thomomys talpoides*, ZAPR = *Zapus princeps.*

Phenacomys intermedius was uncommon in 1993 (19 captures), increased in 1994 (108 captures), and remained relatively high in 1995 (77 captures; Table 2). The total number of captures was similar in the 3 forest types in 1993 and 1995 (Fig. 3A). However, total number of captures was greater in clearcut stands in 1994 (Fig. 3A).

Stand-Level Associations

Closed-canopy

Three species — *Sorex cinereus*, *Sorex vagrans*, and *Clethrionomys gapperi* — constituted about 93%, 79%, and 78% of the captures in the closed-canopy stands in 1993, 1994, and 1995, respectively (Table 2). Whereas *S. cinereus* was the numerical dominant in all years, the ranking of the other 2 species changed between years. The relative abundance of the other small mammal species changed considerably

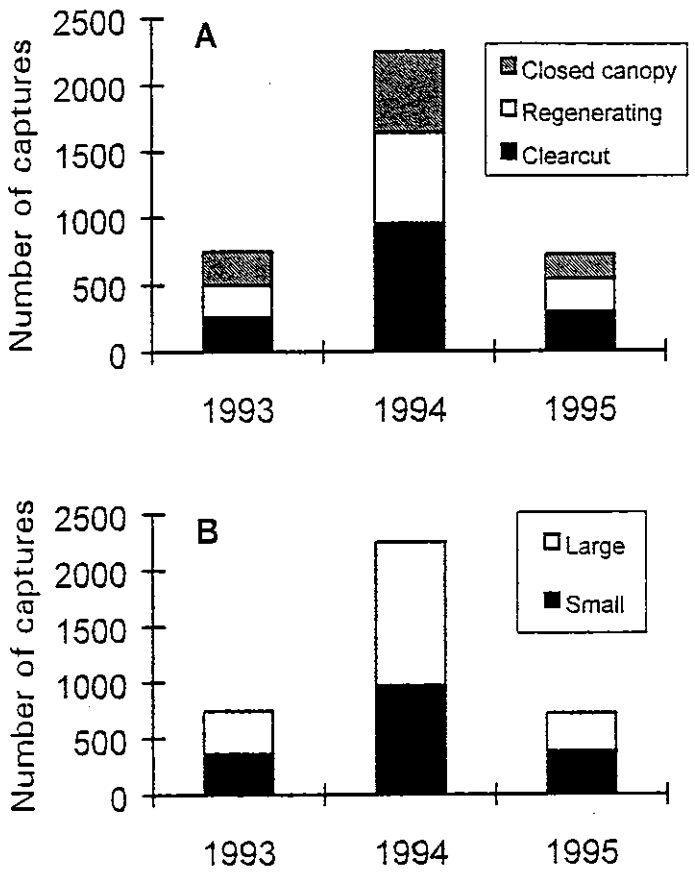

Figure 3. Number of captures of all small mammals during 1993-1995 in (A) the 3 forest types and (B) the 2 stand sizes.

between years in these closed-canopy stands (Table 2). Two species, *Clethrionomys gapperi* and *Sorex cinereus* were captured more frequently at sites in closed-canopy stands ($\bar{x}$ = 5.9, F = 13.8, df = 2, 107, $P < 0.0001$; $\bar{x}$ = 10.6, F = 12.9, df = 2, 107, $P < 0.0001$, respectively) than in either clearcut (2.7, 3.0) or regenerating stands (2.0, 3.7; Fig. 4A).

Multiple regression models of habitat variables on captures of *C. gapperi* were significant in all 3 years (1993: F = 24.8, $P < 0.0001$; 1994: F = 6.65, $P < 0.0001$; 1995: F = 6.36, $P < 0.0001$). Although the specific habitat variables with which *C. gapperi* was associated varied somewhat between the 3 years, this species was associated positively with habitat features such as canopy cover, medium to large d.b.h. trees, low shrubs, large, well-decayed woody debris that are reflective of closed-canopy forest. The predictive power of the models was high, ca. 60-75% over the 3 years (Table 3).

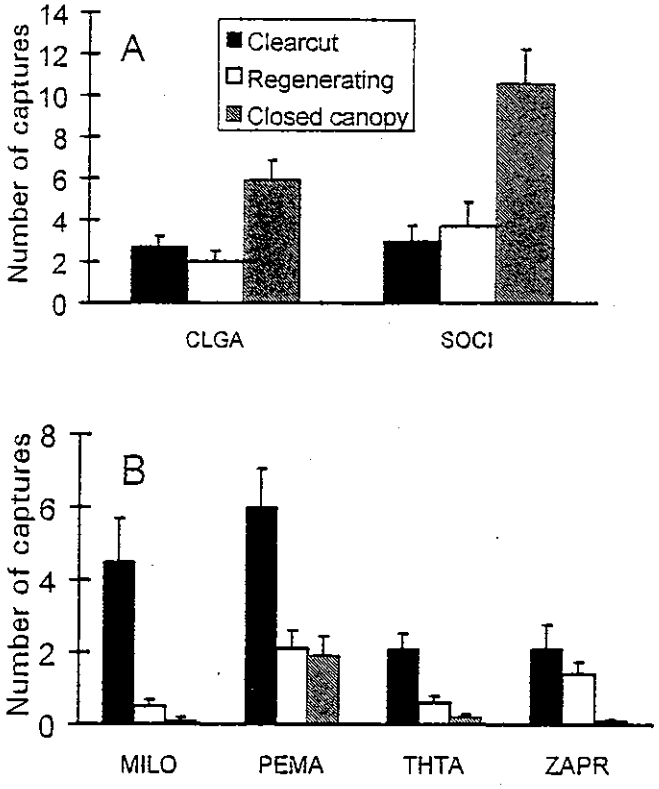

Figure 4. Mean number of captures per site for each forest type for species associated with (A) closed-canopy and (B) clearcut forest types. Species codes are listed in Fig. 2.

The regression models of habitat variables on captures of *S. cinereus* also were significant in all 3 years (1993: $F = 23.6$, $P < 0.0001$; 1994: $F = 48.9$, $P < 0.0001$; 1995: $F = 51.4$, $P < 0.0001$). The variables with which this shrew was associated positively were similar to those for *C. gapperi* –medium to large d.b.h. trees and large, well-decayed woody debris. The predictive power of the models varied from 49% in 1995 to 82% in 1994 (Table 3).

The proportion of reproductive to nonreproductive female *Clethrionomys gapperi* was higher in closed-canopy stands (56:21), but equal in the other stand types. Correspondingly, mean body mass of female *C. gapperi* was greater in the closed-canopy stands (22.9 g) than in regenerating (21.2 g) or clearcut stands (19.2 g; $F = 3.4$, df = 2, $P < 0.04$). Although overall captures did not differ with stand size for either

Table 3. Numbers of captures of small mammals in the 3 forest types in 1993-1995, and results of regression models predicting numbers of captures on quadrants of trapping grids. Regressions were not conducted when number of captures was <20.

	Captures				Habitat variables			
Species	Mature	Regen	Cut	R^2	Overstory	Shrub/regen	Woody debris	Ground cover
C. gapperi								
1993	27	7	10	69.9			LF1, M1, -LS3	
1994	126	45	70	55.9	d.b.h.3	AreaHt1	NS3	
1995	58	19	17	76.4	d.b.h.3		SF2, LFB	
M. longicaudus								
1993	0	0	8					
1994	5	16	138	63.8			M1, SF2, CS4	
1995	0	3	17	27.5			NS1, CS1	Grass
M. montanus								
1993	1	0	1					
1994	2	7	13	50.0		AreaHt2	LF2, -M3	
1995	0	1	4					
P. maniculatus								
1993	3	21	43	47.6			CS1, M2, -M3	
1994	64	42	145	50.9			SF3, SF2	Shrub
1995	2	14	29	49.4	-d.b.h.2		-CR2, -M3	
P. intermedius								
1993	0	8	11					
1994	5	60	43	50.1	- Cancov		-CS4, -M2	
1995	5	34	38	43.0	- Cancov		CS4	-LitDep
S. cinereus								
1993	124	23	18	68.9	Snag4, TreeHt		M4	
1994	193	76	62	82.1			M4, NS3, Snag1	
1995	65	34	27	82.8			LS4, M4, LS1	
S. hoyi								
1993	1	5	1					
1994	10	12	0	76.4		AreaHt2	M4, LFB	
1995	6	7	4					

Species	Captures			R^2	Habitat variables			
	Mature	Regen	Cut		Overstory	Shrub/regen	Woody debris	Ground cover
S. monticolus								
1993	8	3	7					
1994	37	21	26	58.9	- Cancov		M4, LF4	
1995	4	6	11	40.1	AreaHt3		NSB, M4M	
S. vagrans								
1993	80	146	127	62.6		AreaHt2	DR1M, -LFB	
1994	159	379	374	72.8	d.b.h.1	AreaHt3		
1995	37	113	96	67.5		AreaHt3	M2, CS4	
T. talpoides								
1993	2	13	16	39.1		AreaHt2	M1, CS3	
1994	3	4	39	70.0			M1, LF2, CS4	
1995	2	3	20	58.7			M1, CS4	LitDep
Z. princeps								
1993	0	12	17	83.5			SF1, CS4, LF2	
1994	2	24	34	82.3		AreaHt2	SF1, CS4	
1995	0	14	25	84.7			SF1, CS4, LF2	

species, the number of male versus female captures of *Sorex cinereus* did. Males were more common than females in smaller stands (213:97; $\chi^2 = 43.4$, df = 1, $P < 0.05$), but the sexes were equally abundant in larger stands (191:120; $\chi^2 = 1.9$, df = 1, $P > 0.05$).

REGENERATION

Sorex vagrans constituted 61.3%, 55%, and 45.6% of all captures in the regenerating stands in 1993, 1994, and 1995, respectively (Table 2). *Sorex cinereus* was the 2nd most abundant species in 1993 (9.7%) and 1994 (11%), whereas *S. cinereus* (13.7%) and *Phenacomys intermedius* (13.7%) tied for this place in 1995. The abundance of the other species was always <10% in all years and the ranking of abundance varied between each year (Table 2). No species was captured more frequently in the regenerating stands than in the other 2 stand types.

CLEARCUTS

Sorex vagrans was the numerically dominant species across all 3 years, comprising 33-49% of all captures (Table 2). *Peromyscus maniculatus* was the 2nd most abundant species in 1993 and 1994, but the 3rd most abundant in 1995 (Table 2). The relative abundance of the other species in clearcuts changed substantially between years (Table 2). Four species were captured more frequently in clearcuts (Fig. 4B).

The mean number of captures per site of *Peromyscus maniculatus* was greater in clearcuts ($\bar{x} = 6.0$), but did not differ between closed-canopy ($\bar{x} = 1.9$) or regenerating ($\bar{x} = 2.1$) stands ($F = 14.7$, df = 2, 107, $P < 0.0001$; Fig. 4B). Mean body mass of male *P. maniculatus* was greater in the clearcuts (18.9 g) than in closed-canopy (16.2 g) or regenerating stands (16.5 g; $F = 4.13$, df = 2, $P < 0.02$). *Peromyscus maniculatus* was significantly associated with habitat variables in all 3 years (1993: $F = 9.6$, $P < 0.0001$; 1994: $F = 13.9$, $P < 0.0001$; 1995: $F = 14.7$, $P < 0.0001$). This rodent was associated positively with recent woody debris and negatively associated with medium-high shrubs and regenerating conifers (Table 3). The predictive power of the models ranged from 48% (1993) to 60% (1994; Table 3).

The mean number of captures per site of the pocket gopher, *Thomomys talpoides* was greater in clearcuts ($\bar{x} = 2.1$), but did not differ between closed-canopy ($\bar{x} = 0.6$) or

regenerating ($\bar{x}$ = 0.2) stands (F = 13.52, df = 2, 107 P < 0.0001; Fig. 4B). *Thomomys talpoides* was associated positively with medium shrubs, recent to moderately decayed woody debris, and litter depth (Table 3). Regression models of habitat variables on the captures of this gopher were significant in all 3 years (1993: F = 6.9, P < 0.0001; 1994: F = 24.9, P <0.0001; 1995: F = 15.1, P < 0.0001), with predictive power ranging from 39% (1993) to 70% (1994; Table 3).

The mean number of captures per site of *Zapus princeps* differed among the 3 habitats (clearcut = 2.1, regeneration = 1.4, closed canopy = 0.1; F = 6.36, df = 2, 107, P < 0.002; Fig. 4B). The regression models of habitat variables on captures of this jumping mouse indicated significant associations in all 3 years (1993: F = 54.0, P < 0.0002; 1994: F = 49.6, P < 0.0001; 1995: F = 15.1, P < 0.0001). This species was associated positively with medium shrubs, older cut stumps, and recent logs (Table 3). The model R^2 values ranged from 16 in 1993 to 82 in 1994 (Table 3). As shown in the regression model, *Z. princeps* was more common in the smaller stands ($\bar{x}$ = 2.0) than larger stands ($\bar{x}$ = 0.4; F = 11.1, df = 1, 107, P < 0.001); however, sex ratios also differed between stand sizes. Males outnumbered females in the smaller stands (66:40) as compared to the larger stands (12:9; χ^2 = 8.89).

The mean number of captures per site of *Microtus longicaudus* was 4.5 in the clearcut stands, 0.5 in the regenerating stands, and 0.1 in the closed-canopy stands (F = 15.35, df = 2, 107, P > 0.0001; Fig. 4B). The stepwise regressions of habitat variables on captures of *M. longicaudus* were significant for 1994 and 1995 when there were >20 captures (1994: F = 27.4, P < 0.0001; 1995: F = 7.3, P < 0.0001) and had a predictive power of 27 and 64%, respectively. Captures of *M. longicaudus* were positively associated with recent woody debris and grass cover (Table 3). Male *Microtus longicaudus* significantly outnumbered females in 1994 as compared to 1994 or 1995 (χ^2 = 9.64).

OPEN-CANOPY

Three species avoided closed-canopy stands but were equally abundant in clearcuts and regenerating stands (Fig. 5A). The mean number of captures of *Sorex vagrans* was 7.7 in the closed-canopy stands, 16.6 in the clearcuts, and 17.7 in the regenerating

stands (F = 8.69, df = 2, 107, P < 0.0003; Fig. 5A). *Sorex vagrans* was positively and consistently associated with increasing area of shrubs and small trees (Table 3). The model R^2 values were relatively high in all 3 years, ranging from 63% in 1993 to 73% in 1994. The stepwise regression models for this species were significant in all 3 years (1993: F = 17.8, P < 0.0001; 1994: F = 28.5, P < 0.0001; 1995: F = 22.1, P < 0.0001).

Sorex vagrans was more common in larger ($\bar{x}$ = 16.6) than smaller stands ($\bar{x}$ = 11.4; F = 5.7, df = 1, 107, P < 0.01). Twice as many male as female *Sorex vagrans* (163 vs. 82) were captured in 1995, whereas sex ratios were equal during the previous 2 years.

The mean number of captures per site of *Phenacomys intermedius* in the closed-canopy stands was 0.3, 2.6 in clearcuts, and 2.8 in the regenerating stands (F = 12.79, df = 2, 107, P < 0.0001; Fig. 5A). In 1993 and 1995, the distribution of captures among the 3 forest types was similar to the distribution of mean captures, but in 1994 there were more captures in the regenerating stands compared to the clearcuts (Table 3). The stepwise regression models of habitat variables on abundance of *P. intermedius* were significant in the 2 years for which there were >20 captures of this species (1994: F = 10.7, P < 0.0001; 1995: F = 16.3, P < 0.0001). Captures of this species were negatively associated with increasing canopy cover and litter depth. The model R^2 values were about 46% in both years (Table 3).

Sex ratios of *P. intermedius* differed between habitat types. Males outnumbered females (62:30) in the clearcuts but were equally abundant in closed-canopy (5:5) and regenerating (50:52) stands (χ^2 = 6.67). Although overall captures of *Phenacomys intermedius* did not differ with stand size, males were more common than females in the smaller stands (74:30) as compared to the larger stands (43:47; χ^2 = 5.39).

The mean number of captures of *Microtus montanus* was greatest in the clearcuts ($\bar{x}$ = 0.5), which did not differ from the mean number of captures in regenerating stands ($\bar{x}$ = 0.2) but was different from the number in the closed-canopy stands ($\bar{x}$ = 0.1; F = 3.53, df = 2, 107, P < 0.03; Fig. 5A). The annual number of captures was >20 in only 1994 and the stepwise regression model for that year was significant (F = 10.7, P < 0.0001). The predictive power of this model was moderate (50%), and captures of this species were positively associated with grass cover and woody debris (Table 3).

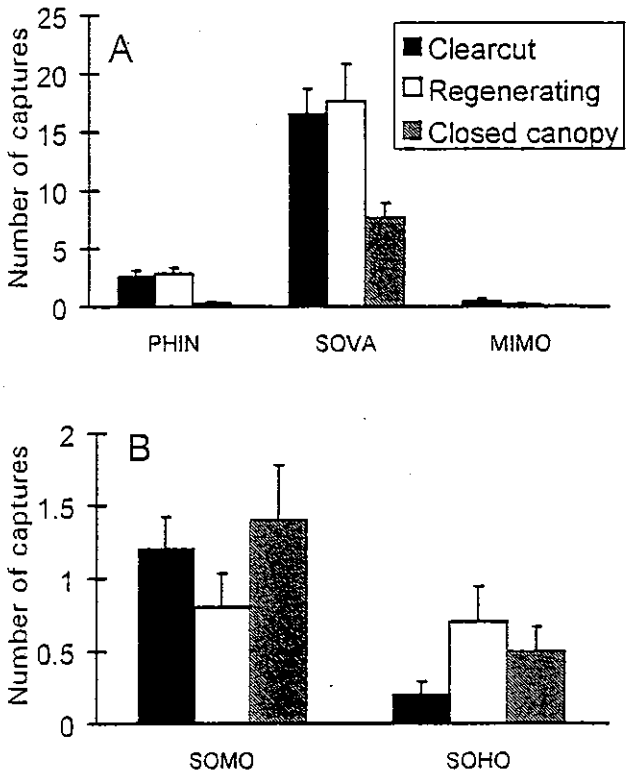

Figure 5. Mean number of captures per site for each forest type for species associated with (A) open-canopy stands and (B) without specific forest associations. Species codes are listed in Fig. 2.

NO FOREST STAND ASSOCIATIONS

Two shrew species were captured in equal abundance across all 3 forest stand types (Fig. 5B). The mean number of captures of *Sorex hoyi* per site over all 3 years was 0.67 for regenerating stands, 0.48 for closed-canopy stands, and 0.14 for clearcuts (F = 1.48, df = 2, 107, $P > 0.20$; Fig. 5B). In contrast, the multiple regressions of the habitat variables on captures of this species were significant for 1994 when captures were >20 (F = 34.6, $P < 0.0001$) and the multiple R^2 value of the model was high (76%). The captures of *S. hoyi* were associated positively with woody debris and area of medium-tall shrubs (Table 3).

The mean number of captures per site of *Sorex monticolus* over the 3 years was 1.4 in closed-canopy stands, 1.2 in clearcuts, and 0.8 in regenerating stands (F = 1.18, df = 1, 107, $P > 0.30$; Fig. 5B). The multiple regressions of captures of this shrew were significant for 1994 and 1995 (F = 15.3, $P < 0.0001$ and F = 7.2, $P < 0.0001$, respectively), with predictive power of the models from 21% in 1995 to 59% in 1994.

However, there was no consistent pattern of association with particular habitat variables (Table 3).

LANDSCAPE-LEVEL ASSOCIATIONS

The stepwise regressions of the landscape variables on annual captures of the small mammal species yielded significant models in 14 of the 25 possible models for species with >20 captures per year (Table 4). For 4 of the 5 species for which there were sufficient captures and significant models for >1 year, the species' associations with particular landscape variables were consistent between years (Table 4). *Clethrionomys gapperi* was associated positively with the total area of closed-canopy habitat and negatively associated with increasing perimeter of closed-canopy stands within a 1-km radius of the trapping grid. *Peromyscus maniculatus* and *Microtus longicaudus* were positively associated with the total area of clearcut habitat within a 1-km radius of the trapping grid (Table 4). *Sorex cinereus* was positively associated with the number of regenerating stands within the 1-km radius of the trapping grid (Table 4). However, the multiple R^2 values were generally low with only 4 models having R^2 values >30% (Table 4).

DISCUSSION

The small mammals varied in their distribution and abundance across these landscapes managed for timber harvest. Community composition and species abundance were explained more by stand-level habitat characteristics than by stand size or landscape context. Inter-year population fluctuations exhibited by many small mammals have important implications for how these species might potentially respond to the spatial and temporal dynamics of forests managed for timber harvest.

Community composition varied among the different forest types within years and within a given forest type among years. In general, the relative ranking of the numerically dominant species was more constant among years than that of the less abundant species. Two shrew species, *Sorex vagrans* and *S. cinereus*, were the numerical dominants across all forest types in all years, the former more common in the

Table 4. Significant variables and the variance explained by each (R^2) in stepwise regressions of landscape variables on small mammal captures for 1993-1995. Sign indicates the direction of association. Regressions were conducted only when the number of captures for a species was >20 in a year. NS = the overall regression was nonsignificant ($P > 0.05$).

	1993			1994			1995		
Species	Variable	Sign	R^2	Variable	Sign	R^2	Variable	Sign	R^2
Rodents									
Clethrionomys gapperi	NS			MatA	+	24.4	MatA	+	13.0
				DisN	-	12.9	MatP	-	10.1
				RegN	+	5.8	RegP	+	8.6
				MatP	-	4.1			
Microtus longicaudus				CutA	+	17.8	CutA	+	11.0
Microtus montanus				MatP	-	27.0			
				CutA	+	10.0			
Peromyscus maniculatus	CutA	+	22.0	NS			CutA	+	10.2
Phenacomys intermedius				NS			NS		
Thomomys talpoides	NS			CutA	+	29.0	NS		
				DisN	-	7.1			
Zapus princeps	NS			NS			NS		
Shrews									
Sorex cinereus	RegN	+	12.3	MatA	+	19.0	RegN	+	17.4
				RegN	+	12.5			
Sorex hoyi				NS					
Sorex monticolus				RegN	+	20.4	RegN	-	20.8
				RegA	-	7.6	MatN	-	5.4
Sorex vagrans	NS			NS			CutA	+	10.4

regenerating and clearcut stands and the latter more common in the closed-canopy stands. *Clethrionomys gapperi* was the numerically dominant rodent in closed-canopy stands across all years, although it shifted in overall abundance ranking between 1993-1994 and 1995. Beyond this, there were no consistent patterns of abundance ranking among the species in the different habitats across the 3 years. As population sizes of individual species fluctuated, dominance ranking shifted. This inter-year shift in ranking was most pronounced in the clearcut and regenerating stands.

The composition and structure of the small mammal communities from these 3 forest stands is similar to those of comparable forest stands in the region. For example, in the closed-canopy forests (managed, naturally young, old-growth) of western Washington, 1 or 2 shrew species (e.g., *Sorex trowbridgii, S. monticolus*) are typically the numerical dominant(s), followed by the red-backed vole (*Clethrionomys californicus* or *gapperi*) (e.g., Bury and Corn 1991, West 1991, Carey and Johnson 1995). The species composition and community structure we observed is similar to uncut and clearcut forests in northwestern Montana (Ramirez and Hornocker 1981).

Forest type was more important than stand size in explaining differences in small mammal distribution in these forests. Captures of 8 species were associated with specific habitat types, whereas overall captures of only 3 species varied with patch size, and in 2 of these cases, sex ratios were biased towards males in the smaller patches. The associations of most of these species with forest type or with habitat variables associated with these forest types are generally documented in forests of the region.

What is less understood is how increases in population size and the corresponding increases in distribution among forest types affects these species-habitat associations. Populations of most species increased in 1994, which resulted in increases in the number of sites at which a species was captured and in the number of captures of individual species across most forest types. However, despite these habitat expansions, no species exhibited pronounced changes in the habitat variables with which captures were associated. This suggests that as individuals disperse into additional habitats, they continue to use similar structural features. Demographic parameters indicate, however, that these habitats might not support reproduction.

For example, captures of *Peromyscus maniculatus*, a species associated with clearcuts, increased from 3 to 64 in closed-canopy forests between 1993 and 1994 and declined to 2 in 1995. However, habitat variables associated with captures of this species did not change to any extent. Mean body mass of males was greatest in clearcuts, and the proportion of nonreproductive males in 1994 (when more were captured outside of the clearcuts) was greater than in other years, suggesting that this habitat expansion might reflect source-sink dynamics (Pulliam 1988).

The associations of red-backed voles (*Clethrionomys*) with closed-canopy forests, in general, and with woody debris, in particular, have been observed throughout its range (e.g., Ramirez and Hornocker 1981, Tallmon and Mills 1994, Carey and Johnson 1995). Captures of this species increased about 6 times in both the clearcut and regenerating stands in 1994. Captures remained associated with woody debris in all years; in 1994, captures were positively associated with more classes of woody debris. Despite the habitat expansion in 1994, reproductive females were more common in closed-canopy stands, also suggesting a source-sink dynamics. These open habitats might provide certain structural features that allow use by dispersing *C. gapperi*, but do not provide the full complement of habitat conditions (e.g., microhabitats supporting hypogeous sporocarps of fungi—Mills 1995) to support sustained populations.

We observed no reduction in abundance or richness of small mammals on the smaller size stands indicating that smaller stands are sufficiently large to support diverse small mammal communities. Our selection of stand sizes for study was determined by the size of management units in the region and by the original research goal to examine "upland management areas". Most upland management areas are similar in size to our smaller stands (N. Sturhan, Department of Natural Resources, pers. comm.). When stand size is reduced to smaller patches, small mammal abundance can be impacted negatively. Mills (1995) observed a decrease in abundance of *Clethrionomys californicus* in forest remnants of 1-4 ha. However, it is unlikely that the harvest prescriptions of the state or federal agencies or private timber companies that manage most of the forests in the region will incorporate units of such small size.

Given that stands of both size classes support populations of these small mammals and that, at least in some years, individual species exhibit population increases that

result in expansion from 1 forest type into surrounding areas, the distribution of forest types relative to one another might potentially impact the dynamics of these populations. However, we found that the associations between captures of small mammals and landscape variables were consistent with observed stand-level associations (i.e., species that were captured more frequently in a particular stand type were associated positively with landscape variables describing the same type). For example, the abundance of *Clethrionomys gapperi*, a closed-canopy species, was greater when the habitat within 1-km radius consisted of large closed-canopy stands. *Peromyscus maniculatus*, a clearcut species, was associated positively with surrounding clearcut habitat in 1993 and 1995. In 1994, when populations were highest, captures of this species were not associated with any landscape variable, reflecting its greater distribution. However, the predictive power of the landscape variables was consistently low across all species, indicating that at the current level of fragmentation, the context of the surrounding habitat is relatively unimportant in determining small mammal distribution and abundance. It is possible that increased fragmentation would adversely affect these species, but at this time, most stands are not that isolated from one another. At current levels of fragmentation, the population pulses, as observed in 1994, will likely ensure that individuals disperse across forest types (Appendix C).

CONSERVATION OF BATS IN MANAGED FORESTS: USE OF ROOSTS BY *LASIONYCTERIS NOCTIVAGANS*[1]

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The erosion of biological diversity with habitat loss or modification is often discussed (e.g., Soulé 1986). Much less attention has been devoted to understanding the importance of "modified" lands for maintaining biodiversity. For example, the biological significance of the remaining old-growth coniferous forests in the northwestern USA has received considerable recent attention (e.g., Ruggiero and others 1991), but the "managed" forests that have replaced them over the last century have not. In north-eastern Washington, managed forests are young (<90 years), lack many of the structural characteristics of old growth, and may have different tree species. Moreover, recent harvest activities have fragmented these forests and created a mosaic of patches of various ages and sizes within a matrix of mature, closed-canopy forest. Determining the consequences of these changes on the diversity of vertebrates

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inhabiting these forests is essential if forest practices are to be modified to mitigate adverse effects.

We chose bats for study because their distinct requirements for roosting and foraging habitats should make them respond to structural characteristics of the forest and to landscape pattern (Thomas and West 1989). Twelve species of bats are predicted to occur in the forests of Washington, making bats the second most diverse group of mammals in the Pacific Northwest (Thomas and West 1989). Of these, 2 species, *Lasionycteris noctivagans* and *Lasiurus cinereus*, have been shown to be more common in older forests within their range in the Pacific Northwest (Perkins and Cross 1988, Thomas and West 1991). The association of these species with older forests is likely due to their roosting requirements. They roost in foliage, in or under the bark of trees, or in tree cavities (Barbour and Davis 1969, Kunz 1982a, Barclay and others 1988). Older forests tend to have a greater number of large trees including standing dead trees (i.e., snags), which provide many potential roost sites for bats. Although little is known about the specific characteristics of roost sites, the overall decline in size and age of forest patches and the loss of large trees and snags are expected to decrease roosting habitat in managed forests.

Reduction in forest habitat also can cause an increase in distance to foraging areas. In a managed landscape, the forest is a collection of different patches. Highly mobile animals, such as bats, can move between patches to obtain required resources. Harvest of a particular patch could greatly increase the distance bats must travel between their roost sites and foraging areas, potentially changing their patterns of habitat use. In a patchy landscape, *Myotis grisescens* was observed traveling to foraging areas along a forested edge even though this route was less direct (Tuttle 1979). Because many bats forage primarily over water, distance from the roost site to water can be an important component in roost-site selection. Distance to foraging areas is particularly important for females because of the higher energy demands placed on them during reproduction and can affect their reproductive success (Tuttle 1976, Barclay 1989).

In this study, we examined the roosting ecology of *Lasionycteris noctivagans* in managed forest. We wanted to determine the consequences of the conversion to

young, managed forest for a species that has a strong affinity for old-growth forest. We selected *L. noctivagans* to study roosting ecology in a managed forest because of its affinity for older forests. Our objectives were to locate roost sites of *L. noctivagans*, to describe the roosts sites and associated habitat, and to examine the use of these habitats relative to their availability.

MATERIALS AND METHODS

STUDY SITE

The coniferous forests of the Selkirk Mountains in northeastern Washington are a mosaic of patches of different sizes and ages. We used Landsat data to classify the forest into 4 predominant patch types—clearcut, regeneration (<30 years old), closed-canopy (typically >30 and <80 years old), and disturbed (areas modified by timber activities and usually with a deciduous component). We mapped the patches in 20 watersheds using ARC/INFO (ESRI, Redlands, CA) with a minimum mapping unit of 2 ha (J.G. Hallett and others, in litt.). We selected the North Fork Calispell watershed (Stevens and Pend Oreille Counties; T32-33N, R42-43E) for study because >42% of its 7,160 ha have been converted from closed-canopy forest, and it contains a large number of forest patches of varying habitat types and sizes. Forest composition is variable; dominant tree species include western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and grand fir (*Abies grandis*). A gravel road bisects the watershed, and logging roads provide access to much of the watershed. The stream system within the basin provides many sites for capturing bats.

SAMPLING METHODS

Bats were captured using mist nets and harp traps. Mist nets were standard, 4-pocket nets, either 6 m or 12 m in length. Harp traps were constructed following the collapsible design of Tidemann and Woodside (1978). Trapping was conducted during July-September 1992 (32 trap nights: 20 mist net, 12 harp trap) and May-August 1993

(46 trap nights: 31 mist net, 15 harp trap). Nets and traps were set across slow moving areas of streams and across shallow ponds (9 sites for 53 trap nights), which are potential drinking and foraging locations for bats, and across narrow roads (10 sites for 25 trap nights). Nets and traps were opened at dusk and run until about 0200 h the next day. Captured bats were identified to species, and sex, age, and reproductive condition were recorded. Reproductive condition of females was determined by abdominal palpation and examination of mammary condition. Males were judged to be reproductive if their testes were scrotal. Length of ear, forearm, and hind foot also were recorded.

ROOSTING ECOLOGY

We used radiotelemetry to determine the location of roosts. *Lasionycteris noctivagans* is typically >9 g in body mass and was not anticipated to experience a drastic reduction in foraging efficiency due to the load of the radiotransmitter (ca. 0.75 g). Aldridge and Brigham (1988) suggested that the addition of transmitters equaling 5% of total body mass of *Myotis yumanensis* could decrease their maneuverability sufficiently to reduce foraging efficiency. Hickey (1992) found no significant difference in foraging efficiency between tagged and non-tagged *Lasiurus cinereus* when the transmitter weighed ca. 3% of body mass. Likewise, Hickey and Fenton (1990) found no difference in foraging ability in red bats (*L. borealis*) with and without transmitters (transmitter mass ca. 6% of body mass). The transmitters we used (Holohil Systems Ltd., Woodlawn, Ontario, Canada) weighed <7.5% of the body mass of the radio-tagged *Lasionycteris noctivagans*. Although this percentage is higher than that in the above studies, observations of adult *L. noctivagans* indicated no adverse effects of radiotagging on flying ability. At the site of capture, transmitters were attached to the bats dorsally using surgical adhesive (Skin Bond Cement--Smith & Nephew United, Largo, FL). We used surgical scissors to clip all hair within an area the size of the transmitter immediately over the scapula. Adhesive was applied directly to the skin, and the transmitter was pressed into place until the adhesive set (1-2 min).

Radio-tagged bats were located at their roosts during the day following capture. Locations of tagged bats were verified twice weekly until the transmitters failed after ca.

21 days. Roost trees were identified to species, and diameter at breast height (d.b.h.), height, and decay class (1-living; 2-dying; 3-dead; 4-loss of some bark, few branches; 5-no bark, no branches--Thomas and others 1979) of the trees were recorded. Approximate location of bats on the roost trees was determined by orienting the receiving antenna until the signal from the radiotransmitter on the bat peaked in strength. We estimated the height of this location from the base of the tree by using a clinometer. In many cases, this location was at a vertical crack or was <1 m from a cavity opening, which gave us confidence that our estimate was within ca. 1 m of the actual location of the bat. Distance from foraging or drinking areas was determined by plotting each roost and capture location on the watershed map and using ARC/INFO to calculate distance between locations. Straight-line distance between each roost and the nearest riparian zone with a permanent water source also was calculated.

HABITAT ANALYSIS

A 15-m radius plot centered on the roost tree was used to describe the habitat of the area immediately surrounding the roost. For each plot, we tallied the number, species, d.b.h., and decay class of all trees >4 cm d.b.h. Based on d.b.h., each tree was placed into 1 of 4 size classes: (1) >4 and ≤10 cm, (2) >10 and ≤25 cm, (3) >25 and ≤50 cm, and (4) >50 cm. We calculated an index of the overall presence of each tree species on the plot by multiplying the number of individuals of each species in each size class by their size class (i.e., 1, 2, 3, or 4), and then summing the results. We chose this index because it places greater weight on larger trees, which seem to be preferred by bats for roosting (Barclay and others 1988, Cross 1988). In addition, we determined the species, d.b.h., decay class, distance from the center, and height for the 5 nearest neighbors of the roost tree. Canopy closure was measured once at the plot center and in each of 4 quadrants with a convex densiometer. Total cover and average height of vegetative understory (to the nearest 0.25 m) were estimated. Slope and aspect were recorded at the plot center.

To evaluate habitat use versus availability, characteristics of the roost plots were compared to those of 45 randomly selected plots. Random-plot locations were produced by defining a polygon encompassing all roost and capture locations on a map

of the watershed. A random number generator provided Universal Transverse Mercator coordinates within the polygon to locate random plots. Plots <50 m apart were discarded. To select a tree for the plot center, we first determined the modal size of ca. 10 trees and then selected the tree nearest to the random location that was in this size class. By choosing a tree of representative size, we sought to minimize observer bias toward size extremes that might have altered the location of the random plot. The species, d.b.h., decay class, and height were recorded for all plot centers, and habitat characteristics of the plots were measured as for roost plots.

Habitat data did not meet the requirements for analysis using parametric tests. Therefore, all comparisons between tree height, size class, decay class, canopy closure, understory height, and cover for roost and random plots were made by Kruskal-Wallis *H* test and the normal approximation to the Mann-Whitney test (*Z*—Zar 1974). Because of small cell values, stem count data by species, d.b.h., and decay class were square-root transformed after 0.5 was added to each variate (Steel and Torrie 1980). All statistical tests were conducted with SAS statistical software (SAS Institute 1988). Tests were considered statistically significant at $P < 0.05$.

RESULTS

Thirty *Lasionycteris noctivagans* were captured including 12 adult males, 14 adult females, 3 juvenile males, and 1 juvenile female. All captures were at water sites. The first juvenile *L. noctivagans* was caught on 4 August 1992. No juvenile bats were captured in 1993 prior to the cessation of trapping in August. A late summer season and prolonged rain and cold weather probably delayed parturition (Grindal and others 1992, Findley 1993).

ROOSTING ECOLOGY

Fifteen bats were radiotagged including 6 adult males, 5 adult females, and 4 juveniles. Although pregnant females were not tagged, several females were or had been reproductively active. Thirteen bats including 3 juveniles were relocated and 15 roost

sites were identified. All 3 juveniles moved to a new roost within 7 days of tagging and did not return to the previous roost site during the monitoring period. All adults were detected at only 1 roost site for the duration of the monitoring period. All but 1 of the roost sites were in snags. Fourteen of 15 roost sites were located in trees with d.b.h. >30 cm (Table 1). Trees in this size class accounted for <16% of all trees on both roost and random plots. All roost trees were decay class 4 or greater (loss of some or all bark, extensive vertical cracks; some had broken tops and cavities). One roost site was located in a dying western red cedar that had a dead top with both cracks and cavities. All but 1 of the roost sites were located in gaps in otherwise closed-canopy patches. The exception was a Douglas-fir snag located in a clump of trees on the edge of a large, partial clearcut. Two females used the same roost tree, but we could not determine if the bats were in close proximity to each other.

Height of snags ranged from 6.9 to 61.5 m. Estimated height of roosting bats ranged from 6.1 to 15.2 m, and bats generally were located ≤50% of the total snag height. Maximum distance between roost and capture sites was 3.4 km for an adult male, but most bats were captured much closer to the roost (juvenile males, $\overline{X}$ = 1.3, range = 0.1-2.5, N = 4; juvenile females, $\overline{X}$= 1.5, range = 1.3-1.7, N = 2; adult males, $\overline{X}$ = 1.8, range = 0.2-3.4, N = 6; adult females, $\overline{X}$ = 0.5, range = 0.1-1.8, N = 3). All roost sites were >100 m from the nearest riparian area with a permanent water source. On average, roosts were on sites with a slope of 38% (range = 3-84%). Aspect of the slope varied considerably, but for 11 of 15 sites, aspect was within ca. 70° to the east or west of north.

HABITAT ANALYSIS

Seven species of trees were used as roosts (Table 1). Twenty-six percent of roosts were in ponderosa pine (*Pinus ponderosa),* and white pine (*P. monticola*) was the next most frequent species at 20%. Although these 2 species accounted for 46% of roosts, they comprised <27% of trees found on roost plots, and only 20% of trees in the same size class as roosts. Ponderosa and white pine were present on ca. 30% and 20%, respectively, of roost and random sites combined. The relative abundance of

Table 1. Species and means and ranges for size (d.b.h.) of snags used as roosts by *Lasionycteris noctivagans*.

		d.b.h. (cm)	
Species	N	$\bar{X}$	Range
Grand fir, *Abies grandis*	1	54	54
Western larch, *Larix occidentalis*	2	48	31-64
Lodgepole pine, *Pinus contorta*	2	26	20-31
White pine, *Pinus monticola*	3	48	37-55
Ponderosa pine, *Pinus ponderosa*	4	49	32-74
Douglas-fir, *Pseudotsuga menziesii*	1	36	36
Western redcedar, *Thuja plicata*	2	52	37-68

these species differed between roost and random sites. Ponderosa pine accounted for only 2.8% of total stems in all classes on random plots but 18% of total stems on roost plots. White pine accounted for <1% of trees on random plots but 9.3% on roost plots. On average, <18% of the total number of stems (living trees and snags) on a plot were the same species as the roost tree, although this value ranged from 2 to 83% of the total number of stems per plot. Twenty percent of roost trees belonged to the species with the highest index value (number of individuals multiplied by their size class) for the respective plot. The roost tree was often 1 of a few trees, generally representing <20% of the plot total, in its size or decay class regardless of species. For 60% of roosts, the roost tree was the only member on the plot in its size and decay classes. On average, roost trees were 14.3 m taller than neighboring trees ($Z = 3.82$; $P < 0.0001$). The height of plot centers on random plots was also significantly different than the heights of nearest neighbors by an average of 5.4 m ($Z = 4.13$; $P < 0.0001$). Roost trees were significantly taller than random plot centers ($Z = 2.15$; $P < 0.03$).

The frequency distribution of tree decay classes was significantly different from uniform on both roost ($H = 38.5$, df = 3, $P < 0.0001$) and random plots ($H = 99.0$, df = 3, $P < 0.0001$). Living trees greatly exceeded the numbers in other decay classes on all plots. On roost sites, size classes 1, 2, and 3 were encountered more often than expected and trees in size class 4 were relatively rare. On random plots, trees of size

classes 1 and 2 were more abundant than expected, whereas classes 3 and 4 were less abundant than expected (roosts, $H = 33.64$, df = 3, $P < 0.001$; random plots, $H = 80.46$, df = 3, $P < 0.001$). When compared to random plots, roost plots showed no significant differences for overall stem number or index value. Few differences in the number of stems in each size and decay class were observed between roost and random sites. For trees in decay classes 3, 4, and 5 (dead trees to decayed snags with exfoliating bark, cracks, broken tops) and size classes >25 cm d.b.h., there were significant differences in stem counts between roost and random sites. Roost sites had significantly more size class 3 trees belonging to decay classes 4 and 5 (size class 3, $Z = -4.04$, $P < 0.0002$; decay class 4, $Z = -3.88$, $P < 0.0002$; decay class 5, $Z = -2.93$, $P < 0.002$). As this is the grouping to which most roost trees belonged, roost plots had more roost-type trees than did random plots.

Canopy closure immediately at the roost tree did not differ significantly from that over the rest of the roost plot. Similarly, there was no significant difference between canopy closure over the plot centers and that over the rest of the random plots. Canopy closure was significantly less at roosts than at random-plot centers (roost, $\bar{X} \pm 1\ SE$ = 62 ± 3%; random, $\bar{X}$ = 73 ± 3%; $Z = 2.34$, $P < 0.02$). Overall, roost plots exhibited significantly less canopy closure than random plots ($Z = -3.24$; $P < 0.001$). Height of understory vegetation was greater on random plots than on roost plots (roost, $\bar{X}$ = 0.42 ± 0.05 m; random, $\bar{X}$ = 0.83 ± 0.06 m; $Z = -4.08$, $P < 0.0001$), as was understory cover (roost, $\bar{X}$ = 34 ± 3%; random, $\bar{X}$ = 53 ± 3%; $Z = -3.55$, $P < 0.0004$).

DISCUSSION

Roost sites are a critical resource for bat populations (Humphrey 1975, Cross 1988). Roosts must provide a safe location with the proper thermal and moisture conditions and must be in the vicinity of foraging and drinking habitat. The North Fork Calispell watershed provided suitable roost sites for both male and female, reproductive and non-reproductive *Lasionycteris noctivagans*. Roosts were typically located in trees whose species, size, and condition are now uncommon on this landscape. Populations

of bat species that require these types of roost sites may not be maintained in managed forests characterized by short rotation cycles.

The 2 species of tree most frequently used for roosts, ponderosa and white pine, are now rare in the watershed. These 2 species were more common on roost plots than on random plots, suggesting that selection of roost sites is occurring. These tree species might be selected for some attribute of their own, or they may be indicative of another habitat feature such as moisture or slope. The use of these species also could be an historical artifact. Fire suppression and timber harvest have changed the community composition of trees in this region. Fire suppression favors shade-tolerant species such as *Abies* that outcompete shade intolerant ponderosa pine. Both white and ponderosa pine are historical remnants of the vegetative landscape prior to conversion to other timber species such as firs and western larch. These could be some of the only trees present that are large enough and old enough to provide the cracks, crevices, and cavities used by *L. noctivagans*. Shade tolerant conifers common in the watershed such as western hemlock, grand fir, and, western redcedar are shallow rooted (Cline and others 1980) and may uproot before they are decayed enough to provide suitable roosts.

The use of ponderosa pine for roosts by bats contrasts with results of Perkins and Cross (1988) who examined bat use in different types of forest habitat in Oregon. These authors rarely found bats in ponderosa pine forests, and suggested that this species probably cannot, as a result of bark structure, provide as many potential roost sites for bats as old-growth Douglas-fir (*Pseudotsuga menziesii*). Brigham (1991), however, reported big brown bats (*Eptesicus fuscus*) using cavities in ponderosa pine in British Columbia. In our study, 1 roost site was in a patch of ponderosa pine, and this species occurred on 30% of roost and random plots. Based on the species of roost trees found in our study, ponderosa pine (N = 4) provided more roost sites than Douglas-fir (N = 1).

Roost trees were large in size and were usually snags in an advanced state of decay. Mean d.b.h. of 47 cm for roosts located in our study area is much higher than the minimum d.b.h. of 30.5 cm suggested in Thomas (1979:382-386) for bat species using tree cavities. Roost trees also were much taller than neighboring trees. This

contrasts to the finding of Barclay and others (1988) that roost trees of migrating *L. noctivagans* were not taller, a result they attributed to the fact that many roosts had broken tops. In our study, roost trees also often had broken tops, but were still significantly taller than neighboring trees. The taller height of roost trees may provide the bat with an above-canopy landmark by which to locate its roost. Our estimated height of bat roosts of 6.1-15.2 m is higher than the 0.87-3.5 m reported by Barclay and others (1988). If the actual roost is above the level of the surrounding canopy, it may provide an easy flying space, free of clutter. These emergent trees may receive a different amount of sunlight or wind than trees within the canopy, changing the thermal environment within the roost. This may be important to *L. noctivagans*, a species which can use torpor to save energy rather than taking advantage of the insulative properties of a roost (Barclay and others 1988). Perhaps using emergent trees as roosts facilitates entrance into and emergence from torpor with the help of a fluctuating roost environment, a strategy that might provide energy savings to the bat. An emergent roost tree also could provide a unique micro-environment for a roost. For example, an emergent roost site on a south-facing slope would provide a much warmer microhabitat due to direct solar radiation than a roost located on a north-facing slope.

Roost plots exhibited significantly less canopy cover, shorter understory height, and less vegetative cover than did random plots. A reduced amount of canopy closure and understory would reduce impediments to flight. This has been shown to be particularly important for newly volant lasiurine bats (Constantine 1966). The reduced understory height and cover allow a greater vertical space in which young bats can practice flying without colliding with the vegetation.

The lack of significant differences in the size and decay class distributions of trees between roost and random plots suggests that bats are not attracted by a higher concentration of trees belonging to a single size or decay class. Roost plots did have a greater concentration of roost-type trees, however. This result corresponds with the findings of Cline and others (1980) that snags in Douglas-fir forests in western Oregon were distributed randomly, but that patches of snags were present.

All roost sites were >100 m upslope from riparian areas. Distance to riparian zones is important because abundance of insect prey is much greater in riparian areas than in

forests (Thomas and West 1989). Consequently, foraging by bats occurs at a much higher rate along riparian areas than in forests (Cross 1988). Older, larger trees are often more abundant in riparian than in upland areas (Cross 1988). These trees may shade the riparian zone and decrease the ambient temperature in these areas. The upslope location of bat roosts may be explained in part by the thermoregulatory constraints discussed above. There may be a trade-off between taking advantage of a warmer environment upslope and being close to foraging areas.

Two roosts were atypical—1 in a dying western red cedar and 1 in a partial clearcut. Both roosts were used by adult males, which may be able to be more opportunistic in their selection of roost sites than females due to their lower reproductive investment. Because of lower energy demands, males also may be able to roost farther from foraging areas. Because *Lasionycteris noctivagans* was only captured at water sites, these individuals may have come from different areas within the basin to drink at the same location. Our results suggest that males and females in this watershed may be in closer proximity than reported in other studies.

Two adult females were found in the same roost tree. Maternity roosts for this species are considered rare (Kunz 1982b, Barclay and Cash 1985, Parsons and others 1986). As these individuals were considered non-reproductive, it is unlikely that this was a maternity roost, although Barclay and Cash (1985) did document the presence of non-parous females in a maternity colony of *Myotis lucifugus*. It is unclear whether either bat was in close proximity to other bats, but this observation is still unusual for this species.

The complexity of patch structure may be an important component in roost site selection. Our results suggest that snag retention and recruitment in managed forests are important for bat conservation. Timber harvest has been associated with a decline in bat abundance when large roost trees are removed (Lunney and others 1985). Australian chocolate wattled bats (*Chalinolobus morio*), a species that roosts in tree hollows, flew 5 km from a logged area to roost in an unlogged area (Lunney and others 1985). In contrast, selective cutting, in which some potential roost trees remain, might provide areas in which bat populations may be maintained. In our study, most roosts were in large snags. Although the distribution of snags seems to be fairly even within

the North Fork Calispell watershed, their density is very low. Further, nearly half of the roosts were in white and ponderosa pine, but these species are now rare in the watershed. If other, more common species can be managed to attain similar size and decay classes, there may be a continuing source of roost trees within the basin. However, it is possible that some attribute of these 2 species of pines makes them particularly suitable roost sites (a certain type of bark or pattern of bark exfoliation, crack development, or ease of cavity excavation). If this is the case, the conversion of the watershed to other species that may not have these attributes may reduce the number of suitable roost sites for bats. Two of the more abundant species, grand fir and Douglas-fir, accounted for just 1 roost each. An examination of the interaction of habitat components may be helpful in identifying more features associated with bat roost sites. Another consideration is the location of roosts upslope from riparian zones. Traditional management of snags has focused on riparian zones <100 m in width. To protect upslope roost sites it will be necessary to expand guidelines for snag management to include upland areas.

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BIRD POPULATIONS IN MANAGED FORESTS OF NORTHEASTERN WASHINGTON

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INTRODUCTION

One of the challenges for maintaining biological diversity over broad regions is to utilize lands that are managed for the production of commodities, especially timber (Harris 1984, Hansen and others 1991). In the Pacific Northwest, considerable research has been focused on the importance of old-growth forests in maintaining late-seral organisms to help resolve the debate over how much of these forests should be retained (Ruggiero and others 1991). This work has pointed to the need for examining species diversity across a broader array of natural and managed forests (Hansen and others 1991). The latter forests are second-growth, mixed-coniferous forests and now encompass millions of hectares in the Pacific Northwest. Managed forests are younger and less structurally diverse than the forests they replaced and because of recent harvesting have been fragmented into a mosaic of patches of various successional stages.

Dramatic changes in avian species diversity following habitat fragmentation were first observed in eastern deciduous forests (e.g., Whitcomb and others 1981, Freemark and Merriam 1986). Alterations in community composition result from a number of factors including the loss of suitable habitat with conversion to new habitat types, and the invasion by species that are able to use new habitat types. These invaders may prey upon (Andrén 1992), parasitize, or compete with native species (review in Schieck and others 1995). The degree to which this may occur may be dependent on the size of habitat patches that remain. The ratio of edge to area is higher for small patches and this may increase the interaction between native species and those entering from new habitats (Wilcove 1985).

Although it is clear that native species may be adversely affected by habitat fragmentation, there are a number of factors that may mitigate these negative effects. First, the degree to which new habitats differ from those they replace will be important. Many studies of the consequences of fragmentation have examined conversion to novel habitats (e.g., forests converted to agricultural lands). The changes that occur on managed forests, however, mimic natural succession to some extent, although the scale and time frame of these changes is different (Hansen and others 1991). Thus the

context of a habitat patch is important. Second, species that have evolved on dynamic landscapes with natural spatial heterogeneity may have strategies to deal with community change. Work conducted on remnants of old growth suggest that fragmentation may not substantially alter the composition of bird communities (Schieck and others 1995).

We examined how size, age, and context of forest patches influenced avian distribution and abundance in managed forests of northeastern Washington. This paper presents initial results on patterns of species diversity and on the habitat and landscape factors that affect the distribution of some species.

METHODS

BIRD SURVEYS

STUDY SITE

Research was conducted in mixed-coniferous forests managed for timber production in the Selkirk Mountains of northeastern Washington (Stevens and Pend Oreille counties). Forest harvest over the past 30 yrs has created a mosaic of patches of different sizes and ages within a matrix of closed-canopy, second-growth forest. Forest composition is variable and is affected by slope, aspect, edaphic factors, fire history, and timber management practices. Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), and grand fir (*Abies grandis*).

We used Landsat data to classify the forest into 4 predominant patch types—clearcut, regeneration (<30 yrs old), closed-canopy (65-80 yrs old), and disturbed (areas modified by timber activities and usually with a deciduous component). We mapped the patches in 20 watersheds using ARC/INFO (ESRI, Redlands, CA) with a minimum mapping unit of 2 ha (Hallett and others, in litt.). We selected 36 sites for study in 7 watersheds, which were moderately to heavily fragmented for this region (30-50% cutover). Six replicates of each of 2 stand sizes (12-15 and >34 ha) and the 3 predominant, upland forest types (mature, closed canopy, >60 yrs; regeneration, 12-20

yrs; and recent clearcuts) were surveyed for birds. The 2 stand sizes reflect those typically produced by forest harvest. The clearcut sites had some standing live and dead trees.

Surveys

We used a circular point-count method for surveying bird populations (Verner 1985, Manuwal 1991). We established 3-4 and 12 point-count stations on the small and large stands, respectively. The point-count stations were 50-m radius circles, and the area covered by these stations was about 35-40% of the total stand area. Point-count stations were >100 m apart and were >100 m from the stand edge and from riparian areas or gaps in the stand.

Point-count surveys were conducted during the breeding season (mid-May to late June) in 1993 to 1995. Surveys were conducted 4 times per site in 1993 and 6 times in 1994 and 1995 between 0500 and 0800 hrs PDT on days with little or no wind and no rain. All birds detected during an 8-min period within a 50-m radius of the point-count station were recorded. Birds observed >50 m or between stations were recorded if it was the first time the species was detected on the site. Birds flying over the 50-m radius circle, but not landing, were recorded as "flyovers". Observers were rotated among the various study sites so as to avoid potential bias. The abilities of observers to identify birds by sight and sound and to conduct point counts were evaluated before the field season commenced.

Habitat Sampling and Landscape Description

Habitat features were sampled during July 1993. At each of the point-count stations we established a 24- x 24-m plot with 4 transects extending from the center point in each of the 4 cardinal directions. In each direction, strip transects with widths of 1, 2, and 3-m were established.

Trees and Snags

Within each 24- x 24-m plot all trees were identified and counted by size class and all snags were counted by size, decay, and height class. We used 4 size classes for trees

and snags based on diameter at breast height (d.b.h.): 1 (4-10 cm), 2 (11-25 cm), 3 (26-50 cm), and 4 (>50 cm). Snags were categorized as either Condition 1 if all bark was essentially intact and Condition 2 if the bark was peeling off or absent. In addition, snags were assigned to 1 of 2 height classes: 1-5 m and >5 m. This yielded 4 potential snag categories that were counted by size class. Tree heights of 4 representative live trees were measured using a clinometer to determine angle to base and to top and a metric tape.

Canopy Cover

Percentage of canopy cover was measured using a spherical densiometer at the center of the plot and at 8 m along each transect for a total of 5 measurements per 24- x 24-m plot.

Shrubs

Along each 1 m-strip transect, all shrubs with stems within the strip were identified. The length and width of each shrub was measured to obtain an estimate of area and each shrub was assigned to 1 of 3 height classes: 1 (0.5-1 m), 2 (1.1-1.5 m), and 3 (>1.5 m).

Woody Debris

The size and decay classes of all logs intersecting or encompassed within the 2-m wide strip transects were recorded. Four size classes were designated: 1 (<15 cm d.b.h., >5 m long), 2 (15-25 cm d.b.h., >2.5 m long), 3 (>25 cm d.b.h., $\leq$5 m long), and 4 (>25 cm d.b.h., >5 m long). Decay classes of logs were as follows: 1 (freshly fallen tree, bark intact, no decomposition), 2 (bark beginning to slough or almost completely gone, decomposition has begun but log still firm), 3 (wood soft and breaks into blocks), and 4 (wood has decomposed to point of soil-like texture, includes hummocks). The type and decay class of all stumps within the 3-m wide transect were recorded. Stumps were divided into 2 types: cut and natural and into the 4 decay classes described above. If a stump had been burned, it was not assigned to a decay class, but recorded as "burned".

Regenerating Trees

The number, type (coniferous or deciduous), and height class (0.5-1.5 m and >1.5 m) of all regenerating trees was counted within the 2-m wide strip transects. Saplings were included if >0.5 m in height and <4 cm d.b.h.

Ground Cover

To measure ground cover, a 20- x 50-cm plot frame was placed at the plot center and along the 4 transects at 4-, 8-, and 12-m intervals. Visual estimates of the cover of vegetative types (herbaceous, grass, fern, shrub, regenerating trees, and moss) and litter types (organic litter, soil, rocks, and logs) were scored between 1 and 6. These scores corresponded to the following levels of cover: 1 (>0-5%), 2 (6-25%), 3 (26-50%), 4 (51-75%), 5 (76-95%), and 6 (96-100%). Only shrubs and regenerating trees <0.5 m were recorded in this measure.

For each point-count transect, we characterized the landscape within a 1 km-radius circle of the center of the transect. Because our earlier work had revealed that some measures of landscape structure were invariant (e.g., perimeter-area fractals) or were highly intercorrelated (e.g., proportion of area in a forest type and pmL-fractals), we examined only the number of patches, total perimeter, and proportion of area in each forest type. In this analysis, we included the disturbed forest category. Variable mnemonics and descriptions are listed in Table 1.

Data Analysis

Two indices of species richness were calculated for each patch. Species richness A (SRA) was a count of all species detected on a patch for each survey including those >50 m away, those observed between stations, and flyovers. Species richness B (SRB) was the total number of species detected within all point-count circles on a patch. It does not include any flyovers or birds detected beyond 50 m, or between points.

The Shannon-Wiener index of species diversity and evenness (E) were calculated for birds detected within the count circle. Species evenness or the proportion of individuals among species is a major component of species diversity. The highest diversity a bird community could have is if all species comprised an equal number of

Table 1. Habitat and landscape variables used in regression analyses.

Variable	Description
Trees and Snags	
Cover	Canopy cover (%)
CC1	Coniferous trees 4-10 cm d.b.h.
CC2	Coniferous trees 11-25 cm d.b.h.
CC3	Coniferous trees 26-50 cm d.b.h.
CC4	Coniferous trees >50 cm d.b.h.
DC1	Deciduous trees 4-10 cm d.b.h.
DC2	Deciduous trees 11-25 cm d.b.h.
Snag1	Snags 4-10 cm d.b.h.
Snag2	Snags 11-25 cm d.b.h.
Snag3	Snags 26-50 cm d.b.h.
Snag4	Snags >50 cm d.b.h.
Shrubs	
Shrub	Area of shrub
Alde	Area of alder
Rupa	Area of thimbleberry (*Rubus parviflorus*)
Vacc	Area of huckleberry (*Vaccinium*)
Regeneration	
Dreg	Broadleaf regeneration
Creg	Coniferous regeneration
Woody debris-type class	
Log	Number of logs
Stump	Number of stumps
Ground cover	
Grass	% of 20- x 50-cm plot frame covered by grasses
Herb	% of 20- x 50-cm plot frame covered by herbaceous dicots
Moss	% of 20- x 50-cm plot frame covered by moss
Fern	% of 20- x 50-cm plot frame covered by ferns
Dshrub	% of 20- x 50-cm plot frame covered by shrubs <0.5 m high
Regen	% of 20- x 50-cm plot frame covered by regenerating trees <0.5 m high
Other	% of 20- x 50-cm plot frame covered by other material
Litter	% of 20- x 50-cm plot frame covered by litter
Dlog	% of 20- x 50-cm plot frame covered by logs
Rock	% of 20- x 50-cm plot frame covered by rock
Soil	% of 20- x 50-cm plot frame covered by bare ground
Landscape metrics (within a 1-km radius of transect center)	
DisN	Number of disturbed habitat patches
DisA	Total area of disturbed habitat patches
DispP	Total perimeter of disturbed habitat patches
CutN	Number of clearcut habitat patches
CutA	Total area of clearcut habitat patches
CutP	Total perimeter of clearcut habitat patches
MatN	Number of closed-canopy habitat patches
MatA	Total area of closed-canopy habitat patches
MatP	Total perimeter of closed-canopy habitat patches
RegN	Number of regenerating habitat patches
RegA	Total area of regenerating habitat patches
RegP	Total perimeter of regenerating habitat patches

the total number of individuals present in the community. The mean number of birds per point also was calculated for each patch. We used number per point in the data analysis rather than total number of birds because of the differences in sampling effort between small and large patches. We examined differences in SRA, SRB, mean number of birds per point, species diversity, and evenness using ANOVA and Bonferroni means separation test.

For each species, 2 values were calculated for each patch: the percentage of surveys when the species was detected and the mean number of birds detected per point. Data were analyzed using a 3-way analysis of variance (ANOVA) and Bonferroni means separation test. The 3 factors were habitat type (closed-canopy, regenerating, or clearcut), patch size (small or large), and year. For each species, we conducted separate ANOVAs using percentage of surveys and mean number of detections per point, respectively.

To examine the relationship between detection frequency and habitat structure at the stand level, we used stepwise multiple regression with the number of birds detected per point as the dependent variable and the habitat variables describing each point as independent variables.

We conducted a second set of stepwise multiple regressions to examine the relationship between number of birds detected per point and the landscape variables. We did not consider variables that were highly intercorrelated as revealed by a principal components analysis. All analyses were conducted using the Statistical Analysis System (PROC GLM; SAS Institute, 1989). All statistical tests were considered significant at $P < 0.05$ unless otherwise noted.

RESULTS AND DISCUSSION

Species Composition, Richness, and Diversity

Mean counts of all birds detected (species richness A) were higher for clearcuts ($\bar{X}$ = 16.7) and regenerating ($\bar{X}$ = 16.0) forests than for closed-canopy forests ($\bar{X}$ = 13.7; F = 16.8, df = 2, $p < 0.0001$; Fig. 1). The same pattern was observed for the mean count of

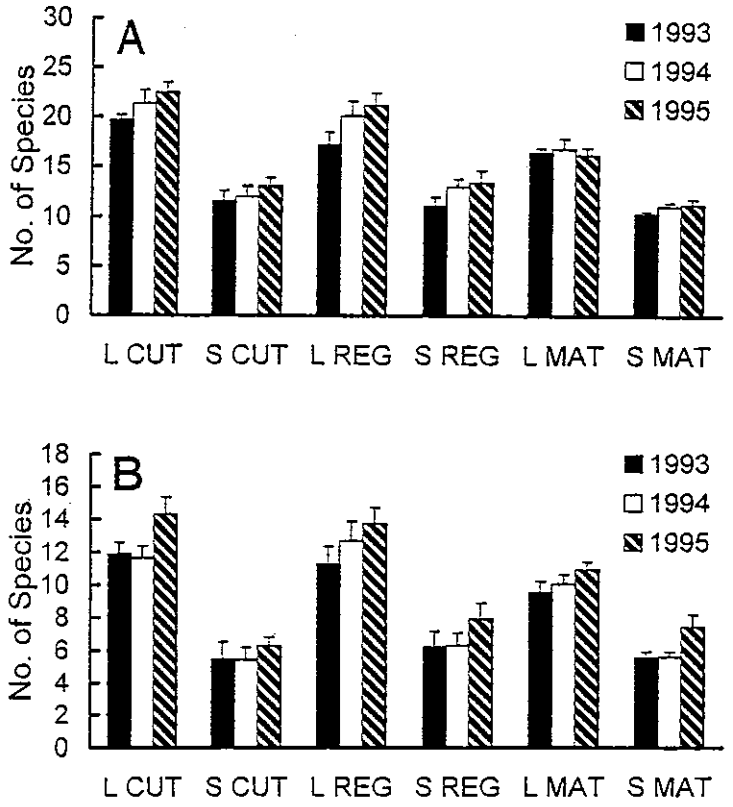

Figure 1. Species richness for (A) all birds detected and (B) only those birds within the 50 m-radius point-count station on large (L) and small (S) stands of the 3 forest types (CUT, clearcut; REG, regeneration; MAT, closed-canopy).

birds detected within the 50-m radius of the point-count station (species richness B, clearcuts = 9.1; regenerating = 9.6; closed canopy = 8.1; $F = 5.8$, df = 2, $P < 0.004$; Fig. 1).

Both measures of species richness were higher on the larger than the smaller stands (Fig. 2). The mean species richness A was 19.0 for the large and 11.9 for the small stands ($F = 223.1$, df = 1, $P < 0.0001$). Mean species richness B was 11.7 and 6.2 for the large and small stands, respectively ($F = 824.2$, df = 1, $P < 0.0001$). However, the comparison of species richness B between the 2 size classes was confounded because there were more point-count stations on large patches than on small patches.

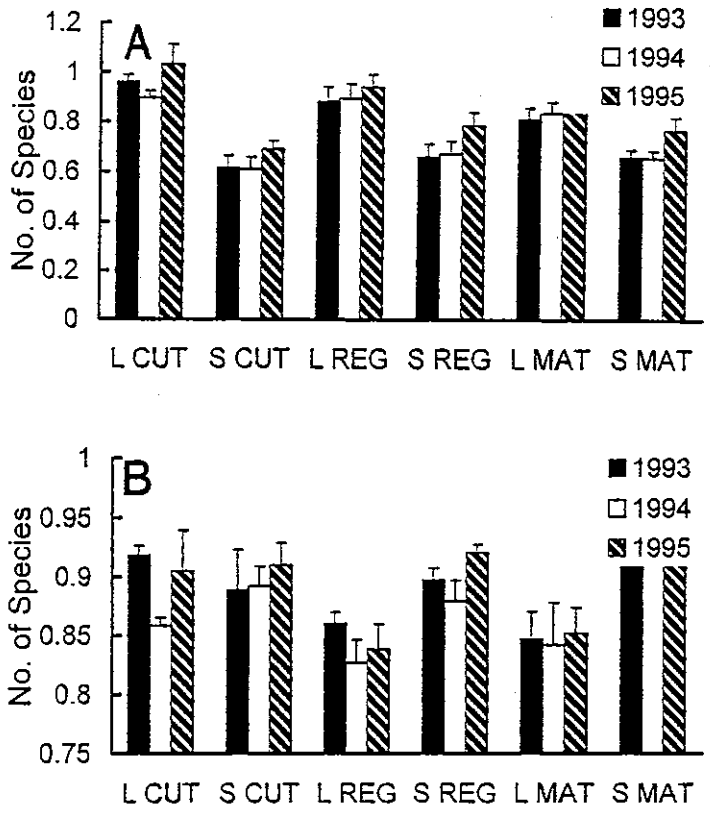

Figure 2. (A) Shannon-Wiener diversity and (B) evenness for large (L) and small (S) stands of the 3 forest types (CUT, clearcut; REG, regeneration; MAT, closed-canopy).

There were significant effects of year on both measures of species richness (Fig. 1). Species richness A was lower in 1993 (14.4) than in the other 2 yrs (15.8 and 16.2 for 1994 and 1995, respectively; $F = 6.3$, df = 2, $P < 0.003$), but this partly reflects the lower sampling effort in 1993. Species richness B was higher in 1995 (10.1) than in either 1993 (8.3) or 1994 (8.6; $F = 8.7$, df = 2, $P < 0.0004$).

The number of birds per point was significantly higher in regenerating forest (4.0) than either the closed-canopy (3.2) or clearcut (3.1) forests ($F = 10.2$, df = 2, $P < 0.0001$). Small patches had more birds per point (3.7) than larger stands (3.2; $F = 7.1$, df = 1, $P < 0.009$).

The Shannon-Wiener species diversity index was 0.8 for all 3 forest type ($F = 1.29$, df = 2, $P = 0.28$). Likewise, evenness was similar (0.8 to 0.9) across the 3 forest types (F= 2.67, df = 2, $P = 0.07$). In contrast, large sites had significantly higher species

diversity (0.9), but lower evenness (0.86) than small patches (diversity = 0.7; $F = 114.0$, df = 1, $P < 0.0001$; evenness = 0.9, $F = 24.9$, df = 1, $P < 0.0001$) (Fig. 2).

Stand-level Associations

Closed-Canopy

Fifteen species were detected more often in closed-canopy forest than in either clearcut or regenerating forests (Table 2). More species were restricted to the closed-canopy forest than to either of the other forest types, although overall avian abundance, richness, and diversity of these stands was lower. Moreover, some of the species associated with the closed-canopy forests, such as chestnut-backed chickadees and Townsend's warblers, are restricted to this habitat throughout their range.

Five of these species had a sufficient number of detections to be included in the regression analyses and each was significantly associated with 1 or more habitat variables (Table 3). Abundance of Townsend's warbler was associated positively (R^2 = 0.95) with 2 key habitat features of closed-canopy forest: number of medium to large coniferous trees and canopy closure. Golden-crowned kinglets also were associated positively with medium-large trees, but not as closely to canopy closure. The predictive power of the habitat variables on the distribution of the other 3 species was lower (<30%; Table 3). Swainson's thrush was associated positively with canopy closure and a dense understory of shrubs or regenerating trees. The abundance of brown creepers was associated with the number of large d.b.h. coniferous trees and canopy closure and that of red-breasted nuthatches with medium-large snags and canopy closure.

Clearcut

Five species were detected more often in clearcuts than in either closed-canopy or regenerating forests (Table 2). One species, the hairy woodpecker, had sufficient detections for analysis and was significantly associated with 6 habitat variables (Table 3). This woodpecker was associated positively with snags and open canopy cover, both characteristics of this forest type. However, the predictive power of the regression model was low.

Table 2. Habitat and patch size associations of avian species in northeastern Washington. These associations are based on significant ANOVA F-tests and means separation tests.

	Closed-canopy	
Pileated woodpecker	Cassin's vireo	Winter wren
Chestnut-backed chickadee	Brown creeper	Golden-crowned kinglet
Swainson's thrush	Hermit thrush	Varied thrush
Evening grosbeak	Townsend's warbler	Red crossbill
Gray jay	Red-breasted nuthatch	
	Closed-canopy and regenerating	
Ruffed grouse		
	Regenerating	
Dusky flycatcher	Warbling vireo	Nashville warbler
Orange-crowned warbler	Wilson's warbler	Black-headed grosbeak
Chipping sparrow	Brown-headed cowbird	
	Regenerating and clearcuts	
Northern flicker	Olive-sided flycatcher	American robin
MacGillivray's warbler	Dark-eyed junco	
	Clearcuts	
Red-naped sapsucker	Hairy woodpecker	Clark's nutcracker
Townsend's solitaire	Pine siskin	
	Clearcuts and closed-canopy	
Mountain chickadee	Western tanager	
	Large patch size	
Clark's nutcracker	Townsend's solitaire	Nashville warbler
Yellow-rumped warbler		
	Small patch size	
Northern flicker	Brown creeper	Golden-crowned kinglet
Cassin's vireo	Orange-crowned warbler	Townsend's warbler
Chipping sparrow	Dark-eyed junco	Pine siskin

Table 3. Results of regression models predicting numbers of detections of 15 common bird species. Sign indicates the direction and R^2 indicates the strength of the association.

	Hairy woodpecker		Northern flicker		Dusky flycatcher		Red-breasted nuthatch		Brown creeper		Golden-crowned kinglet		Swainson's thrush	
	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2
CC1	-	0.01									+	0.01		
CC2														
CC3									+	0.15	+	0.37		
CC4									+	0.02	+	0.02		
DC1	+	0.01			-	0.01								
DC2													-	0.01
SC1														
SC2									+	0.01				
SC3							+	0.01			+	0.01		
SC4	+	0.05			-	0.01								
Shrub	-	0.01									-	0.03	+	0.04
Alde									+	0.00	+	0.02		
Rupa					+	0.07	-	0.01						
Vacc														
Log			+	0.01	-	0.03								
Stump					+	0.12								
CReg					+	0.00					+	0.00	+	0.03
DReg					+	0.02	-	0.03			-	0.01		
Herb	-	0.07												
Litter									+	0.01				
Grass			+	0.01										
Regen											-	0.00		
Other					+	0.01								
Fern														
Rock											+	0.00		
Soil														
Moss							-	0.00						
DLog					-	0.01								
DShrub														
TrHeight					-	0.01	+	0.13					-	0.01
Cover	-	0.03	-	0.10			+	0.02			+	0.05	+	0.22
Total		0.17		0.12		0.28		0.20		0.19		0.52		0.31

Table 3. Continued.

	American robin		Warbling vireo		MacGillivray's warbler		Yellow-rumped warbler		Townsend's warbler		Dark-eyed junco		Chipping sparrow		Western tanager	
	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2	Sign	R^2
CC1			+	0.00	-	0.03									-	0.01
CC2					-	0.01					-	0.01				
CC3					-	0.09			+	0.39	-	0.01			-	0.01
CC4					-	0.01			+	0.03	-	0.01				
DC1			-	0.01												
DC2			+	0.00							+	0.00				
SC1									+	0.02						
SC2			-	0.00												
SC3																
SC4			-	0.00												
Shrub			+	0.35			+	0.07	-	0.08	-	0.01	-	0.01		
Alde					-	0.02										
Rupa			+	0.02	+	0.03			-	0.01	-	0.01				
Vacc					+	0.00	+	0.00								
Log							-	0.01	-	0.01	-	0.01	-	0.01		
Stump			+	0.05			+	0.01			+	0.01			-	0.00
Creg							-	0.00	+	0.01			+	0.01		
Dreg			+	0.10					-	0.01	+	0.00				
Herb							-	0.01								
Litter	-	0.02							+	0.00	-	0.01			+	0.02
Grass			-	0.00	-	0.00									-	0.01
Regen					-	0.01			-	0.00						
Other			+	0.01	-	0.00										
Fern			+	0.02												
Rock															+	0.02
Soil													+	0.00		
Moss			+	0.01			+	0.00			+	0.00				
DLog											-	0.01				
DShrub															+	0.01
TrHeight			-	0.01	+	0.01							-	0.01	+	0.03
Cover	-	0.11	+	0.00			+	0.05	+	0.39	-	0.35	-	0.08		
Total		0.12		0.60		0.22		0.17		0.95		0.43		0.11		0.10

Regenerating

Eight species were detected more often in regenerating forests than in either closed-canopy or clearcut forests. Detections of the dusky flycatcher, warbling vireo, and chipping sparrow were sufficient for regression analysis and regression models for these species were significant (Table 3). The predictive power of the regression model was greatest for warbling vireos (60%) and analysis indicated an association of this species with shrubs, stumps, and regenerating trees. Detections of dusky flycatchers also were associated positively with number of stumps, number of regenerating trees, and shrub cover, but the predictive power of the model was less (Table 3). The abundance of chipping sparrows was not closely associated with any of the measured habitat features; avoidance of closed-canopy explained the most variance, but the R^2 was only 0.08.

Combination of Types

A few species were detected more commonly in 2 of the 3 forest types (Table 2). The ruffed grouse was detected more often in closed-canopy and regenerating forests. Five species were detected more commonly in open-canopy stands of clearcut and regenerating forests (Table 2).

Regression models of habitat variables on detections of 4 of these open-canopy species–dark-eyed junco, MacGillivary's warbler, American robin, and northern flicker–yielded significant associations (Table 3). In all cases, the R^2 was low (<0.50). For these species, the variance was explained by a negative association with closed-canopy, number of coniferous trees, or a combination of the 2 features (Table 3).

Two species, mountain chickadees and western tanagers, were detected more often in clearcut and closed-canopy forests than in regenerating forests (Table 2). The regression of habitat variables on detections of western tanagers was significant, but the R^2 was only 0.10 and no single variable or combination of variables explained the variance observed (Table 3).

Stand Size

Few species were detected more frequently in one stand size as compared to the other. Four species were more abundant in the larger stands whereas 9 were more common in the smaller stands (Table 2).

Landscape-level Associations

Many of the associations revealed by our landscape analysis reflect the stand-level patterns described above (Table 4). However, for many species the predictive power of the landscape variables, in at least 1 year, was greater than the predictive power of the individual habitat variables (Tables 3 and 4). The 5 closed-canopy forest species, Townsend's warbler, red-breasted nuthatch, golden-crowned kinglet, Swainson's thrush, and brown creeper, were all associated positively with the total area of closed-canopy forest within the 1-km radius of the transect (Table 4). Most of these species also occur in old-growth forests elsewhere in the Pacific Northwest (Manuwal 1991, Schieck and others 1995). These species were typically associated negatively with increasing perimeter of closed-canopy stands, suggesting a positive association with larger tracts.

The landscape variables also explained a much larger proportion of the variance in the abundance of the hairy woodpecker, than did the habitat variables. This species was associated positively with area of clearcut habitat, but also was associated with perimeter of closed-canopy patches, suggesting that juxtaposition of the 2 forests is important. Elsewhere in Washington, old-growth Douglas-fir forests are considered optimal (Manuwal 1991).

None of the regenerating forest species (warbling vireo, dusky flycatcher, chipping sparrow) were closely associated with the amount of regenerating forest that surrounded the transect (Table 4). The warbling vireo presents an interesting case. On the stand-level, 60% of the abundance of this species was explained by the presence of habitat features reflective of a young forest. On the landscape-level, for at least 1 year, 60% of the variance in abundance was explained by the area of closed-canopy forest surrounding the transect.

Table 4. Significant variables and the variance explained by each (R^2) in stepwise regressions of landscape variables on number of detections for 1993-1995. Sign indicates the direction of association. NS = the overall regression was nonsignificant ($P > 0.05$).

	1993			1994			1995		
Species	Variable	Sign	R^2	Variable	Sign	R^2	Variable	Sign	R^2
Hairy woodpecker	CutA	+	50.7	CutA	+	10.5	CutA	+	9.5
	CutP	-	7.3	CutN	-	5.7			
	MatP	+	3.4	MatP	+	5.4			
Northern flicker	CutA	+	16.7	MatA	-	20.9	CutA	+	25.3
	CutP	-	20.9	CutP	-	10.7	CutP	-	19.4
	RegP	+	10.8	RegA	-	19.0	MatP	+	8.0
	RegA	-	3.4	RegN	+	9.1	DisA	+	3.2
Dusky flycatcher	CutN	-	12.9	RegN	-	13.0	RegN	-	17.2
				RegA	+	6.8	RegP	+	11.6
Red-breasted nuthatch	MatA	+	32.5	RegA	-	20.7	RegA	-	22.4
	MatP	-	11.4	CutP	-	14.7	CutN	-	7.1
Brown creeper	RegN	-	6.9	MatA	+	33.5	MatA	+	15.9
				MatP	-	9.3	MatP	-	7.6
				DisA	+	9.1	DisA	+	8.7
Golden-crowned kinglet	MatA	+	17.3	MatA	+	23.8	MatA	+	22.5
	MatP	-	7.2				MatP	-	5.0
	DisA	+	12.6				DisA	+	9.2
Swainson's thrush	RegN	-	8.5	MatA	+	16.4	CutA	-	15.3
	MatA	+	11.3	MatP	-	7.9	RegN	-	14.1
							DisN	-	9.8
American robin	RegP	+	16.0	RegA	+	24.0	CutN	-	11.7
	RegA	-	22.3	RegP	-	8.7	RegP	-	6.2
				DisN	+	6.4	DisN	+	6.4
				CutP	-	6.2			
Warbling vireo	NS			MatP	+	63.0	CutP	+	26.4
				CutP	-	13.4			
MacGillivray's warbler	CutN	-	15.8	CutA	+	41.7	CutA	+	33.8
				CutP	-	16.3	CutP	-	19.0
Yellow-rumped warbler	DisN	-	20.1	RegN	-	22.3	CutP	-	19.1
	MatA	+	11.4	DisA	-	14.6	MatA	+	14.3
	RegN	-	13.8	CutA	-	9.3	RegN	-	13.7
Townsend's warbler	MatA	+	41.0	MatA	+	33.9	MatA	+	34.5
	MatP	-	12.5	MatP	-	4.5			
Dark-eyed junco	MatA	-	15.7	RegA	+	12.5	MatP	+	14.3
	MatP	+	10.2	RegP	-	7.4	CutA	+	10.4
	CutA	+	8.8						
Chipping sparrow	DisN	+	10.0	MatN	+	21.1	CutP	-	12.0
	DisP	-	7.7	CutP	-	10.9	MatA	-	4.6
				DisP	-	5.3	CutN	-	8.7
Western tanager	RegP	-	25.7	RegP	-	23.6	RegP	-	29.3
	MatN	-	8.4	RegN	-	7.5			
				DisA	-	7.2			
				DisP	+	4.3			

ANOVA of detections of the western tanager classified these birds as occupants of closed-canopy and clearcut forests, but regression of specific habitat variables revealed little insight into which features of the habitat were important. In contrast, the predictive power of the landscape variables to explain abundance was greater for this species and indicated that western tanagers were consistently and negatively associated with the perimeter of regenerating forest surrounding the transect in which they were detected.

The individual habitat variables explained little of the variance in the abundance of 2 common species (American robin and northern flicker) associated with more open-canopy forests. In contrast, regression of the landscape variables on abundance resulted in larger R^2 values (Table 4). For example, the northern flicker was associated positively with the total area of clearcut forest surrounding the transect and negatively associated with the perimeter of clearcut habitat, suggesting association with larger tracts.

The abundance of the yellow-rumped warbler did not vary with forest type, nor was much of the variance in abundance of this species explained by the specific habitat variables. This species was associated with larger forests (Table 2). Examination of the landscape-level associations of yellow-rumped warblers indicate that these birds are associated positively with the area of closed-canopy forest surrounding the transect and negatively associated with the number and area of regenerating, clearcut, or disturbed patches surrounding the transect (Table 4).

CONCLUSIONS

The avifauna of managed forests in northeastern Washington is diverse. Unfortunately we do not have a benchmark for comparing the present-day situation with conditions prior to the initial harvesting of forests in this region. However, many species restricted to closed-canopy forests also are associated with old-growth forests elsewhere in Washington (Manuwal 1991). Retention of these species over the long term may require that some large tracts (>35 ha) of closed-canopy forest remain intact. Planning for the production and retention of large snags is a critical element in management for some of these species (e.g., pileated woodpecker). We do not have information on

nesting success for any species and thus cannot assess whether current populations are viable. It is possible that at current levels of fragmentation, some populations are maintained by dispersal from other stands.

The juxtaposition of forest types is important for some species, such as the hairy woodpecker. This species utilizes clearcuts where some green trees and snags have been retained, but these areas also are adjacent to closed-canopy forests.

A large component of the avifauna is benefitted by the production of clearcut and regenerating forest. Some of these species may prey upon (e.g., corvids) or parasitize (e.g., brown-headed cowbird) the nests of closed-canopy species. We are currently examining the local habitat and landscape factors that allow invasion by the brown-headed cowbird.

APPENDIX. Common and scientific names and migratory status of birds species surveyed.

Common name	Scientific name	Migratory status
Ruffed grouse	*Bonasa umbellus*	Permanent resident
Red-naped sapsucker	*Sphyrapicus nuchalis*	Short-distance migrant
Downy woodpecker	*Picoides pubescens*	Permanent resident
Hairy woodpecker	*Picoides villosus*	Permanent resident
Northern flicker	*Colaptes auratus*	Short-distance migrant
Pileated woodpecker	*Dryocopus pileatus*	Permanent resident
Olive-sided flycatcher	*Contopus cooperi*	Nearactic-neotropical
Hammond's flycatcher	*E. hammondii*	Nearactic-neotropical migrant
Dusky flycatcher	*E. oberholseri*	Nearactic-neotropical migrant
Cassin's (solitary) vireo	*Vireo cassinii*	Nearactic-neotropical migrant
Warbling vireo	*Vireo gilvus*	Nearactic-neotropical migrant
Gray jay	*Perisoreus canadensis*	Permanent resident
Steller's jay	*Cyanocitta stelleri*	Permanent resident
Clark's nutcracker	*Nucifraga columbiana*	Permanent resident
Black-capped chickadee	*Poecile atricapilla*	Permanent resident
Mountain chickadee	*Poecile gambeli*	Permanent resident
Chestnut-backed chickadee	*Poecile rufescens*	Permanent resident
Brown creeper	*Sitta canadensis*	Short-distance migrant
Winter wren	*Certhia americana*	Short-distance migrant
Golden-crowned kinglet	*Troglodytes troglodytes*	Short-distance migrant
Townsend's solitaire	*Regulus satrapa*	Short-distance migrant
Hermit thrush	*Cathrus guttatus*	Short-distance migrant
Swainson's thrush	*Myadestes townsendi*	Nearactic-neotropical migrant
Varied thrush	*Ixoreus naevius*	Short-distance migrant
Orange-crowned warbler	*Vermivora celata*	Nearactic-neotropical migrant
Nashville warbler	*Vermivora ruficapilla*	Nearactic-neotropical migrant
Yellow warbler	*Dendroica petechia*	Nearactic-neotropical migrant
Yellow-rumped warbler	*Dendroica coronata*	Short-distance migrant
Townsend's warbler	*Dendroica townsendii*	Nearactic-neotropical migrant
MacGillivray's warbler	*Opornis tolmiei*	Nearactic-neotropical migrant
Wilson's warbler	*Wilsonia pusilla*	Nearactic-neotropical migrant
Western tanager	*Piranga ludoviciana*	Nearactic-neotropical migrant
Dark-eyed junco	*Junco hymalis*	Short-distance migrant
Brown-headed cowbird	*Molothrus ater*	Short-distance migrant
Pine siskin	*Loxia curvirostra*	Short-distance migrant
Red crossbill	*Carduelis pinus*	Short-distance migrant
Evening grosbeak	*Coccothraustes vespertinus*	Short-distance migrant
Black-headed grosbeak	*Pheucticus melanocephalus*	Nearactic-neotropical migrant
Chipping sparrow	*Spizella passerina*	Nearactic-neotropical migrant

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APPENDICES

APPENDIX A

MICROSATELLITE CHARACTERISTICS AND POPULATION GENETIC STRUCTURE FOR *RANA LUTEIVENTRIS* AND *HYLA REGILLA*

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Abstract

Recent literature about microsatellite loci provides theoretical support for the assumption of a stepwise mutation process and also provides several new estimates of population structure and genetic distance for use with microsatellite markers. Empirical evidence, however, suggests that the stepwise process is not perfect and estimates derived from an infinite alleles model may provide better descriptions of population structure and genetic distance for natural populations. I explored these issues using 7 microsatellite markers for 2 frog species (*Rana luteiventris* and *Hyla regilla*). The distribution of alleles suggested the markers mutate in a stepwise fashion, but as much as 11% of mutations may involve multiple steps. Most loci were in Hardy-Weinberg equilibrium within individual populations (8 and 3, respectively), but I also found evidence of null alleles for all 3 *R. luteiventris* markers. I found a broad scale pattern of isolation-by-distance that was consistent with earlier findings with allozyme data. Isolation-by-distance regression models suggested neighborhood sizes of 19 to 274 frogs for *R. luteiventris* populations. Because neighborhood size is an upper limit for effective population size, I used a mutation rate (10^{-4}) that produced an estimate of effective population size (128 frogs) consistent with the neighborhood estimates. Variance for estimates of F_{ST} and for isolation-by-distance models was greater for estimators derived from stepwise mutation models. Four recently proposed estimates of genetic distance for microsatellites failed to recover the correct geographic relationships for *R. luteiventris* populations, although an IAM derived estimator was successful. More research is needed to determine the general applicability of estimators derived specifically for microsatellite markers. Estimators derived from an infinite alleles model may be adequate for descriptions of genetic diversity in natural populations.

INTRODUCTION

Microsatellite markers are increasingly used to describe the behavioral ecology and population structure of a wide range of taxa. Microsatellites are particularly attractive because they reveal high levels of variation where other markers may not (Bruford and Wayne 1993, Hughes and Queller 1993). In addition, these markers appear to be randomly distributed throughout eukaryotic genomes, as well as being associated with noncoding regions and inherited in a Mendelian fashion (Tautz and others 1986, Tautz 1989, Bruford and Wayne 1993). Thus, these markers could provide an extensive source of neutral genetic variation for analysis of natural populations.

Microsatellites are composed of short units of DNA (<6 nucleotides) that are repeated tandemly many times. Different alleles for a given marker are defined as having a different number of tandem repeats. Increases and decreases in the number of tandem repeats appear to arise from strand slippage during DNA replication (Fieldhouse and Golding 1991, Schlötterer and Tautz 1992) and the rate of change can be quite high (10^{-3} to 10^{-5} per gamete; Bruford and Wayne 1993) relative to detectable changes in conventional protein markers (10^{-6}; Voelker and others 1980). This variation in length provides the genetic variability for analysis of population genetic structure, but the mutation process itself generates some interesting properties. Strand slippage usually results in a change of 1 or 2 repeat units; a process that has been approximated with a stepwise mutation model (SMM; Shriver and others 1993, Valdes and others 1993). One consequence of an SMM is that derived alleles are not independent of their ancestral state. Thus, there is a higher probability of homoplasy which results in a decreased number of alleles and a lower level of heterozygosity relative to an infinite alleles model (IAM) with a comparable rate of mutation (Shriver and others 1993). In addition, microsatellites appear to be limited in total length (<100 units; Valdes and others 1993) which restricts the range of possible alleles below what would be expected for an IAM.

Despite the strong case that has been developed for a single-step mutation process, there is growing empirical evidence suggesting that microsatellite variation

conforms more frequently to an IAM at the population level. Di Rienzo and others (1994) used a 2-phase mutation model to explain differences from expectation under the SMM in their study of human population structure in Africa. Their model incorporated single repeat mutations with a smaller probability of larger mutation steps. This model provided a better fit to known relationships of these populations compared to a strict SMM (also see, Goldstein and others 1995b). Estoup and others (1995a,b) found evidence that a departure from SMM expectations with honey bee (*Apis mellifera*) microsatellites was attributable to compound motifs of repeat sequences. These irregular microsatellites may give rise to larger mutations (>1 step) more frequently than an uninterrupted sequence although the rate of mutation may be lower for complex motifs (Bruford and Wayne 1993). De León and others (1997) also found the number of alleles and level of heterozygosity in European sea bass (*Dicentrarchus labrax*) populations conformed more closely to the expectations of the IAM.

In all of these cases, multi-step mutations can produce more novel alleles in a population and consequently the structure is more likely to conform to either a multi-step SMM or an IAM (Slatkin 1995, Rousset 1996). A consequence of this process is that parameter estimates for population subdivision and genetic distance derived from an SMM will have greater variance than estimates derived from an IAM (Slatkin 1995, Rousset 1996). Parameter estimates incorporating a step-wise process also are prone to higher variances due to local genetic drift. These estimators incorporate differences in allele size as indicators of coalescence time where larger differences represent more generations since the alleles had a common ancestor. Thus, if drift produces large gaps in the distribution of allele sizes then the variance will be higher relative to measures based solely on relative frequencies of different alleles. Genetic drift will have the most effect on SMM estimates of subdivision when populations fluctuate in size and undergo different rates of genetic drift.

I chose 2 anuran species as subjects for examining mutation processes of microsatellites and the relative contribution of genetic drift to the frequency distribution of microsatellite alleles. *Rana luteiventris* (Green and others 1997) is a pond and stream dwelling frog that appears to be restricted to perennial water supplies. *Hyla regilla* is also a pond breeder, but it takes advantage of ephemeral water supplies and can often

be found some distance from perennial water outside of the breeding season. *R. luteiventris* is a particularly good candidate for study because previous work with allozymes showed a significant pattern of isolation-by-distance which suggests that this species may be in genetic equilibrium at a broad spatial scale (Wright 1943, Slatkin 1995, Green and others 1996). This pattern of isolation-by-distance provides a potential contrast with results expected from hypervariable markers such as microsatellites. Slatkin (1995) demonstrated that even if drift and migration are at equilibrium, high mutation rates ($>10^{-5}$) can obscure the pattern when population sizes are large. Consequently, failure to detect a pattern of isolation-by-distance may suggest a high rate of marker mutation relative to allozymes. Alternatively, if a significant isolation-by-distance pattern does exist then it will provide some insight into the average size of a genetic neighborhood (Slatkin and Maddison 1990, Slatkin 1993). Because genetic neighborhoods should be regarded as the upper limit of effective population size (N_e) (Crawford 1984), this estimate will provide the upper bounds for estimates of N_e that incorporate mutation rates (Crow and Kimura 1970, Ohta and Kimura 1973). Thus, mutation rate can be estimated within an order of magnitude by finding the best fit between neighborhood size and N_e. My objectives were to (1) develop and evaluate the characteristics of microsatellite markers for *R. luteiventris* and *H. regilla*, (2) test for a pattern of isolation-by-distance which I will use to estimate the average mutation rate, and (3) evaluate the variance for genetic parameter estimates derived from IAM and SMM models.

METHODS

STUDY AREA

H. regilla tissues were collected at 49N Pond, Little Muddy and Smoot Hill locations (Table 1). The first 2 collection sites are located in mixed-coniferous forests of the Selkirk Mountains in northeast Washington State. Smoot Hill is located approximately 165 km south of 49N Pond at an ecological preserve near Albion, WA. *R. luteiventris* samples were collected from 8 locations (Table 1). Bob's Pond, Ruby NW, and 49N Pond are all located in the Selkirk Mountains. Clarkia is located in mixed-coniferous

Table 1. *Rana luteiventris* and *Hyla regilla* populations sampled in this study. Universal transverse mercator (UTM) coordinates are provided for zone 11. Owyhee tissues were pooled from 3 different locations.

Population	Elevation (m)	UTM east	UTM north
R. luteiventris			
Bob's Pond	1060	465340	5392590
Ruby NW	1190	463270	5378740
49N Pond	1130	457500	5351000
Pullman	730	487200	5173700
Clarkia	910	547700	5204300
Alpine Lake	2500	687700	4994100
Egg White	2500	688550	4997950
Owyhee	~ 1200	508380	4708320
		538190	4726600
		529755	4714840
H. regilla			
Little Muddy	770	466300	5399200
49N Pond	1130	457500	5351000
Smoot Hill	670	480500	5187200

forest in northern Idaho, whereas Alpine Lake and Egg White populations are located in high-elevation basins in the Big Horn Craig Wilderness (D. Pilliod, pers. comm., Idaho State Univ., Pocatello, ID). Samples from the Owyhee population were collected from 3 localities (J. Munger, pers. comm., Boise State Univ., Boise, ID), but I pooled data across sites to increase my sample size. This population is located in desert-scrub habitat at the northern end of the Great Basin.

DNA Extraction and Genomic Libraries

Frogs were captured opportunistically (by hand or with a net) and a single toe was excised and stored in 95% ethanol. Genomic DNA was extracted using a proteinase K digest followed by 2 chloroform extractions and ethanol precipitation (Sambrook and others 1989). DNA was resuspended in TE or water and concentration was adjusted between 50 and 250 ng/ml using a TKO 100 fluorometer (Hoefer). I digested 5 µg of purified DNA with 3 restriction enzymes (*Hae*III, *Rsa*I, and *Alu*I) and size selected

fragments between 200 and 400 base pairs (bp) using low melting temperature agarose. After purification, fragmented DNA was ligated to pUC-19 and transformed by electroporation into *E. coli* (DH10B™, GibcoBRL). Genomic libraries were stored at -80° C until ready for screening.

Screening Libraries for Microsatellite Repeats

Transformed cells were incubated overnight on LB plates (75 µg/ml ampicillin) and resulting colonies (*ca.* 2,500 per plate) were transferred to a positively charged nylon membrane using manufacturer's protocols (Magnacharge, MSI). Hybridization methods follow Spruell and others (1994) with the following modifications. Membranes were incubated in blocking solution (10 ml) for 45 min (55° C) followed by incubation in hybridization solution (8 ml) with 1.0 µl of probe mix. Probe mix was composed of equal proportions of different oligonucleotides that were labeled with alkaline phosphatase. Each probe consisted of a series of *n* repeats and most colonies were screened with a mixture of at least 4 probes: (CA)*n*, (GA)*n*, (GC)*n*, and (AT)*n*. The probe manufacturer (FMC Corp.) does not provide data on probe concentrations (fmol) or the number of repeats, but in practice there appear to be a minimum of 7 to 10 repeat units. After probes were hybridized to the membrane (45 min, 55° C), hybridization solution was removed and the membrane was rinsed 3 times and incubated in an alkaline solution (Spruell and others 1994). I then applied chemiluminescent substrate (CSPD or Lumi-Phos® 480) and exposed the membrane to autoradiograph film for 6–12 hr. Colonies containing inserts positive for microsatellites showed up as dark spots on the film.

Each region of the LB plates that encompassed a positive colony was scraped and cells were resuspended in LB. These cell suspensions were replated on LB plates and colonies were again lifted and screened for DNA repeats as described above. One positive colony from each secondary LB plate was cultured in 4.5 ml LB or Terrific broth and I isolated plasmid DNA from the cultures using a modified alkaline-lysis/PEG miniprep (Applied Biosystems). Purified plasmid was submitted for automated sequencing (Applied Biosystems, Model 373A, Murdock Molecular Lab, University of Montana, Missoula). Primers for product amplification were designed with PRIMER (Lincoln and others 1991).

Scoring Microsatellite Genotypes

Polymerase chain reaction (PCR) was carried out in an Amplitron thermalcycler and I used the same conditions for all loci. Reaction mixtures contained 1X Promega reaction buffer (50 mM KCL, 10 mM Tris-HCL (pH 9.0), 0.1% Triton® X-100), 2.5 mM $MgCl_2$, 200 nM of each primer (GibcoBRL), 200 nM of each dNTP, 0.5-1.0 units *Taq* polymerase and 50-200 ng DNA template for a 25.5 µl total reaction volume plus 1 drop of mineral oil. Thermal cycling included a 3 min predwell (95° C) followed by 35 cycles of 95° C denaturization (30 s), 55° C annealing (40 s), 72° C extension (40 s) and a 5 min postdwell (72° C) after cycling was completed. PCR products were separated in an 8% acrylamide denaturing gel (8 M urea) for 3.5 h (60 watts constant). Microsatellites were transferred to a nylon membrane using a capillary blot (1.5 h) and the appropriate repeat probe (FMC Corp.) was hybridized to the DNA as described above (40° C hybridization temperature, 12–24 hour film exposure). Known standards were run in flanking and center lanes so that allele sizes could be estimated to an exact base pair.

Allele Sizes and Distribution

I examined the distribution of allele size differences by arranging all alleles in ascending order (by size) and calculating the number of 2-base, 4-base and >4-base pair differences for adjacent alleles. This was done separately for each locus and comparisons were made by pooling alleles (within loci) across populations and by considering populations separately. I also summarized the range of allele size differences relative to the median allele for each locus. This involved arranging all alleles for a given locus in ascending order and dividing alleles into equally spaced quartiles on either side of the median allele size. I then tallied the mean base pair size difference for each quartile and pooled data within species. This analysis provided a convenient summary of the largest gaps in allele sizes relative to the range of observed alleles.

Hardy-Weinberg Equilibrium and Null Alleles

I used GENEPOP (ver. 3.0) to test the assumption that each locus was in Hardy-Weinberg equilibrium (HWE) using a Fisher's exact probability test or a Markov

approximation of the exact test (Guo and Thompson 1992, Raymond and Rousset 1995). I set the parameters for the Markov approximation so that the standard error for the probability estimate was always <0.01. I also used GENEPOP to test for linkage equilibrium both within and between populations using either an exact test or the Markov chain method.

Several factors contribute to departures from genotypic frequencies expected under HWE, including the Wahlund effect, nonrandom mating, genetic drift, and selection. Microsatellite genotypes also can show heterozygote deficiencies when null alleles are present in the population (Chakraborty and others 1992, Pemberton and others 1995, Brookfield 1996, Ishibashi and others 1996). Null alleles arise when mutations prevent 1 of the primers from binding to the template DNA. If a sample is heterozygous for the mutation, only 1 allele will be visible so the genotype will be incorrectly tallied as homozygous. If sample sizes are small, it is still possible for a sufficient number of null alleles to be present in the sample to produce an excess of visible homozygotes. I used 3 methods to estimate the frequency of null alleles in a population, assuming the locus was in HWE. Chakraborty and others (1992) (Eq. 1) developed an estimate from their work with low-resolution gels where they considered missing alleles a result of electrophoresis errors so missing products were not informative. Brookfield (1996) incorporated missing products implicitly (Eq. 2) and explicitly (Eq. 3) into his estimates of null allele frequencies. After estimating the frequency of null alleles, I tested the "fit" of the estimates by incorporating the null alleles back into the original data set and again testing for HWE. For instance, suppose 2 of 12 samples yielded blank lanes and the estimated frequency suggested there were 6 null alleles present in the original sample. I would assign 4 of these 6 alleles to the blank lanes and distribute remaining null alleles proportionately among visible homozygotes and test for HWE. A blank lane was assigned the status of a potential null homozygote when I was able to use the same template DNA to successfully generate genotype data for other loci. This suggests that failure to produce the product was not an artifact of degraded DNA or PCR inhibitors in the sample. Although this is not a definitive test for other artifacts, in most cases I also replicated the blank results using an independent round of PCR.

ISOLATION-BY-DISTANCE

I used a model of isolation-by-distance to determine if populations of *R. luteiventris* are at genetic equilibrium for microsatellite markers. Slatkin (1993) showed that under certain assumptions, $\hat{M}$ is a reasonable measure of the extent of gene flow between pairs of populations where $\hat{M} = \frac{1}{4} \times [(1/F_{ST}) - 1]$, and F_{ST} is Wright's estimate of population subdivision (Wright 1951). Under the assumption of genetic equilibrium with restricted dispersal and low rate of mutation, there is a simple log-log relationship between $\hat{M}$ and geographic distance. I used a least-squares regression ($\log(\hat{M}) = b_o + b_1 \times \log(\text{distance})$) to estimate the slope of this relationship. A significant negative slope indicates a pattern of isolation-by-distance and suggests that the system is in genetic equilibrium. A statistical evaluation of the slope parameter (H_o: $b_1 = 0$) is not possible using parametric distributions because the pairwise population comparisons are not statistically independent (Slatkin 1993). Instead, I evaluated the significance level using a resampling algorithm to build bootstrap confidence intervals (15,000 iterations) for each regression parameter and for the correlation coefficient (r^2) (Slatkin and Maddison 1990, Crowley 1992, Green and others 1996). I calculated $\hat{M}$ using 2 estimators for F_{ST}. The IAM based estimator ($\hat{\theta}$, Weir and Cockerham 1984) uses allele frequencies to estimate the correlation between alleles from different individuals in the same population. The SMM based estimator ($\hat{\rho}$, Rousset 1996) for the same correlation is calculated from the variance of the distribution of allele sizes within and between populations. I calculated $\hat{\theta}$ using FSTAT ver. 1.2 (Goudet 1995) and $\hat{\rho}$ with GENEPOP ver. 3.0. I generated bootstrap estimates for regression parameters based on $\hat{\theta}$ and $\hat{\rho}$ as well as for data from Green and others (1996). There was a slight discrepancy between my analysis and that of Green and others because of a potential error in their reported data set (Green and others 1996; Table 4).

ESTIMATOR VARIANCE

To test the applicability of IAM and SMM based estimators, I calculated $\hat{\theta}$ and $\hat{\rho}$ for each locus and evaluated the coefficient of variation for the mean estimate of F_{ST}. I also tried to recover the basic phylogeographic distribution of *R. luteiventris* populations using several estimates of genetic distance. Estimators developed for microsatellite

markers (SMM estimators) include (1) *Ddm*, a squared mean difference between alleles of 2 populations (Goldstein and others 1995a, Goldstein and others 1995b), (2) *Dsw*, an extension of Nei's minimum distance estimate (Shriver and others 1995), (3) *Dps*, the proportion of shared alleles between populations (Bowcock and others 1994), and (4) R_{ST}, the ratio of within and between population variance in allele lengths (Slatkin 1995). The IAM based estimators included (5) F_{ST}, as estimated by a coefficient of coancestry (Reynolds and others 1983), and (6) *Ds*, Nei's standard genetic distance (Nei 1972). I used Microsat ver. 1.5b (Goldstein and others 1995b) to calculate the above estimates of genetic distance. Phylogeographic trees were constructed using the neighbor-joining method with PHYLIP ver. 3.5c (Saitou and Nei 1987, Felsenstein 1993) and visualized using TREEVIEW ver. 1.4 (Page 1996).

MUTATION RATE AND N_E

I estimated the inbreeding effective population (N_e) size using estimators derived from both IAM and SMM (De León and others 1997). Crow and Kimura (1970) found that for a finite population at genetic equilibrium, an IAM can be used to approximate N_e as (H_e / 1 - H_e) / 4μ where H_e represents observed heterozygosity and μ is the mutation rate. Ohta and Kimura (1973) also derived an estimate of N_e for a population at genetic equilibrium, but using an SMM. In this case, $N_e = [(1 / (1 - H_e)^2) - 1] / 8\mu$. I averaged estimates of H_e across populations for each locus and used an estimate of μ that produced N_e values consistent with estimated neighborhood sizes.

RESULTS

I developed 7 highly polymorphic microsatellite loci (Table 2). All of the microsatellite clones included dinucleotide sequences that varied from simple tandem repeats to complex motifs of different nucleotide combinations. Based on the original clone sequences, I estimated the number of tandem repeats to range between 9 and 63 for the *R. luteiventris* loci and between 15 and 52 for the *H. regilla* loci. The frequency distribution for alleles was variable between loci (Fig. 1, Appendix). With the exception of HYRE59, no alleles exceeded a frequency of 45% although each locus tended to be

Table 2. Characteristics of 3 *Rana luteiventris* (RALU) and 4 *Hyla regilla* (HYRE) microsatellites. N represents the number of individuals screened for allelic variation. The number of repeat units was estimated from the size of the alleles relative to the original microsatellite sequence which is available through Genebank.

Locus	Repeat motif	Primers (5' => 3')	N	Number of alleles (range)	Mean size (%CV)	Number of repeat units	Genebank accession number
RALU47	$(CA)_{34}N_4(CA)_5$	TGTATATTGATTGGTTTGTGGGCAAAG TGCCAGATTGCCC	136	27 (160 – 252)	188.1 (4.5)	10 – 56	U92272
RALU48	$(CT)_{25}$	GGAGCCCAATCTACTTATGCCGAGCA GCCAATTCTTCCG	180	10 (196 – 228)	214.6 (4.5)	9 – 25	U92273
RALU50	$(GT)_{11}(ATGT)_2(AT)_{39}$	ACAGATCCCAATTGATTGGCTGGGAG AAATATACCTACCCCC	110	22 (164 – 236)	203.9 (9.2)	28 – 63	U92274
HYRE58	$(GT)_8(TGTGT)_6$	GAGTTTATGCCGTTCTTGGGACAAGG GGGAGACACAGGC	53	9 (189 – 225)	206.3 (4.9)	15 – 33	U92275
HYRE59	$(AC)_9(TC)_{13}$	ATCCTGGATAACCCTTTCAGGGCTATT TCATCGTATGATCCCA	56	5 (196 – 214)	197.4 (1.9)	22 – 33	U92276
HYRE64	$(AT)_{19}(AC)_3(AT)_1$ $(AC)_5(GC)_1(CA)_4$	ATGGAAGCGTTTAGCCCACTCTTCCCT CTTGCCCCAG	49	15 (150 – 192)	176.9 (4.8)	18 – 39	U92277
HYRE65	$(AT, CT, GT)_{50}$, interrupted	CTGCCTATCTAAACATGAAGCCGGGG ATGCATCATCAGGG	48	11 (201 – 225)	210.4 (3.1)	41 – 52	U92278

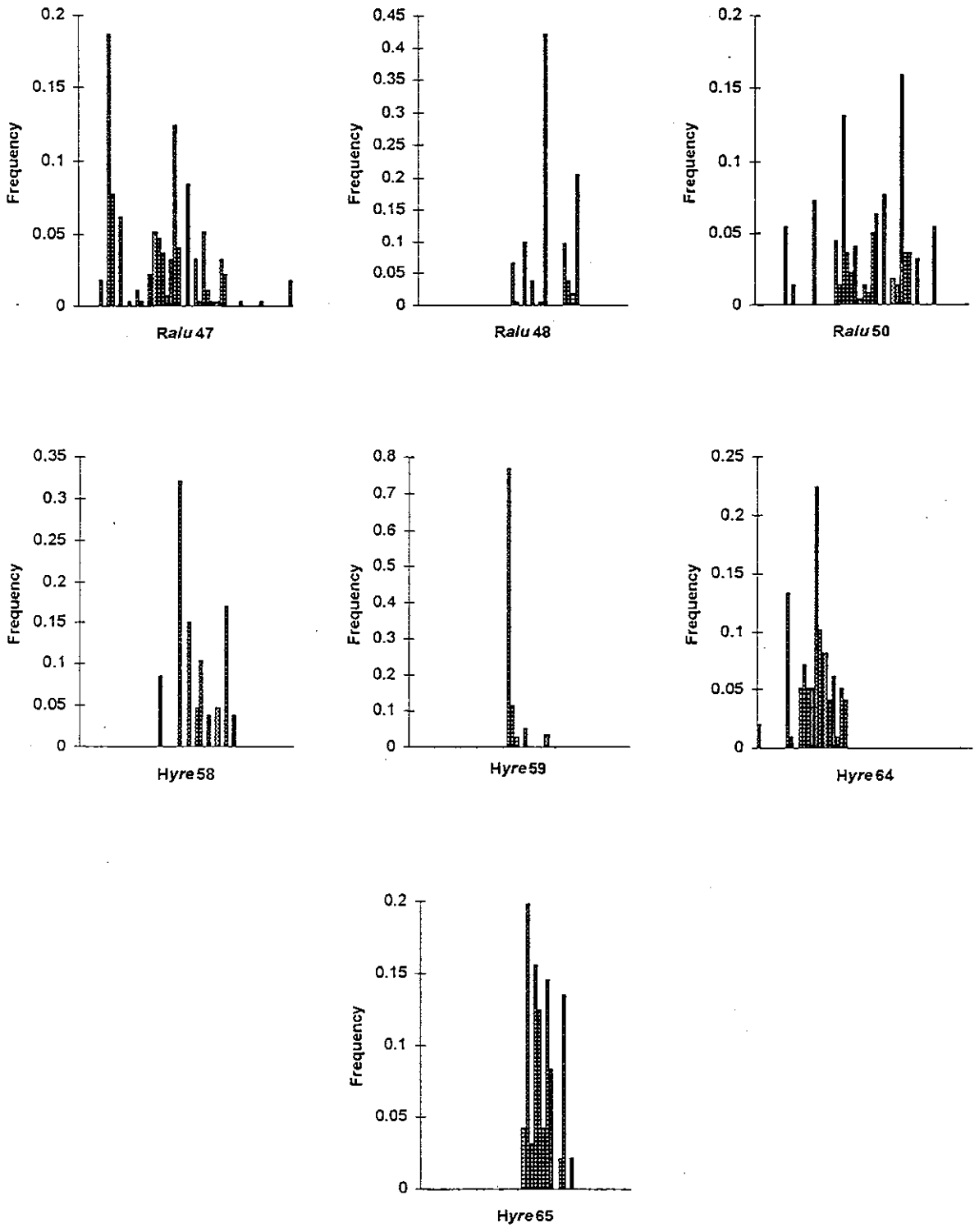

Figure 1. Frequency distribution of all alleles observed for *Rana luteiventris* and *Hyla regilla* microsatellite loci. The x-axis is the same for all graphs (150-250-bp).

dominated by a 1 allele. With the exception of HYRE58, over 59% of differences between alleles lengths were represented by 2-base pair gaps and 89% of these differences were no more than 4 bases (Fig. 2A). The distribution of gaps was similar for all loci (χ^2 = 17.3, 12 df, P = 0.14) and there was no significant difference between the distribution of gaps for *R. luteiventris* ($\bar{x}$ = 3.5 ± 0.36 (±SD), range 2–14) and *H. regilla* ($\bar{x}$ = 3.3 ± 0.64, range 2–14; χ^2 = 0.42, 2 df, P = 0.8). The distribution of gaps in allele size was not equally distributed across the range of observed alleles. The average gap in the 4th quartile was significantly greater than the other 3 quartiles for *R. luteiventris* (Fig. 3A, F = 6.06, 52 df, P = 0.0014). The *H. regilla* allele distribution demonstrated a similar pattern, although it was not statistically significant (Fig. 3b, F = 1.93, 31 df, P = 0.15). When I considered gaps between allele sizes at the population level, the overall frequency of 2-base, 4-base and >4-base changes was approximately equal (33.8%, 30.2% and 36%, respectively, Fig. 2B). *R. luteiventris* populations had larger gaps ($\bar{x}$ = 8.5 ± 0.11, range 2–60) compared with *H. regilla* populations ($\bar{x}$ = 4.1 ± 2.8, range 2– 6; χ^2 = 12.7, 2 df, P = 0.002).

Hardy-Weinberg Equilibrium and Null Alleles

Three populations were monomorphic at 1 locus and several potential null alleles were observed at 8 *R. luteiventris* populations and 1 *H. regilla* population (Table 3). Eight of the null alleles in the Pullman sample (RALU50) came from samples that also produced null alleles at the RALU47 locus. I replicated both results twice to confirm the null observations and all samples were used successfully to produce products at the RALU48 locus. There were no distinct advantage of any of the 3 methods used to estimate null alleles, except that Eq. 3 generally produced a better fit for the expected number of heterozygotes under HWE. In some cases the estimated number of alleles was insufficient to explain the existence of all the observed null alleles (e.g., Eq. 1 and Eq. 2, 49N Pond, RALU47) or predicted more null alleles than could be explained by the number of observed null homozygotes and visible heterozygotes (e.g., Eq. 1, Egg White, RALU50). In 1 case (Pullman, RALU50), Eq. 3 yielded nonsensical results (frequency = 1.0) and the remaining equations failed to account for all null homozygotes. Consequently, more than 1 null allele may be present in this population.

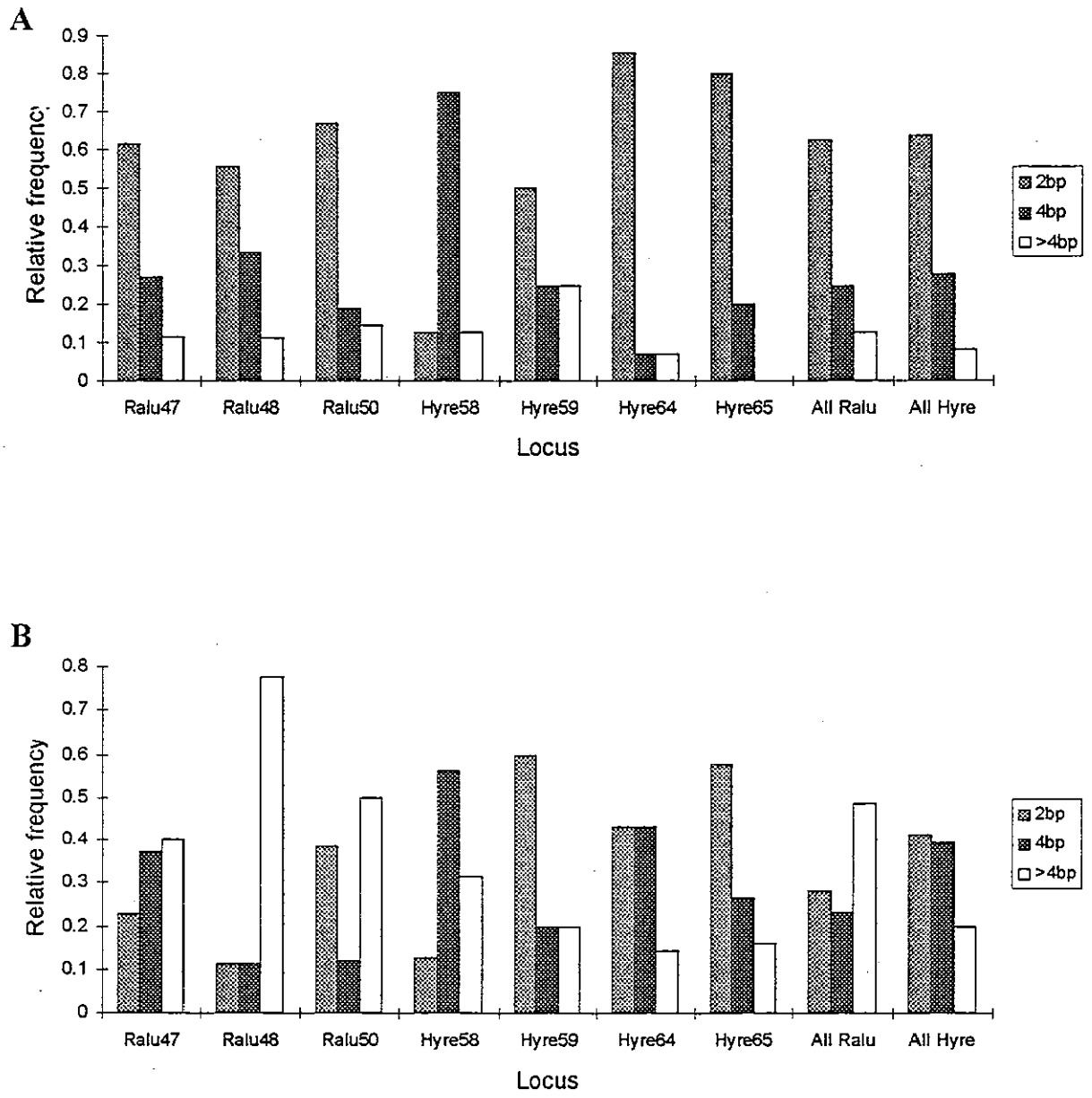

Figure 2. Relative frequency of allele size differences (A) for all alleles pooled across populations, and (B) for all alleles within populations.

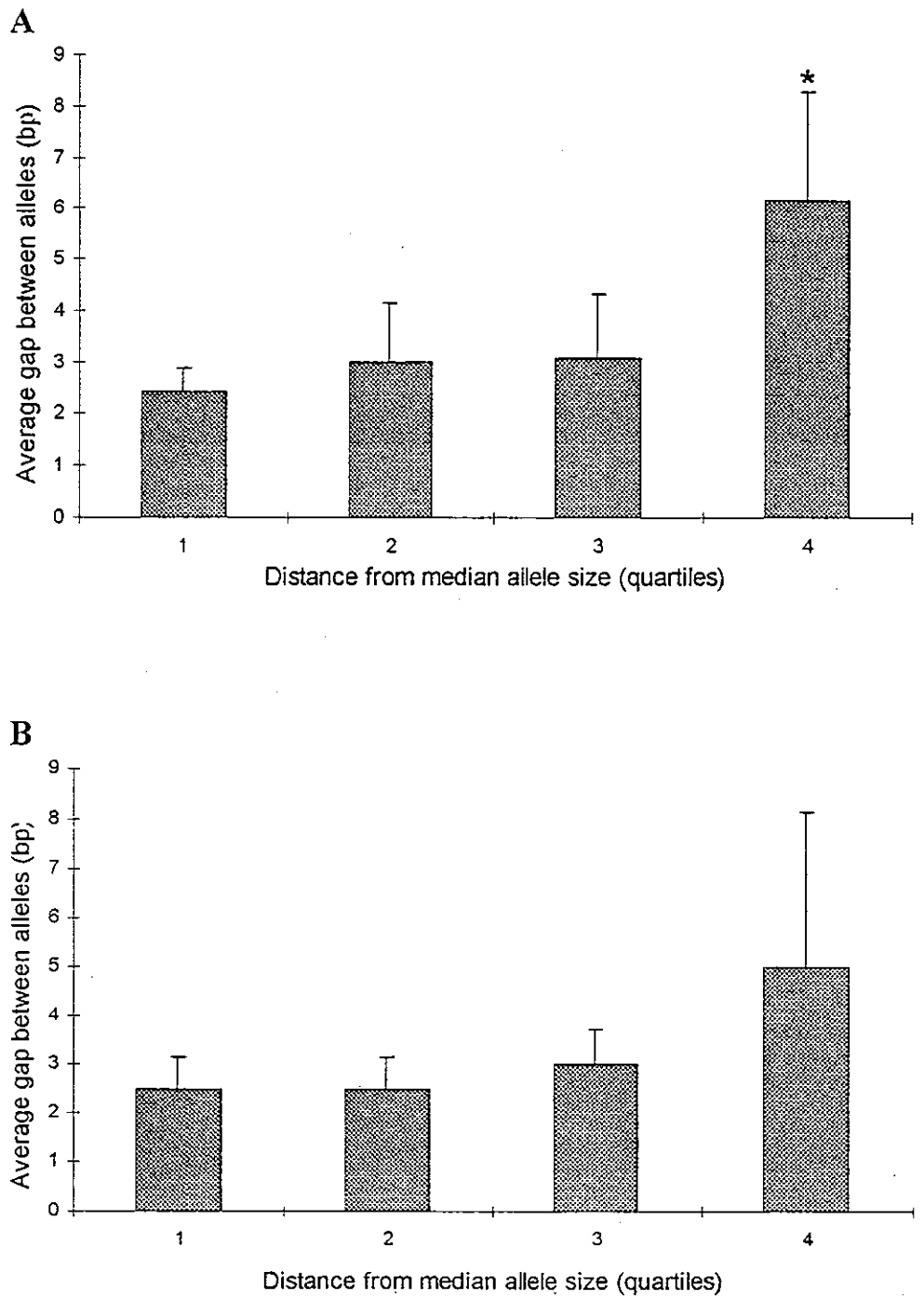

Figure 3. Distribution of average allele size differences relative to the median allele size for each locus. Bars represent 1 standard deviation (* $P < 0.05$). (A) *Rana luteiventris* loci, and (B) *Hyla regilla* loci.

Table 3. Microsatellite variation within 8 *Rana luteiventris* and 3 *Hyla regilla* populations. HWE *P* is the probability of observing a larger deviation from expected heterozygosity under Hardy-Weinberg equilibrium. Frequency of null alleles was estimated from Chakraborty and others (1992) (Eq. 1) and Brookfield (1996) (Eq. 2, Eq. 3). *P*-values are given for HWE tests after incorporating estimates of the number of null alleles in the original sample.

Locus and population	N	Number alleles	Null alleles	Obs. H_e	Exp. H_e	HWE *P*	Frequency of null alleles			*P*-values		
							Eq 1	Eq 2	Eq 3	Eq 1	Eq 2	Eq 3
RALU47–Bob's Pond	11	12	0	1.00	0.91	1.00						
Ruby NW	11	6	1	0.60	0.76	0.19	0.11	0.09	0.15	0.24	0.04	0.24
49N Pond	13	5	2	0.64	0.70	0.38	0.05	0.04	0.21	----	----	0.12
Clarkia	13	8	2	0.55	0.83	**0.02**	0.21	0.16	0.25	0.01	<0.01	0.56
Pullman	19	1	17									
Alpine	14	5	0	0.50	0.51	0.67						
Egg White	10	4	0	0.60	0.71	0.54						
Owyhee	28	2	0	0.18	0.16	1.00						
RALU48–Bob's Pond	12	2	0	0.33	0.38	1.00						
Ruby NW	16	2	0	0.26	0.19	0.31						
49N Pond	27	2	0	0.48	0.46	1.00						
Clarkia	13	3	5	0.13	0.57	**0.01**	0.64	0.28	0.61	1.00	0.92	1.00
Pullman	19	3	0	0.53	0.53	0.85						
Alpine	14	2	0	0.36	0.38	1.00						
Egg White	10	2	0	0.10	0.46	**0.02**	0.64	0.24	----	----	0.55	----
Owyhee	12	2	9									
RALU50–Bob's Pond	10	8	0	0.70	0.85	**0.02**	0.09	0.08	----	0.43	0.41	----
Ruby NW	12	10	0	0.75	0.86	0.05						
49N Pond	25	5	0	0.56	0.64	0.11						
Clarkia	13	10	0	0.77	0.88	**0.01**						
Pullman	19	4	8	0.45	0.62	**0.01**	0.16	0.10	----	----	----	----
Alpine	8	4	0	0.75	0.73	0.68						
Egg White	10	2	4	0.00	0.28	0.09	1.00	0.63	0.77	----	1.00	1.00
Owyhee	15	1	0									
HYRE58–Little Mud	20	5	0	0.60	0.72	0.16						
49N Pond	19	6	0	0.79	0.77	0.11						
Smoot Hill	20	5	0	0.60	0.72	0.16						
HYRE59–Little Mud	15	1	0									

Table 3. Continued

Locus and population	N	Number alleles	Null alleles	Obs. H_e	Exp. H_e	HWE P	Frequency of null alleles			P-values		
							Eq 1	Eq 2	Eq 3	Eq 1	Eq 2	Eq 3
49N Pond	19	3	0	0.37	0.42	0.41						
Smoot Hill	22	4	0	0.50	0.55	0.64						
HYRE64–Little Mud	15	9	0	0.87	0.80	0.24						
49N Pond	19	7	0	0.68	0.75	0.63						
Smoot Hill	15	8	0	0.80	0.83	0.34						
HYRE65–Little Mud	15	7	0	0.80	0.79	0.24						
49N Pond	19	8	1	0.67	0.83	0.12	0.11	0.091	0.091	0.28	0.11	0.11
Smoot Hill	15	8	0	0.80	0.75	0.65						

Two out of 5 cases which departed from HWE did not include any null homozygotes, but this does not mean that null alleles were absent in the populations. For Bob's Pond there was a 93% chance of missing the null homozygote (frequency = 0.085, N = 10, binomial distribution) and for Egg White there was 55% chance of missing a null homozygote in a sample of 10 toes (frequency = 0.24). The mean observed H_e (± SD) was significantly greater for *H. regilla* ($\bar{x}$ = 0.68 ± 0.15) than for *R. luteiventris* populations ($\bar{x}$ = 0.49 ± 0.25, F = 4.6, 30 df, P = 0.04). In the 49N Pond population the RALU47 and RALU50 loci appeared to be in linkage disequilibrium (P = 0.023) as well as the RALU47 and RALU48 loci (P = 0.046). All remaining loci within and between populations were in linkage equilibrium (P > 0.13).

ISOLATION-BY-DISTANCE

All 3 regression models suggested a strong pattern of isolation-by-distance (Fig. 4). The $\hat{\theta}$ estimate for $\hat{M}$ generated a highly significant slope (P < 0.0001) that explained 63% of the variance (Fig. 4A). The $\hat{\rho}$ based estimate of $\hat{M}$ also produced a statistically significant model for isolation-by-distance (P = 0.0004, Fig. 4B, Table 4), but explained less variation (r^2 = 0.31). The regression from Green and others (1996) was significant (P < 0.0001, Table 4) and explained 35% of the variance (Fig. 4C). The 2 microsatellite regressions excluded the pairwise comparison between Egg White and Alpine Lake. Inclusion of this data point in the $\hat{\theta}$ model still produced a significant regression, but the model explained much less variance (r^2 = 0.35). Inclusion of the data point with the $\hat{\rho}$ model produced a statistically significant model (P = 0.023), but it explained little of the variance (r^2 = 0.09).

ESTIMATOR VARIANCE

The lower r^2 value for the $\hat{\rho}$ based isolation-by-distance model suggested a higher variance for this SMM estimator. This was also true when each locus was evaluated separately. The coefficient of variation was 4 times larger using $\hat{\rho}$ to estimate *R. luteiventris* subdivision compared with $\hat{\theta}$ estimates (14.5% vs. 58.2%, respectively). A similar, although less pronounced pattern was evident for *H. regilla* loci (56% vs. 22.4%, respectively). The phylogeographic trees were not intended to be an exhaustive

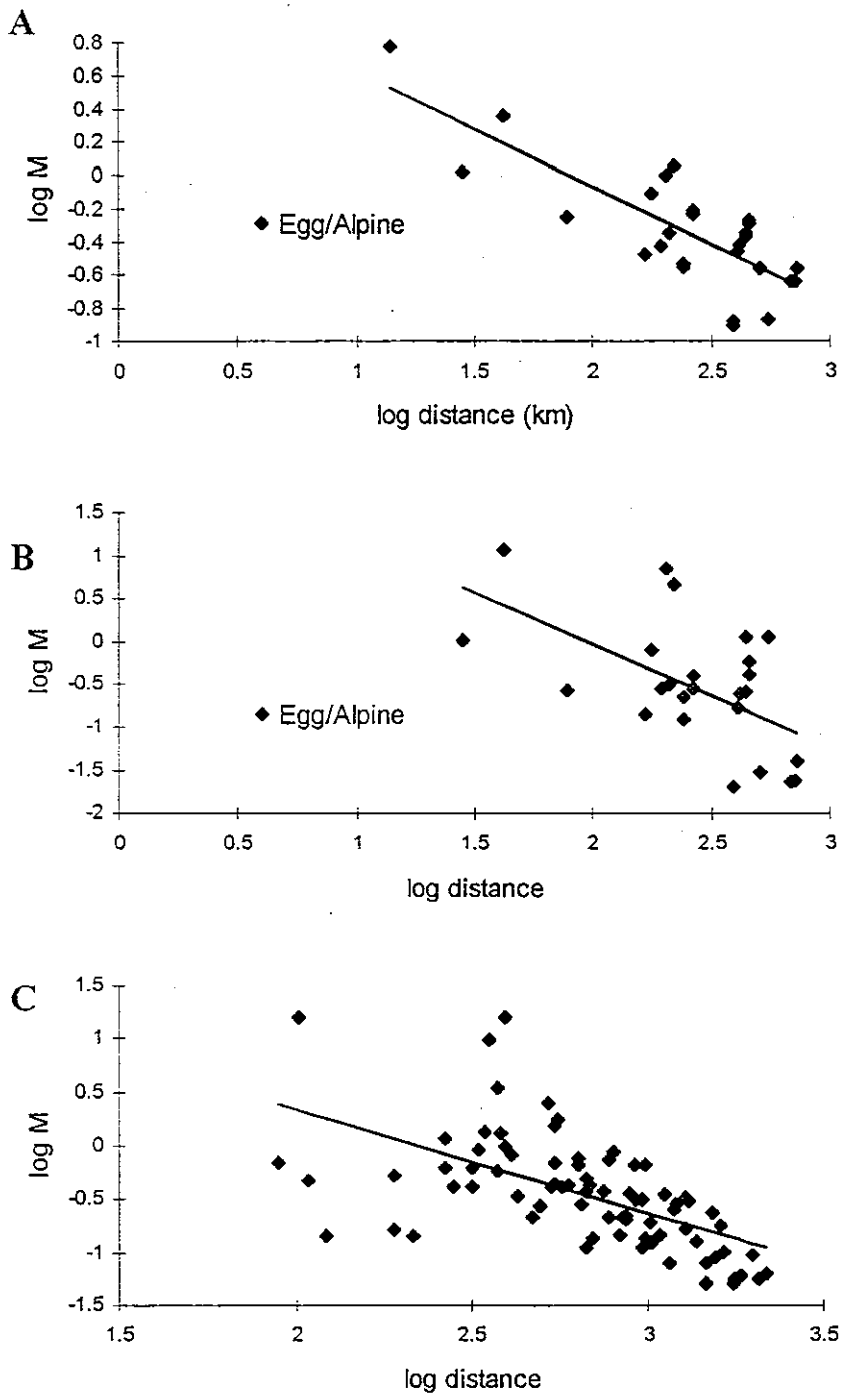

Figure 4. Isolation-by-distance models for *Rana luteiventris* populations. (A) $\hat{M}$ estimated from $\hat{\theta}$, where $\log_{10}(\hat{M}) = 1.3057 - 0.6875 * \log_{10}(\text{km})$, $r^2 = 0.63$, $P < 0.0001$, (B) $\hat{M}$ estimated from $\hat{\rho}$, where $\log_{10}(\hat{M}) = 2.3482 - 1.1919 * \log_{10}(\text{km})$, $r^2 = 0.306$, $P = 0.0004$, and (C) $\hat{M}$ estimated from G_{ST} (allozyme data, Green and others 1996), where $\log_{10}(\hat{M}) = 2.2573 - 0.9605 * \log_{10}(\text{km})$, $r^2 = 0.35$, $P < 0.0001$. Egg/Alpine estimate of $\hat{M}$ was not included in the regression models.

Table 4. Mean parameter estimates and bootstrap confidence intervals (95%) for regressions of $\log_{10}(\hat{M})$ on $\log_{10}$(distance, km) for *Rana luteiventris* populations (N = 8). $\hat{M}$ estimates were based on $\hat{\theta}$ and $\hat{\rho}$ estimators for this study whereas Green and others (1996) used G_{ST} to estimate $\hat{M}$.

Regression data set	Y-intercept (b_o)	Slope (b_1)	Correlation (r^2)
$\hat{\theta}$	1.27	-0.67	0.60
	0.63 – 1.75	-0.87 – (-0.42)	0.26 – 0.82
$\hat{\rho}$	2.44	-1.23	0.32
	0.73 – 4.60	-2.08 – (-0.51)	0.07 – 0.60
Green and others	2.29	-0.97	0.36
(1996)	1.20 – 2.91	-1.40 – (-0.76)	0.17 – 0.46

analysis of the distance estimators. It is instructive, however, that all 4 estimates of genetic distance derived specifically for microsatellites failed to recover the correct population structure based on the geographic relationships of the populations (Fig. 5, A, B, C, D). None of these estimators correctly grouped the Selkirk populations (49N, Bob, RNW) and Nei's standard genetic distance failed as well (Fig. 5F). The F_{ST} estimate based on the coefficient of coancestry (an IAM estimator), however, appeared to recover the correct pattern of population structure (Fig. 5E).

MUTATION RATE AND N_E

Converting the y-intercept of the isolation-by-distance models into neighborhood size yielded estimates between 19 and 274 frogs, although there was a wide range of estimates based on the y-intercept confidence intervals (Table 5). The best match for N_e was obtained with a mutation rate of 10^{-4}. Given this rate of mutation, the estimated N_e for *H. regilla* was 4-fold greater than that for *R. luteiventris*.

DISCUSSION

The distribution of alleles observed in this study was qualitatively very similar to the distribution of 108 dinucleotide loci in human populations (Valdes and others 1993). Valdes and others (1993) showed that the pattern of allele size differences generally conform to an SMM. Nevertheless, a strict stepwise mutation process would not lead to

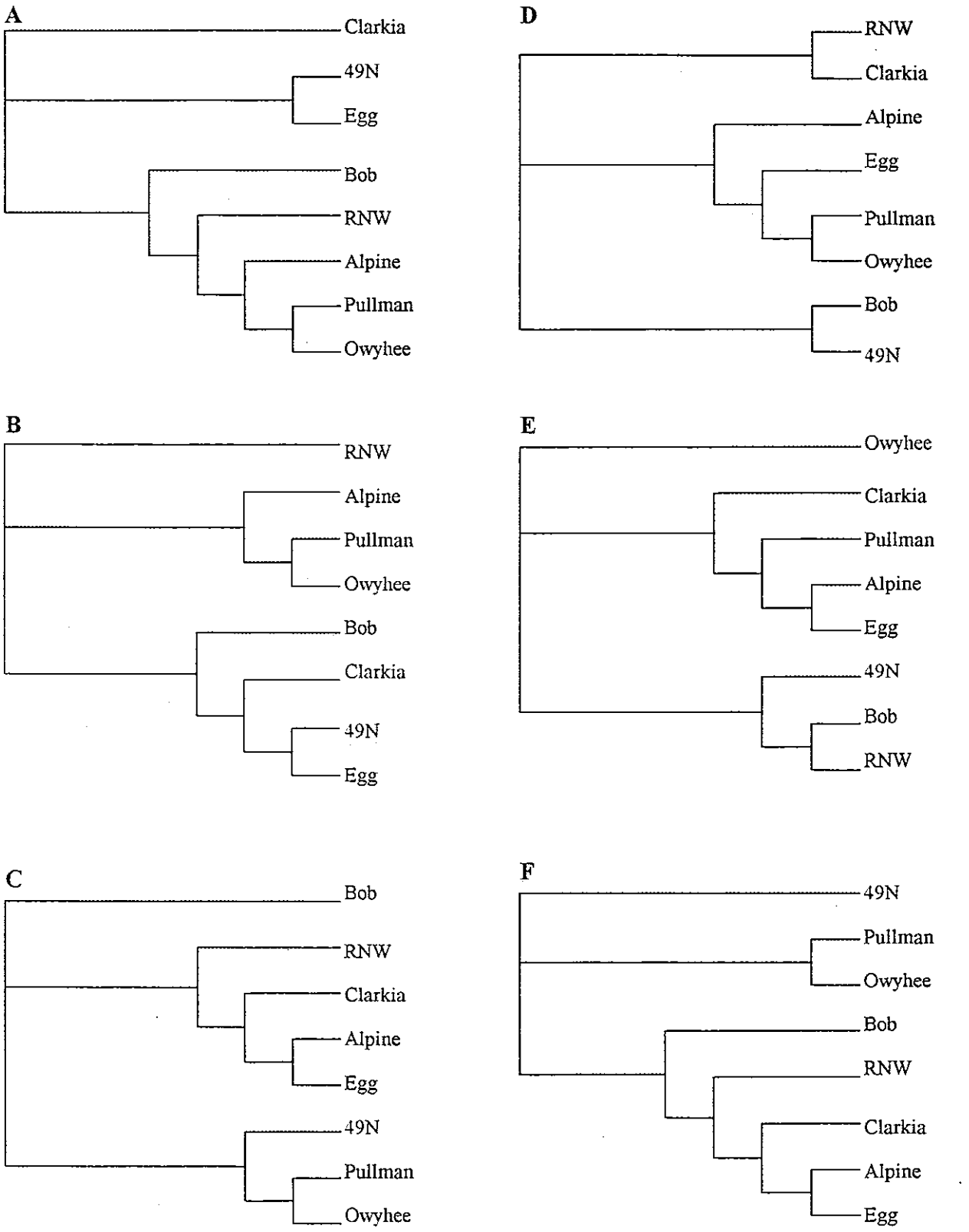

Figure 5. Neighbor-joining cladograms for 8 *Rana luteiventris* populations using 6 estimates of genetic distance. (A) *Ddm* (Goldstein and others 1995b), (B) *Dsw* (Shriver and others 1995), (C) *Dps* (Bowcock and others 1994), (D) R_{ST} (Slatkin 1995), (E) F_{ST} (Reynolds and others 1983), and (F) D_S (Nei 1972).

Table 5. Estimated effective population size (N_e) for *Rana luteiventris* and *Hyla regilla* populations. Estimators were derived from an infinite alleles model (IAM) (Crow and Kimura 1970) and a stepwise mutation model (SMM) (Ohta and Kimura 1973). Heterozygosity (H_e) was averaged across all loci. Neighborhood sizes for *R. luteiventris* were estimated from the y-intercept of the isolation-by-distance models. The G_{ST} estimate is based on allozyme data (Green and others 1996). The range of sizes is based on bootstrap confidence intervals for the y-intercept.

Species	Average H_e	N_e from IAM	N_e from SMM	Neighborhood size		
				$\hat{\theta}$	$\hat{\rho}$	G_{ST}
R. luteiventris	0.49	128	352	19 (4 - 60)	274 (5 - 40,050)	194 (16 - 816)
H. regilla	0.68	531	1221			

many allele differences greater than 1 or 2 repeats. Sampling error and genetic drift will produce larger gaps in the distribution, but this pattern should be random and thus average gap sizes would be equal across the range of observed alleles. Instead, the largest gaps in my allele frequencies were found in the 4th quartile where I would expect to detect occasional multi-step mutations. Di Rienzo and others (1994) estimated the proportion of multi-step mutations for human loci to range between 0.05 and 0.2 which is consistent with my estimate of 11% gaps greater than 4-base pairs in size. Valdes and others (1993) found allele length differences ranged from 2 to 30 units whereas I found gaps between 2 and 14 when data were pooled across populations. Although none of these results prove that microsatellite marker mutation is a stepwise process, the results are consistent with this pattern with the addition of occasional larger mutations. Gaps in allele sizes were considerably larger within populations which probably resulted from a combination of sampling error, multi-step mutations, and genetic drift.

HARDY-WEINBERG EQUILIBRIUM AND NULL ALLELES

I found evidence of null alleles for all *R. luteiventris* markers and 1 possible null allele for a *H. regilla* marker. Null alleles have been found or suggested as possible reasons for departure from HWE for several genetic markers and a range of taxa (Foltz 1986, Chakraborty and others 1992, Paetkau and Strobeck 1995, Pemberton and others 1995). Some of the null alleles I observed may have been an artifact of my hybridization

procedure. Two alleles had as few as 10 repeats which is at the lower end of detectability of my short oligonucleotide probes. Regardless of the source of the missing alleles, in most cases at least 1 estimator (Eq. 1, 2 or 3) predicted a frequency of null alleles consistent with expectations under HWE. The 1 exception was the Pullman population where more than 1 null allele may be present. One *R. luteiventris* population (49N Pond) showed potential linkage disequilibrium. This can result from several factors, but genetic drift is a likely candidate in this particular case. Over 3 years I never observed more than 8 egg masses at 49N Pond. Such a small breeding population will be subject to rapid genetic drift.

Isolation-by-Distance

I justified the exclusion of the Egg White–Alpine Lake estimate of gene flow from my regression models because it was clearly an outlier. These 2 populations are very close (4 km) and yet the allele frequencies suggested gene flow consistent with a minimum of 31 km separation. The populations are located in adjacent, high-elevation basins separated by a steep cirque wall (>300 m) that is probably a barrier to migration. The nearest downstream migration corridor is 22 km and includes a >300 m drop in elevation. If this result is typical of other basins, it suggests that alpine populations may experience an extended absence of frogs following local extinction (e.g., Bradford and others 1993).

The significant isolation-by-distance relationship is consistent with the assumption of equilibrium between genetic drift and migration for both allozyme and microsatellite markers. Slatkin (1993) suggested that a steeper regression slope (-1.0) represents a 1-dimensional dispersal system while less slope (-0.5) represents 2-dimensional dispersal. My IAM results are consistent with 2-dimensional dispersal whereas results from Green and others (1996) are consistent with a 1-dimensional system (e.g., stream corridors). The discrepancies between slope estimates may reflect the larger spatial scale incorporated into the Green and others (1996) model.

ESTIMATOR VARIANCE

Rapid mutation and increased departures from a strict SMM will produce higher variances for estimators derived from an SMM (Slatkin 1995, Rousset 1996). In these cases, IAM-derived estimators may be more accurate for predicting relationships between populations. In addition, if an insufficient number of mutations has occurred, then an IAM estimator should perform at least as well as the SMM estimators (Slatkin 1995, Rousset 1996). The variances for SMM estimators used here were clearly larger for the isolation-by-distance model and estimates of F_{ST}. In addition, the phylogeographic trees based on SMM estimators did not reflect the actual geographic relationships between populations. Because the isolation-by-distance relationship appears to hold for *R. luteiventris*, it is reasonable to assume that geographic distance is closely related to phylogeographic structure. It is noteworthy that the only phylogeographic tree to correctly reflect the geographic relationships for *R. luteiventris* populations was based upon an IAM estimator (Reynolds and others 1983). This particular measure assumes that populations fluctuate in size and mutation rate is negligible relative to the rates of genetic drift and migration—a result that is consistent with the isolation-by-distance models. Further work is needed to clarify the usefulness of SMM derived estimators for population subdivision and genetic distance. My study supports other results which show IAM derived estimators perform better for describing genetic diversity within and between natural populations (e.g., De León and others 1997).

MUTATION RATE AND N_E

The average neighborhood size for *R. luteiventris* (19–194) was well within what I would expect based on the number of frogs that I encountered while collecting tissue samples (generally <40). Given that neighborhood size is an upper boundary for N_e (Crawford 1984), the best fit for mutation rate was 10^{-4} for the IAM model which yielded an estimate of 128 frogs. This rate of mutation is well within the range of mutation rates reported for human microsatellite loci (10^{-2}–10^{-5}, Di Rienzo and others 1994) and contrasts sharply with estimates of mutation rates for mitochondrial DNA. Rand (1994) found a pattern of 5-fold faster rates of mutation for homeotherms compared with

poikilotherms. The factors suggested for this discrepancy (e.g., rate of oxidative damage) are probably not affecting the rate of nuclear DNA mutation in the frogs I studied.

The estimated N_e is reasonable considering reported population sizes for another closely related species of pond-dwelling frog. Berven (1995) studied 11 populations of *R. sylvatica* for at least 7 years and found populations sizes that varied from <50 to >9,000. All populations experienced bottlenecks, complete reproductive failures in some years, and highly skewed sex ratios (up to 17:1). These dynamics contribute to a lower harmonic mean for N_e which may be similar to what I found for *R. luteiventris*. I did not quantify *R. luteiventris* population dynamics, but I have seen 1 population that varied from no frogs in 1 survey to a sufficient density that I was able to capture over 40 adults with 2 hours of effort during a survey 2 years later. Thus, the estimate for mutation rate, neighborhood size and N_e all appear to be biologically reasonable. In addition, if this mutation rate is appropriate for *H. regilla* loci, then the 4-fold larger estimate of N_e is consistent with a slower rate of genetic drift as may be reflected by the smaller average gap in alleles sizes within *H. regilla* populations.

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Appendix. Allele frequencies for 3 *Rana luteiventris* and 4 *Hyla regilla* microsatellite loci. Allele sizes are shown in bold type with allele frequencies for each population directly below. Populations are abbreviated as follows: Bob's Pond (Bob), Ruby NW (RNW), 49N Pond (49N), Clarkia (Cla), Pullman (Pul), Alpine Lake (Alp), Egg White (Egg), Owyhee (Owy), Little Muddy (LMU), and Smoot Hill (Smo).

Locus	Allele frequencies																				
RALU47	**160**	**164**	**170**	**174**	**178**	**184**	**186**	**188**	**190**	**192**	**194**	**196**	**198**	**202**	**206**	**210**	**212**	**214**	**218**	**220**	**252**
Bob	0	0	0	0.05	0.14	0.09	0.05	0.14	0.05	0	0.14	0.09	0	0.09	0.05	0	0.09	0	0	0	0.05
RNW	0	0	0	0	0	0.05	0.4	0	0.2	0	0	0.1	0	0.15	0	0	0	0	0	0	0.1
49N	0	0	0	0	0	0.09	0	0.46	0	0.05	0.23	0	0	0	0	0	0	0	0.18	0	0
Cla	0	0	0	0	0	0	0.18	0	0	0.05	0	0.09	0	0.18	0	0.05	0	0.05	0.23	0.18	0
Pul	0	0	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alp	0	0	0	0	0	0	0	0	0.4	0	0	0.68	0.14	0	0.04	0.11	0	0	0	0	0
Egg	0	0	0	0	0	0	0	0	0.2	0	0	0	0.35	0.35	0.1	0	0	0	0	0	0
Owy	0.09	0.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RALU48	**196**	**206**	**210**	**212**	**222**	**224**	**226**	**228**													
Bob	0	0	0	0.75	0	0	0	0.25													
RNW	0	0	0	0.84	0	0	0	0.16													
49N	0	0	0	0.65	0	0	0	0.35													
Cla	0	0.56	0	0.13	0	0.31	0	0													
Pul	0.63	0	0	0	0	0.24	0	0.13													
Alp	0	0	0	0	0.75	0	0.25	0													
Egg	0	0	0	0	0.65	0	0	0.35													
Owy	0	0	0.33	0.67	0	0	0	0													
RALU50	**164**	**168**	**178**	**180**	**188**	**190**	**192**	**194**	**196**	**198**	**200**	**202**	**204**	**206**	**208**	**212**	**216**	**218**	**220**	**224**	**228**	**236**
Bob	0	0	0.25	0	0.05	0	0	0.12	0	0	0	0.05	0.1	0.15	0	0.15	0.1	0	0	0	0	0
RNW	0	0	0	0	0.13	0	0	0.04	0	0.25	0.04	0.08	0.04	0.17	0.04	0.13	0.08	0	0	0	0	0
49N	0	0	0.22	0	0	0	0.52	0	0	0.02	0	0	0	0.06	0.18	0	0	0	0	0	0	0
Cla	0	0	0	0	0.12	0.12	0.12	0.15	0.19	0.08	0	0	0	0	0.08	0.04	0	0.08	0	0.04	0	0
Pul	0	0.14	0	0.09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.23	0	0	0.55
Alp	0	0	0	0	0.19	0	0	0	0	0	0	0	0	0	0	0.38	0	0	0	0.19	0.25	0
Egg	0.83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.17	0	0
Owy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	0	0	0
HYRE58	**189**	**199**	**203**	**207**	**209**	**213**	**217**	**221**	**225**												
LMU	0	0.25	0.21	0.04	0.04	0.04	0.14	0.14	0.14												
49N	0	0.26	0.26	0.03	0.26	0	0.03	0.16	0												
Smo	0.23	0.43	0	0.08	0	0.08	0	0.2	0												

Appendix. Continued.

Locus	Allele frequencies													
HYRE59	**196**	**198**	**200**	**204**	**214**									
LMU	1.0	0	0	0	0									
49N	0.74	0.16	0	0	0.11									
Smo	0.64	0.16	0.07	0.14	0									
HYRE64	**150**	**164**	**170**	**172**	**174**	**176**	**178**	**180**	**182**	**184**	**186**	**188**	**190**	**192**
LMU	0	0.03	0.03	0	0.1	0.17	0.2	0	0.17	0.13	0	0.03	0	0.13
49N	0.05	0.34	0	0	0.03	0	0.29	0.21	0.05	0	0.03	0	0	0
Smo	0	0	0.13	0.23	0.03	0	0.17	0.07	0.03	0	0.17	0	0.17	0
HYRE65	**201**	**203**	**205**	**207**	**209**	**211**	**213**	**215**	**221**	**225**				
LMU	0.07	0.33	0	0.2	0.07	0	0.13	0.03	0.17	0				
49N	0.06	0.25	0.06	0.22	0.06	0.08	0	0.14	0.14	0				
Smo	0	0	0.03	0.03	0.27	0.03	0.4	0.07	0.1	0.07				

APPENDIX B

DETECTING EARLY DIFFERENTIATION BETWEEN SMALL, NONEQUILIBRIUM POPULATIONS

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Abstract

Genetic markers are important for describing population structure and making inferences about migration, but there may be limitations when using these tools to analyze smaller, nonequilibrium populations. We use a simulation model to evaluate how quickly and consistently we might detect genetic isolation between small populations resulting, for example, from recent habitat fragmentation. Genetic drift is the only evolutionary force in the model and reproduction replaces mortality at each iteration. All populations are initialized with similar allele frequencies to mimic isolation of previously panmictic populations. In nearly all cases, initial mean differentiation is rapid and approximately linear whereas the variance for mean differentiation is a function of population size, number of loci, and number of alleles. Detecting early differentiation ($\leq$30 iterations) between groups of populations is feasible when populations are small (e.g., N = 50) and several markers are employed (e.g., $\geq$6 loci, 2 alleles each). With more markers ($\geq$8 loci) we can detect statistically significant differences within a single iteration. A more biologically meaningful level of significance (i.e., equivalent to <1 migrant/generation) can be detected within 31 iterations using 10 hypervariable markers (10 alleles each). For larger populations (N > 300), we may be unable to detect biologically significant differentiation until after 150 iterations. Although genetic isolation can be detected between groups of small populations of approximately equal size, pairwise comparisons between individual populations may produce conflicting interpretations despite identical model parameters.

INTRODUCTION

Molecular markers can be very powerful tools for detecting population structure and inferring migration or historical associations between populations (Avise 1994). Conservation biologists have used molecular markers for management of breeding programs (e.g., Haig and others 1994), identifying fish stocks (e.g., Cummings and others 1997), and for identifying evolutionarily unique populations (e.g., Milligan and others 1994, Moritz 1994, Moritz 1996). These markers also may be used to infer gene flow between populations either directly (e.g., Handel 1983, Breden 1988) or indirectly (e.g., Ellstrand and Marshall 1985, Slatkin 1985, Avise 1994). The latter application is of particular interest to the study of natural populations because indirect inferences of gene flow can help identify metapopulation structure and identify potential barriers to gene flow that might affect population viability (e.g., Reh and Seitz 1990). When estimating gene flow or describing genetic structure for a group of populations, molecular markers are particularly advantageous because it is possible to collect the necessary data within one season in contrast to the multiple seasons that might be required for direct observations for cryptic species. In addition, recent techniques (e.g., polymerase chain reaction) provide the means for limiting impacts on individual animals as well as for comparing current and past patterns of genetic structure using museum specimens (Hillis and others 1996).

As with most analytical tools, however, there are probably spatial and temporal sampling scales at which we cannot draw reliable inferences from genetics data (Lewontin 1974, 1985; Pickett and others 1994). Scale is defined here relative to the vagility and longevity of the species being studied. We evaluated the potential application of molecular markers for testing hypotheses about population structure at what is arguably the smallest scale of inference – contemporary gene flow and isolation. We used a simulation model focused on small populations because these are of most concern to conservation biologists, and because smaller populations are more likely to generate patterns of differentiation over shorter time scales that are relevant to land management agencies (i.e., <150 years). Short time scales are particularly relevant in systems where we need to identify metapopulation structure to mitigate for

increased habitat fragmentation from resource development. Small populations, however, present special problems because they are unlikely to be in equilibrium with respect to genetic drift, mutation, and migration. In addition, small populations may fluctuate dramatically during the short periods typical of empirical investigations. Thus, changes in relative levels of genetic distance may be nonlinear in these systems and estimates of gene flow from equilibrium models may be invalid.

We limited our investigation to exploring a relatively simple model to determine if these markers are appropriate for addressing questions about contemporary changes in genetic structure. Thus, our model reflects a "best case scenario" for which additional complexity would only add additional variance to the results. We were specifically interested in using genetic data to identify populations that were recently isolated (e.g., due to habitat fragmentation) and to determine if relative differences in gene frequencies can provide useful information about gene flow or time since genetic isolation.

METHODS

We designed a stochastic population model that tracks the sex and genotype (diploid) for individuals in isolated populations. In this model, each population originates from a uniform distribution of alleles to mimic initial panmixia followed by isolation and subsequent differentiation due to genetic drift. Simulations are initialized by assigning a randomly drawn genotype to each individual in the populations. Consequently, initial populations will have very similar, but not necessarily identical initial allele frequencies. Model iterations begin by subjecting the populations to a mortality pulse where each individual has a 50% chance of surviving. This is followed by a reproduction pulse where mating is polygamous and random and 4 offspring are produced from each pairing. Reproduction exceeds mortality so offspring are randomly selected for recruitment into the next breeding cohort and excess offspring are eliminated. Offspring become mature adults at the next breeding pulse so that populations begin each cycle with the same number of individuals and generations overlap. Mutation can affect differentiation over short periods of time if severe bottlenecks allow rapid fixation of

novel alleles. Because breeding populations remain relatively constant in size and we are concerned primarily with short temporal scales, mutations were not included in these simulations. Each locus behaves as a Mendelian marker that is selectively neutral and no migration is permitted between populations. Each simulation repeats the survivorship and reproduction pulses for 150 iterations and results are summarized for 1,000 simulations under each set of conditions unless otherwise noted.

After each pulse of reproduction, we quantified genetic differentiation between pairs of populations using G_{ST} (Nei 1973). G_{ST} provides an index of the amount of genetic variation attributable to population subdivision, where

$$G_{ST} = (\sum_{i=1}^{L} H_{Tt} - \sum_{i=1}^{L} H_{St}) / \sum_{i=1}^{L} H_{Tt}$$

H_T is the expected heterozygosity when all populations are pooled together whereas H_S represents average heterozygosity within populations, and L is the total number of loci. In the special case where all loci have fixed on the same alleles within each population, G_{ST} is mathematically undefined ($H_T = 0$). The proportion of undefined cases at fixation is equivalent to $(1/a)^L$ where a is the number of alleles. Undefined comparisons were eliminated from the simulation statistics because it is biologically impossible to ascertain whether this result is a function of complete panmixia or complete isolation (Weir 1996). Mean G_{ST} ($\overline{G}_{ST}$) is asymptotic at unity after a sufficient number of iterations.

G_{ST} is equivalent to a multilocus estimator for Wright's F_{ST} statistic (Wright 1951). We also explored characteristics of short-term differentiation using another estimator for F_{ST} (β, Cockerham and Weir 1987, 1993) and a coefficient of coancestry (Reynolds and others 1983). β estimates can be upwardly biased compared with G_{ST}, but G_{ST} is sensitive to the number of populations included in the analysis (Cockerham and Weir 1993). Most of our simulations involved only 2 populations and both β and the coefficient of ancestry behaved very similarly to G_{ST} with respect to short-term patterns of differentiation so we do not report these results.

Before proceeding to our primary questions, it was necessary to explore the behavior of G_{ST} for several parameter values to validate performance of the model and because conclusions may differ depending on the values of these parameters. We

began by simulating populations of different size (N = 25, 75, 150, or 300) for 1 locus and 2 alleles. We also varied the number of loci (n = 1, 2, 4, 6, 8, or 10) and alleles (n = 2, 4, 6, 8, or 10) for populations of N = 50. When more than 1 locus was included, every locus had the same number of alleles. For each set of conditions, we calculated $\overline{G}_{ST}$ and its standard deviation (SD) for each iteration (n = 1,000 simulations).

One of our primary questions is whether genetic markers can be used to detect genetic differentiation soon after populations are isolated. A simple approach to this question is to consider how many iterations are required for $\overline{G}_{ST}$ to be statistically >0. We estimate this quantity by determining at what iteration a 95% confidence interval (CI) no longer overlaps zero. Although this approach is not strictly appropriate for hypothesis testing, it can provide a reasonable indication of the parameters necessary for detecting statistically significant differentiation. The 95% CI is defined as $\overline{G}_{ST} \pm$ 1.96*SD and it might also be interpreted as a 1-tailed t-test (α = 0.025). In all cases SD for each iteration is asymptotic within 150 simulations (data not shown). We focus our attention on the first 30 iterations of the model which might correspond to the minimum period required for a forest canopy to close following a large disturbance (e.g., fragmentation caused by logging activities, assuming 1 year per iteration).

We also consider if differentiation is biologically significant. For instance, if we have no *a priori* knowledge about the population structure for the system we are studying, we might consider Wright's infinite island model an appropriate starting point for making inferences (a common practice in the literature; see Slatkin 1985). With this model 2 populations will differentiate independently when migration (Nm) involves fewer than 1 individual per generation (Wright 1951). Nm is defined as 0.25 ($1/F_{ST}$ - 1). Thus, we define biologically significant differentiation at the point where the lower 95% CI for $\overline{G}_{ST}$ no longer overlaps 0.2 (i.e., Nm < 1).

Finally, if it is feasible to use genetic markers to address questions about individual populations, then estimates of differentiation should be relatively similar for all populations that become isolated at the same time. To evaluate this question, we plotted pairwise G_{ST} values for 10 populations (N = 50) originating from the same panmictic population.

RESULTS

When genetic drift is the sole evolutionary force for genetic differentiation, it is intuitive that population size will govern the rate of increase in $\overline{G}_{ST}$ (Fig. 1A). $\overline{G}_{ST}$ for the smallest populations (N = 25) rapidly approaches 1.0 (1 locus, 2 alleles), whereas $\overline{G}_{ST}$ for the largest population (N = 300) barely exceeds 0.2 after 150 iterations. SD for small populations increases initially as populations diverge, but eventually begins to decline as $\overline{G}_{ST}$ approaches 1.0 (Fig. 1B). SD for larger populations (N > 75) continues to increase beyond 150 iterations. SD is also a function of the number of loci and alleles considered in the analysis (Fig. 2). Increasing both of these variables reduces the variance, but there is a diminishing return with the addition of each new locus or allele. The addition of more loci provides a greater reduction in variance compared with the addition of more alleles.

Our ability to detect significant differentiation is clearly a function of population size and both the number of loci and alleles. For relatively small populations (N = 50), we cannot expect to detect significant differentiation ($\overline{G}_{ST}$ > 0) within 30 iterations if we employ ≤4 loci (Fig. 3A). With ≥6 loci, however, we can detect statistically significant differentiation even though the magnitude may be quite small (Table 1). Using a single locus for this same scenario would require >8 alleles to have reasonable confidence that $\overline{G}_{ST}$ is significantly >0 within 30 iterations (Fig. 3B).

Detecting biologically significant differentiation (i.e., $\overline{G}_{ST}$ > 0.2, 95% CI) is very difficult over short time scales unless populations are relatively small (e.g., N = 50, Table 1). With only 1 locus (2 alleles) we would need 122 iterations, and the addition of 8 more alleles only reduces this to 92 iterations (Table 1). Even with 10 loci (2 alleles each), 49 iterations are necessary before $\overline{G}_{ST}$ > 0.2 with 95% confidence. If we employ 10 hypervariable loci (10 alleles each) we can expect to detect biologically significant differentiation after 31 iterations.

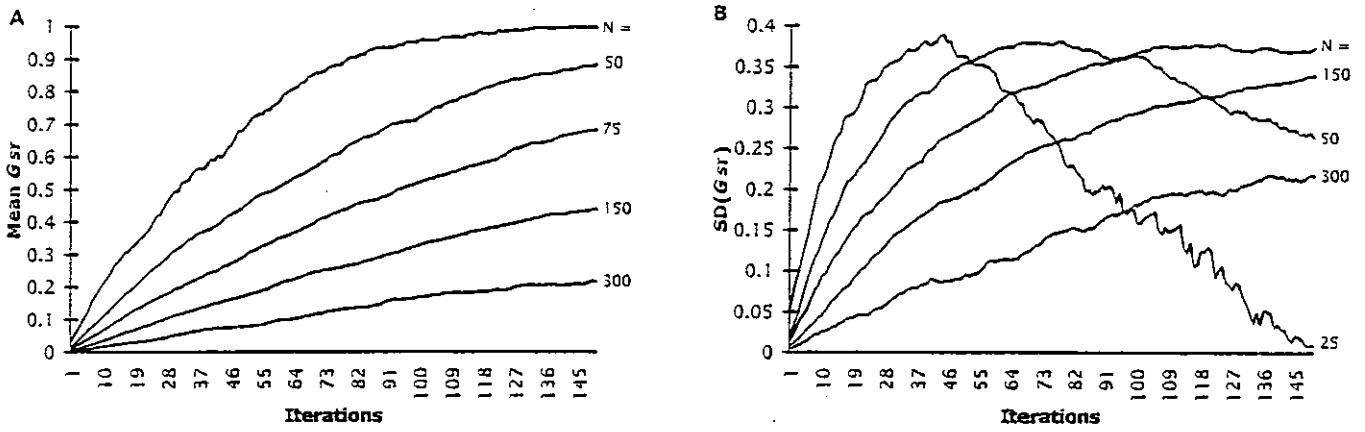

Figure 1. Patterns of genetic differentiation for 2 populations that were initially panamictic followed by complete genetic isolations. (A) Relationship between $\overline{G}_{ST}$ and population size and (B) standard deviation for 1,000 simulations of 2 populations. All simulations considered 1 locus with 2 alleles and all populations began with similar allele frequencies.

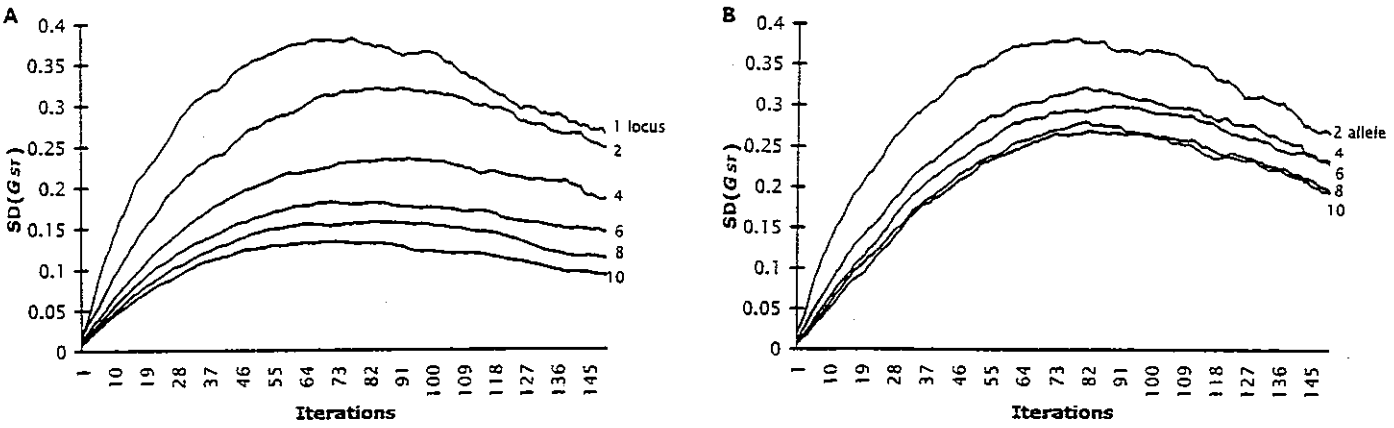

Figure 2. Relationship between genetic differentiation and the number of loci or alleles for 2 populations that were initially panmictic followed by complete genetic isolation. (A) Standard deviation for 1,000 simulations of equal sized populations (N = 50) with different numbers of loci (2 alleles each), and (B) different numbers of alleles (one locus).

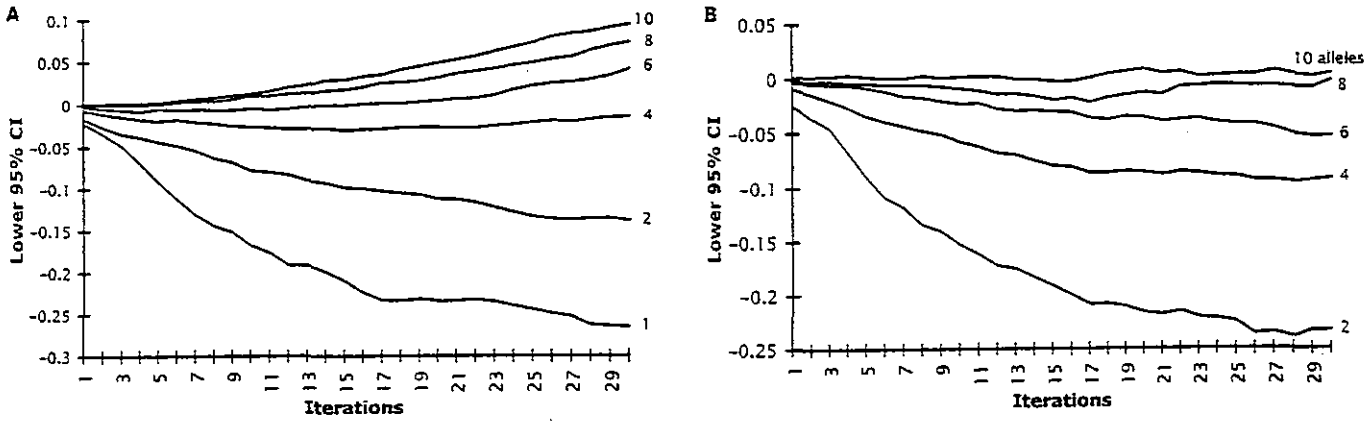

Figure 3. Lower limit for the 95% confidence interval (CI) for $\overline{G}_{ST}$ based on 1,000 simulations of 2 populations that were initially panmictic followed by complete genetic isolation. (A) Different number of loci, and (B) different number of alleles. Mean differentiation was considered statistically significant when the lower 95% CI was >0 and biologically significant when >0.2.

Table 1. Number of iterations required for genetic differentiation to be statistically ($\overline{G}_{ST} > 0$) or biologically ($\overline{G}_{ST} > 0.2$) significant. $\overline{G}_{ST}$ was generated from 1,000 simulations for pairs of isolated populations ($N = 50$).

Number of loci	Number of alleles	$\overline{G}_{ST} > 0$		$\overline{G}_{ST} > 0.2$	
		Iterations	$\overline{G}_{ST}$	Iterations	$\overline{G}_{ST}$
1	2	102	0.73	122	0.82
2	2	88	0.64	122	0.79
4	2	37	0.34	88	0.67
6	2	16	0.16	65	0.56
8	2	3	0.03	57	0.51
10	2	1	0.01	49	0.45
1	4	82	0.64	114	0.79
1	6	69	0.56	112	0.77
1	8	41	0.39	94	0.73
1	10	17	0.17	92	0.72
10	10	1	0.01	31	0.31

The variance associated with individual G_{ST} estimates (i.e., between 2 populations) can be considerable (Fig. 4). With only 1 locus, estimates of G_{ST} range between 0 and 1 within 30 iterations despite each population having nearly identical allele frequencies at the beginning of the simulation (Fig. 4A). This picture improves somewhat with the addition of more alleles, but the variance is still high (Fig. 4B). When 10 loci are considered in the analysis, variance is significantly reduced (Fig. 4C), but much tighter confidence intervals will be expected if each locus is hypervariable (Fig. 4D).

DISCUSSION

Only 4 variables affect the genetic structure between populations (i.e., effective population size, selection, migration, and mutation), but they interact in a multivariate, nonlinear fashion (Lewontin 1974, 1985). Based on our simple simulation model that incorporates only genetic drift, we can begin to outline the boundary conditions for resolving patterns of genetic divergence at short temporal and spatial scales using molecular markers. For populations that are not in genetic equilibrium, the rate of mean differentiation ($\overline{G}_{ST}$) increases linearly just following isolation for small populations of about equal size (Fig. 1A). This is an important characteristic if genetic markers are going to be used effectively for detecting genetic isolation or for testing hypotheses about changes in gene flow following environmental disturbances.

The rate of increase in $\overline{G}_{ST}$, however, is inversely related to population size. Our simulations suggest that the rate of differentiation for larger populations (e.g., $N > 150$) may be too slow to be detected relative to the temporal influence of a disturbance event or to the typical planning horizon of natural resource managers. For instance, larger populations separated by fragmentation in a managed forest may never show significant differentiation before plant succession re-establishes migration corridors between surviving populations. This is particularly true if a criterion of biological significance is required. Despite these limitations, there may be natural populations that are sufficiently small for effective study with genetic markers (Crawford 1984, Wilcove and others 1993).

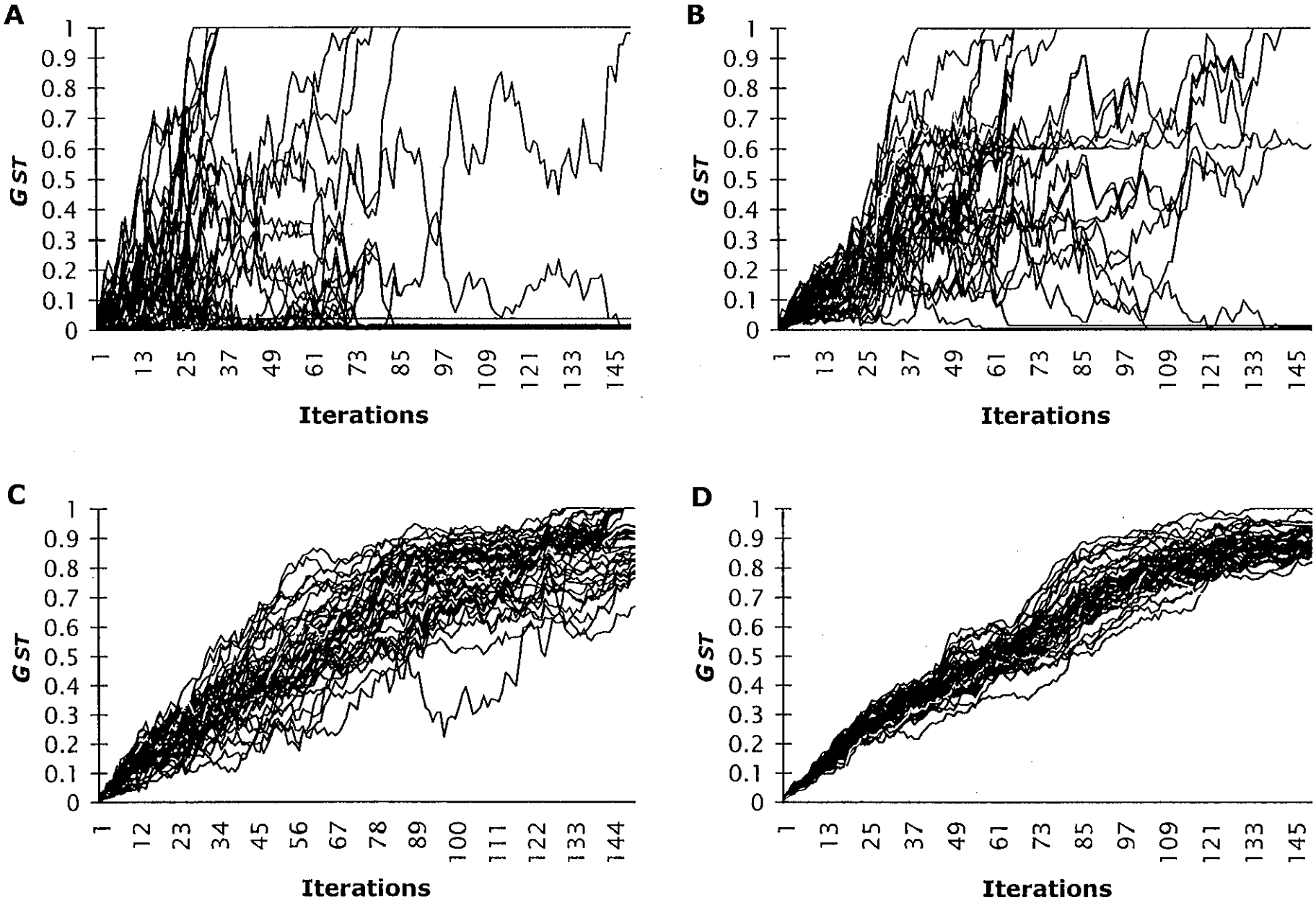

Figure 4. Example of all pairwise comparisons of genetic differentiation (G_{ST}) between 10 populations (N = 50). Populations were initially panamictic followed by complete genetic isolation. Data are shown from single simulations with (A) 1 locus, 2 alleles, (B) 1 locus, 10 alleles, (C) 10 loci, 2 alleles, and (D) 10 loci, 10 alleles.

We can decrease the variance in $\overline{G}_{ST}$ and consequently increase the likelihood of detecting differentiation simply by increasing the number of loci included in the analysis. Nei and Roychoudhury (1972) were the first investigators to show this relationship and our results reiterate their findings. A similar effect, although of less magnitude, is evident when more alleles are present in the initial population. With enough markers (e.g., 10 loci) it is possible to detect statistically significant differentiation within the 1st iteration for small populations (Table 1). Indeed, it is clearly possible to detect differences that may exist between the initialized populations before the 1st mortality pulse. These differences arise because the random assignment of genotypes to individuals will inevitably generate some G_{ST} values >0. Consequently, the apparent power to detect differentiation with a large number of markers should be considered carefully with respect to biological relevance of the result.

Our model calculates G_{ST} using all members of each population, but increasing the number of loci or alleles also can dramatically improve the precision of estimates that are based on subsampling. For instance, Verheyen and others (1995) examined 2 groups of populations using data from 3 minisatellite markers (24.3 alleles each, SD = 8.6) and detected significant differentiation even though the magnitude was extremely low (F_{ST} = 0.006). They examined relatively large numbers of individuals ($\overline{n}$ = 56.6 ± 26.0), but only small sample sizes may be required if genetic differentiation is reasonably high (Nei 1978).

Although we demonstrate that short-term isolation can be detected for small (N = 50) simulated populations (i.e., $\overline{G}_{ST} > 0$), interpretation of such findings for natural systems requires caution. Detection of significant differentiation, of course, does not necessarily equate to low rates of migration or to increased time since common ancestry. Nürnberger and Harrison (1995) found high levels of genetic differentiation between populations of whirligig beetles (*Dineutus assimilis*) despite high levels of observed migration. The authors concluded that this pattern reflected rapid turnover of populations at a regional scale. Thus, lack of concordance between direct observation and indirect inference was probably due to genetic drift. It is noteworthy that genetic drift can lead to large differences between small populations even when strong selective pressures are involved (e.g., Falconer 1977, Abplanalp 1988). In reality, vastly

different demographic and genetic processes can lead to very different or very similar patterns of genetic differentiation so any inferences about the processes that generated differentiation need to be considered carefully (Lewontin 1974, 1985; Nichols and Beaumont 1996).

Our results suggest that drawing inferences from comparisons of differentiation between individual populations may be quite difficult. Even with large numbers of loci and alleles, estimates of G_{ST} between populations may vary considerably from genetic drift alone (Fig. 4). Moreover, unless population sizes are known, a high G_{ST} value may only be different from a lower G_{ST} value because of disparate population sizes rather than because of migration or historical associations (Fig. 1). This can be more problematic for populations which undergo frequent extinctions, colonizations, and bottlenecks as we might expect for metapopulations (Gilpin and Hanski 1991, Whitlock 1992). Failure to consider different rates of genetic drift can lead to unlikely *post-hoc* explanations for observed patterns of differentiation (e.g., Travis and others 1996).

Our results represent a conservative illustration of the challenges associated with detecting genetic differentiation because several other factors will increase variance when we study natural populations. For instance, problems can arise when loci are under the influence of different mutation mechanisms and selection regimes as well as due to investigator sampling error (Slatkin and Arter 1991). In addition, occasional migration may extend the time needed to detect significant differentiation, even for very small populations.

Molecular markers would best be used for studies of small populations where differentiation can be analyzed in terms of treatment or replicate groups – a challenging task with natural populations (Hurlbert 1984). Both natural and sampling variation for pairwise comparisons may be so great that it will be difficult to infer correct historical associations between individual populations. This problem will diminish for comparisons between larger populations where genetic equilibrium can be satisfied, but the time scale necessary for differentiation will increase accordingly. Clearly, more accurate inferences will be made when more genetic markers are used and new techniques such as amplified fragment length polymorphisms (AFLP's; Vos and others 1995) may provide a cost effective means to address these questions.

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APPENDIX C

SMALL MAMMAL USE OF CORRIDORS IN A FRAGMENTED LANDSCAPE

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INTRODUCTION

Contiguous forests are broken into smaller units by harvesting practices. The resulting fragmentation of forest landscapes may have profound effects on the distribution, abundance, and persistence of wildlife species (Wilcove and others 1986, Burkey 1995, Newmark 1995). Corridors have been proposed as a means to preserve species in a landscape by mitigating the isolating effects of fragmentation (Wegner and Merriam 1979, Harris 1984, Bennett 1990a, Hansson 1991, Saunders and others 1991). In theory, corridors provide connections between otherwise isolated patches of forest habitat and facilitate dispersal between populations (McEuen 1993, Noss 1993). Corridors also have been suggested as serving as additional habitat to support resident populations (Simberloff and others 1992, Noss 1993, Bennett and others 1994).

Whether corridors actually ameliorate the negative effects of fragmentation and facilitate the maintenance of wildlife populations is uncertain (Simberloff and Cox 1987, Hobbs 1992, Simberloff and others 1992). Other factors may influence the utility of corridors including surrounding habitat, habitat quality, corridor size, barriers or gaps within the connecting strip, and the ability of species to disperse (Bennett 1990a, Henein and Merriam 1990, Gates 1991, Hill 1995). Investigation of such factors is essential for understanding the value of corridors in the landscape.

The use of corridors as a dispersal route or as habitat depends on the requirements of species and how they perceive the landscape (Gates 1991, McEuen 1993, Hill 1995). Certain habitat types may act as barriers for some wildlife species by preventing

movement between isolated habitat patches. For these species, habitat strips between patches may allow movement that otherwise would not occur. For other wildlife species, however, few barriers to movement exist, enabling them to use the entire habitat matrix. Thus, only forest-restricted species would need, or even be able to perceive, forested corridors to move between forest stands. Species distribution across habitat types should reflect these requirements.

Habitat suitable for colonization may be left vacant because of barriers surrounding isolated forest patches (Merriam and others 1989). The absence of forest-restricted species in suitable, but isolated, forest patches would indicate that corridors may be necessary to allow colonization. Alternatively, the relative amount of corridor use may indicate the conditions in which a population would be effectively isolated. Comparisons between isolated and connected forest stands should provide insight into how corridors affect species occurrence and abundance.

Corridors also may play an important role in determining the need to use larger spatial scales in management planning to increase connectivity between patches. Many forest environments have been severely affected by fragmentation and have become a major focus of conservation efforts, but the few studies on corridor use have focused mainly on agricultural landscapes (e.g., Wegner and Merriam 1979, Lorenz and Barrett 1990, Merriam and Lanoue 1990, La Polla and Barrett 1993). Responses to forest fragmentation are likely to be very different because managed forests are characteristically different from agricultural landscapes, with more complex structure, greater habitat heterogeneity, and varied species composition.

Habitat strips between larger patches may be crucial to facilitate species movements, reduce inbreeding depression, lower extinction rates for small, isolated populations, and maintain overall species diversity. The realized function of corridors, however, may be drastically different than its hypothesized value. Our objectives were: 1) to identify forest-restricted small mammal species capable of perceiving forested corridors, 2) to assess corridor use by examining presence, abundance, and movements of species, and 3) to relate corridor use to habitat quality, corridor size, and requirements of species.

METHODS

STUDY AREA

Study sites were located in North Fork Calispell (T32N R42E), East Fork Small (T33N R43E), and Little Muddy (T38N R42E) watersheds in Stevens and Pend Oreille counties, Washington. The area consisted primarily of second growth, mixed coniferous forest, fragmented by clearcuts and regenerating stands. The extent of fragmentation varied, with North Fork Calispell, East Fork Small, and Little Muddy watersheds being 42%, 35%, and 50% cutover, respectively (Hallett and others in litt.). The level and pattern of fragmentation in each of the watersheds created distinct corridors and isolated forest patches that could be identified easily. Tree species included grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and western redcedar (*Thuja plicata*). Forest understory was sparse but varied locally depending on the degree of canopy closure. Wood rose (*Rosa gymnocarpa*), myrtle boxwood (*Pachistima myrsinites*), prince's pine (*Chimaphila umbellata*), and false and starry Solomon's seal (*Smilacina racemosa* and *S. stellata*) were the dominant understory species. Vegetation in areas with little or no canopy cover was composed predominately of shrub and herbaceous species, mainly shinyleaf and redstem ceanothus (*Ceanothus velutinus* and *C. sanguineus*), thimbleberry (*Rubus parviflorus*), and fireweed (*Epilobium angustifolium*).

A total of 22 study sites was chosen across 5 different stand types: clearcut, regeneration, isolated forest, contiguous forest, and forested corridors. Corridors were defined as linear strips of forest habitat connecting 2 larger forest stands. Riparian zones were not included in this study because of their characteristic difference from upland forest habitat. Four structurally similar forested corridors were selected to minimize variability in habitat quality. Three corridors were not independent of one another, but instead shared common forest end patches. This lack of independence was accepted because of the scarcity of distinct, non-riparian corridors. The corridor sites ranged in length and width from 200-350 m and from 50-150 m, respectively. Stands on either side of each corridor were chosen preferentially to obtain information

on small mammal occurrence directly outside the corridors. Clearcut stands varied in age from 5-10 years from harvest, but only had sparse regeneration. Regenerating stands were >10 years in age and appeared to be the result of natural seeding because of the various seedling ages, mixed species composition, and characteristic random structure. Sizes of clearcut and regenerating stands varied considerably from about 10 to >100 ha. Isolated forest patches were chosen based on their size (<15 ha) and well defined stand boundaries. These stands ranged in size from 0.3-13.3 ha. Conversely, contiguous forest stands were all >100 ha in size. Contiguous forest sites comprised the end patches to the corridors and their selection was the result of corridor location. Mean stand age for the forested sites, as calculated from tree cores, was approximately 95 years ranging from 75-125 years of age. Mean tree height varied between 20 and 25 m. All 22 study locations, ranging in elevation from 750-1210 m, generally had an easterly aspect with a mean slope of 15%.

Small Mammal Distribution and Abundance

In 1993, we selected 4 clearcut, 4 regeneration, 4 isolated forest, and 6 contiguous forest patches, and 4 forested corridors to examine the distribution of small mammals across the landscape. In 1994, we sampled only in 6 contiguous forest and 4 corridor stands to further evaluate corridor use. Clearcut, regeneration, and isolated forest stands were sampled using 250-m long trapping transects. Transects were placed in approximately the center of the stands with a >15-m buffer from stand edges or riparian areas, and parallel to the length of the corridor if next to a corridor site. Shorter transects were used when the standard size would have extended beyond the stand edge. Two Sherman live traps baited with oats were placed at each station spaced 10 m apart along the transect. Traps were placed along logs or near rodent holes to increase the chance of small mammal capture. Each site was trapped for 5 nights (dusk to dawn) during the breeding season (June-August). Species, sex, age, reproductive condition, body mass, and general morphometrics were recorded for every individual captured. Age determination was based on both reproductive condition and body mass (Pucek and Lowe 1975). Reproductive condition of males was assessed by examining the position of the testes (scrotal or abdominal). Females were recorded as non-

reproductive, receptive, pregnant, lactating, or post-reproductive based on vaginal perforation, opening of the pubic symphysis, nipple condition, and palpitation for embryos. Each individual also was marked uniquely with a numbered ear tag for identification.

Trapping grids were used to intensively trap the corridor areas and increase the probability of capture and detection of individual movements through the corridor. A 5-station grid with 10-m spacing was placed in the center of the corridor and a 10-station grid with 10-m spacing was placed at each end of the corridor in contiguous forest stands. Corridor width was the main determinate of corridor grid size. One live trap was placed at each station and mark-recapture techniques, as described above, were used.

VEGETATION SAMPLING

In summer 1994, we measured variables describing vegetative structure at all 22 sites to compare macrohabitat differences between stand types. Each site was sampled using three 20-m plots, systematically placed within the trapping grids. Slope and aspect were recorded for each plot. Five convex densiometer readings were used to estimate percent canopy cover. Total understory cover and composition for each plot were estimated using five 20-cm plot-frame samples following Daubenmire (1970). Shrub cover was calculated by measuring the size and distance of the nearest 4 shrubs from the center point of each plot, using the point-centered quarter method. The number of regenerating coniferous trees >0.5 m in height and <4 cm diameter at breast height was tallied in 2 diagonally opposed 100-m^2 areas within the plot. Logs and stumps were grouped into size and decay classes and also counted in the same 100-m^2 areas. Size classes of logs included 2 length [S ($\leq$5 m), L (>5 m)], and 3 diameter [S (5-15 cm), M (16-24 cm), F ($\geq$25 cm)] categories. Degree of decay was broken into 4 classes adapted from Maser and others (1979), with class I being the least and class 4 being the most decayed. The combination of length, diameter, and decay classes was used as a naming convention for logs (e.g., LF4 class logs are logs that are in the length class L, diameter class F, and decay class 4). Stumps were grouped into natural (NS) or cut (CS) categories, based on their method of origin and combined with degree

of decay to form 8 stump classes (e.g., CS1 class stump is a cut stump in decay class 1). Tree and snag density was determined using a variable-radius plot with a 20-basal area factor prism. Mean tree and snag height were estimated using a clinometer. A total snag count in the 400-m^2 plot also was tallied.

We also conducted a microhabitat analysis by comparing vegetation characteristics at trapping stations with and without captures of red-backed voles. Approximately 50 trapping stations of each type (54 vole capture, 48 no-vole) were selected randomly from the 1993 and l994 capture data for all sites. Two perpendicular point-intercept transects, 5 m in length, were established to characterize the vegetation at each station. Sampling points were located at 0.5-m intervals along the transects. Percent canopy cover and an index of log biomass also were estimated. The index of log biomass was calculated by tallying the number of logs in each size and decay class and measuring their length to the nearest 0.5 m within a 2.5-m radius plot. The total was obtained by weighting each of the log classes, multiplying these values by their length, and then summing these weighted lengths for each plot. Log classes were weighted by assigning values to each of the length, diameter, and decay classes. Decreases in length and diameter class decreased the weight by ½ and ⅓, respectively, whereas increases in decay class were assigned decreasing values.

Statistical Analysis

Statistical analyses were performed using SYSTAT (Wilkinson 1989), SAS (SAS Institute Inc. 1985), JMP (SAS Institute Inc. 1992), and StatView (Abacus Concepts Inc. 1987). We considered tests significant at the 0.05 level. To meet model assumptions, all parametric models were tested for constant variance and normality using Bartlett's test for homogeneity of group variances and the Shapiro-Wilks W-test for normality.

Relative abundance of small mammals was compared among stand types. Number of individuals captured was adjusted by the number of trap nights to standardize capture numbers across sites. Any traps triggered by factors not attributable to small mammals were deducted from the total number of traps set to increase accuracy in the total number of trap nights used in calculations. Analysis of variance (ANOVA) was used to test for significant differences in relative abundance of each species across the

5 stand types. Tukey's multiple comparison tests were used to identify significant differences among treatments. Animal captures in corridor stands also were compared to those in contiguous forest stands for each year and between years using a repeated measures ANOVA with weighted least squares to control for nonconstant variance. Chi-square tests were used to compare differences between sex (male, female), age (adult, juvenile), and reproductive condition (non-reproductive, reproductive) classes for animals captured in contiguous forest and corridor stands for both years. The number of recaptures, grouped into 2 categories (captured once or multiple times), also was analyzed using chi-square tests. Fisher's 2-tailed tests were used for comparisons with <5 observations per category.

Red-backed voles were used as the target species for the corridor study. The relationship between vole captures and macrohabitat differences in vegetation across stand types was analyzed using a multivariate approach. First, means for each habitat variable were calculated by site and correlations between variable means were analyzed across sites. Because of intercorrelations among variables, a principal components analysis (PCA) on the correlation matrix was used to reduce the variable set and to create independent linear combinations of variables. Second, a multiple linear regression was constructed with the number of vole captures as the dependent variable and the PCA factors that significantly contributed to the regression model as the independent variables. A Mann-Whitney U-test was used to compare pairwise differences of macrohabitat within and between stand types.

Microhabitat variables were analyzed for differences between stand types and for differences between sites with and without vole captures. Mean and variance were calculated for each variable, and correlations between variables were analyzed. Mann-Whitney U-tests were conducted to identify variables that significantly differed between corridor and forest trapping stations with and without captures of voles.

RESULTS

SMALL MAMMAL DISTRIBUTION AND ABUNDANCE

A total of 1,097 individual small mammals in 9 genera were captured during 10,600 trap nights in 1993 and 1994. Only the 3 most common species had sample sizes adequate for statistical analysis. Deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Clethrionomys gapperi*), and yellow-pine chipmunks (*Tamias amoenus*) comprised the most captures in both years (Tables 1 and 2). The remaining taxa (*Glaucomys sabrinus, Mustela frenata, Zapus princeps, Neotoma cinerea, Microtus* spp., and *Sorex* spp.) comprised about 6% of total captures in both years. In 1993, deer mice had the highest capture numbers (71%) and were similar in abundance in all 5 stand types ($F = 2.60$, $P = 0.07$). Yellow-10
pine chipmunks and red-backed voles were the next most abundant species, each comprising 11% of total captures. Yellow-pine chipmunks and red-backed voles, however, had different distributions across the 5 stand types. Yellow-pine chipmunks were found in all 5 stand types, but occurred in highest abundance in corridors ($F = 5.79$, $P = 0.004$). In contrast, red-backed vole captures were restricted to forested stands with the exception of 1 regeneration stand ($F = 4.75$, $P = 0.009$). Furthermore, no voles were captured in clearcut and regeneration stands on either side of the corridors. The number of vole captures in clearcuts was significantly less than in other stand types (Tukey's pairwise comparisons). However, the ANOVA model was nearly significant when clearcuts were excluded from the analysis, indicating that capture differences between the remaining stand types still existed ($F = 2.98$, $P = 0.067$).

The PCA of macrohabitat variables produced 2 components that were useful in characterizing habitat use by voles. PC 1 is a forest component, explaining 45% of the total variance in the macrohabitat variables across sites. This factor correlated positively with overstory cover, distance to nearest shrub, snag and tree density and height, tree age, and percent litter and log cover; it was correlated negatively with understory cover and percent fern, grass, herb, and shrub cover. PC 2 is a low regeneration density component and accounted for 12% of the variation. Each

Table 1. Mean number of small mammals captured per 100 trap nights in 5 stand types in the Colville National Forest, Washington, during summer 1993.

Species	Clearcut (N = 4)		Regeneration (N = 4)		Isolated forest (N = 4)		Contiguous forest (N = 6)		Corridor (N = 4)		Total capture (N = 22)	% of total capture
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD		
Clethrionomys gapperi	0	0	0.62	1.23	2.10	0.93	1.65	0.63	0.52	0.79	22.85	11.38
Tamias amoenus	0.21	0.42	0.57	0.78	0.44	0.64	0.51	0.51	3.74	2.56	22.92	11.42
Peromyscus maniculatus	9.52	5.54	6.34	4.92	1.34	1.36	3.97	2.71	12.61	10.08	143.04	71.24

Table 2. Mean number of small mammals captured per 100 trap nights in forest and corridor habitat in the Colville National Forest, Washington, during summer 1994.

Species	Contiguous forest (N = 6)		Corridor (N = 4)		Total capture (N = 10)	% of total captures
	$\bar{x}$	SD	$\bar{x}$	SD		
Clethrionomys gapperi	5.38	3.01	5.84	2.24	55.66	36.23
Tamias amoenus	0.65	0.43	4.39	1.79	21.50	13.99
Peromyscus maniculatus	5.15	3.19	8.99	7.05	66.86	43.53

remaining component explained <10% of the total variance and did not significantly contribute to the multiple linear regression model.

A positive relationship was found between vole captures and PC 1 scores (R^2 = 0.317). Three outliers influenced both normality and model significance. Excluding these outliers increased the degree of linear association (R^2 = 0.746), but did not significantly change the overall relationship. Two outliers were forest stands with the lowest mean canopy cover and the other outlier was the 1 regeneration site with vole captures. The relationship between vole captures and the outlying points was better described when PC 2 was added to the regression model. As coniferous regeneration density decreased so did the relative abundance of voles. The variance created by the 3 outlying sites also was better explained and normality was attained. Despite this contribution, the forest component factor still remained the only statistically significant variable in the model. Thus, red-backed voles appeared to be forest-restricted.

Because voles were captured only in 1 regenerating stand, comparisons were made with the other 3 regenerating sites to explain this distinction. The site with vole captures was the oldest (15 yrs) of the regenerating stands and had significantly more overstory cover, percent litter and regeneration cover, and SS3 class logs (Mann-Whitney U-test, $P < 0.05$). These habitat differences correspond with the results obtained in the linear regression model, and reinforce the significance of forest habitat in vole distribution.

Stand size did not appear to be a major factor in determining vole presence or abundance. In 1993, voles were found in equal abundance in isolated (<15 ha) and contiguous (>100 ha) forest stands (Tukey's test, $P = 0.93$; Table 1). Sex and age ratios for these 2 stand types also did not significantly differ (chi-square tests, $P > 0.05$). The isolated forest stands strongly resembled the larger forest stands for most vegetation characteristics. Differences between isolated and contiguous forest were not found for any of the significant variables in the forest component factor, but were found for stump (CS 1, NS4), log (LS2) and western redcedar density (Mann-Whitney U-test, $P < 0.05$).

CORRIDOR USE

Although voles were present in all contiguous forest sites, use of forested corridors by voles was variable (Table 3). Relative abundance of voles was significantly higher in 1994 than in 1993 for both corridor and contiguous forest stand types ($F = 23.98$, $P < 0.001$; Tables 1 and 2). Relative abundance of voles was found to be significantly lower in corridor than in contiguous forest habitats in 1993 ($F = 6.35$, $P = 0.036$; Table 1), but not in 1994 ($F = 0.068$, $P = 0.80$; Table 2). The capture difference between these 2 stand types was masked by the inter-year variation in the repeated measures ANOVA model ($F = 0.02$, $P = 0.90$). No interaction was found between stand type and year ($F = 1.31$, $P = 0.27$).

Sex ratios did not significantly vary between years or between corridor and contiguous forest stand types. Age ratios also did not differ between stand types, but did differ between years across both stand types ($\chi^2 = 13.71$, $P < 0.001$). This age ratio difference was not significant in corridors ($\chi^2 = 3.04$, Fisher's $P = 0.15$), but was highly significant in the forest ($\chi^2 = 9.69$, $P = 0.002$). However, more juvenile males were captured in corridor stands than in the forest in 1994, although this result was only marginally significant ($\chi^2 = 3.47$, $P = 0.063$). The proportion of animals in reproductive condition significantly differed between years ($\chi^2 = 24.56$, $P < 0.001$) with a greater proportion of non-reproductive individuals captured in 1994. No significant difference between reproductive condition in forest and corridor stand types for either year was found ($P > 0.05$). The number of voles that were recaptured did not significantly differ between the 2 stand types for either year, nor between years for either stand type (chi-square tests, $P > 0.05$). Red-backed voles did show a significant difference in recapture frequency between adults and juveniles for both years ($\chi^2 = 12.91$, $P < 0.001$), with juveniles more likely to be captured only once.

Table 3. Corridor size and number of red-backed vole individuals captured per 100 trap nights, Colville National Forest, Washington, summers 1993-94.

	Corridor dimensions		Relative abundance	
Site	Length	Width	1993	1994
1	300	75	0.00	6.10
2	200	75	1.67	8.04
3	350	50	0.00	2.71
4	250	150	0.41	6.52

Capture differences between corridor and forest stands may relate to differences in vegetation characteristics. Corridor stands typically had greater shrub cover, especially ocean-spray (*Holodiscus discolor*), than forest stands (Mann-Whitney U-test, $P < 0.05$). Corridors also had higher frequencies of highly decayed cut stumps (CS4), SM2 class logs, herbaceous species, shrubs, and dead shrubs (Table 4). Greater differences existed between capture sites with and without voles and between the 2 stand types at locations where voles were captured (Table 4). Voles were found at trapping stations with increased log biomass ($t = 2.052$, $P = 0.043$), but were correlated negatively with log class LF4 ($t = -2.46$, $P = 0.016$; Table 4). In the forest habitat, voles were captured at locations with greater densities of stumps and LF2 class logs, and with less exposed ground (soil) and LF4 class logs. Conversely, in the corridor habitat, there was little difference between locations where voles were captured and where they were not, except for an increased frequency of regeneration at stations with vole captures. Comparisons between forest and corridor vole capture sites similarly show that corridor capture locations had higher regeneration, exposed ground, dead shrubs, moderately decayed natural stumps (NS2), and SM4 class logs.

No movement of voles between corridor and forest trapping grids was observed in 1993 and only 1 juvenile male moved between grids in 1994. This individual was captured on the 2 closest trapping lines between grids, and moved approximately 100 m from a forest end-patch into the adjacent corridor.

Table 4. Significant vegetation differences between forest and corridor capture sites with and without voles, Colville National Forest, Washington.

Microhabitat attributes	Total		Corridor			Forest		
	No-vole (N = 48)	Vole capture (N = 54)	No-vole (N = 6)	Vole capture (N = 6)	Total (N = 12)	No-vole (N = 34)	Vole capture (N = 39)	Total (N = 73)
	$\bar{x}$ (SD)							
Log biomass index[a] stump class:	96.57 (55.30)	120.89 (63.42)	72.54 (46.76)	89.54 (64.12)	81.04 (54.24)	98.71 (58.29)	119.69 (58.81)	109.92 (59.11)
CS4[b]	0.02 (0.14)	0.00 (0.00)	0.17 (0.41)	0.00 (0.00)	0.08 (0.29)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
NS2[c]	0.06 (0.24)	0.04 (0.19)	0.00 (0.00)	0.17 (0.41)	0.08 (0.29)	0.09 (0.29)	0.00 (0.0())	0.04 (0.20)
Log class								
LF2[d]	0.09 (0.65)	0.44 (1.21)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13 (0.77)	0.60 (1.39)	0.38 (1.16)
LF4[ad]	0.98(1.63)	0.33 (0.98)	0.33(0.82)	0.17(0.41)	0.25 (0.62)	1.29(1.81)	0.41 (1.13)	0,82(1.54)
SM2[b]	0.04 (0.23)	0.19 (0.92)	0.08 (0.20)	0.00 (0.00)	0.04 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
SM4[c]	0 18 (0.54)	0.32 (1.04)	0.00 (0.00)	0.83 (1.33)	0.42 (1.00)	0.15 (0.50)	0.10 (0.56)	0.12 (0.53)
Point intercept frequency								
Herb[b]	7.04(8.43)	8.13(9.89)	11.00(7.32)	10.83(8.45)	10.92(7.54)	5.21(7.11)	7.13(9.28)	6.23(8.34)
Regen[ce]	5 17 (7.32)	7.98 (9.53)	3.33 (4.46)	14.33 (10.56)	8.83 (9.63)	4.24 (6.89)	6.28 (8.77)	5.33 (7.96)
Dead shrub[bc]	0.02 (0.14)	0.15 (0.49)	0.00 (0.00)	0.83 (0.98)	0.42 (0.79)	0.00 (0.00)	0.05 (0.32)	0.03 (0.23)
Shrub[b]	2.38 (4.14)	3.54 (6.83)	2.17 (2.93)	5.33 (5.32)	3.75 (4.41)	1.32 (2. X6)	1.72 (3.66)	1.53 (3.30)
Soil[cd]	0.58(0.92)	0.50(1.84)	0.83(1.17)	2.50(5.17)	1.67(3.68)	0.56(0.89)	0.23(0.63)	0.3X(0.7X)
Stump[d]	0.06(0.43)	0.39(1.11)	0.00(0.00)	0.17(0.41)	0.08(0.29)	0.09(0.51)	0.44(1.21)	0.27(0.96)

[a] Significant difference between total no-vole and vole capture sites using t-test ($P < 0.05$).
[b] Significant difference between forest and corridor total micro-habitat using Mann-Whitney U-test ($P < 0.05$).
[c] Significant difference between forest and corridor vole capture sites using Mann-Whitney U-test ($P < 0.05$).
[d] Significant difference between forest no-vole and vole capture sites using Mann-Whitney U-test ($P < 0.05$).
[e] Significant difference between corridor no-vole and vole capture sites using Mann-Whitney U-test ($P < 0$ 05).

DISCUSSION

SMALL MAMMAL DISTRIBUTION AND ABUNDANCE

The use of linear strips of forested habitat as corridors depends on how a species perceives the landscape, which should be reflected in its spatial distribution across the habitat matrix. The spatial distribution of small mammals in this study area indicated that deer mice and yellow-pine chipmunks occurred in all 5 stand types, but that red-backed voles were restricted to forested stands. Small mammal populations significantly differed between years, with abundance increasing overall in 1994. Reproductive rates also were higher in 1994 compared to 1993, shown by the increase in juvenile, non-reproductive red-backed vole captures. Use of other, non-forested habitat by red-backed voles was minimal during periods of low population numbers. In fact, no voles were found in stands bordering corridors in 1993. However, these stands were not sampled in 1994 because of logistical constraints.

Avoidance of open areas with little overstory cover or log density has been well-documented for red-backed voles (e.g., Ramirez and Hornocker 1981, Szacki 1987), and thus they have been categorized as a forest species (Merritt 1981). Although occurrence in clearcuts tends to be minimal (Probst and Rakstad 1987, Mills 1993, 1995), others have found that red-backed voles remain common or increase in clearcuts immediately following harvest (review in Kirkland 1990). The reason for this pattern is unknown, but may be related to the presence of low-lying cover provided by slash piles and herbaceous or shrubby vegetation. Martell (1983) found that voles remained common in unscarified clearcuts with relatively undisturbed shrub cover for at least 2 years after harvest. However, red-backed voles were shown to decrease in number in scarified clearcuts with little available cover and increase with years since selective cuts, as the amount of protective cover increased.

These data support the assumption that clearcuts are significant barriers to movement, but can provide limited microhabitats suitable for voles in some cases. However, if red-backed voles are able to move into clearcuts, the probability of finding suitable habitat within or near the clearcut is small and depends on the degree of fragmentation and risk of mortality (Szacki 1987). Gaines and McClenaghan (1980)

reviewed factors influencing survivorship among dispersers. Dispersal increases mortality by subjecting individuals to numerous hazards. Consequently, the probability of survival or of finding suitable habitat in sub-optimal areas, such as clearcuts, may be low. Corridors, depending on their quality, may increase the chance of survival for dispersing individuals by providing direct linkages between forest habitat (Herein and Merriam 1990).

Mature forest may represent optimal habitat for voles, but older regenerating stands also appear to be suitable habitat (Probst and Rakstad 1987, Nordyke and Buskirk 1991). Considering the scale at which a small mammal operates, tall regeneration may act similarly to forest habitat by providing adequate cover and protection from predators, as well as creating an ideal mesic microclimate (Nordyke and Buskirk 1991). Voles were present in the 1 regeneration stand with the greatest amount of vegetative cover and in relatively high abundance (2.47 individuals per 100 trap nights; Table 1). Voles also seemed to select forested sites with high regeneration density in the understory, both at a macro- and micro-scale.

Despite this habitat selection, regenerating stands only seemed to be used when adequate forest interior cover was unavailable. For example, the regeneration factor of the PCA explained the variance in vole capture for the outliers in the forest component regression model; these outlying captures were in isolated forest and corridor stands, which are both edge-influenced stands. An increase in regeneration also was found at corridor vole capture sites compared to those in the forest (Table 4). Likewise, in a study conducted in fragmented coniferous forests, Mills (1993) found that the few California red-backed voles (*Clethrionomys californicus*) captured in clearcuts were located in areas of dense regeneration and logs.

Red-backed vole distribution can be grouped into 3 categories: (1) high abundance in isolated and contiguous forest stands, (2) moderate abundance in corridors and older regenerating stands, and (3) absence in clearcut and young regeneration habitat with little overstory cover. The absence of voles in clearcut and young regeneration indicates that these stand types are probably perceived as barriers to movement. Consequently, red-backed vole populations and individual movements are confined to

forested habitat. Red-backed voles should therefore perceive habitat patchiness and forested corridors within a fragmented landscape.

STAND SIZE

Besides habitat requirements, stand size and degree of isolation have been shown to influence forest species distribution (Bennett 1990b, Fitzgibbon 1993, Mills 1993, 1995, Newmark 1995). Occupancy by red-backed voles, however, was not limited by the size of forest stands in our study. Similarly, Rosenberg and Raphael (1986) found no relationship between abundance of California red-backed voles and stand area. In fact, most species of small mammals in Douglas-fir forests of northwestern California did not respond negatively to decreased patch size nor increased clearcut edge. Small forest patches that remained largely undisturbed in terms of microhabitat were able to support forest-interior species, even near a clearcut edge. Conversely, Mills (1995) found significant negative edge effects for California red-backed voles.

Possible explanations for vole presence in the isolated forest stands in our study include: (1) forest stands were not truly isolated, (2) patch sizes were large enough to maintain a stable population, or (3) populations in these stands were in decline and given time, will go extinct. Two of 4 isolated forest sites were surrounded by older regenerating habitat, which also had vole captures. Effective stand size was the sum of all 3 sites (>100 ha) because voles would be able to freely disperse within these habitats. This demonstrates the importance of considering the surrounding habitat when assessing patch isolation for a particular species. Population viability analysis was beyond the scope of this study, and differentiation between explanations 2 and 3 above was not possible. However, local extinctions of small isolated populations have been shown to be likely for many species (van Apeldoorn and others 1992, Mangel and Tier 1994, Burkey 1995). Environmental and demographic chance events can lead to local population extinctions, influencing species persistence in fragmented landscapes (Fahrig and Merriam 1985, Henderson and others 1985). Because red-backed voles are restricted to forest cover, corridors could provide a necessary route to recolonize vacant patches, and allow higher rates of emigration and immigration to reduce the risk of local extinction.

Corridor Use

Although voles should be able to perceive corridors in the landscape, use of corridors by voles in our study was highly variable across years. In 1993, red-backed voles occurred in only 2 of the 4 corridors and at very low levels. Corridor habitat, however, was quickly colonized, with vole abundance equaling that in the forest in 1994. The age ratio and probability of recapture were equivalent across contiguous forest and corridor stand types, but significant differences might have been masked by the overall increase in juveniles. In 1993, at low population density, individual voles were captured only once (with no recaptures) in corridors whereas multiple captures comprised 42% of the total in contiguous forest stands. One would expect to capture resident individuals multiple times because they would remain near trapping stations, whereas dispersers may only be captured a single time as a chance event during travel through a trapping grid. Although the difference in recapture rates between corridors and forest stands was not significant because of small sample size and decreased statistical power, the lack of recaptures in corridors supports the premise that individuals captured in the corridors were dispersing and not residents. Furthermore, a trend was found in the occurrence of juvenile males in corridor habitat in 1994, with a higher proportion of juvenile, compared to adult, males captured in corridors than in contiguous forest. As population density increases and the habitat becomes saturated, individuals are more likely to disperse to find suitable, unoccupied space (Lidicker 1975, Gaines and McClenaghan 1980). Most of these dispersing individuals are juveniles, especially males (Lidicker 1975, Gaines and McClenaghan 1980, Bondrup-Nielsen and Karlsson 1985, Bondrup-Nielsen 1987). All of these data suggest that corridor habitat is mainly suitable for dispersal and colonization by subordinate individuals. Although only 1 movement between grids was recorded, the presence of voles in corridors suggests the utility of corridors to allow movement between forest stands.

Corridor Quality

Results of the habitat analysis support the hypothesis that corridor stands were suboptimal for red-backed voles. Corridor stands typically had greater shrub and overstory cover, both of which were negatively correlated on the forest component

factor in the PCA. Red-backed voles have been shown to prefer areas with forest cover, dense shrub cover, high moisture, brush piles, logs, stumps, dense leaf litter, and rocky microhabitat (Gunderson 1959, Getz 1968, Miller and Getz 1972, 1973, Wolff and Dueser 1986, Wywialowski and Smith 1988, Barry and others 1990, Stewart 1991). In our study, red-backed voles showed an affinity for locations with high log biomass, but that lacked long (>5 m), large (>25 cm), and highly decayed logs (class LF4). Although there was no significant difference between forest and corridor habitats for these 2 log variables (biomass and LF4), forest sites with vole captures had a lower frequency of LF4 logs compared to sites without voles. Despite a similarity in litter frequency, forest vole capture sites also tended to have less exposed ground. Furthermore, forest vole capture sites had more long, large, relatively undecayed logs (class LF2) and stumps, both of which correspond with microhabitat preferences recorded by other researchers for red-backed voles.

Performing a similar study on microhabitat selection, Wywialowski and Smith (1988) also found that red-backed voles occurred predominately at sites with more recently fallen logs rather than highly decayed logs (decay class 2 vs. 4). A similar trend was found for California red-backed voles (Hayes and Cross 1987). Undecayed logs may function as protective runways for vole movements. Nordyke and Buskirk (1991) and Tallmon and Mills (1994), however, found a positive correlation between vole abundance and degree of log decay. This correlation was explained by the preference of *Clethrionomys* for fungi as a food source (Rhoades 1986, Nordyke and Buskirk 1991, Tallmon and Mills 1994). However, due to the breadth of forested habitats red-backed voles can occupy, their dependence on fungi is variable and habitat dependent (Ure and Maser 1982, Maser and Maser 1988). Red-backed vole diets consist of seeds, green plants, berries, fungus, and insects, and are not as restricted to fungal sporocarps as some other *Clethrionomys* species (Martell 1981, Maser and Maser 1988).

Corridor trapping stations with vole captures and those without captures, on the other hand, basically did not differ in microhabitat. This contrast between forest and corridor vole capture and no-vole sites, however, may simply be an artifact of the small sample size in the corridor habitat. Nevertheless, corridor vole capture locations had a

greater frequency of smaller logs (classes SM4 and SS2), shrubs, regeneration, and exposed ground than forest vole capture sites. These habitat attributes appear to contribute to habitat that is suitable for some red-backed voles under certain conditions, such as those that induce and maintain dispersal.

Edge and Size Effects on Corridor Quality

The differences found in vegetation in corridor and contiguous forest stands relate to the level of habitat disturbance in these stand types. Edge effects include an increase in light and wind penetration into a stand, and a subsequent increase in the amount of understory cover, regeneration, and exposed ground. Mills (1995) found that the density of California red-backed voles decreased towards the edge of remnant forest stands and concluded that voles were negatively affected for at least 90 m from the stand edge into the stand interior. Because 3 of the 4 corridors in this study were only between 50 and 75 m in width at their narrowest point, the impinging edge may have affected the entire habitat, potentially eliminating any forest interior habitat. Population fluctuations tend to be greater in patches of sub-optimal habitat quality, as found for the bank vole (*Clethrionomys glareolus*; van Apeldoorn and others 1992). Edge effects appear to have reduced the quality of the corridor habitat, as shown by the differences in forest and corridor vegetation and by the differential use of corridors between years of low and high vole abundance.

Qualitative comparison of relative vole abundance with corridor size in this study also supports the hypothesis that edge effects reduce habitat quality. The widest (150 m) and shortest (200 m) corridors, which had the least amount of edge relative to stand area, had the greatest relative abundance of voles in both years (Table 3). Similarly, the longest and narrowest corridor (350 m x 50 m) had the least relative abundance in both years. These data support the theory that corridor size strongly influences its quality and subsequent use. This phenomenon may be a function of red-backed vole dispersal capability, as well as habitat quality within the corridor. Immature red-backed voles have been reported moving up to 200 m across grids (Bondrup-Nielsen 1987). Szacki and Liro (1991) found bank voles moving >1000 m, with movements of several hundred meters to be common. Thus, red-backed voles probably have the ability to

disperse through the corridors we studied, but as corridor length increases, their ability to move through the entire corridor in 1 dispersal event may be reduced. Continuous movement through the corridor becomes more critical when the corridor is unsuitable for colonization due to poor habitat quality. Subsequently, corridor suitability appears to decrease with increasing length and decreasing width, which was reflected in the differential use of corridors of varying size.

Corridors in our study, however, were colonized during high population pressures, with the proportion of adults and recaptures equaling that in the forest. Potentially forced to be less selective because of intensified interactions between individuals, voles were able to use corridors as additional habitat strips. Similarly, Bock (1972) found that bank voles used a wider range of habitats when population size increased. The pattern of corridor use indicated that the corridors were adequate for dispersal of individuals from 1 forest patch to another at times of low abundance, and also could serve as additional habitat in years of high abundance.

CONCLUSION

Corridor use by red-backed voles was variable in our study and appeared to depend on habitat quality, corridor size, and population dynamics. In assessing quality, habitat preferences of species need to be considered. Corridor habitat did not contain certain habitat attributes preferred by red-backed voles and therefore was considered to be of lower quality than that in the contiguous forest. Corridor size also influenced use, with fewer individuals occupying longer, narrower habitat strips. Optimal habitat attributes and corridor width would tend to be more important for residents within the corridor, whereas linear continuity and corridor length would be important for dispersers (Bennett and others 1994).

Population fluctuations of red-backed voles caused high inter-year variation in corridor use. When population density was high, the corridors served as valuable habitat for expanding vole populations, but when population density was low, corridors acted, at most, as a dispersal route. Understanding population dynamics of species also would provide insight into the relative importance of corridors for maintaining

species populations in otherwise isolated forest stands. Red-backed voles were present and in nearly equal or greater abundance in isolated forest stands as in contiguous forests. Consequently, the necessity of corridors to ensure population viability was not demonstrated in this short-term study.

Nevertheless, corridors acted as additional habitat and potentially could facilitate movement between forest stands. In this sense, corridors fulfill their intended function of providing connections between populations, and their utility should be considered significant. Although conclusive information on the utility of corridors is lacking, corridors should be incorporated into forest management plans to preserve connectivity in managed forest landscapes. Preserving remnant strips of habitat between forest stands and planning timber harvests accordingly would obviously be easier than attempting to reconstruct forested corridors when proven to be valuable. In planning for connections between forest stands, the size, configuration, and habitat characteristics of corridors need to be considered, especially in relation to the particular forest-dependent species. Additional research into the relationship between corridors and forest-restricted species is essential for further understanding of the importance of corridors to maintain species in fragmented landscapes.

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APPENDIX D

SHREW ASSEMBLAGES OF NORTHEASTERN WASHINGTON: EFFECTS OF BODY SIZE AND DIET

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Soricid shrews are characterized by high species diversity across many habitat types (Hanksi 1992, Kirkland 1997). Body size and competition for food resources have been suggested as important factors in structuring shrew communities (Dickman 1991). In this research I examined the community structure of shrews in northeastern Washington, and focus on how body size and diet impact community composition.

The small size of shrews (2-20 g) results in a very high metabolic rate, with most species foraging 24 hrs a day (Kirkland 1991, Hanksi 1992). Smaller species metabolize food more rapidly than larger individuals. Consequently, they must spend more time feeding with shorter resting periods (Kirkland 1991). Little temporal separation is expected between different *Sorex* species. This raises the question of how several similar species can coexist in 1 area. Applying species assembly rules, partitioning taxonomically related species by unique characteristics, has been 1 approach to address this question.

Diamond (1975) introduced species-specific assembly rules in an attempt to predict where individual species would occur. These rules matched resource utilization functions for congeneric species to resource production curves for specific habitats. He predicted the number of species present in an assemblage would be limited by the diversity of available food. Connor and Simberloff (1979) questioned whether these assemblages could be predicted by deterministic rules, or if they simply occurred by chance. Intense debate over the issue (Strong and others 1984) led recent research to include the statistical generation of random species assemblages to compare to the

observed. Fox (1987) introduced assembly rules for functional groups of species arguing that there is a much higher probability that each species entering a community will be drawn from a different functional group until each group is represented.

Functional groups consist of individuals from the same genus or other taxonomically related groups of species with similar diets. Fox (1987) defined functional groups for Australian small mammals based on trophic category and observed that species entering an assemblage were drawn from a different functional group, until each group was represented. Fox and Kirkland (1992) applied an assembly rule to eastern North American shrew communities using functional groups based on body mass in an attempt to predict patterns of community organization. They separated 6 species of shrews into 3 functional groups of large, medium, and small based on body mass. They hypothesized that body mass differentiation serves as an evolutionary mechanism to reduce competition by allowing shrews to utilize different microhabitats within an area. The 6 species occurred in assemblages in a non-random pattern, indicating that community composition followed an assembly rule. Assemblages with elevated diversity, they concluded, should only exist when food resources are abundant.

Wilson (1975) noted that large predators often have a competitive advantage over smaller predators because they typically utilize food sizes unavailable to smaller species, whereas the reverse situation occurs very rarely. Large species of shrews typically eat larger prey items (Churchfield 1991), although it has been observed that in the absence of a larger individual, smaller species also may utilize these items. Dickman (1988) showed that removal of the larger of 2 shrew species resulted in the smaller switching to more productive microhabitats and feeding on larger food resources. The rate of prey capture in smaller species increased after removal of the dominant species (Dickman 1991). Malmquist (1986) observed that the crania of a smaller shrew species were larger when allopatric than when sympatric with larger species. Shvartz and Demin (1986) suggest that differences in the strength of the masticatory musculature is an important factor in allowing sympatric species to exist due to their ability to handle different prey items. The size of prey an individual takes

might therefore be determined by the interference of a dominant competitor and not the inability to handle certain sized prey.

These above studies suggest that body size of soricid shrews and size of food available to them are important in structuring communities. To examine these issues I had the following objectives: (1) to characterize the shrew communities of northeastern Washington, (2) to determine if shrews in northeastern Washington follow an assembly rule for functional groups based on size, (3) to examine the diet of shrews to determine if size of shrew species determines size of prey consumed, and (4) to determine if prey items consumed by individual shrew species changes depending on the number of species present in an assemblage.

MATERIALS AND METHODS

FIELD SAMPLING

STUDY AREA

I examined patterns of shrew assemblages in managed forests of the Selkirk Mountains in northeastern Washington. These forests are a mosaic of habitat types resulting from differences in slope, aspect, soil and water properties, fire history, and timber management practices. Composition of forests is variable; dominant species of trees include western hemlock (*Tsuga heterophylla*), western larch (*Laris occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and grand fir (*Abies grandis*). Prevalent shrub species include thimbleberry (*Rubus parviflora*), serviceberry (*Amelanchier alnifolia*), ninebark (*Physocarpus malvaceas*), snowberry (*Symphoricarpus albus*), and red osier dogwood (*Cornus stolonifera*). Logging roads provide access to much of the study area. Shrew populations were sampled on a total of 72 sites from late May to mid-July, 1993-1995. Sites consisted of 18 riparian and adjacent upland sites, including mature, closed-canopy and recently harvested stands, and 36 sites in 3 upland forest types (mature, >60 years; regeneration, 15-20 years; and recent clearcuts) and 2 stand sizes (~12 and $\geq$36 ha).

SMALL MAMMAL SAMPLING

Pitfall (18,144 trap nights/year) and snap-traps (20,736 trap nights/year) were used to sample shrew populations from the 18 riparian and adjacent upland sites. Two parallel transects 720 m in length, were placed 8 m from the stream and 100 m upslope. A total of 72 snap-trapping stations was spaced at 10-m intervals along each transect. Two snap-traps were placed within 3 m of each station, baited with a mixture of oats and peanut butter, and checked for 3 consecutive days. Eighteen pitfall traps constructed of 2 #10 coffee cans taped together and buried in the soil, were placed at 15-m intervals. Approximately 5 cm of water were placed in each can. Pitfall traps were checked every other day for 2 weeks.

Pitfall traps also were used to sample shrew populations in the 3 upland forest types. Pitfall grids were established in a 6 x 6 array with 10-m spacing between traps, with a 50-m buffer away from any edge habitat or water sources. As for the riparian sites, these traps were left open for 14 days for a total of 18,144 trap nights/year.

Specimens were weighed and measured upon capture, then frozen for later autopsy. Species identification was based on dental characteristics, relative body measurements, and pelage. Shrews were considered unidentifiable when these characters were damaged or missing.

INVERTEBRATE SAMPLING

To determine prey availability and size, I sampled invertebrates in 1995 at the 24 study sites which, when combined, detailed the range of shrew assemblages possible, based on 1994 data. Sticky boards, pitfall traps, and soil core samples were used to sample these specimens.

On the riparian and upland transects, I established 4 invertebrate trapping stations at 50-m intervals within the portion of the transect containing mammalian pitfall traps. In the 3 upland forest types, 4 stations were placed at the center of each of the 4 quadrants of the pitfall grid. I marked these stations with flags to serve as reference points for the invertebrate sampling stations. I placed 1 of each trap type within 3 m of each sampling station for a period of 7 days and a total of 5,376 trap nights.

I constructed sticky board traps from 30-cm strips of flypaper stapled to 35- x 30-cm plywood boards. I placed these traps in shallow trenches which allowed the surface of the trap to be flush with the soil surface to increase the likelihood of invertebrate capture.

Pitfall traps were constructed of 1 #10 coffee can in which I placed a funnel to prevent the inadvertent capture of any small mammals. I also placed these traps flush into the ground with the soil surface. Finally, I obtained 3 soil core samples within 3 m of the sampling station, to a depth of 15 cm, to sample subterranean species.

Trapping of invertebrates occurred within 2 weeks of the small mammal sampling period to ensure prey items sampled were possible food items for shrews captured. The invertebrates I collected were preserved in 85% isopropyl alcohol and keyed in the laboratory using Borror and Delong (1971). I then measured the body length, leg width and length, and antennae width of these specimens to establish a reference of measurements to compare with invertebrates from the stomach contents of field-collected shrew specimens.

I removed the stomachs of 674 specimens from the 24 study sites at which invertebrates were sampled in 1995. At the time of removal, I cut the stomachs open and preserved them in microcentrifuge tubes containing 85% isopropyl alcohol. I then examined the stomach contents under a dissecting scope and prepared microscope slides with all identifiable parts from the stomach contents such as legs, wings, and antennae. I also took one 2-ml sample with a pipette from each stomach to check for smaller items such as setae. Prey items were keyed to class or order using Borror and DeLong (1971). I measured the length and width of leg parts and wings, and width of antennae of the invertebrate prey.

DATA ANALYSIS

SPECIES CHARACTERIZATION

To determine the size relationships of the 5 *Sorex* species, I measured 15 jaw and cranial traits (van Zyll de Jong 1980) and body mass. All jaw and cranial measurements were made using a Bausch and Lomb dissecting scope and Mitutoyo digimatic calipers. Only adult specimens were measured to reduce the variability that

would occur from sampling across age classes. No pregnant females were used in assessing differences in body mass to ensure a common size pool. Fifty specimens were used for *S. cinereus* and *S. vagrans*, but fewer specimens of adults of the other species were available (*S. monticolus*, N = 46; *S. hoyi*, N = 24; *S. palustris*, N = 11). Principal components analysis was conducted on cranial and body mass measurements to examine correlation among variables and the distribution of the 5 species on the components (SAS Institute Inc. 1989).

To examine patterns of association I conducted a Spearman correlation analysis for the frequency of capture of shrews at each pitfall trapping station from 1993-1995. I conducted all statistical tests with SAS (SAS Institute Inc. 1989) and used a significance level of $P \leq 0.05$ unless otherwise noted.

GENERATION OF RANDOM SPECIES ASSEMBLAGES

I used Monte-Carlo simulations following the procedure outlined in Fox and Kirkland (1992) to generate the expected distribution of assemblages based on random sampling. The simulation program was written using Microsoft Fortran Powerstation (Microsoft 1995) on a Pentium Pro computer. The following constraints were placed on the simulation. First, the number of sites at which each individual species occurred in a year was divided by the total number of sites (N = 72). This determined the probability of a species being drawn into an assemblage, thereby reducing the likelihood of a rare species occurring as compared to a common one. Second, I determined how many assemblages were observed with 1, 2, 3, 4, and 5 species present so that this frequency distribution would be repeated in the simulation. Finally, the number of species from any size class in an assemblage was limited to that observed on the sites.

There are 17 possible outcomes for shrew assemblages in northeastern Washington. For example, an assemblage of 1-1-0 indicates that there are 1 small-sized, 1 medium-sized, and 0 large-sized species present in each functional group. Likewise, an assemblage of 2-2-1 indicates 2 small, 2 medium, and 1 large species. The assembly rule predicts that each of the 3 size classes should have 1 species present before a 2nd species can be added to any 1 of the 3 groups. Therefore, assemblages in which a 2nd species enters a functional group before a single species

is present (e.g., 2-1-0) in each of the other 2 groups are unfavored states. A chi-squared analysis was conducted to compare observed to random species assemblages.

ANALYSIS OF PREY

I conducted an analysis of variance (ANOVA) to determine the mean number of prey taxa occurring at the 24 study sites, and a Duncan's means separation test to determine significant differences in these numbers. I compared the mean percentage of the consumption of prey items per study site for each *Sorex* species. At all sites where the invertebrate taxa was present, I calculated the percentage of the prey item in individual shrew stomachs, then the mean of these percentages for the species overall.

I conducted a regression analysis on leg, wing, and antennae measurements compared to body length measurements for invertebrates in the reference collection to predict the size of insects found in the stomach contents (Table 1). Ten specimens from each of the 14 taxa and 45 families were measured, except in the cases of Diplopoda, Hemiptera, and Lepidoptera, where sample sizes were too low. In these cases, I measured 4 specimens from each taxa and took an average of the different measurements compared to body size. I considered prey items found in the stomachs to be from the same invertebrate when leg and wing parts were still attached.

When 2 or more measurements of a single prey item were available in the stomach contents, I conducted a multiple regression combining these different measurements to obtain a more appropriate estimate of the body length of the invertebrate. When I compared individual body part measurements to body length, all values were significant at $P \leq 0.001$. To ensure the predictive power of the regression model, I accepted a minimum R^2 value of 75%. I conducted an ANOVA to compare mean prey lengths of the taxa found in the stomachs of different shrew species. I also conducted an ANOVA to determine if the mean length of prey items consumed changed for species when present in different assemblages.

Table 1. R^2 values for regression of body measurements on total body length of different invertebrate prey taxa. All values significant at $P \leq 0.001$.

Measurement	Araneae	Chilopoda	Coleoptera	Collembola	Diplopoda	Homoptera	Microcoryphia	Diptera	Hymenoptera	Orthoptera	Phalangida
ANT		0.94	0.92						0.96	0.99	
ANT*TARL*TARW		0.98									
ANT*TARL*TARW*TIBW		0.99									
ANT*TARW										0.99	
ANT*TARW*TIBW			0.94						0.98		
ANT*TIBW			0.93								
FEMW	0.98							0.94			0.99
FEMW*TARL*TARW*TIBW	0.98										
FEMW*TARW*TIBW											0.99
FEMW*TIBW	0.98										0.99
TARL	0.96	0.87			0.75			0.95			
TARL*TARW		0.99						0.99			
TARL*TARW*TIBW	0.98	0.99						0.99			
TARL*TARW*TIBW*WINL*WINW								0.99			
TARL*TARW*TIBW*WINW								0.99			
TARL*TARW*WINL								0.99			
TARL*TARW*WINL*WINW								0.99			
TARL*TARW*WINW								0.99			

Table 1. Continued

Measurement	Araneae	Chilopoda	Coleoptera	Collembola	Diplopoda	Homoptera	Microcoryphia	Diptera	Hymenoptera	Orthoptera	Phalangida
TARL*TIBW		0.99									
TARW	0.96	0.98	0.96	0.97		0.88	0.89	0.97	0.98	0.99	0.99
TARW*TIBW			0.93			0.93		0.98	0.98	0.99	
TARW*TIBW*WINL								0.99			
TARW*TIBW*WINL*WINW								0.99			
TARW*WINL								0.99			
TARW*WINL*WINW								0.99			
TARW*WINW								0.99			
TIBW	0.97	0.98				0.93		0.97	0.90	0.99	0.90
TIBW*WINL								0.99			
TIBW*WINL*WINW								0.99	0.98		
TIBW*WINW								0.99	0.97		
WINL								0.99	0.95		
WINL*WINW								0.99	0.95		
WINW								0.99	0.89		

ANT = antennae width; FEMW = femur width, TARL = tarsus length, TARW = tarsus width, TIBW = tibia width, WINL = wing length, WINW = wing width.

Kulzynski's Similarity Index (Oosting 1956) was used to indicate the similarity of diets between intra- and interspecific samples when individuals occurred in different species assemblages. This expression is calculated by the formula:

$$\frac{2\sum_{i=1}^{s}(w_i)\ (100)}{\sum_{i=1}^{s} a_i + b_i}$$

where a_i represents the mean percentage of food item i in the diet of group X, b_i represents the mean percentage of food item i in group Y, and w_i represents a_i if $a_i \leq b_i$ and b_i if $b_i \leq a_i$.

RESULTS

CHARACTERIZATION OF SHREW COMMUNITIES

A total of 6,170 individuals was captured during the 3 years. Five species of shrews were present in the study area: *S. hoyi*, the pygmy shrew (3.6 g); *S. cinereus*, the masked shrew (4.4 g); *S. vagrans*, the vagrant shrew (5.8 g); *S. monticolus*, the montane shrew (4.7 g); and *S. palustris*, the water shrew (8.6 g).

Sorex cinereus and *S. vagrans* were the most abundant of the 5 species and each was present on ≥58 sites each year. I observed substantial interyear variation in the total number of individuals captured as well as the number of sites at which species were present (Table 2). The number of captures of each species more than doubled in 1994 as compared to 1993 and 1995. *Sorex hoyi* expanded from 11 sites in 1993, to 17 in 1994, and was reduced to 15 in 1995. *Sorex monticolus* displayed the greatest change in site distribution, increasing from 29 sites in 1993, to 58 in 1994, then decreasing to 24 in 1995.

Yearly variation in the number of unique species communities occurred, increasing from a total of 8 in 1993, to 11 in 1994, and 13 in 1995 (Table 3). Two new species combinations in 1994 resulted from the addition of *S. hoyi*, the third from *S. monticolus*.

Table 2. Total number of captures (number of sites) of 5 *Sorex* species from 1993-1995.

	Year					
Species	1993		1994		1995	
S. hoyi	16	(11)	34	(17)	27	(15)
S. cinereus	511	(60)	1,024	(66)	510	(58)
S. vagrans	982	(72)	1,981	(70)	803	(62)
S. monticolus	43	(29)	173	(58)	46	(24)
S. palustris	5	(3)	12	(8)	3	(3)
Total	1,557		3,224		1,389	

Table 3. The presence (+) or absence (-) of the 5 *Sorex* species and number of sites at which species combinations were found from 1993-1995. SOHO = *S. hoyi*, SOCI = *S. cinereus*, SOVA = *S. vagrans*, SOMO = *S. monticolus*, and SOPA = *S. palustris*.

Small		Medium		Large	No. of Sites		
SOHO	SOCI	SOVA	SOMO	SOPA	1993	1994	1995
-	-	+	-	-	5	2	5
-	+	-	-	-	0	2	0
-	-	-	+	-	0	0	1
-	+	+	-	-	29	6	24
-	+	-	+	-	0	0	1
-	-	+	-	+	1	0	0
-	+	+	-	+	2	1	2
+	+	+	+	+	0	2	1
-	-	+	+	-	6	4	3
+	+	-	-	-	0	0	1
-	+	+	+	-	18	37	14
+	-	+	+	-	0	0	1
+	+	+	-	-	6	1	9
+	+	+	+	-	5	12	3
-	+	+	+	+	0	3	0
+	+	+	-	+	0	2	0

In 1995, *S. hoyi* and *S. monticolus* were each added to a species combination forming 2 new groups.

Analysis of cranial and body mass measurements showed that the 5 species were distinctly distributed on 2 principal components. The first principal component accounted for 78% of the variation among the species and had a positive association and equal loading amongst all of the size variables. Association with this component indicated an overall increase in size of the species. Principal component 2 described an additional 10% of the variation and was associated with the width across the upper incisors and length of the lower incisor. For example, *S. hoyi* had a positive association with this component compared with *S. cinereus*, indicating it possesses wider upper incisors and a longer lower incisor. This analysis resulted in assigning species to the following size classes: small, *S. hoyi*, *S. cinereus*; medium, *S. vagrans*, *S. monticolus*; large, *S. palustris*.

Captures of *S. vagrans* were negatively correlated with the other medium-sized species, *S. monticolus*, and with *S. cinereus* in all years (Table 4). *Sorex hoyi* and *S. cinereus* were negatively correlated only in 1993, and *S. palustris* showed no significant correlation with any other species.

SPECIES ASSEMBLY

Seven of 17, 11 of 17, and 10 of 17 possible assemblages of small, medium, and large species were observed on the 72 sites in 1993, 1994, and 1995, respectively (Table 5). In 1993, the distribution of observed assemblages differed from those based on random assembly ($X^2 = 40.98$, df = 16, $P \leq 0.05$). Thirty-seven favored states were observed, compared to 24 expected from random. The 1-1-0 state comprised 30 of the favored states. Only 35 of the expected 48 unfavored states occurred in this same year. Distribution of observed assemblages also differed from random in 1994 ($X^2 = 52.82$, df = 16, $P \leq 0.05$). Unfavored states were observed 54 times, compared to 18 favored. Most of the unfavored states were of the 1-2-0 combination, with 37 observations compared to 16 expected from random. No significant differences were observed in 1995 ($X^2 = 21.88$, df = 16, $P \leq 0.05$) as observations of favored and unfavored states

Table 4. Correlation of the frequency of captures at each pitfall trapping station for 5 *Sorex* species for 72 study sites sampled from 1993-1995. Numbers indicate significant negative correlation between species ($P \leq 0.001$). (+) and (-) signs indicate non-significant correlations in trends ($P \geq 0.05$). SOHO = *S. hoyi*, SOCI = *S. cinereus*, SOVA = *S. vagrans*, SOMO = *S. monticolus*, and SOPA = *S. palustris*.

	SOCI			SOVA			SOMO			SOPA		
Species	93	94	95	93	94	95	93	94	95	93	94	95
SOHO	-0.08	+	-	-0.14	-0.09	-0.16	-	-	-	-	-	-
SOCI				-0.54	-0.38	-0.50	-	+	-0.18	-	-	-
SOVA							-0.13	-0.12	-0.17	+	+	+
SOMO										-	+	-

Table 5. The expected and observed species assemblages for 5 *Sorex* species (unfavored states in bold).

	1993		1994		1995	
States	Expected	Observed	Expected	Observed	Expected	Observed
0-0-1	0.04	0.00	0.15	0.00	0.17	0.00
0-1-0	2.69	5.00	2.33	2.00	4.90	6.00
0-1-1	0.32	0.00	0.43	0.00	0.48	0.00
1-0-0	2.07	0.00	1.52	2.00	4.11	3.00
1-0-1	0.27	0.00	0.31	0.00	0.45	0.00
1-1-0	15.39	30.00	4.32	6.00	14.44	25.00
1-1-1	0.31	2.00	1.47	1.00	0.61	2.00
1-2-1	0.18	0.00	1.89	3.00	0.15	0.00
2-1-1	0.07	0.00	0.88	2.00	0.12	0.00
2-2-1	0.00	0.00	3.00	2.00	1.27	1.00
0-2-0	**8.42**	**6.00**	**3.47**	**4.00**	**6.97**	**3.00**
0-2-1	**0.33**	**0.00**	**1.48**	**0.00**	**0.49**	**0.00**
1-2-0	**14.73**	**18.00**	**16.11**	**37.00**	**13.91**	**15.00**
2-0-0	**7.93**	**0.00**	**1.47**	**0.00**	**6.73**	**1.00**
2-0-1	**0.27**	**0.00**	**1.13**	**0.00**	**0.42**	**0.00**
2-1-0	**11.96**	**6.00**	**19.18**	**1.00**	**12.32**	**9.00**
2-2-0	**4.57**	**5.00**	**12.85**	**12.00**	**2.75**	**3.00**

were similar to random values. The frequency of assemblages observed with a large species present was consistent with expected values in all years.

DIET ANALYSIS

INVERTEBRATE REFERENCE

A total of 1,055 invertebrates was collected in 1995 (Table 6). Pitfall and sticky board traps accounted for 61 and 39% of all captures, respectively. Soil core samples collected did not contain any invertebrate items. Invertebrates from the orders Diptera and Phalangida were significantly more numerous on all sites, accounting for 52% of the captures. Seven of the 14 taxa sampled occurred at <25% of the study sites, whereas only 3 were present at all sites.

Table 6. Total number of captures (number of families), mean (± 1 SD) of captures per site, and number of sites of 14 invertebrate taxa in 1995. Means with the same letter are not significantly different (F = 10.4, df = 13, 299, $P \leq 0.05$).

Taxa	Total	Mean/Site	Sites
Diptera	279 (8)	11.6 ± 8.0[a]	24
Phalangida	271 (1)	11.3 ± 8.6[a]	24
Hymenoptera	194 (5)	8.1 ± 8.0[b]	24
Araneae	102 (3)	4.3 ± 3.4[c]	21
Coleoptera	83 (8)	3.5 ± 3.1[c,d]	21
Orthoptera	54 (4)	2.3 ± 2.2[c,d,e]	18
Microcoryphia	28 (1)	1.2 ± 1.5[d,e]	12
Collembola	21 (4)	0.88 ± 2.4[e]	5
Chilopoda	8 (3)	0.33 ± 0.76[e]	5
Lepidoptera	4 (2)	0.16 ± 0.48[e]	3
Diplopoda	4 (2)	0.17 ± 0.48[e]	3
Homoptera	3 (2)	0.13 ± 0.34[e]	3
Trichoptera	2 (1)	0.08 ± 0.28[e]	2
Hemiptera	1 (1)	0.33 ± 1.2[e]	1

DESCRIPTION OF DIET

A total of 462 of the 674 stomachs contained identifiable prey items (*S. hoyi*, N = 7; *S. cinereus*, N = 193; *S. vagrans*, N = 251; *S. monticolus*, N = 9; *S. palustris*, N = 2). The low sample size of *S. palustris* did not allow statistical analysis. The number of stomachs containing 1, 2, 3, or 4 prey items was: (*S. hoyi*, N = 5:2:0:0; *S. cinereus*, N = 138:42:11:2; *S. vagrans*, N =174:70:7:0; *S. monticolus*, N = 6:1:2:0). Overall, there was a high degree of variance in the percentage of the diet that invertebrate taxa comprised at different sites (Table 7). The most common prey item consumed by *S. hoyi* were Diplopoda (millipedes). Both the small *S. cinereus* and the medium-sized *S. vagrans* preyed on >60% Chilopoda (centipedes), Lepidoptera larvae (moths), and Homoptera (aphids) across the sites. *Sorex vagrans* also consumed a high percentage of Araneae (spiders) and Diptera (flies).

Table 7. Mean percentage of prey (± 1 SD) in the diet of 4 *Sorex* species across study sites where listed invertebrate taxa were present in 1995 (number of individuals/number of sites).

	Species							
	Small				Medium			
	S. hoyi		*S. cinereus*		*S. vagrans*		*S. monticolus*	
Diptera	10.0 ± 22.4	(1/5)	46.2 ± 37.9	(66/23)	68.3 ± 32.9	(88/21)	23.8 ± 37.1	(3/7)
Phalangida	20.0 ± 44.7	(1/5)	41.9 ± 41.8	(20/23)	36.4 ± 39.4	(6/14)	19.0 ± 37.8	(2/7)
Hymenoptera	20.0 ± 44.7	(1/5)	29.9 ± 42.5	(11/23)	47.5 ± 39.5	(32/19)	7.14 ± 18.9	(1/7)
Araneae			39.2 ± 39.5	(35/23)	62.4 ± 33.9	(46/19)	16.7 ± 40.8	(1/6)
Coleoptera	10.0 ± 22.4	(1/5)	40.5 ± 41.3	(25/22)	49.8 ± 39.1	(35/19)		
Orthoptera			27.6 ± 43.2	(7/19)	30.4 ± 44.0	(6/14)		
Microcoryphia					18.3 ± 33.7	(3/10)	8.33 ± 16.7	(1/4)
Collembola					50.0 ± 50.0	(3/5)		
Chilopoda	50	(1/1)	65.8 ± 32.5	(48/19)	67.9 ± 33.9	(61/14)	58.3 ± 50.0	(3/4)
Lepidoptera			70.8 ± 34.1	(16/10)	87.5 ± 21.2	(12/10)		
Diplopoda	91.7 ± 14.4	(4/3)	35.0 ± 48.7	(3/5)	37.5 ± 47.9	(2/3)		
Homoptera			76.2 ± 24.1	(25/15)	80.5 ± 24.3	(25/16)	36.7 ± 41.5	(3/5)
Hemiptera			46.7 ± 50.6	(7/5)	75.0 ± 27.4	(6/6)		

Table 8. Mean prey length (± 1 SD, mm) compared by analysis of variance for 4 species of *Sorex* at 24 sites in 1995. Means with the same letter are not significantly different ($F = 6.15$, df = 3, 617, $P \leq 0.05$).

Species	Mean	N
S. hoyi	15.0 ± 8.3 [a]	7
S. cinereus	7.6 ± 5.5 [b]	193
S. vagrans	7.2 ± 5.4 [b]	251
S. monticolus	8.7 ± 5.4 [b]	9

Overall, *S. hoyi* consumed the longest prey (Table 8). Mean prey length of the 2 medium-sized species, *S. vagrans* and *S. monticolus*, and the small *S. cinereus*, were similar. Comparing prey taxa length consumed by species assemblage revealed similar results (Table 9). In the absence of *S. hoyi*, in the 1-2-0 state, the similarly sized *S. cinereus*, and the 2 medium-sized species did not show an increase in prey size consumed.

Similarity of Diet

The percentage similarity of food items consumed varied depending on species assemblage (Table 10). The intraspecific diet of *S. cinereus* in the presence of the medium-sized *S. vagrans* (1-1-0) was highly similar in the 1-2-0 and 2-1-0 states, in the absence of *S. hoyi* and *S. monticolus*, respectively. When both of the former species were present (2-2-1, 2-2-0), and when alone with *S. hoyi* (2-0-0), similarity was reduced. The intraspecific diet of *S. vagrans* (0-1-0) was highly similar when 1 or fewer species were present in the other functional groups (1-1-0, 1-1-1); however, with the addition of a 2nd species into a functional group, this similarity drops by 17-20%.

Interspecific similarity in the diet of *S. vagrans* and *S. cinereus* was high in the 1-1-0 and 2-1-0 state. The addition of the 2nd medium-sized species, *S. monticolus*, and the large species, *S. palustris*, lowers the degree of similarity markedly (1-1-1, 2-2-1, 1-2-0). *Sorex vagrans* and *S. monticolus* could only be compared in the 1-2-0 assemblage, where a moderate degree of similarity was observed.

Table 9. Results of analysis of variance comparing mean prey length (± 1 SD, mm) for 4 species of *Sorex* for assemblages in 1995. Within rows, means with the same letter are not significantly different. SOHO = *S. hoyi*, SOCI = *S. cinereus*, SOVA = *S. vagrans*, and SOMO = *S. monticolus*.

	Mean						
State	SOHO	SOCI	SOVA	SOMO	*F*	df	*P*
2-2-1	16.3 ± 9.4[a]	4.96 ± 2.2[b]	5.11 ± 3.2[b]	3.65 ± 0.0[b]	6.73	4, 29	0.0006
1-1-0		8.05 ± 5.8[a]	7.50 ± 5.5[a]		0.59	1, 281	0.7400
0-2-0			6.77 ± 5.4[a]	8.62 ± 5.7[a]	1.07	1, 69	0.3000
1-2-0		9.93 ± 6.6[a]	7.42 ± 6.0[a]	8.35 ± 6.0[a]	1.49	2, 78	0.2300
2-0-0	14.6 ± 8.3[a]	6.63 ± 4.9[b]			22.1	1, 141	0.0001
2-1-0	14.1 ± 9.7[a]	6.73 ± 4.6[b]	6.84 ± 5.8[b]		4.81	2, 153	0.0090
2-2-0	16.3 ± 9.4[a]	7.17 ± 6.5[b]	5.37 ± 3.3[b]	8.95 ± 6.0[b]	3.39	3, 43	0.0300

Table 10. Intra- and interspecific similarity indices of percent diet of *Sorex* species for different assemblages in 1995. SOCI = *S. cinereus*, SOVA = *S. vagrans*, and SOMO = *S. monticolus*.

	Combination			
(*)	SOCI (1-1-0) vs. SOCI (*)	SOVA (0-1-0) vs. SOVA (*)	SOVA vs. SOCI	SOVA vs. SOMO
1-1-0		81	87	
1-1-1	46	83	56	
2-2-1	55	64	71	
1-2-0	74	66	64	60
2-1-0	77	61	84	
2-0-0	54			
2-2-0	58			

DISCUSSION

Shrew communities of northeastern Washington include up to 5 species dominated by *S. vagrans* and *S. cinereus* in both abundance and distribution. *Sorex monticolus* was distributed moderately throughout the area but was encountered in low numbers. The remaining 2 species, *S. hoyi* and *S. palustris*, had limited distributions and were never abundant. These communities are dynamic with a high degree of between-year variation in both species composition and abundance. This was displayed in the substantial population increase of 1994 for all species. With this increase, new combinations of species were observed as *S. hoyi* and *S. monticolus* expanded into additional study sites. In 1995, numbers of individuals returned to levels very similar to 1993, but the number of combinations of species did not decrease. Despite a reduction in numbers in 1995, the greater number of *S. hoyi* and *S. monticolus* in 1994 might have created a sufficient population to expand their distribution in this year.

My results indicate that these shrew communities do not always follow assembly rules based on size. High between-year variation in the number of individuals is the most important factor influencing this observation. In 1993, more favored states were observed than expected, with the state of 1-1-0 the most common. This is explained by the high abundance of *S. cinereus* and *S. vagrans*, small and medium-sized species, respectively. The population rise in 1994 most dramatically increased the number and distribution of *S. monticolus*, a habitat generalist, which in turn increased observations of the unfavored 1-2-0 state. In fact, most unfavored states occurring more frequently than expected were influenced by the presence of *S. monticolus*. Fox and Kirkland (1992) demonstrated the successful application of an assembly rule for functional groups of shrews based on body mass in eastern North America. They applied the rule to specimens sampled in 1 season and did not consider possible between-year variation. My results indicate that inter-annual variation must be taken into account in the application of these rules, especially when generalized species can expand their range freely, altering assemblages on different sites. Conversely, the distribution of habitat specialists such as *S. palustris* will not expand as readily.

Shrews showed no change in mean length of prey consumed in different assemblages. Interestingly, the smallest species, *S. hoyi*, consumed the longest prey. Most prey items consumed by this species were Diplopoda (millipedes) and Chilopoda (centipedes), long and slender invertebrates, which likely increases the ease of capture and consumption. Smaller shrews have a high stomach surface area-to-body ratio and must eat proportionally more than larger species (Saarikko 1989), therefore ease of capture is an important determinant of their diet.

The diet of *S. cinereus* and *S. vagrans* included a high percentage of Chilopoda (centipedes), Lepidoptera (moths), and Homoptera (aphids). Only *S. vagrans* preyed heavily upon Diptera (flies), 1 of the 3 orders that was captured most frequently. With this exception, none of the other 3 species consumed a significant portion of the most frequently captured invertebrates, of the orders Diptera, Phalangida (Daddy-Longlegs), or Hymenoptera (bees, ants). These findings contrast with those of Churchfield (1982) who sampled invertebrates in a similar fashion, and found the major constituents in the diet of shrews to be the most numerous in the habitat.

Comparing the percentage similarity of food items consumed in different assemblages indicates that though there is no differentiation in prey-size selection, the type of prey consumed does change. The reduced intraspecific similarity in the diet of *S. cinereus* in the presence of both *S. hoyi* and *S. monticolus*, or alone with *S. hoyi*, supports these findings. The wider upper incisors and longer lower incisor of *S. hoyi* might result in a competitive advantage over *S. cinereus* in its ability to seize and consume the centipedes that are so prevalent in both of their diets. *Sorex vagrans* showed a similar reduction in diet similarity in assemblages where there was more than 1 species present in a functional group. Introduction of *S. monticolus* and *S. palustris* into an assemblage reduced the similarity of diet between *S. cinereus* and *S. vagrans*. This is supported by Churchfield (1991), who found that overlap in diet between *S. araneus* and *S. minutus* decreased in a 3-species community as compared to 2. In all communities, the exploitation of food resources will depend on the distribution and occurrence of the different prey available in their habitat.

My results suggest that shrews in the interior Pacific Northwest are likely foraging in different microhabitats. The abundance of *S. vagrans* was negatively correlated with *S.*

cinereus and *S. monticolus* in all years, indicating these species are likely foraging in different areas. Therefore, it is not surprising there is no difference in prey size selection by these species. In these dynamic communities, it is not likely that the character displacement described by Malmquist (1986) has had the chance to evolve. Shrews in this area appear to be foraging in different microhabitats, therefore it is unlikely that removal of a larger species would change the feeding habits of smaller individuals as Dickman (1991) observed.

Several studies provide evidence that shrews have adapted strategies to optimize foraging in diverse communities by utilizing different microhabitats (Whitaker and Maser 1976, Hanski 1984, Inoue and Maekawa 1990, Hanksi 1992). Hanski (1989) and Feldhamer and others (1993) have demonstrated that in multi-species shrew communities, habitat generalists are typically numerically dominant over habitat specialists due to their decreased sensitivity to temporal variation in food availability and environmental stochasticity.

Changes in managed forests of northeastern Washington alter the habitat and have a strong influence on the presence of species and prey taxa. Previous work conducted by Terry (1981) and Belk and others (1990), indicate habitat preferences of *S. vagrans* and *S. monticolus*, with the former preferring areas with a high water table, and the latter areas with a highly herbaceous ground cover. Hawes (1977) found that interspecific competition and territoriality disputes of these similarly sized species are alleviated by the evolution of marked habitat preferences. *Sorex monticolus* has slightly more robust and slower wearing teeth allowing it to eat a higher proportion of small-bodied invertebrates found in its acidic western hemlock habitat, whereas *S. vagrans* shows a higher reproductive rate which may be a factor of the less resource-limiting regime of its richer redcedar habitat. Studying *S. cinereus*, Geier and Best (1980) found that the removal of woody plant debris such as logs, brush piles, and stumps reduced the number of individuals present. Changes in habitat in the managed forests of this region might further increase the negative correlation of *S. cinereus* and *S. vagrans*, providing more suitable habitat for the former species.

Extreme between-year variation in shrew species abundance makes it difficult for assembly rules to predict species composition in northeastern Washington. Habitat

variables change with forest management practices, which result in a changing community, and diversity of food availability.

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APPENDIX E

NEST PREDATION IN MANAGED CONIFEROUS FORESTS: EFFECTS OF PATCH TYPE AND SIZE

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Understanding the relationship between landscape dynamics and biodiversity is a critical element in attempts to mitigate the effects of land-use practices on wildlife species (Hansen and Urban 1992). Habitat fragmentation may adversely affect the reproductive success of bird species. Robinson and others (1995), for example, found that nest predation and brood parasitism both increased with reduced forest cover for 9 landscapes in the midwestern United States. Nest predation was earlier recognized as a major influence on the population dynamics (Ricklefs 1969) and community relationships (Martin 1988a, b) of many bird species. The creation of open-canopy patches and edge habitats can allow predators to invade the landscape and forest interiors, respectively (e.g., Andrén 1992, Møller 1988). Consequently, nest predation can increase with habitat fragmentation (Wilcove 1985).

In much of the Pacific Northwest, conversion of old-growth to second-growth forests prior to the 1930s has been followed more recently by timber harvesting that has fragmented the landscape into a complex mosaic of habitat patches of differing ages and sizes. Because "managed" forests encompass >7,000,000 ha in Washington alone, there has been increasing interest in understanding the effects of forest practices on native wildlife species (e.g., Hansen and others 1991).

As in several earlier studies (review in Major and Kendal 1996), we examined rates of predation on artificial nests and how they varied with size and type of habitat patches

in managed forests of NE Washington state. An evaluation of the role of nest predators in these habitats is of particular importance for understanding the processes that might affect avian diversity following fragmentation. We tested the hypotheses that predation would be lower in large, closed-canopy patches than in small patches, and would be higher in open-canopy habitats.

METHODS

Study Area

The study was conducted on 7 watersheds managed primarily for timber production in NE Washington (Stevens and Pend Oreille counties; T32-33N R42-43E, T35N R42-43E, T37-38N R42-43E). The watersheds varied in size from 2,937 to 7,160 ha. Second-growth mixed-coniferous forest of <90 yrs is the predominant habitat type. We classified Landsat thematic mapper imagery for the region into 4 forest classes: (1) closed canopy of >30 yrs, (2) regeneration of <20-30 yrs, (3) open canopy from timber harvest, and (4) deciduous and open ground usually related to harvesting activities. We converted the raster image into an ARC/INFO polygon coverage using a minimum mapping unit of 2 ha (Hallett and others in litt.). This map assisted us in selecting 5 replicate patches of 2 size classes (small:16-20 ha; large: >35 ha) and 3 forest types (closed canopy, 60-90 yrs; regeneration, 15-20 yrs; and open canopy, <6 yrs) for a total of 30 patches. The open-canopy patches were clearcuts that retained a few seed or dead trees. The smaller size class is representative of the minimum patch size typically created by harvest in this region. The 3 forest types are the most common, comprising 82% of the total area. The watersheds have been converted from closed-canopy forest to the other types by about 27.8 to 50.7%.

Measuring Nest Predation

Because of the difficulties in locating natural nests and in obtaining adequate sample sizes, we examined nest predation by using artificial nests provisioned with quail eggs (George 1987, Martin 1987, Wilcove 1985). This approach allows large sample sizes and replication. The disadvantage is that artificial nests cannot have the placement,

construction, and defensive response that a bird would provide. Some predators may follow adult birds to the nest. Thus the rates of predation on artificial nests are likely to differ from those on natural nests. Martin (1987), however, found that when natural materials were added to artificial nests, predator response was similar to that for natural nests. We camouflaged wicker nests by wrapping them with dried grasses. As Yahner and Mahan (1996) have argued, artificial nests do allow comparison between local habitats.

Beginning in late May 1994, 20 nests were placed at each of the 30 patches for a total of 600 nests. We used disposable latex gloves when handling eggs and nests. Nests were baited with 3 quail eggs and were placed throughout each forest patch with >25-m spacing between nests. Nests were >100 m from the edge of each patch to reduce edge effects. Nest locations were unmarked to prevent recognition by visual predators such as jays and ravens. To subsequently find the nests, we recorded the distance (>25 m) and bearing of each nest from a transect that bisected the patch. This transect was established in 1993. Nests were positioned up to 1.0 m off the ground next to trees, logs, stumps, or shrubs. The absence of tall trees in some habitats precluded examination of nest height. The nests were checked and removed after 7 days. This corresponds to typical egg-laying or incubation times for small passerine birds (Martin 1987). Between 5 and 7 patches could be visited each day. The experiment was repeated 21 days after completing the first trial. Repeated sampling was necessary because predation rates might change with time due to changes in resource availability or predator behavior. On completion of the second trial, nests were removed and the nest locations were flagged.

At each check, the condition of each nest and the number and condition of eggs present were recorded. A predation event was considered to be any disturbance that destroyed or displaced the nest or 1 or more eggs. Some small mammals are unable to break the shells of quail eggs, whereas they are able to consume the smaller eggs of many passerines (Haskell 1995). Consequently, nests found with eggs that were scratched by the incisors or claws of small mammals were considered to be depredated. We categorized the likely predator at each disturbed nest as mammalian, avian, or unknown based on the condition of the nest and eggs. Mammalian predators

characteristically leave fragments of egg shell, and often disturb or tear the nest. Eggs attacked by avian predators have peck holes or are completely removed from the nest, which is otherwise left undisturbed.

We estimated the relative abundance of some probable nest predators using data from avian point-count surveys conducted on each patch during the breeding season (mid-May to late June) in 1993 to 1995. Sampling in the years before and after the experiment allowed us to assess variability in predator occurrence. We established transects with 3-4 and 12 point-count stations on small and large patches, respectively. Point-count stations were >100 m apart and >100 m from the edge of the patch. Surveys were conducted 4 times in 1993 and 6 times in 1994 and 1995 between 0500 and 0800 PDT on days with little or no wind and no rain. All birds detected within a 50-m radius of the point-count station were recorded during an 8 min period. Birds flying over the 50-m radius circle, but not landing, were recorded as "fly-overs". For potential avian predators, including the common raven (*Corvus corax*), Steller's jay (*Cyanocitta stelleri*), and gray jay (*Perisoreus canadensis*), we used the total number of observations per point-count station per sampling day as an index of abundance for each patch. Relative abundance of red squirrels (*Tamiasciurus hudsonicus*) was determined similarly by tallying the number of individuals seen or heard vocalizing within the 50-m radius circle during each survey.

We sampled small mammals using pitfall traps in a 6 x 6 grid with 10-m spacing. Trapping grids were placed in representative areas of each patch and were run for 2 weeks in June or early July 1993-1995. We tallied the total number of deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Clethrionomys gapperi*) captured on each grid for each year, and used this as a relative measure of abundance.

The habitat surrounding a nest may provide different degrees of protection from predation (e.g., dense shrubs may reduce access or visibility by predators). Following the experimental trials, we measured habitat characteristics within a 5-m radius circle centered on the artificial nest and divided into 4 quadrants along the cardinal directions. Presence of logs >6 cm in diameter, saplings >4 and <10 cm diameter at breast height (d.b.h.), trees $\geq$10 cm d.b.h., stumps >16 cm d.b.h., and shrubs both within 1 m and 5 m of the nest was determined in each quadrant. The total number of coniferous,

deciduous, and dead trees in 2 size classes (4 to <10 cm d.b.h. and ≥10 cm d.b.h.) was tallied in the circle. Horizontal cover was measured at the nest with a 25- x 25-cm coverboard divided into 5-cm squares. Cover was estimated as the percentage of squares that were >50% obstructed by vegetation when viewed at a distance of 5 m. Measurements were taken from the 4 cardinal directions and then averaged. Vertical cover was determined with a convex spherical densiometer held at 1.5 m above the nest location. A 20- x 50-cm cover plot was placed at the nest and the cover of herbs, stumps, logs, litter, soil, trees, shrubs, and rocks was scored into 7 classes: 0, no cover; 1, >0-5%; 2, >5-25%; 3, >25-50%; 4, >50-75%; 5, >75-95%; 6, >95-100%. We used the midpoint of each percentage class in the analyses.

Data Analysis

We used repeated measures analysis of variance to examine differences in degree of predation with patch size and habitat type over time. The dependent variable was the number of disturbed nests per patch repeated on patch for the 2 trials. Patch size and type were independent classification variables. We tested our specific hypotheses using planned orthogonal comparisons (Sokal and Rohlf 1995).

The relative abundance of red squirrels and potential avian predators for 1993-1995 was examined by analysis of variance with respect to habitat type and patch size. Because of significant heterogeneity in the distribution of red squirrels, we conducted an analysis of covariance for the first trial to predict the number of depredated nests per patch using dummy variates representing 2 of the 3 habitat types and the relative abundance of red squirrels as a covariate.

To examine the microhabitat features affecting predation on the artificial nests, we conducted logistic regression. The dependent variable was the state of each nest, designated as 1 if disturbed and 0 otherwise. The independent variables were the habitat variables describing each nest location. We used a forward-selection procedure to select variables retained in the model using $P = 0.1$ for entry. We obtained identical results using backward-elimination. All statistical analyses were conducted using GLM or LOGISTIC procedures in SAS (SAS Institute 1989).

RESULTS

SPATIAL AND TEMPORAL DISTRIBUTION OF NEST PREDATION

Totals of 262 and 412 of the 600 nests available during each trial were disturbed during the 1st and 2nd trials, respectively. The mean number of disturbed nests varied significantly among patches during the 1st trial ($F = 2.3$, df = 3,26, $P < 0.05$; Fig. 1), but not the 2nd ($F = 1.9$, df = 3,26, $P > 0.15$). The number of disturbed nests increased significantly during the 2nd trial ($F = 78.3$, df = 1,27, $P < 0.001$; Fig. 1). Differences during the 1st trial were associated with habitat type ($F = 4.1$, df = 2,26, $P < 0.03$), but not with patch size ($F = 0.6$, df = 1,26, $P > 0.4$). Planned orthogonal comparisons indicated that during the 1st trial, greater predation occurred in closed-canopy forest than in regeneration and clearcut patches ($t = 2.52$, df = 1,27, $P < 0.01$), but not between regeneration and clearcut patches ($t = 0.65$, df = 1,27, $P > 0.5$).

TYPES OF PREDATION

In the 1st trial, 52 and 193 predation events were attributable to avian and mammalian predators, respectively (Fig. 2). The number of predation events increased in the 2nd trial to 85 and 312 attributable to birds and mammals, respectively, but there was no proportional change in predation by the 2 taxa between trials (*G*-test for heterogeneity, $G = 0.003$, df = 1, $P > 0.9$). The number of predation events attributable to mammals was significantly greater than for birds (*G*-test on pooled data, $G = 224.3$, df = 1, $P < 0.001$).

No relationship was observed between the number of nests depredated by birds or by mammals on a patch during the 1st trial ($r = 0.10$, N = 30, $P = 0.58$), but there was a negative correlation in the 2nd ($r = -0.36$, N = 30, $P = 0.049$). The latter result was due to 8 sites that had very high levels of predation by mammals (≥16 of 20 nests).

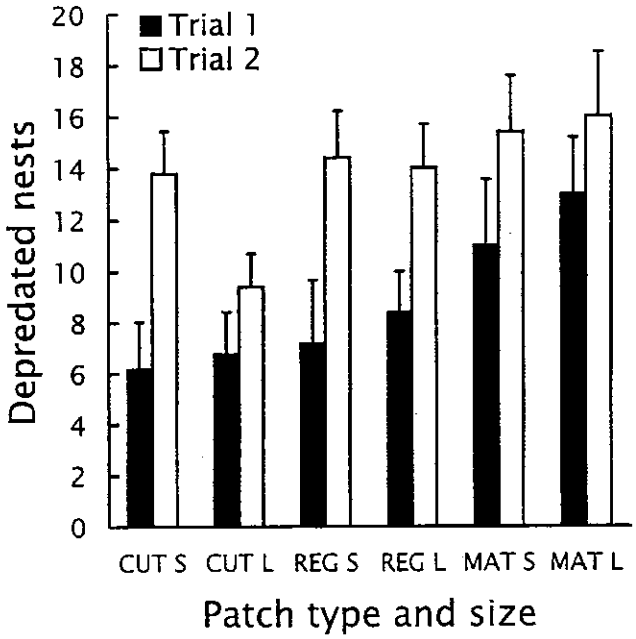

Figure 1. Mean number of nests (±1 SE) that were depredated during the 2 experimental trials for patches in 3 habitat and 2 size classes. Habitat types are clearcut (CUT); regeneration (REG); and mature, closed-canopy forest (MAT). Size classes are small (S) and large (L).

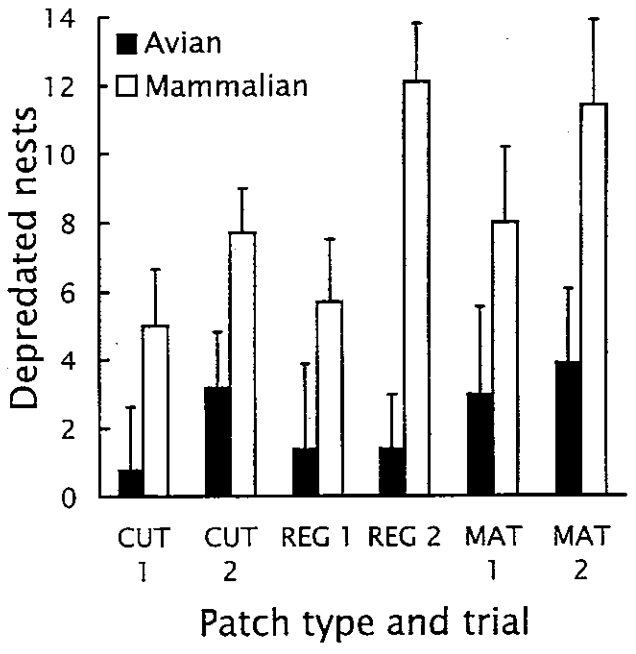

Figure 2. Mean number of depredated nests (±1 SE) for 10 patches of 3 habitat types for the 2 experimental trials that were attributable to avian and mammalian predators. Habitat types are clearcut (CUT); regeneration (REG); and mature, closed-canopy forest (MAT).

Distribution of Nest Predators

Relative abundance of red squirrels increased significantly in all patch types from 1993 to 1994, but returned to previous levels in 1995 (repeated-measures ANOVA, Wilk's $\lambda = 0.24$, df = 2,26, $P < 0.001$). Although squirrels varied in abundance among patches (Fig. 3), red squirrels were observed significantly more often in closed-canopy forest than in regeneration and clearcut patches in all years ($t > 3.2$, $P < 0.004$ for all comparisons). A significant interaction between time and habitat type (Wilk's $\lambda = 0.4$, df = 4,52, $P < 0.001$) reflected the dramatic increase in sightings of squirrels in closed-canopy patches in 1994 (Fig. 3).

Relative abundance of potential avian predators decreased significantly in all habitats from 1993 to 1994 ($F = 4.7$, $P = 0.04$) and remained low in 1995 ($F = 0.32$, $P = 0.74$; Fig. 4). Although avian abundance was significantly greater in closed-canopy forest than in regeneration or clearcut patches in 1993 ($t = 2.51$, $P = 0.02$), there were no differences between habitats in 1994 or 1995.

We examined several ANCOVA models to determine the importance of habitat and relative abundance of red squirrels in predicting the number of depredated nests per patch. When dummy variates for habitat were placed in the model, only closed-canopy forest was significant as expected ($R^2 = 22.4$, $F = 8.1$, df = 1,29, $P = 0.008$). Using squirrel abundance as the only independent variable increased the variance explained ($R^2 = 32.8$, $F = 13.5$, df = 1,29, $P < 0.001$). Addition of a variate for closed-canopy forest did not provide significant improvement over the model for squirrel abundance alone ($F = 0.09$, df = 1,29, $P = 0.77$). Relative abundance of avian predators was not a significant predictor of the number of depredated nests ($F = 0.02$, df = 1,29, $P > 0.88$).

Microhabitat Characteristics of Depredated Nests

We conducted logistic regression only for the 1st trial. Number of coniferous trees $\geq$10 cm d.b.h. within 5 m of the nest location and percentage cover of logs at the nest were positively related to predation (Wald $X^2 = 15.0$ and 8.3, respectively, $P < 0.004$), whereas percentage cover of herbaceous vegetation was negatively related to predation (Wald $X^2 = 2.95$, $P = 0.086$).

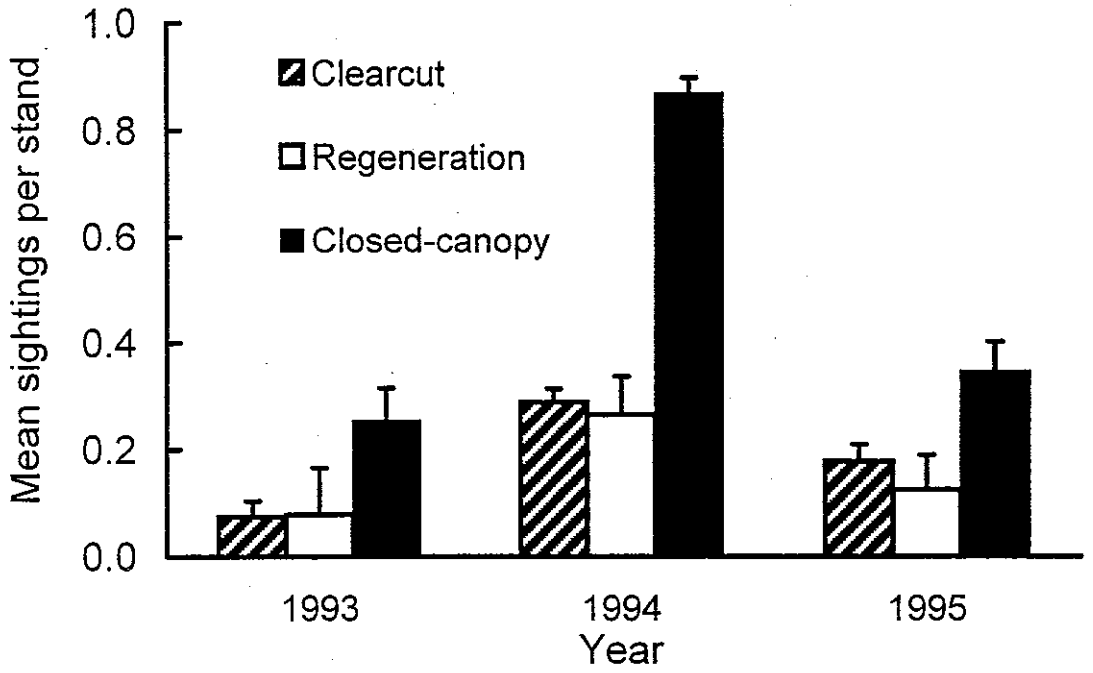

Figure 3. Mean number of sightings of red squirrels per stand (±1 SE) for each habitat type and year. The number of sightings per patch was adjusted for differences in the number of point-count stations on each patch and for the lower number of surveys in 1993.

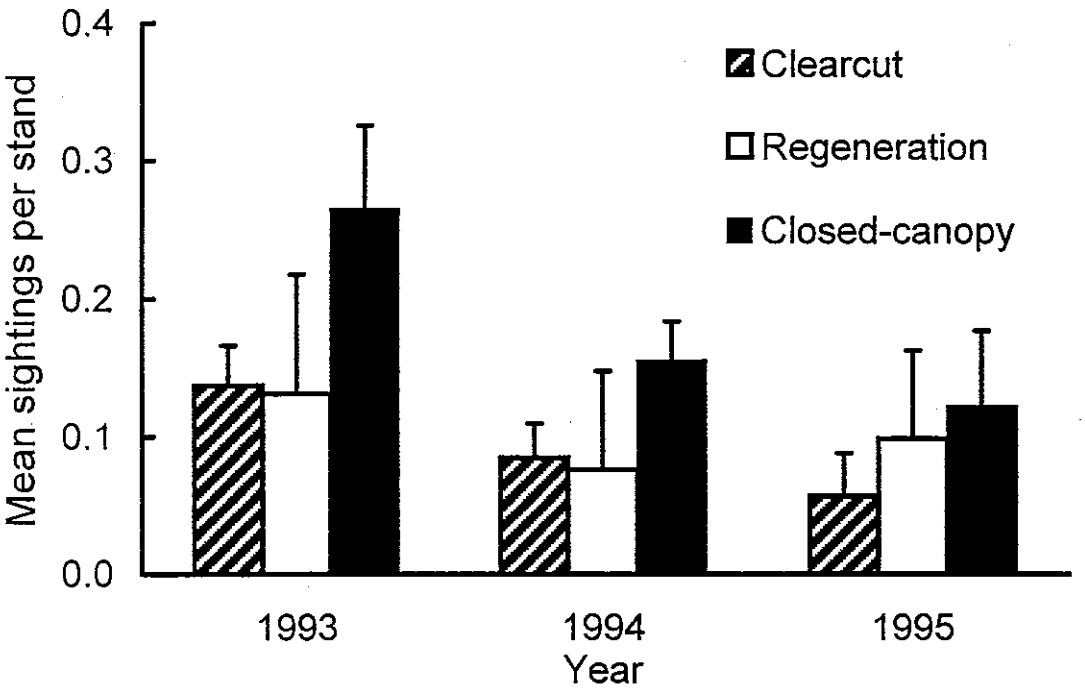

Figure 4. Mean number of sightings of potential avian predators per stand (±1 SE) for each habitat type and year. The number of sightings per patch was adjusted for differences in the number of point-count stations on each patch and for the lower number of surveys in 1993.

DISCUSSION

Unlike some other studies of predation on artificial nests, we found no effect of patch size. Rather, the pattern of nest predation was largely explained by the distribution of 1 principal predator, the red squirrel. In the following we consider these results in turn, and view them in light of some recent criticisms of nest-predation experiments (e.g., Haskell 1995).

We were somewhat surprised that patch size did not contribute to the likelihood that a nest would be preyed upon because earlier studies (e.g., Small and Hunter 1988, Wilcove 1985) found higher rates of predation in smaller patches. There are several explanations for this finding. First, it is possible that our small patch size was above some critical threshold below which predation might increase because of a higher ratio of edge to total area. Because our patch sizes were selected to be representative of those created by current forest practices, we did not examine smaller patches and further work is necessary to test this hypothesis. Second, the minimum distance from the edge of a patch to a nest was >100 m in our study. Consequently, if patch size differences are largely the result of predation at the edge of a patch, these differences would go undetected in our design. Third, the context of a patch may influence rates of predation. Wilcove (1985), for example, found that small forest patches generally had higher predation in suburban than in rural areas. Many other studies of nest predation have been conducted in agricultural areas where the matrix surrounding forest fragments has been modified completely. These studies contrast markedly with ours because we studied fragments that are still within a matrix of closed-canopy forest. Fourth, the patterns of predation that one observes are determined by the types of predators in an area, and by our ability to detect them in an experiment (Haskell 1995). Primary predators have differed between studies. Wilcove (1985) and Yahner and Scott (1988) found that birds were the dominant predators in their study areas. Nour and others (1993) found that most attacks were by avian predators (>70%), but that mammalian predators increased in importance in larger patches and away from the forest edge.

Haskell (1995) argued that effects of patch size could result from problems detecting predators in studies using quail eggs. Some small mammals, such as deer mice (*Peromyscus*) and eastern chipmunks (*Tamias striatus*), are unable to break quail eggs, although they can feed on the smaller eggs of passerines.

The significantly greater predation in closed-canopy forest than in regeneration or clearcut patches, also ran counter to our predictions. This result is explained largely by the greater importance of mammalian predators and particularly the distribution of the red squirrel. The relative occurrence of red squirrels paralleled the distribution of depredated nests in the 1st trial. Relative abundance of red squirrels was the best predictor of degree of predation across patches for the 1st trial. Reitsma and others (1990) found that removing red squirrels did not alter rates of predation and attributed this to compensatory mortality inflicted by other predators.

We did not randomize the distribution of nests for the 2nd trial, and predation increased substantially over the 1st trial. This result likely reflects the development of a search image by predators for the artificial nests. The increase in predation was large enough to swamp initial differences in habitat. We concur with Yahner and Mahan (1996) that nests should be randomized.

Yahner (1996) urged that the types and numbers of potential predators be determined. Mammalian predators were most important in our study, and changed substantially in abundance between years. Thus the results of nest predation experiments may also vary depending on when and where they are conducted. Variation in the numbers of squirrels and small mammals between years could alter the results of artificial nest predation studies depending on when the study is conducted relative to predator densities. In our study, populations of small mammals including squirrels were all much higher than in either the preceding or following year.

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