

WILDLIFE USE OF MANAGED FORESTS: A LANDSCAPE PERSPECTIVE



A Workshop

**October 8, 1996 - Westside - Olympia, Washington
October 10, 1996 - Eastside - Cheney, Washington**

Table of Contents

	Page
Overview of the Landscape Project in Washington State	1
Keith B. Aubry ¹ , James G. Hallett ² , and Stephen D. West ³	
Overview of the West Side portion of the Landscape Project.....	3
Keith B. Aubry and Stephen D. West	
Avian survey results: habitat occupancy patterns.....	14
David A. Manuwal ³	
Amphibian survey results: habitat occupancy patterns	18
Keith B. Aubry	
Small mammal survey results: habitat occupancy patterns.....	28
Stephen D. West	
Bat survey results: habitat occupancy patterns.....	33
Janet L. Erickson ³	
Nesting success and habitat selection of the Pacific-slope Flycatcher	36
Scott F. Pearson ³	
Northwestern salamander movement patterns and habitat use	39
Angela B. Stringer ³	
Habitat utilization and home range size of the bobcat in managed forests of western Washington.....	43
Levon P. Yengoyan ³	
Roost site characteristics of the long-legged myotis (<i>Myotis volans</i>) in the Teanaway River Valley of Washington.....	46
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Table of Contents

	Page
Overview of the East Side portion of the Landscape Project.....	51
James G. Hallett ⁴ and Margaret O'Connell ⁵	
Avian survey results: habitat occupancy patterns.....	55
Deborah Beutler ⁴	
Small mammal survey results: habitat occupancy and population patterns	58
Margaret O'Connell and James G. Hallett	
Bat survey results: habitat occupancy patterns and roost use by silver-haired bats (<i>Lasionycteris noctivagans</i>)	61
Lori A. Campbell ⁶ , James G. Hallett, Margaret A. O'Connell	
Patterns of shrew community composition	64
Robert E. Griffith ⁵	
Predation on artificial nests: effects of patch size and type.....	68
James G. Hallett and Margaret O'Connell	
Analyzing movement patterns of vertebrates on fragmented landscapes.....	71
Douglas R. Call ⁴ and Stephen G. Mech ⁴	
Spatial dynamics of snowshoe hares in managed forests	74
Jason A. Thomas ²	

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Overview of the Landscape Project in Washington State

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As of 1991 most of the major research effort spent in understanding wildlife habitat relationships in forests of the Pacific Northwest targeted the investigation of old-growth forests. Knowledge of wildlife habitat relationships in landscapes managed for timber production was not well known for many species. There was general agreement within the scientific community that this was a critical shortcoming that needed to be addressed. In late 1990 the TFW Wildlife Steering Committee issued a request for proposals to meet this need, and a research group consisting of researchers from the University of Washington, Washington State University, and the U.S. Forest Service were selected to conduct the work. Following a May 1991 workshop with researchers, TFW Wildlife Steering Committee members, and outside consultants, the objectives of the Landscape Project were revised from the original request for proposals.

The revised objectives were to:

- 1) describe the species composition and abundance levels of wildlife and plant communities occurring in forest stands of varying seral stages, size-classes, and landscape configurations in watersheds managed primarily for timber production,
- 2) develop methods for analyzing wildlife responses to landscape-scale habitat conditions in managed watersheds.

In addressing these general objectives we planned for similarly-structured, parallel investigations east and west of the Cascade crest. The original design for replicated sampling was modified in late 1991 in response to ecological and historical differences on either side of the crest. The changes resulted in a west-side research design that emphasized stand-level habitat differences related to forest management more than the east-side design. The details and rationale for the divergent approaches are discussed by Keith Aubry for the west-side and by Jim Hallett for the east-side work.

The sampling of vertebrate and plant communities was done on 24 sites west and 36 sites east of the crest during 1992-1995. Six replicates of all forest conditions were sampled. Information was gathered on breeding birds, bats, terrestrial amphibians, small mammals, and on the composition and structure of the plant communities. Details of the field methodologies and the results are given in the following presentations.

We have organized the symposium to report not only the results of the core landscape project, but also several closely related projects that were conducted as graduate thesis research. These ancillary projects have extended the core project's scope and usefulness. Some of these projects are complete and available as theses and others are still works in progress. In the morning and afternoon sessions we present the core project findings first, followed by the thesis research.

Such intensive, large-scale investigations are essential if we are to understand the basic relationships between wildlife and forested habitats. It is also clear that such investigations cannot be done without extraordinary levels of cooperation among landowners, managers, biologists, and researchers. We have been fortunate.

Overview of the Westside Portion of the Landscape Project

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INTRODUCTION

The managed forests of Washington State encompass approximately 17,305,000 acres (7,003,333 ha) of which about 63% are on State and private lands (Card et al. 1985). The Timber Fish and Wildlife (TFW) Agreement (1987) introduced both a framework for management practices on State and private forests, and a mechanism to evaluate and modify management practices to achieve stated resource goals. A critical question facing TFW resource managers is how to balance the TFW wildlife goal to "provide the greatest diversity of habitats (particularly riparian, wetlands and old growth), and to assure the greatest diversity of species within those habitats for the survival and reproduction of enough individuals to maintain the native wildlife of Washington forest lands" with the timber resource goal of "...continued growth and development of the State's forest products industry..." (Timber Fish and Wildlife 1987).

Franklin and Forman (1987) have proposed that the number, size, and arrangement of stands in a managed forest landscape could be modified to achieve different wildlife objectives. However, we must first be able to analyze and predict wildlife responses to varying landscape conditions. The response of wildlife species to local stand conditions has been hypothesized for certain species (see Thomas 1979, Brown 1985, Irwin et al. 1989), but so far, these responses have only been evaluated in the field in unmanaged forests (Ruggiero et al. 1991); no comprehensive research on wildlife communities in managed forest stands has been conducted in the Pacific Northwest. Even less is known of the response of wildlife populations and communities at the landscape scale.

Analysis of wildlife habitat relationships can be approached from a hierarchical perspective (e.g., Irwin et al. 1989, Urban et al. 1987). Irwin et al. (1989) identified 3 spatial scales in managed forests - landscape, stand, and gap - with 3 corresponding wildlife habitat analysis levels. At the stand scale, we are concerned with habitat features such as stand size, shape, and seral stage. When we view managed forests from a landscape perspective, however, we are concerned with the spatial and temporal patterns occurring among stands. At the landscape scale we consider, for example, the kinds (e.g., seral or structural stages) of stands that are present, distances between stands, connectivity of stands, and conditions surrounding stands. The response of wildlife populations at stand and landscape scales will depend upon the particular life history characteristics of a species, the environment (habitat and other species present), and the species' population structure.

The objectives of this study are two-fold:

- describe the species composition and abundance levels of wildlife and plant communities occurring in forest stands of varying structural classes in watersheds managed primarily for timber production;
- develop methods for analyzing wildlife responses to landscape-scale habitat conditions in managed watersheds.

METHODS

We sampled diurnal breeding birds, forest-floor small mammals, bats, and amphibians for 3 successive years (fall 1992 through spring 1995) in stands occurring in a variety of landscape conditions with a long history of intensive forest management. Selected stands vary in both structural stage and landscape context.

Development of a Landscape-Scale GIS Database

The first step was to develop a means of discriminating between landscapes according to the age, size, and pattern of forest stands, and the intensity and manner in which these landscapes have been logged. We used Landsat Thematic Mapper (TM) imagery to create a seral-stage classification based on species, canopy structure, and stand age. With these data, we developed a GIS methodology for characterizing landscapes according to their composition and management history (see Young et al. 1993 for a detailed description of our analytical approach).

We quantified the range of landscape patterns present in our dataset by subdividing the area within the TM scene into major watersheds (60,000-81,000 ha) using boundaries provided by the Washington State Water Resource Inventory Area (WRIA) classification. This divided the area encompassed by the satellite imagery (scene) into 68 whole or partial major watersheds (basins). To ensure that basins considered for sampling in this study were similar in ecological and physiographic characteristics, so that major differences among landscapes would result primarily from management history, we selected the subset of 19 basins located west of the Cascade crest and east of the Puget Trough Physiographic Province (Franklin and Dyrness 1973) for further analysis (Fig. 1).

We assessed variation in landscape conditions in each of these 19 basins by calculating standard landscape indices (diversity, dominance, and fragmentation) and found that the range of index values among watersheds was narrow, i.e., most of the variation in landscape pattern was occurring within basins. To provide a more useful unit of landscape analysis, we subdivided each basin into sub-basins (3rd-order watersheds) ranging in size from 4,000-12,000 ha according to guidelines provided by the Washington State Department of Natural Resources (DNR) for delineating a Watershed Administrative Unit (WAU). This procedure resulted in 119 sub-basins mapped by age class (Fig. 2).

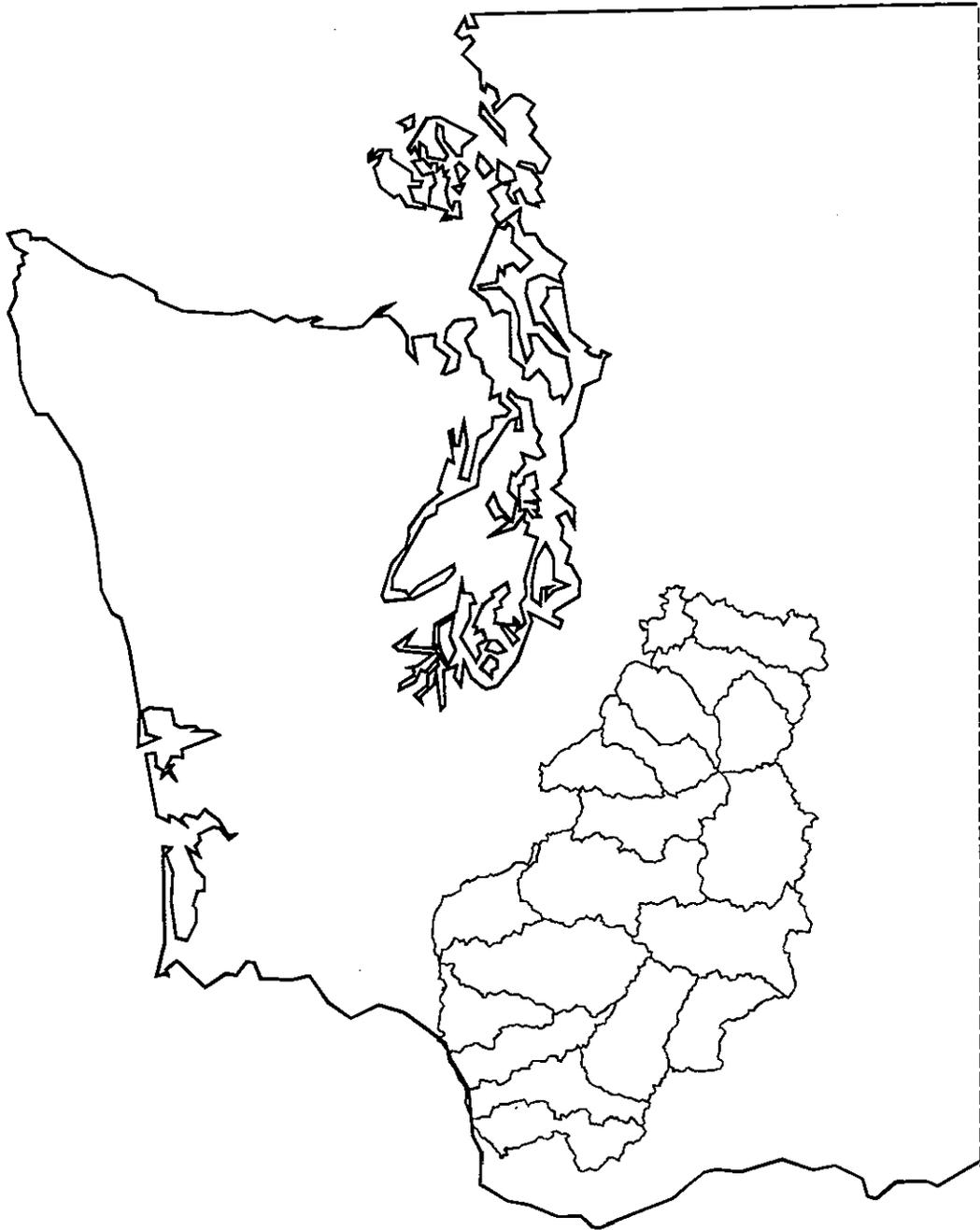


Fig. 1. Map of the GIS analysis area subdivided into 19 WRIs (Water Resource Inventory Areas).

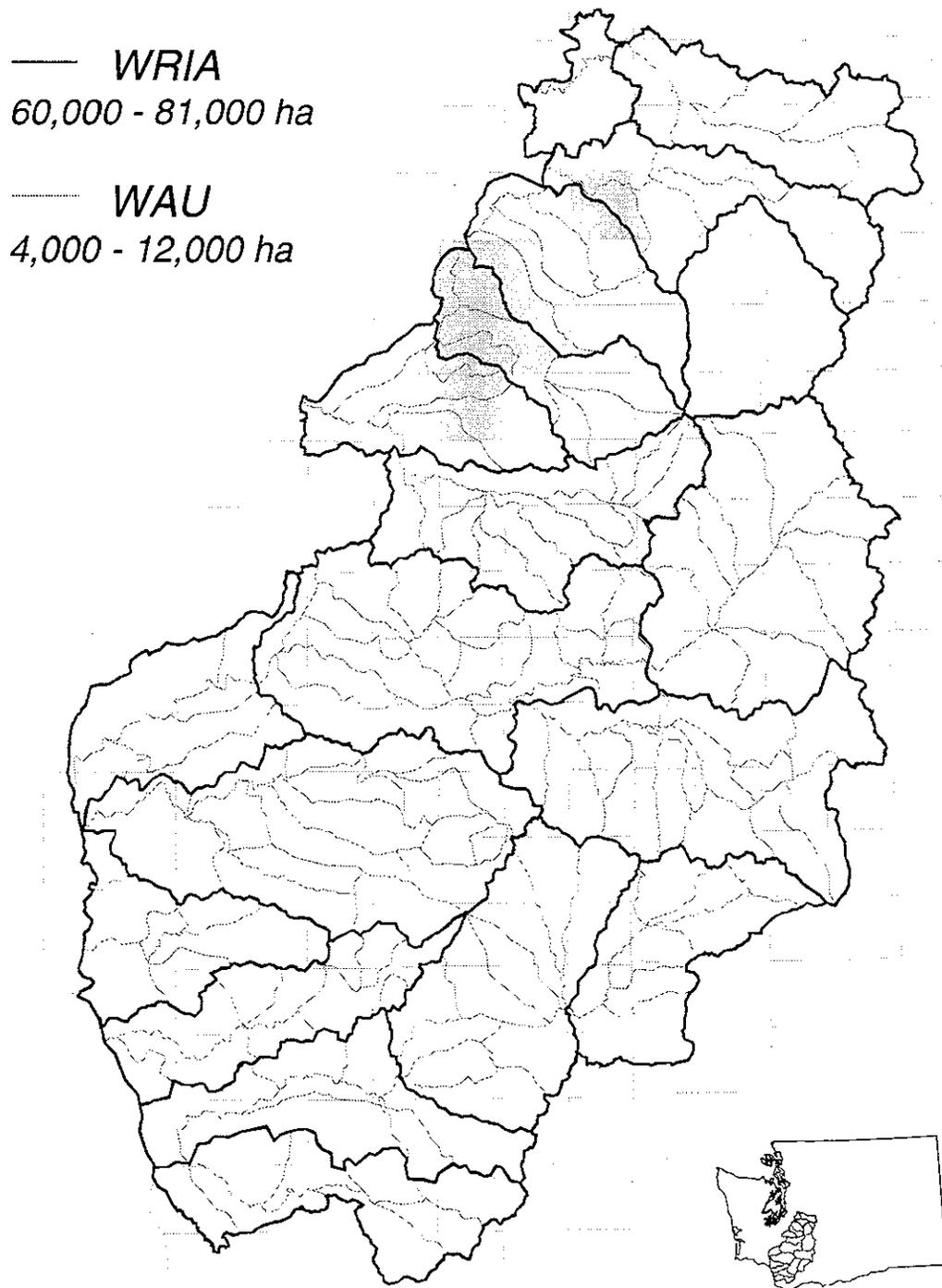


Fig. 2. Map of the 19 WRIsAs subdivided into 119 WAUs (Watershed Administrative Units) for analysis of landscape composition and structure. The shaded areas are the 6 Townships in which the TFW Landscape study sites are located (see Fig. 3).

To further refine this dataset for our study objectives, we screened out those sub-basins that were over 5000 ft in elevation; located in Wilderness Areas, National Parks, National Monuments, or Wildlife Refuges; or that had been strongly influenced by the 1980 eruption of Mount St. Helens. We also eliminated sub-basins that had >20% old-growth forest or less than 20% in the 3-8 yr age class, as these landscapes would not be representative of intensively managed landscapes. This resulted in a total of 79 sub-basins to use in describing the range of landscape conditions occurring in managed forest landscapes in the southwestern Washington Cascade Range.

Our landscape analysis showed that sub-basins could be classified into 5 different groups. The 5 groups represent different landscape configurations and establish a classification of landscape pattern resulting from differing intensities of fragmentation and varying natural and cultural influences. In other words, these groups represent the range of landscape structure types occurring in managed forest landscapes at low to mid-elevations in the Douglas-fir/western hemlock forest zone of western Washington. One of the groups (Group 4) was composed of landscapes dominated by younger seral stages and high contagion or clumpiness. This type was typified by forests in varying stages of regrowth, having approximately equal proportions of patches in the clearcut, young, and mature seral stages with little, if any, old growth. This suggests a managed landscape harvested in rotations. We focused our study-site selection efforts at landscapes within this group to ensure that the stands we selected for wildlife sampling would be located in intensively managed forest landscapes. These landscapes provided similar seral stages, an intensive management history, and a variety of patch sizes and configurations to choose from.

Selection of Study Areas

We then used our reclassified satellite imagery, topographic maps, orthophotos, and ground reconnaissance to locate our primary study areas within sub-basins classified in Group 4 in the area encompassed by the 19 WRAs. We initially focused our efforts on Weyerhaeuser and DNR lands in the southern Cascades near the Columbia River. We excluded this area from further consideration, however, because we typically encountered only extensive areas containing very large patches dominated by only 1 or sometimes 2 of our target age classes. In addition, we found that many areas to the south were not suitable due to confounding environmental influences from the Yacolt burn, the 1980 eruption of Mount St. Helens, or high amounts of residual old growth.

After several months of reconnaissance, we decided to locate 20/24 study sites on the Kapowsin and Buckley tree farms on land owned and managed by Champion International in southern Pierce County. The remaining 4 stands are located in the Vail Tree Farm on land owned and managed by Weyerhaeuser (Fig. 3). We chose these study areas for a number of reasons:

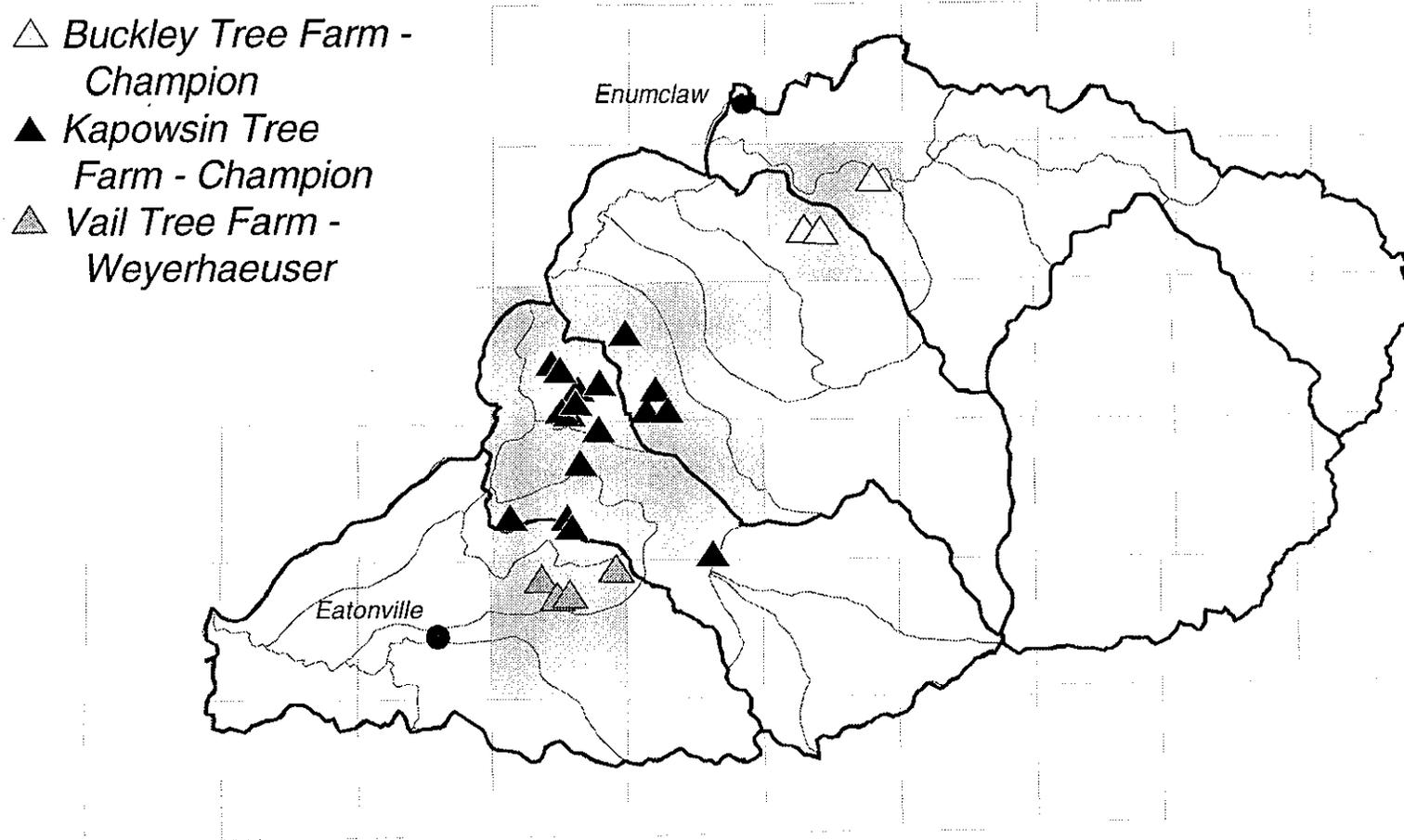


Fig. 3. Map of the 24 TFW Landscape study sites by ownership; sites were located in 4 WRIAs and 7 WAUs.

the landowners were extremely cooperative and were clearly interested in participating in the study; the area had been entirely cutover in the last 70 yrs or so, and is virtually devoid of residual old growth; there is a great deal of heterogeneity in stand composition and juxtaposition on these tree farms; much of the area is fragmented into many relatively small patches; and, lastly, it is only about 1 hour's drive from both Seattle and Olympia, which kept logistical constraints and travel costs to a minimum.

We selected a total of 24 stands: 6 replicates in each of 4 structural classes in stands ranging in size from 80-200 ac.

Description of the 4 Structural Classes

General Selection Criteria

No entry for 3 years (thru December 1995)

Within 1/2 mile of road; year-round access to sites

Avoid stands with riparian zones larger than headwater creeks (i.e., no large riparian zones with distinctive vegetation)

Must have a 75 x 75 m area where target structure is present for pitfall grid

Stands should contain Douglas-fir as the dominant species

Bogs/marshes OK if minor component of stand

Steep slopes OK as long as site is not excessively drained or too steep for effective pitfall trapping

Roads OK as long as contiguous area is present for pitfall grid

Elevation < 3000 ft

Structural Class 1 - Clearcut Stage

Site characteristics at the initiation of sampling include the following:

Age: 2-3 yr since cutting

Tree Height: Herb stratum; seedlings generally < 3 ft tall

Reproduction: Planted, or natural regeneration in progress.

Other Species Present: Weedy invaders, red alder.

Landscape Context: Adjacent stands at least 5 yr older.

Structural Class 2 - Pre-Canopy Stage

Age: 12-20 yr

Tree Height: Mid-canopy approx. 20-30 ft tall

Silvicultural Treatment: Pre-commercial thinning has occurred in stand within the last 5 yr.

Other Species Present: Red alder, big-leaf maple, shade tolerant conifers; herbs and shrubs present in lower strata.

Landscape Context: Adjacent stands recently clearcut or with fully developed tree canopy.

Target Stand Structure: Canopy closure is mid-way between clearcut and a fully closed canopy. Lower branches on conifers dead or dying. Light interception at ground level is high; light reaches ground between trees. Low to moderate amounts of slash resulting from thinning operation may be present.

Structural Class 3 - Closed-Canopy Stage

Age: 30-40 yr

Tree Height: Full canopy height

Silvicultural Treatment: Not yet commercially thinned, history of pre-commercial thinning preferable, but not required.

Other Species Present: Few, maybe some residual alders or maples in patches. Little or no herbs or shrubs present.

Landscape Context: Adjacent stands in any other stand structure.

Target Stand Structure: Stand is densely stocked with a wide range of stem diameters. Light interception within stand is low. Small snags and forest floor woody debris common in stand.

Structural Class 4 - Harvest Stage

Age: 50-70 yr

Tree Height: Full canopy height

Silvicultural Treatment: Stand has been commercially thinned, history of pre-commercial thinning preferable, but not required.

Other Species Present: Herb and shrub layers re-established, salal, Oregon grape, and *Vaccinium* typically present; vine maples occur in openings, sword fern in moist sites.

Landscape Context: Adjacent stands in any other stand structure.

Target Stand Structure: Uniform stem diameters; trees widely spaced with a stocking level of approx. 100-150 trees per acre. Canopy closed, but light is filtering into stand.

Sampling Methodologies

We surveyed vertebrate communities at the stand scale using techniques that provide estimates of species abundances. All taxa were sampled for 3 consecutive years (fall 1992 through spring 1995) to provide an adequate index of temporal variation in wildlife community composition. We implemented more intensive studies for 2 species groups (northwestern salamanders and bats) that we predicted would be sensitive to the effects of forest fragmentation.

Terrestrial Amphibians and Small Mammals--We sampled terrestrial amphibians and small mammals with pitfall traps. Thirty-six traps were placed in a 6 x 6 grid with 15-m intervals between traps in each stand. We opened pitfall traps after the onset of fall rains, which usually occurred in early October, checked each trap weekly for a total of 4 weeks. Mean captures were used to compare relative abundance estimates among structural classes and to investigate patterns of association with various stand and landscape-scale habitat variables.

Breeding Birds--We used a modified point count method for surveying bird populations. The point count method is superior to other methods for sampling forest birds due to relatively poor visibility in forested habitats, and the rugged topography typical of Washington mountains. The modified point count method we used involves estimating the distance to birds detected within 50 m, and then simply recording birds seen or heard in 1 of 2 concentric bands beyond 50 m: 51-75 m and >75 m. Twelve evenly spaced bird-count points (or stations) were located within each stand. Points were spaced 100 m apart and located at least 50 m from the edge of the stand. Counts began within 15 minutes of dawn and were completed within 3 hours. During the survey period, the observer recorded the birds heard or seen for a period of 8 minutes. Each stand was surveyed 6 times each year between mid-April and mid-June. Surveys were spaced throughout the breeding season to account for different breeding phenologies of bird species in this region.

Bats--We sampled bats using ANABAT II automated divide-by-N ultrasonic detectors. These devices yield a frequency count of bat passes per unit time by automatically recording bat echolocation calls on cassette tape after they have been electronically transformed into frequencies audible to humans. We sampled bats on each site for 2 nights in June, July, and August, and used several bat detectors (5 or 6) simultaneously so that we could complete the surveys each month within a 2-week period.

Vegetation--We measured general site characteristics and structural and vegetational components of stands at 3 scales in each pitfall grid and at each bird sampling point (Figure 4). We sampled herbs, low shrubs, and ground cover in 3 x 3 m square plots (9 m²); tall shrubs, small to medium-sized trees and snags (≤ 50 cm d.b.h.), and coarse woody debris in 15 x 15 m square plots (225 m²); and large trees, snags, and stumps (>50 cm d.b.h.) in 45 x 45 m square plots (2025 m²). Sampling included live and dead tree densities by species according to height and diameter classes, percent cover, and presence/absence variables.

We used 3 decay-classes to characterize logs: intact (bark intact, freshly fallen); moderately decayed (bark sloughing to absent, sapwood soft); and well-decayed (log completely in contact with the ground, bark absent, and all wood soft). For snags, we used the same 3 decay-classes, but with slightly different definitions: intact (bark and branches mostly intact, sapwood firm); moderately decayed (limbs either stubs or absent, sapwood soft); and well-decayed (all wood soft, bark and sapwood usually sloughed). We defined fine woody debris as logs (or leaning snags at < 45° angle) < 10 cm in average diameter and coarse woody debris as ≥ 10 cm in average diameter.

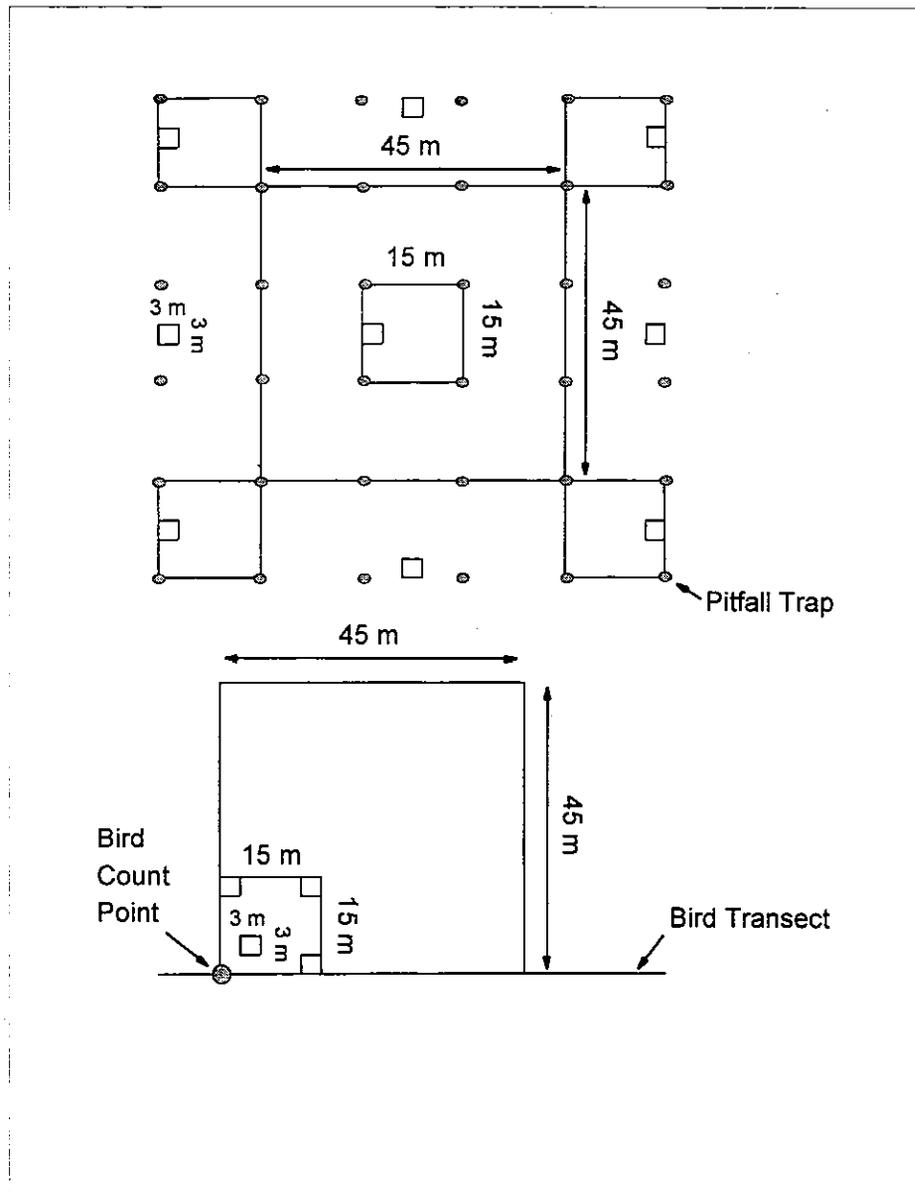


Fig. 4. Configuration of vegetation sampling plots on pitfall grids and bird count points.

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Avian Habitat Occupancy Patterns in Managed Douglas-fir Forests in the Western Washington Cascade Mountains

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The primary objectives of this study were to describe bird species composition and abundance across a gradient of seral managed Douglas-fir forests and to develop methods to evaluate avian habitat occupancy patterns at a landscape level. The study design included 24 managed forest stands consisting of 6 replicates in each of the following four structural age-classes: type A (early regeneration stage: 2-4 years old), type B (pre-commercial thin stage: 12-20), C (commercial thin stage: 30-40) and D (harvest age: 50-70).

Whether a species occupies a given location depends on four sets of factors: 1) various temporal aspects such as territoriality and seasonal residency patterns; 2) within-stand structural characteristics, 3) landscape level considerations such as patch size and shape; and 4) special habitat features that include snags and woody debris.

Seventy-three bird species were recorded in this study. Total age class species richness varied from 35 in the commercial thin stage to 50 in the pre-commercial thin stage (Figure 1). The avifauna of the early regeneration stage differed substantially from later stages since a typical forest environment had not yet developed. Species such as orange-crowned warbler, willow flycatcher, white-crowned sparrow, American goldfinch, dark-eyed junco, rufous-sided towhee, and song sparrow were common in this type of habitat but were either absent or in small numbers in later stages

There were substantial variations in the numbers of species occupying individual stands (Figure 2). In stage A, number of species varied from 18 to 30. In stage D, the largest number of species was 31, whereas the lowest was 20. Presumably, differing structural or landscape-level factors contributed to these differences.

Total avian abundance followed a similar pattern as that shown by species richness in that the lowest levels were found in stage C (Figure 3). The ten most abundant species were (in descending order of abundance): winter wren, Pacific-slope flycatcher, golden-crowned kinglet, chestnut-backed chickadee, dark-eyed junco, white-crowned sparrow, Wilson's warbler, hermit-Townsend's warbler, Swainson's thrush, and song sparrow (Table 1). These 10 species made up 69% of all bird detections. Total bird abundance sometimes varied substantially among stands within a stand type (Figure 4). Furthermore, individual species showed dramatic differences in abundance among stands. For example, total winter wren detections for all stands in stage B sites varied from about 24 to almost 120 (Figure 5). Likewise, similar variability was shown by the white-crowned sparrow in clear-cuts. Several species showed a clear and predictable pattern of habitat occupancy. The winter wren, for example, is primarily a bird of forest habitat and so it is largely missing in the breeding

season from early regeneration sites (Figure 6). Even so, it still shows differences in abundance within the forest landscape.

Based on the habitat occupancy patterns described here and our current knowledge of habitat needs of bird species, forest managers should probably be most concerned with three groups of birds: cavity-nesters, conifer seed-eating finches, and the Vaux's swift. Among the cavity-nesters, the red-breasted nuthatch shows the largest disparity in abundance between natural and managed forests (e.g. Manuwal 1991). The pine siskin and evening grosbeak were less abundant in managed forests than natural ones. Because they depend on a variety of tree species for seeds, a reduction in tree species diversity might reduce their numbers, especially in years when Douglas-fir does not produce cones. The absence of the Vaux's swift, an aerial insectivore, is potentially most troubling from a conservation perspective. This species is a colonial species that nests in large hollow trees. The rarity of hollow large trees in managed forests undoubtedly impacts this species' habitat occupancy pattern.

Figure 1. Number of Bird Species Detected in Each of Four Forest Age Classes, 1993-95.

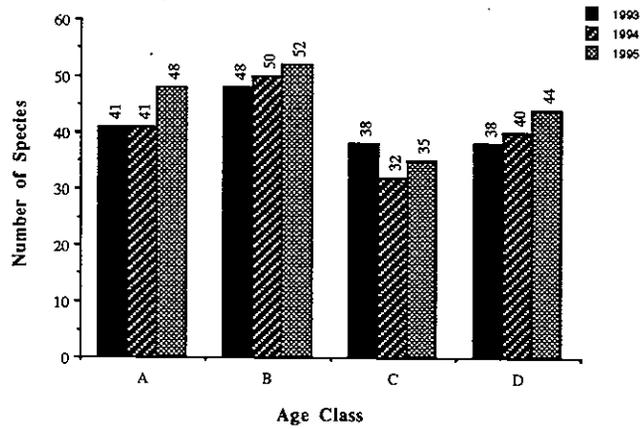


Figure 2. Variation in the Number of Bird Species Detected in Six Managed Forest Sites, 1993-95.

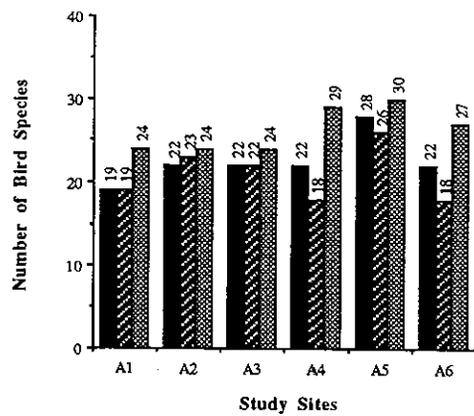


Table 1. Most abundant bird species in managed Douglas-fir forests in the Western Washington Cascades

Species	No. Detections	Percent of Total	Stage Age (yrs)
winter wren	3171	15.5	D 50-70
Pacific-slope flycatcher	1892	9.3	D 50-70
golden-crowned kinglet	1883	9.2	C 30-40
chestnut-backed chickadee	1487	7.3	D 50-70
dark-eyed junco	1169	5.7	A 2-4
white-crowned sparrow	1137	5.6	A 2-4
Wilson's warbler	961	4.7	B 12-20
hermit-Townsend's warbler	881	4.3	C 30-40
Swainson's thrush	755	3.7	B 12-20
song sparrow	675	3.3	A 2-4
Cumulative percent		68.6	

Figure 3. Total Number of Birds Detected in Four Age Classes of Forests in 1993-95.

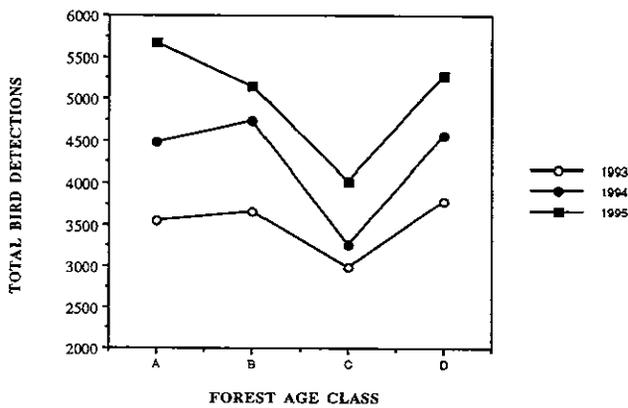


Figure 4. Total Bird Detections by Forest Stand Age Class in 1994.

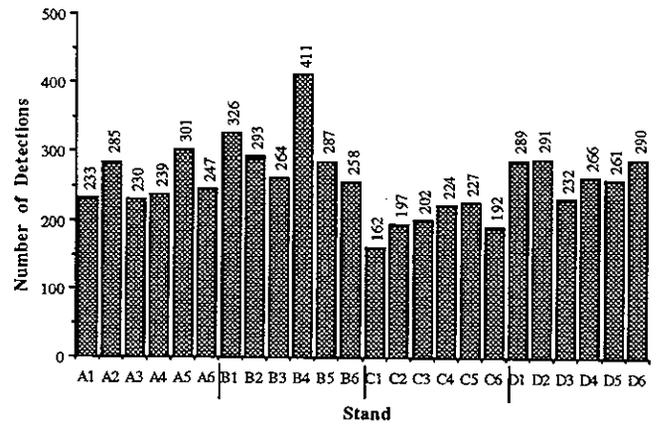


Figure 5. Variation in the Number of Winter Wrens Detected in Six Stands 12-20 Years Old.

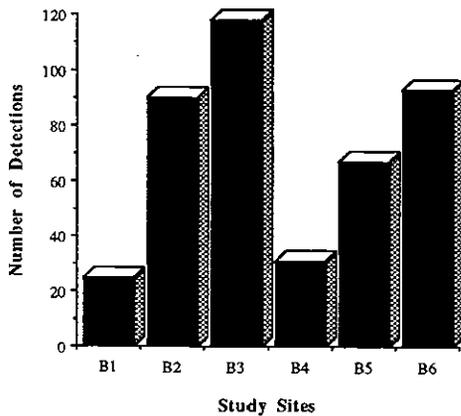
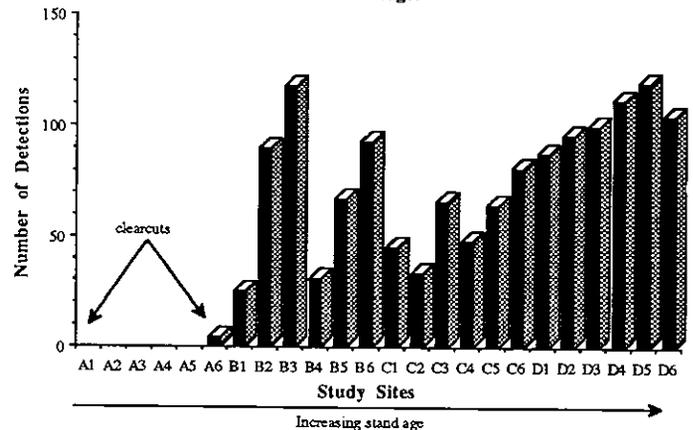


Figure 6. Variation in Abundance of Winter Wrens Across the Gradient of Forest Ages



Amphibian Survey Results: Habitat Occupancy Patterns

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AMPHIBIAN CAPTURES

Three years of pitfall trapping resulted in capture of 842 amphibians of 11 species (Table 1). Three species dominated the terrestrial amphibian communities in all 4 structural classes: the Northwestern salamander, western redback salamander, and ensatina. These 3 species each accounted for over 200 captures; no other species had more than 34 captures. Each of the 4 structural classes was unique in community composition (Fig. 1). Clearcut stands were dominated by western redback salamanders, with relatively low captures of northwestern salamanders and ensatinas. Roughskin newts were captured most frequently in this structural class. Pre-canopy stands had relatively high diversity, but were dominated by northwestern salamanders. Other species present in relatively high numbers included western redback salamanders, ensatinas, roughskin newts, and tailed frogs. Tailed frogs were captured in highest numbers in this structural class. Closed-canopy stands were similar in community structure to Pre-canopy stands, but had virtually no captures of species other than the 3 dominant ones. The Harvest-age class was the only class in which all 11 species were captured at least once; western toads and long-toed salamanders were only captured in this structural class. Harvest-age communities were dominated by ensatinas, but also had high captures of western redback and northwestern salamanders. Although sample sizes were low, red-legged frogs were over 5 times more abundant in this structural class than in any other. Total captures of amphibians in this age class was almost twice as high as in any other class.

SPECIES RICHNESS

Species richness differed significantly among structural classes (Fig. 2). Harvest-age stands had the highest mean richness, whereas Closed-canopy stands were depauperate. Clearcut and Pre-canopy stands were similar and intermediate in mean species richness. Closed-canopy stands had significantly lower species richness than either Clearcut or Harvest-age stands. In accordance with findings in other studies, however, amphibian species richness in forested habitats in this region is negatively and significantly correlated with elevation; i.e., as elevation increases, species richness decreases proportionately (Fig. 3). Because amphibians are ectotherms and generally avoid cold climatic conditions, such a relationship is not unexpected. However, since there is variation in the elevational range of the stands sampled, whereby most Clearcuts were at lower elevations and most Closed-canopy stands were at higher elevations, this relationship is a potentially confounding influence on comparisons among structural classes. It is noteworthy that all species captured during previous amphibian surveys in late-successional forests in this area of Washington also occur in the intensively managed forest landscapes we surveyed.

Amphibian Community Composition

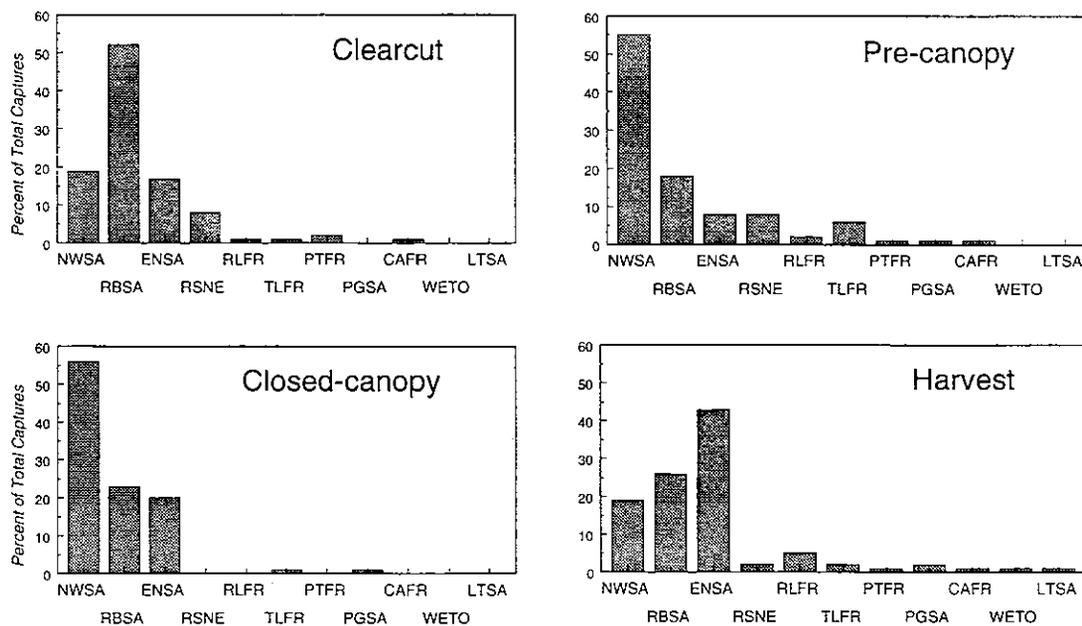


Fig. 1. Histograms showing the percent contribution of each species to total captures within each structural class.

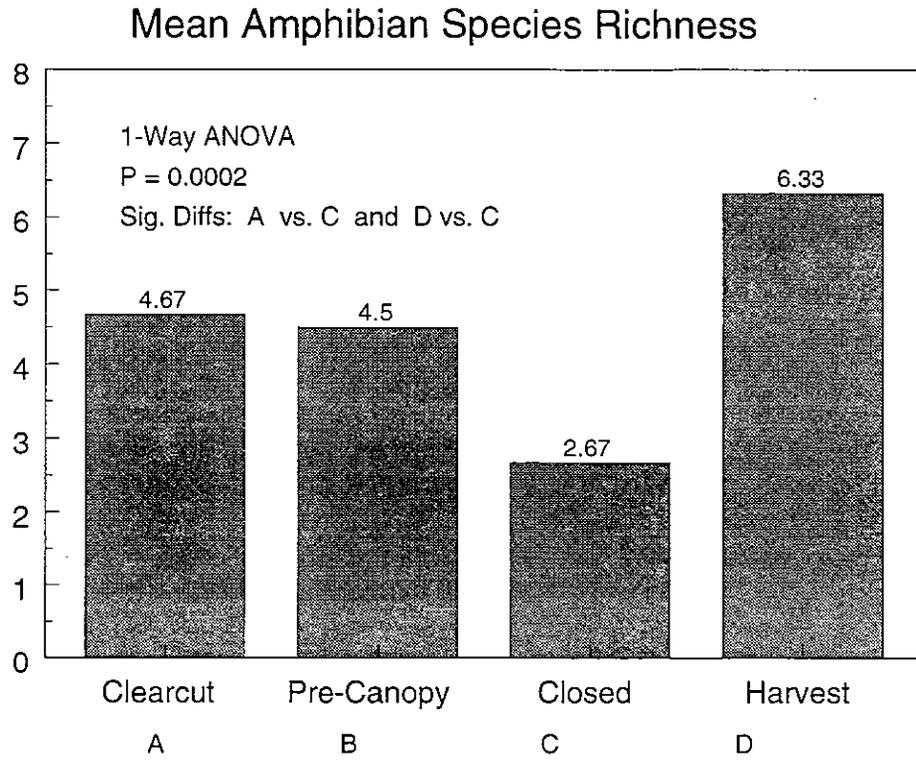


Fig. 2. One-way ANOVA of mean amphibian species richness among structural classes.

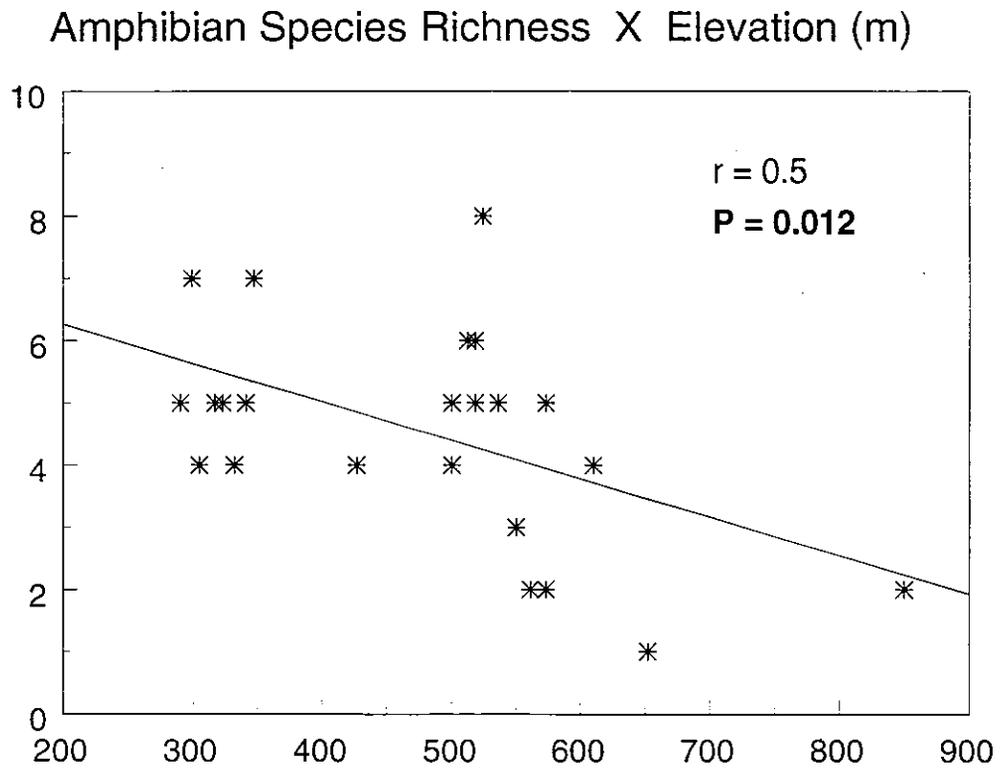


Fig. 3. Linear regression of cumulative amphibian species richness per stand on elevation.

Table 1. Total captures of all amphibian species by structural class, 1993-1995.

SPECIES	CLEAR-CUT	PRE-CANOPY	CLOSED-CANOPY	HARVEST	TOTAL
Northwestern salamander	37	85	95	60	277
W. red-back salamander	102	28	39	84	253
Ensatina	33	12	34	137	216
Roughskin newt	15	12	0	7	34
Red-legged frog	2	3	0	17	22
Tailed frog	1	9	1	5	16
Pacific treefrog	4	2	0	4	10
Pacific giant salamander	0	2	2	5	9
Cascades frog	1	1	0	1	3
Western toad	0	0	0	1	1
Long-toed salamander	0	0	0	1	1
TOTAL	195	154	171	322	842

COMPARISONS OF ABUNDANCE ACROSS STRUCTURAL CLASSES

Of the 11 species captured, only 5 had more than 20 total captures. Comparisons across the structural classes were only made for these 5 species. Northwestern salamanders were captured most frequently in Pre-canopy and Closed-canopy stands. A 1-Way ANOVA of mean captures among structural stages, however revealed no significant differences (Fig. 4). Captures for western redback salamanders exhibited the reverse of this pattern, with the highest number of captures occurring in Clearcut and Harvest-age classes. As with northwestern salamanders, however, none of the differences among structural classes were significant (Fig. 5).

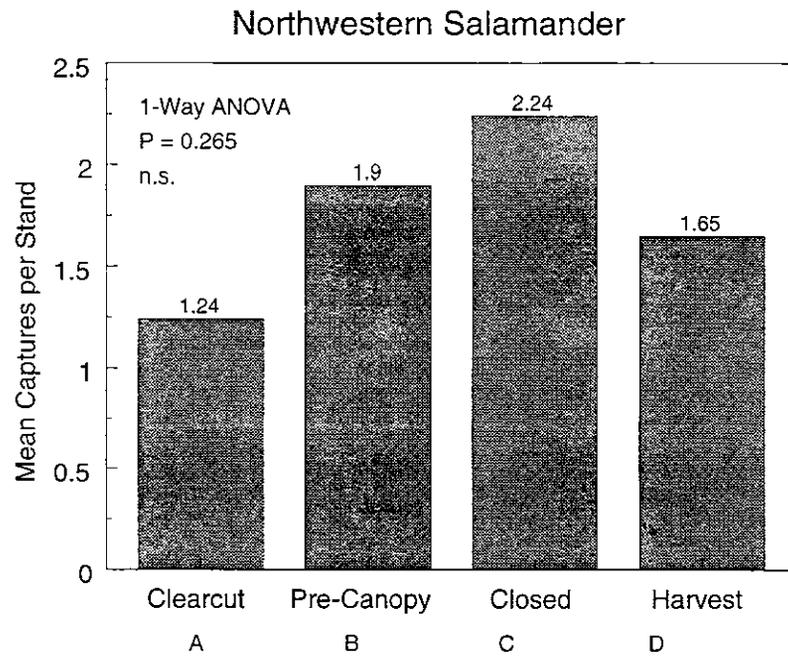


Fig. 4. One-way ANOVA of mean northwestern salamander captures among structural classes.

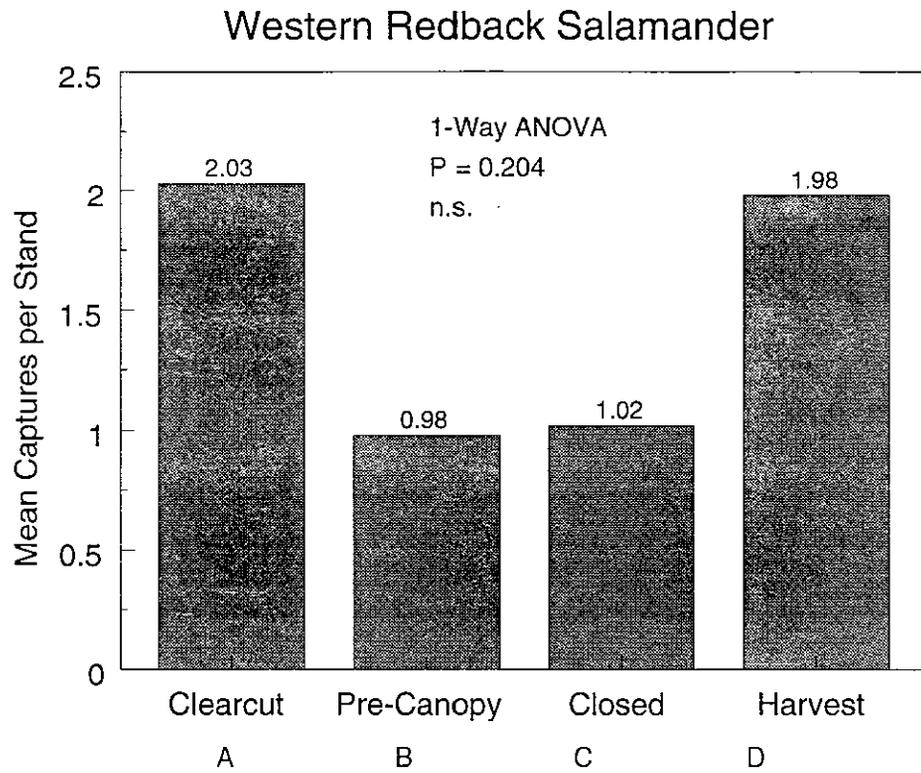


Fig. 5. One-way ANOVA of mean western redback salamander captures among structural classes.

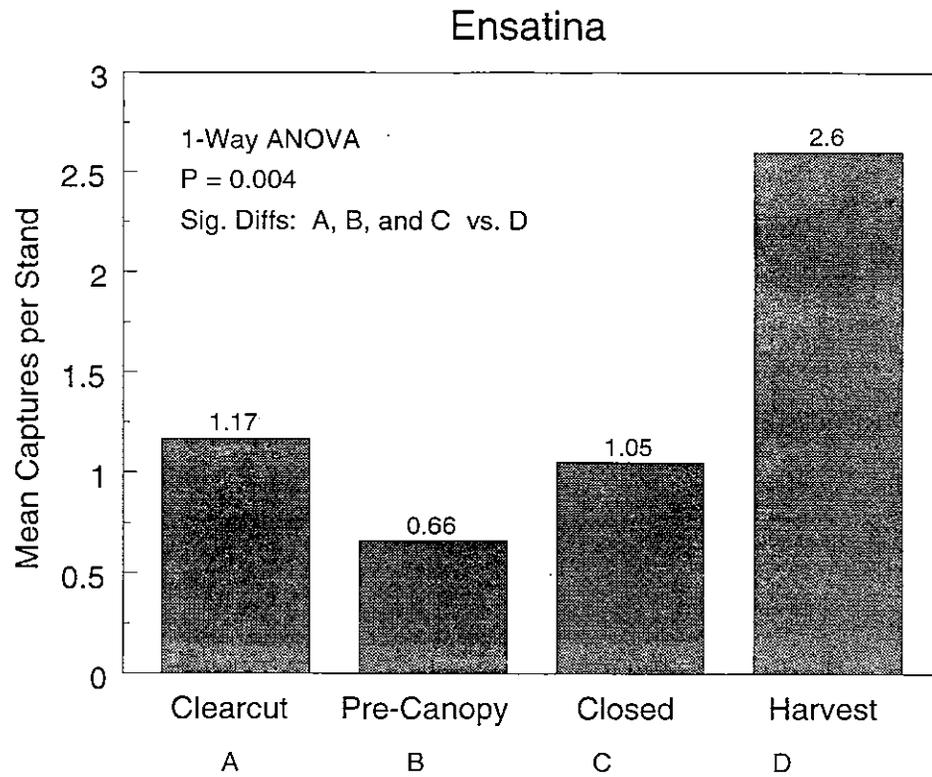


Fig. 6. One-way ANOVA of mean ensatina captures among structural classes.

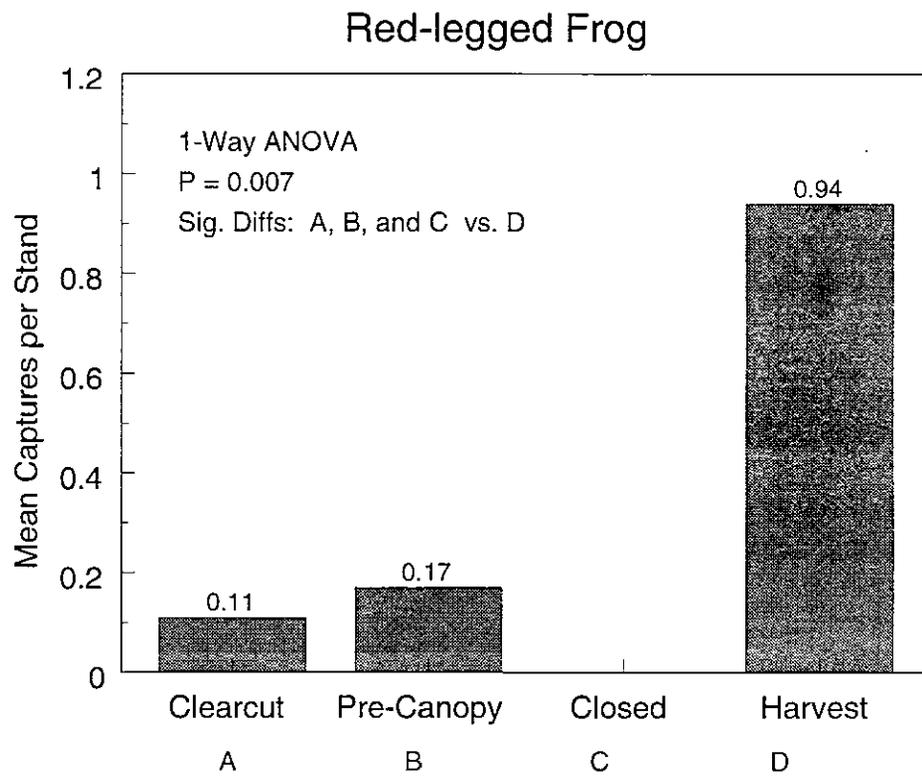


Fig. 7. One-way ANOVA of mean red-legged frog captures among structural classes.

Both the ensatina and the red-legged frog were significantly more abundant in harvest-age stands than in any other structural class. Patterns for all 4 of these species were consistent among years, Repeated Measures ANOVA revealed no significant interactions between structural class and year. Abundance patterns did vary from year to year for the roughskin newt, however. In 1992, captures were significantly higher in Clearcuts than in Closed-canopy stands, but in subsequent years, no pattern was evident. For this reason, and because sample sizes were relatively small, comparisons of abundance values among structural classes were not made for this species.

Significant effects of elevation on amphibian species' abundances were also evident. Abundance values for all 5 species used in the analyses are significantly associated with elevation (Table 2). With the exception of northwestern salamanders, all species were negatively associated with elevation. Northwestern salamanders are common in subalpine zones and are known to occur at elevations exceeding 3,000 m. Although the presence or absence of potential breeding ponds may strongly influence patterns of relative abundance, these results indicate that, unlike the other 4 species analyzed, northwestern salamanders prefer higher elevations. This could result from lesser competition with other species of pond-breeders, most of which favor lower elevations and warmer water temperatures.

Table 2. Results of linear regressions of Elevation on Mean Captures for all species with >20 captures.

	Northwestern Salamander	Western Redback Sal.	Ensatina	Roughskin Newt	Red-legged Frog
Correlation Coeff.	0.66	- 0.68	- 0.40	- 0.46	- 0.43
P Value	0.000	0.000	0.05	0.023	0.034

Small Mammal Survey Results: Habitat Occupancy Patterns

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The goal of the small mammal work was to compare the occupancy patterns of small mammals across the four structural classes [clearcut (A), canopy closure (B), young unthinned (C), and mature (M)] identified for study. Although patterns of habitat occupancy are fairly well understood in such forest classes for some of the common rodents, our understanding of the patterns for many insectivores and the smallest rodents remains poor. To sample those species that are often underrepresented in capture totals generated from box and snap traps, we used pitfall traps which simultaneously sampled terrestrial amphibians. Thirty-six traps were set in a 6 X 6 array with 15-m spacing and operated continuously for 4 weeks beginning in the first week of November 1992, 1993, and 1994.

Over the 3-year period 3,720 individuals of 18 species were captured (Table 1). Reflecting the capture method, most of these were Insectivores (2,564). The remaining captures consisted of rodents (1,134) and ermine (22). For species with at least 20 captures I analyzed habitat occupancy patterns using repeated measures ANOVA of sites across years after logarithmically transforming the capture totals. Where significant interactions were found between forest structural class and years, I tested for differences among classes and years with separate one-way ANOVAs and Tukey's HSD test for multiple comparisons. At least 20 individuals were captured for 13 of the 18 total species (Table 1). Statistically significant differences ($\alpha=0.05$) among structural classes were found for nine species (vagrant shrew, montane shrew, marsh shrew, Trowbridge's shrew, shrew-mole, coast mole, creeping vole, forest deer mouse, and ermine) with strong trends ($P\leq 0.08$) for two others (southern red-backed vole and deer mouse). Statistically significant differences among years were found for six species (marsh shrew, shrew-mole, creeping vole, long-tailed vole, Townsend's vole, and ermine). The most common pattern was for a given species to favor early (Figure 1) or mature (Figure 2) classes. Only the forest deer mouse favored the young unthinned forest (Figure 3). Differences among years were more pronounced in the rodents, which reached highest abundance in 1994 and showed a disproportionate preference for the clearcut forest class. Average species number per site reflected these general trends and was significant across classes and years for both insectivores and rodents.

To see whether the patterns of habitat occupancy as revealed by the capture totals would yield distinct small mammal communities across the structural classes, I added detections of Townsend's chipmunk and Douglas squirrels taken in the breeding bird surveys to the capture totals and clustered the resultant species by site matrix into a hierarchical tree using Pearson similarity coefficients. This procedure grouped sites most similar in their mammalian composition and abundance at the left of the tree and more dissimilar sites to the right (Figure 4).

Agreement between the four structural classes and the resultant mammalian clusters was very good, indicating the strong influence that the plant communities had on the small mammal communities.

Although the study was established primarily to elucidate the influence of structural classes on small mammal communities, I investigated the effect that watershed context might have on the communities by overlaying the Watershed Administrative Unit (WAU) designation for each site on the hierarchical tree. If adjacent or surrounding sites had a strong influence on small mammal communities, one should see a pattern of WAUs segregating with respect to the mammalian clusters. This did not seem to be the case, and typically a given WAU occurred across clusters.

Of the five species caught in numbers insufficient for statistical analysis, two are not sampled well with pitfall traps. Northern flying squirrels and Townsend's chipmunks must be studied with other techniques. The masked shrew has a very large species range in North America, but this region is the southwestern edge of its continental distribution where it is rarely encountered and its habitat affiliations largely unknown. The water shrew occurs at higher elevations than the sites in this study and is a riparian habitat specialist. The Townsend's mole is found commonly in deep soil at low elevations in western Washington, and is replaced at higher elevations and in shallower soil by the coast mole.

These small mammal communities are quite sensitive to the differences among structural classes. It should be possible to predict with reasonably good accuracy the species memberships in forested sites with similar structural features, and plan for desired mammalian communities. Species numbers and individual species' abundances were greatest in early and mature classes. The young unthinned forest class, characterized by a dense, closed canopy and very sparse understory was strikingly depauperate. This class should be moved toward the structure of a mature class to enhance the productivity of its small mammal community. This may be best achieved by vigorous thinning. The only species found in this class in consistently high numbers was the forest deer mouse, a species that will do very well in mature and old forest conditions.

Table 1. Pitfall captures of small mammals in clearcut (A), canopy closure (B), young unthinned (C), and mature (D) forest classes 1992-1994.

SPECIES	FOREST STRUCTURAL CLASSES			
	A	B	C	D
INSECTIVORES				
Vagrant shrew	92	41	10	18
Montane shrew		75	114	60
Water shrew	0	0	1	0
Marsh shrew	4	18	7	28
Trowbridge's shrew		224	517	423
Masked shrew	0	2	0	0
Unidentified shrew		8	8	7
Shrew-mole	34	43	21	110
Coast mole	2	11	6	1
Townsend's mole		1	2	1
RODENTS				
Townsend's chipmunk	0	4	0	1
Northern flying squirrel	0	1	4	2
Deer mouse	115	68	27	38
Forest deer mouse		6	42	87
Unidentified deer mouse	51	9	2	9
Southern red-backed vole		3	22	12
Creeping vole	335	68	5	43
Long-tailed vole		10	11	1
Townsend's vole		5	12	0
Unidentified vole		1	0	0
CARNIVORES				
ermine		12	7	1

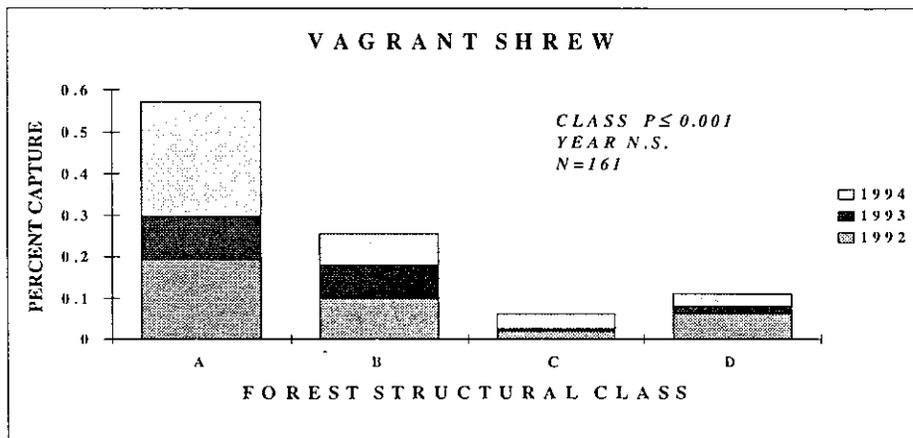


Figure 1. Percent capture of vagrant shrews across forest structural classes.

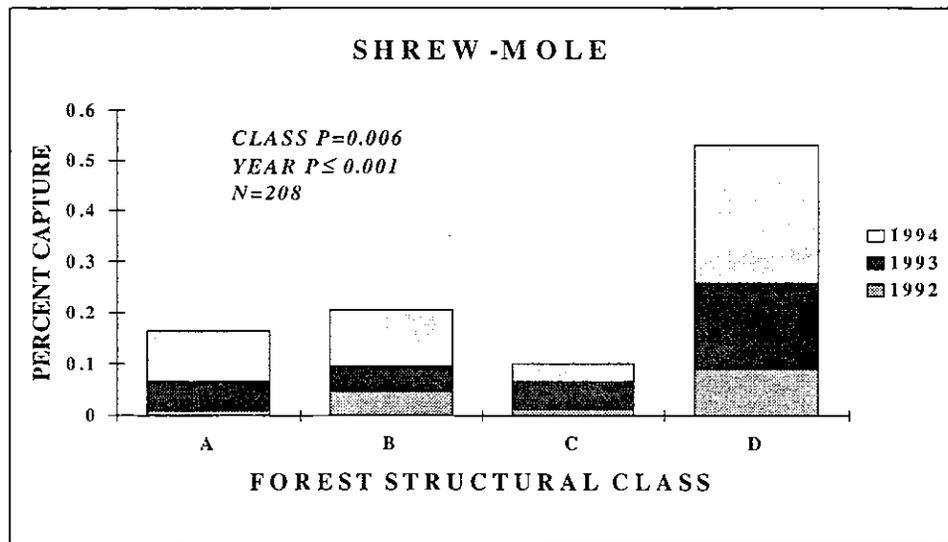


Figure 2. Percent capture of shrew-moles across forest structural classes.

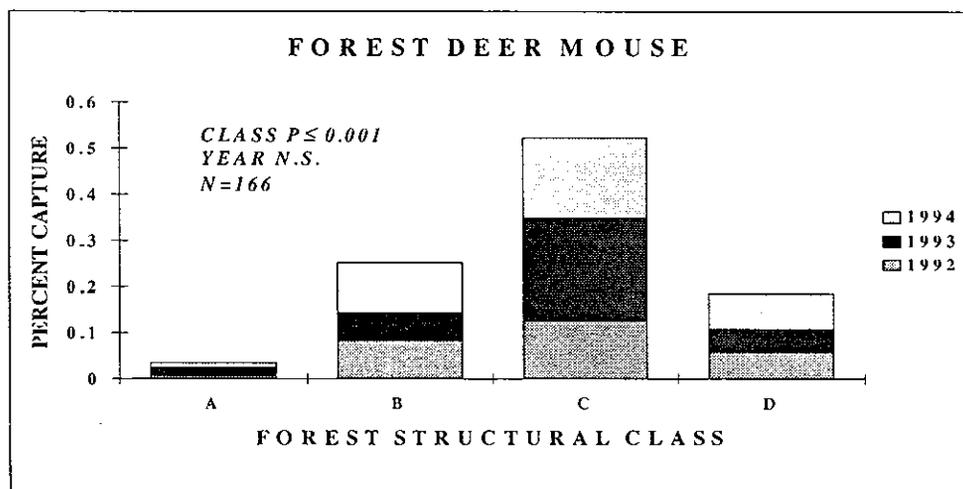


Figure 3. Percent capture of forest deer mice across forest structural classes.

SITES CLUSTERED BY MAMMALIAN CAPTURES

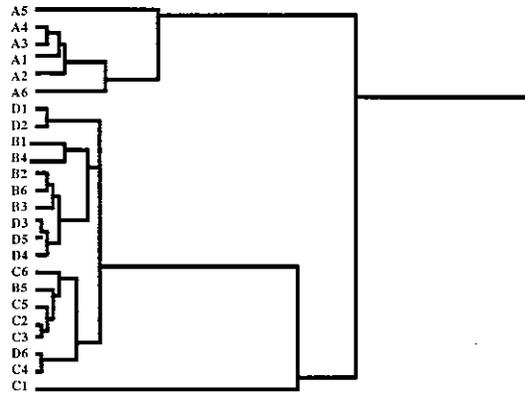


Figure 4. Small mammal community similarity clustering. Sites with similar small mammal communities join to the left of the tree, dissimilar sites join to the right. Sites labeled by forest structural class: clearcut (A), canopy closure (B), young unthinned (C), and mature (D).

Bat Survey Results: Habitat Occupancy Patterns

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Among mammals of their size, bats are unique in having long lives, low reproductive rates and relatively long periods of infant dependency. This combination of characteristics places them at risk of population decline in the presence of habitat alteration. In western Washington, where approximately 9.6 million acres of forest is managed for timber harvest, there is growing concern over the status of forest-dwelling bats. Mitigating for effects of timber management activities is difficult due to a lack of knowledge concerning bat response to forest age and structure.

In 1983, the U.S. Forest Service's Old Growth Wildlife Habitat Program (OGWHP) was initiated to determine the degree to which wildlife, including bats, were associated with old growth Douglas-fir (*Pseudotsuga menziesii*) stands. Using ultrasonic detection, bat activity was monitored over a broad range of unmanaged forest conditions in the southern Washington Cascade and Oregon Coast Ranges. In Washington, detection rates were 2.5 to 9.8 times greater in old growth (200+ yrs.) than in younger stands (35-195 yrs.). These findings suggest that old-growth is an important habitat for forest dwelling bats and that its conversion to younger managed stands may be detrimental to bat populations.

Recognizing the need to extend research from unmanaged to managed stands, a stand-level survey of bat activity within intensively managed forests in the western Cascade range was conducted during the summers of 1993 and 1994. Using ANABAT II bat detectors, six sites from each of four distinct seral stages were surveyed for bat activity. Over 2500 hrs. were monitored resulting in a total of 967 echolocation calls recorded. Overall, activity levels were low with 46.2% of the nights having no detections. The number of detections were not significantly different between years, but were different among seral stages (Table 1). The differences in bat use among seral stages are likely related to the differential availability of food and roost resources.

The highest detection rates were recorded in clearcut stands while young unthinned stands had no detections. The high detection rate, presence of feeding buzzes, and low abundance of roosting structures within clearcut stands suggest these sites were used for foraging. The absence of activity in young unthinned sites suggests that these stands were unsuitable habitat for forest dwelling bats. Although a high density of snags were present, these were typically small-diameter Douglas-fir whose lack of crevices and hollows make them unlikely roost sites.

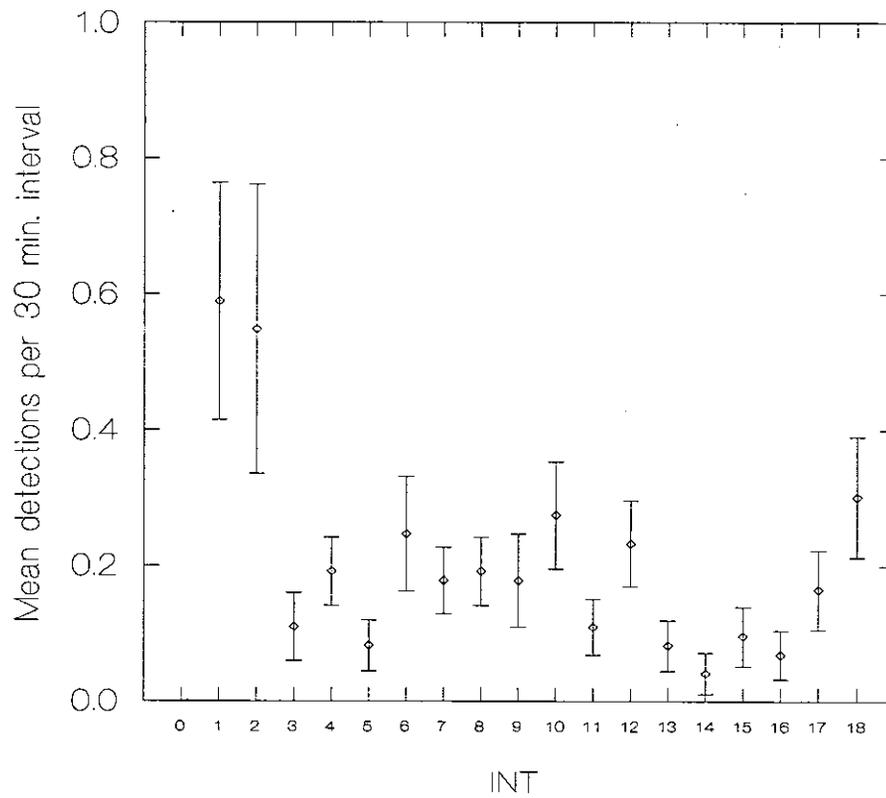
Mature sites had the second highest detection rates and were the only seral stage to have a secondary peak in activity during the early morning hours (Fig. 1). This pattern is easily reconciled with a pattern of intensive feeding, night roosting, and a second period of feeding before returning to the day roost.

If this interpretation of the observed activity patterns is accurate, it would appear that some species of forest dwelling bat can also roost in mature second-growth. Large trees (50-100 cm d.b.h.) and snags (>50 cm d.b.h. and > 15 m tall), which are "roost-type" trees for certain species in Washington state, were most abundant in these stands. Suitable roosting conditions may not be present for all forest dwelling species, however, as suggested by the absence of calls for the big brown bat and silver-haired bat within the mature stands.

Table 1. Mean detection rates for bats in clearcut (CC), pre-commercially thinned (PCT), young unthinned (YU), and mature (M) stands. Where ANOVA was significant, means not significantly different from each other are indicated with letters; $\alpha = 0.05$.

Species	CC	PCT	YU	M
	x (se)	x (se)	x (se)	x (se)
Big brown bat	0.808 (0.185)	0.031 ^a (0.021)	0 ^a	0 ^a
Silver-haired bat	2.327 (0.627)	0.407 ^a (0.164)	0 ^a	0 ^a
Townsend's big-eared bat	0.113 ^a (0.056)	0.031 ^a (0.021)	0 ^a	0 ^a
Hoary bat	0.587 ^a (0.267)	0.150 ^a (0.080)	0 ^a	0.194 ^a (0.194)
Myotis group	2.093 ^a (0.580)	0.405 ^b (0.157)	0 ^b	1.959 ^a (0.532)
Yuma myotis	0.788 ^{abc} (0.329)	0.394 ^{ab} (0.210)	0 ^{bc}	0.910 ^a (0.224)
All <i>Myotis</i> spp.	1.107 ^{ab} (0.262)	0.408 ^{ac} (0.160)	0 ^c	1.266 ^b (0.248)
All Non- <i>Myotis</i>	0.834 (0.200)	0.154 ^a (0.061)	0 ^a	0.053 ^a (0.039)
TOTAL	7.504 ^a (1.300)	1.989 ^{b,c} (0.652)	0 ^b	4.058 ^c (0.738)

Figure 1. Mean number of detections per interval in mature stands.



Nesting Success and Habitat Selection of the Pacific-slope Flycatcher in the Southern Cascades of Washington

Scott F. Pearson

Introduction

Predation is the major factor influencing reproductive success of open-nesting birds across geographic locations and habitat types. There is evidence that birds use nest sites with characteristics that reduce the risk of predation. Therefore, given that birds choose habitat features that increase chances of nesting success, identification of such features is important for effective management. Features critical to nesting success are more likely to be identified in areas with high levels of nest predation because selective pressures will be very strong. The influence of habitat structure on predation rates may vary with distance from the nest, therefore it is necessary to consider different spatial scales in studies of predation.

Here I examine nesting success and habitat selection by the Pacific-slope Flycatcher (*Empidonax difficilis*) in the southern Cascades of Washington. The Pacific-slope Flycatcher is an open-cup nesting neotropical migrant. It breeds in the coniferous forests of the Pacific states west of the Cascades and Sierra Mountain Ranges. In this study I examine the following questions: 1) What is the nesting success rate and what are the major causes of mortality? 2) What are the habitat features that contribute to habitat selection at the nest substrate scale and nest patch scale? 3) Is there a difference in habitat selection between managed and natural forests? The results and discussion below are preliminary and will be submitted to a scientific journal for publication after additional analysis.

Methods

Nesting success and causes of mortality. In 1993 I systematically searched three 10 ha study sites in both managed and natural forest stands. From 1994-1996 field assistants and I located nests in both the study areas and by searching territories located in adjacent forests. Once located, we checked nests every two to three days during egg laying and as fledging approached. Nests were checked every four to five days during the incubation and brooding periods to minimize disturbance. I determined the nesting success rate using the Mayfield method. I considered a nest successful if at least one nestling fledged. I assumed predation to be the cause of nest failure if the eggs or nestlings disappeared from the nest before fledging.

Habitat selection - substrate scale. The following variables were measured on nest substrates and on the nearest potential nest site of the same substrate type: diameter at breast height; nest height; number of branches supporting the nest; percent cover above, below, and on the side of the nest; percent moss cover surrounding the nest; and number of potential nest sites on the substrate.

Habitat selection - nest site scale. I measured nest site variables on three 10 ha sites in natural and managed forests. I measured the following variables in 11.2 m circles centered on nest sites and unoccupied random sites: number of Douglas-fir, red alder, western hemlock, western redcedar, and deciduous trees other than red alder in the canopy; number of deciduous and coniferous trees in the subcanopy; number of snags; percent canopy cover; and percent shrub foliage volume.

Results

Nesting success and causes of mortality. The nesting success rate for 30 nests using the Mayfield method was 17%. Predation was the primary mortality factor, accounting for 56% of the nesting mortality.

Habitat selection - substrate scale. Red alder and snags were the primary nest substrates used, accounting for 72% of all nests. Flycatchers had the highest reproductive success on these two substrates. When comparing habitat features on nest substrates, there was no difference between successful nests and depredated nests. Therefore, for further analyses I pooled successful and depredated nests. When comparing red alder nest trees to random unoccupied red alder trees, Flycatchers selected nest sites with more supporting branches ($p = .027$) and higher cover above ($p = .004$) and on the side ($p = .05$), and with a greater number of potential nest sites ($p = .006$) than expected.

Habitat selection - nest site scale. Natural forests had significantly more red alder trees in the canopy ($p = .01$), more conifer trees in the subcanopy ($p < .0001$), snags ($p < .0001$), and fewer western hemlocks and western redcedars in the canopy ($p = .004$) than managed forests. There was no difference between the means of habitat variables from successful ($n=7$) and depredated ($n=18$) nests. Therefore, for further analyses, I pooled successful and depredated nests. In natural forest stands, Flycatchers selected nest sites with fewer Douglas-fir ($p = .029$) and more western hemlock/redcedar in the canopy ($p = .006$), and more conifers in the subcanopy ($p = .05$) than expected. In managed forest stands, flycatchers selected nest sites with fewer Douglas-fir ($p = .024$) and more red alder trees ($p < .0001$), more conifers in the subcanopy ($p = .002$), and with higher volume of shrub foliage ($p = .06$) than expected. Finally, Flycatchers selected nest sites near a temporary or permanent water source; 50% of the nest plots contained water compared to 6% of the random sites that contained water.

Discussion

Large scale census studies in the southern Cascades of Washington indicate that Pacific-slope Flycatchers are most abundant in wet and riparian sites and in old-growth stands. In this study I looked at relatively young, upland stands with few wet or riparian areas. These conditions, where predation rates were very high and where few suitable habitats or substrates were available for nesting, are ideal for identifying habitat features important to reproductive success.

Like many studies I found no differences between successful and depredated nests at either the substrate or nest site scale; all flycatchers appear to be selecting sites with reduced probability of predation and with favorable foraging conditions. Flycatchers are selecting wet conditions that likely provide ideal foraging conditions (presence of emerging insects). Flycatchers select substrates with relatively high concealment immediately around the nest thereby reducing its visibility to potential predators. In addition, they select nest substrates with many potential nest sites. This outcome supports the "needle in a haystack" theory that states that a nest is placed in a common substrate so that predators must search many potential sites before locating a nest. At the nest site scale, Flycatchers select sites with more potential nest substrates (snags & red alder), and with high shrub and conifer tree cover in the subcanopy. In both managed and natural forest stands, Flycatchers used sites with fewer Douglas-fir trees in the canopy and more conifer trees in the subcanopy than expected. In natural forests, where there were fewer western hemlock/redcedar in the canopy than managed stands, Flycatchers select nest sites with more of these trees than expected. While on managed stands, where there are fewer red alder trees in the canopy and where the shrub foliage volume is lower, Flycatchers select nest sites with more of these two variables than expected. These data illustrate the importance of investigating habitat selection in habitats with different structural and floristic characteristics in order to identify the features that influence reproductive success and they illustrate how these features may change across habitat types. The very low nesting success rate may simply be the result of poor habitat conditions for Flycatchers (young and dry sites). We are currently investigating habitat selection and reproductive success in what we predicted to be optimal conditions, i.e., wet old-growth stands and riparian forests.

Intensive Study: Northwestern Salamander Movement Patterns and Habitat Use

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University of Washington

Current research on amphibian response to forest management has largely focused on forest age and structural components, and on stream quality. However, the landscape ecology of pond-breeding salamanders and their response to forest management is poorly understood. These amphibians are thought to be highly sensitive to changes in microclimate variables (soil moisture, ground temperature, etc.) in their habitat because of their dependence on the external environment for water balance and thermal regulation. Yet, in the TFW Landscape Study, a comparison of relative abundances the Northwestern Salamander (*Ambystoma gracile*), the only abundant pond-breeding salamander captured in the pitfall surveys, suggests that their distributions are not related to stand age. In order to interpret these results, a more detailed understanding of pond-breeding salamander movement patterns and habitat use, both at breeding ponds and in upland (non-breeding) habitat is required. Our research incorporates two approaches: trapping and individually marking migrating and dispersing populations at breeding ponds; and following selected large individuals using radio-telemetry.

Research at Breeding Ponds

The purpose of this research is to investigate the reproductive ecology and breeding pond use of Northwestern Salamanders. Data on the size and demography of populations of migrating breeding adults and dispersing metamorphosed juveniles, and the types of adjacent habitat from which the salamanders enter and leave breeding habitat, were collected at two ponds.

Two ponds with known Northwestern Salamander breeding populations were encircled with a continuous drift fence with pitfall traps located at three meter intervals. During the spring breeding migration, salamanders were individually marked as they entered the ponds, and checked for their number as they left the ponds. Dispersing juveniles were also captured and marked as they left the ponds in the fall. Capture numbers at the two ponds are shown in Figure 1.

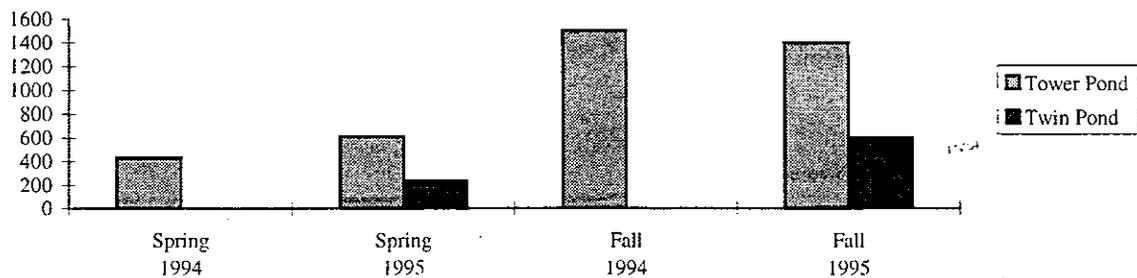


Figure 1. Numbers of salamanders caught at breeding pond drift fences in the spring (breeding migration) and the fall (dispersal of metamorphosed juveniles).

The upland habitat surrounding both ponds is divided almost equally into forested habitat and open habitat. Figure 2 shows the percentage of all captures that occurred in traps adjacent to each habitat type. These data suggest a strong preference for forested habitat by both adults and juveniles. Orientation towards wooded sections of pond edge by emigrating juveniles and adults has also been observed in other pond-breeding salamanders. Mature forested habitat provides a buffered moist, cool microclimate relative to more open or younger forest types where there are much greater extremes in temperature and relative humidity.

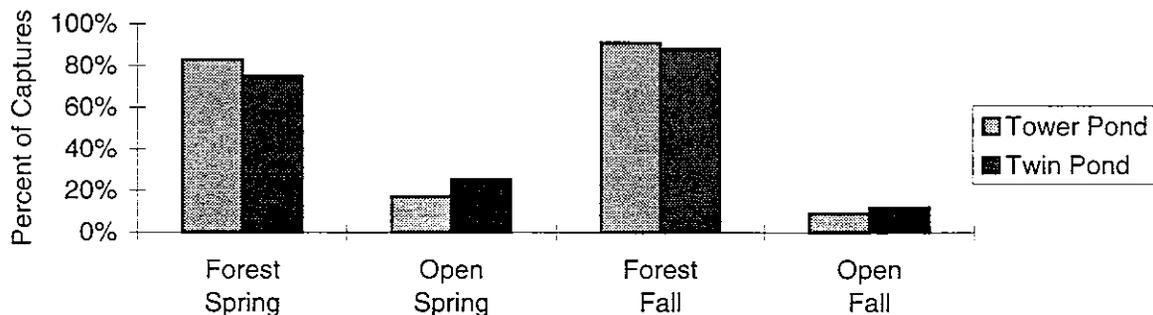


Figure 2. Percent of salamanders caught in traps adjacent to forested and open habitat at Tower and Twin Ponds.

Research Using Radio-telemetry

The purpose of this research is to quantify movement patterns and habitat use of salamanders. Radio-telemetry methods allow data collection on the direction (compass bearing) and distance of each movement, the duration of time between moves, and the surface structures and microhabitat of locations.

Selected large (>25g) salamanders were surgically implanted with radio-transmitters. After recovery from surgery, the salamanders were released at their capture locations and relocated at least twice per week. The compass direction and distance of each salamander movement

was recorded and mapped. Descriptions of general weather conditions, and substrate and cover type for each location point were also recorded. Eleven salamanders were tracked during the winter (pre-breeding season) months, and eight during the spring (post-breeding season) months.

Movement activities were generally characterized by a single large movement followed by an extended stay at a single location point. Locations were never revisited. The directions of pre-breeding season movement were random and post-breeding season movement direction was consistently away from the breeding pond.

Table 1. Ranges (and means) of distance (meters) between locations and duration of stay (days) at points for pre- and post-breeding season movements.

	Pre-breeding Season	Post-breeding Season
Distance Between Locations (m)	1-55 (8)	1-45 (12)
Duration of Stay (days)	2-75 (13)	1-24 (10)
Number of Salamanders	11	8

During the winter and spring rainy season, the salamanders were usually located at or near a cover object (Table 2) and were buried at a depth of one to five centimeters at the soil-duff interface. Once the rains stopped in late spring, the salamanders became increasingly difficult to locate as they moved into small mammal burrows more than a meter deep, presumably to avoid desiccation.

Table 2. Number of location points associated with each cover object type.

Cover Object	Sword Fern	Log	Stump	Tree Roots	Slash Pile	Cookie
Number	26	12	8	4	4	1

Within the a given time period, the movements of all radioed salamanders were often synchronous with each other and with a change in weather conditions (Figure 3). Although the total number of moves during the study period varied between individuals, days when only one of the salamanders moved were rare. Synchronized movement occurred within 24 hours of the first rain after a short dry spell. These data, along with the observed onset of migrational and dispersal movements at the breeding ponds, suggest a strong correlation between weather dependent microclimatic variables (e.g. temperature and relative humidity) and movement initiation. Other researchers have reported similar observations of pond-breeding salamander migration and dispersal movements coinciding with weather variables, especially precipitation.

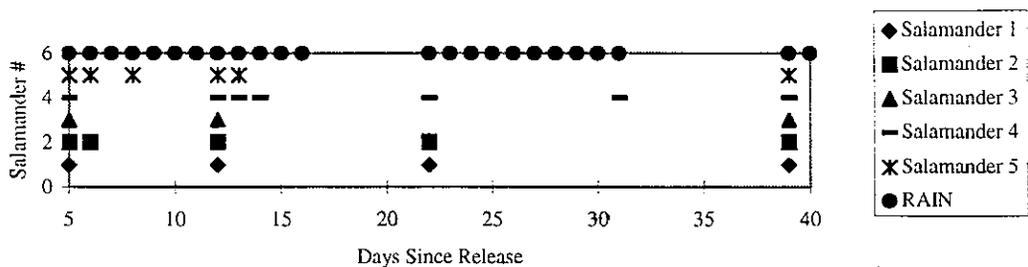


Figure 3. Days of rain and days on which individual salamanders (#1-5) moved over a 40 day period during winter telemetry, 1994.

The results of the research presented here suggest that Northwestern Salamanders are sensitive to the microclimate of their habitat and show a preference for wetter and milder conditions such as those found in forested habitat. This comes as no surprise given their dependence on the external environment for temperature and water regulation. However, these salamanders are not excluded by open habitat, as shown by their presence in clearcuts and young forest stands. Exactly how suboptimal microclimatic conditions may effect their ability to live in or pass through stands to reach breeding ponds is still unknown. Current research is under way to identify exactly which microclimatic variables are most strongly correlated with salamander habitat preference, and to continue mapping their breeding and non-breeding season movements in a variety of habitat types.

Habitat Utilization and Home Range Size of the Bobcat in Managed Forests of Western Washington

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Habitat utilization and home range size of bobcats (*Felis rufus*) in managed forests of western Washington were investigated from May 1993 through September 1994 with the use of radio-telemetry and Geographic Information Systems (GIS). A total of 751 independent locations were obtained for the six male and four female bobcats captured. Home range analysis was performed using three different home range estimators: Minimum Convex Polygon (MCP), 95% Harmonic Mean (HM), and 95% Adaptive Kernel (ADK). Correlation analysis showed the 95% ADK to be least correlated ($r = 0.158$) with number of locations used in the estimation and is generally thought to be the best estimator of the three. The MCP and 95% HM were included in the analysis to allow comparisons with other studies. The 95% ADK method indicated a mean annual home range size of 14.4 km^2 for males and 8.4 km^2 for females. Home range size and movement indexes differed between sexes ($P < 0.05$) with males moving further between successive locations and having larger home range sizes. Home range size and movement indexes did not differ between seasons; winter vs. summer and breeding vs. non-breeding. Adaptive kernel home range estimators were also calculated at a 50% contour levels to indicate the cats core areas or areas of greater use. Intra-sexual overlap of core areas did not occur for either sex. Intra-sexual overlap did occur with male core area overlapping those of females more than females overlapped those of males. A density estimate of 0.22 cats / km^2 was calculated based on mean home range size and a mean home range overlap of 27.24%. Home range and density results from this study were consistent with those from a 1978 study conducted on the same study area and indicate similar population dynamics.

Availability of six habitat types defined by structural differences resulting from timber management was determined from Landsat digital imagery. The six habitat types used in the analysis were newcut, clearcut, reprod, young, mature, and harvest. Habitat analysis based on availability within the study area showed that differences in use versus availability were not the same for all habitat types ($P = 0.012$).

The ordering of habitat types and significant differences determined by the multiple comparisons procedure from least to most preferred (left to right) were:

Harvest Clearcut Mature Newcut ReprodYoung

Habitat types underscored by the same line were not different from each other. A lack of an underscore indicates that the habitat types differed based on the multiple comparison test.

Differential use of habitat ($P < 0.05$) was detected for three cats based on availability within individual home ranges. Young stands were the most consistently preferred. Clearcuts (2-5 years old) and harvest-age stands were mostly avoided. Habitat use differed by season and by time of day. Preferred habitat appeared to be related to abundant understory vegetative cover and prey availability. Thick understory vegetation provides bobcats with cover for stalking their prey as well as security when ledges or rock outcroppings are not available. The primary bobcat prey species, the snowshoe hare and mountain beaver, have also been shown to prefer densely vegetated areas.

It appears that logging, like fire, returned forests to early successional stages that provide good cover and abundant prey for bobcats. The managed forests of Washington provide a continuous cycles of harvest and regrowth that creates a variety of habitat types. Bobcats appear to be adaptable enough to survive in the marginal habitats created by timber harvest, while taking advantage of the preferred habitat types with high prey abundance. They may therefore benefit from the patchwork mosaic of seral stages found in managed forest of western Washington.

Wildlife Use of Managed Forests: A Landscape Perspective

Table 1. Home range sizes and mean distance between successive relocations for 10 bobcats on Kapowsin Tree Farm, Pierce Co., WA, 1994. Home range methods used were Minimum Convex Polygon (MCP), Harmonic Mean (HM), and Adaptive Kernel Estimator (ADK) at various contour levels. Area measurement in km². Movement distance in km. Grid cell size in m.

I.D. #	100% MCP	95% HM	100% ADK	95% ADK	50% Mean ADK	Grid Distance	Cell Size
<u>Males</u>							
00	9.22	6.82	15.18	10.89	1.77	14.08	170.9
12	13.67	10.43	25.80	16.66	3.42	16.76	164.2
41	17.03	6.94	24.76	18.68	2.73	18.35	191.7
43	13.72	10.62	22.89	13.75	2.96	16.24	188.8
45	13.17	7.74	25.05	14.28	2.36	14.29	149.6
47	11.23	8.83	16.92	11.96	3.06	15.07	138.9
Mean	13.01	8.57	21.77	14.37	2.72	1.58	
<u>Females</u>							
05	16.00	11.52	27.27	13.56	2.15	14.75	198.4
07	16.82	8.95	30.05	9.95	1.73	14.22	205.0
14	4.59	2.34	9.29	5.88	0.75	8.90	122.9
31	2.90	1.08	5.93	4.36	0.66	9.31	64.3
Mean	10.08	5.97	18.14	8.44	1.33	1.18	

Table 2. Preference / avoidance of cover types available within each home range for bobcats exhibiting significant differences in use versus availability on the Kapowsin Tree Farm, Pierce Co., WA, 1994. Bonferroni Z statistic confidence intervals were calculated at a P < 0.05 significance level. P = Preference. A = Avoidance. N = No preference or avoidance detected.

Cover Type	05	07	100% ADK				95% ADK		
			12	14	31	43	05	14	43
Newcut	--	N	--	--	--	--	--	--	--
Clearcut	A	N	N	--	A	A	A	--	A
ReprodN	P	N	--	N	A	N	--	A	
Young N	N	N	--	P	P	N	--	P	
MatureN	N	N	P	--	N	N	P	A	
Harvest	N	N	A	A	--	A	N	A	N

Roost Site Characteristics of Long-Legged Myotis (*Myotis volans*) in the Teanaway River Valley, Washington

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Very little is known about the roosting needs of many of Washington's bat species. This study was carried out to identify both macro and micro characteristics associated with the roost sites of one native Washington bat, the long-legged myotis. The study area is located on Boise Cascade and U.S. Forest Service property in the Teanaway River Valley of eastern Washington. The area is composed of approximately fifty thousand acres and encompasses a diverse array of habitats, from heavily harvested dry ponderosa pine forests to nearly pristine grand fir and Douglas fir stands. Elevations range from approximately 610 to 1465 meters.

The long-legged myotis was selected due to its relative abundance in the study area and the fact that most adults are large enough to carry a radio transmitter. Mist nets and Tuttle traps were used to capture bats during July and August of 1995. A total of 127 bats were trapped. Eighteen long-legged myotis were fitted with radio-telemetry transmitters for the identification of roost site locations and nocturnal movement patterns. We attempted to locate the roost site of each bat every day for four weeks after release. Additionally, telemetry locations were taken at night to help identify the nocturnal movement patterns of the bats.

The telemetry efforts resulted in the location of 28 different roost sites. Eighty-two percent of the roost sites were snags (Fig. 1). The other 18 percent were classified as live trees, although all but one were partially dead. No roost sites were found in houses, ground, rock crevices, caves or any structure other than trees. The bats used most of the area's common tree species as roosts, including grand fir (57%), ponderosa pine (25%), and Douglas fir (14%). One bat roosted in a cottonwood on one occasion, but that specific occurrence is probably due to the time of release of the bat after it was tagged and the close proximity of the cottonwoods to the release site. The diameters and heights of the roost trees and snags were not extraordinarily large for the stands in which they occurred.

In all habitat types, the bats appeared to use snags that were in relatively open areas, either at the edge of the stand or in an open area within the stand. Most of the roost snags had large amounts of exfoliating bark. Those roost trees and snags that did not have extensive exfoliating bark usually had readily apparent cavities (e.g. cracks or a broken and decayed top). Distance from water appeared to have little influence on the selection of roost sites. Slope and aspect appear to have little influence as well.

Several of the roost sites were used more than once by the same bat. While most roosts were used only once, some roosts were used on 6 or 7 different occasions by the same bat (Fig. 2). Additionally, many bats returned to the same area to roost on a regular basis, even if they did not return to the same tree. The bats returned to these sites even when telemetry data from the interim night indicated that they had moved significant distances (up to several kilometers) to feed. While no analysis has been performed on this data yet, it appears that there is some type of roost site fidelity occurring. Other bats appeared to choose roosts dependent upon where they were feeding or on other factors and did not return to the same roost sites repeatedly.

The Teanaway study area has been divided into habitat classes based on current and potential vegetation classes. These classes are being used to compare roost site habitat use versus the availability of the different habitat types on the study area landscape. At this point, the bats appear to be using the habitat types in approximate proportion to the habitat's availability on the landscape (Fig. 3). This use pattern implies that the bats are more dependent on specific roost structures than the habitat type in which those structures occurred.

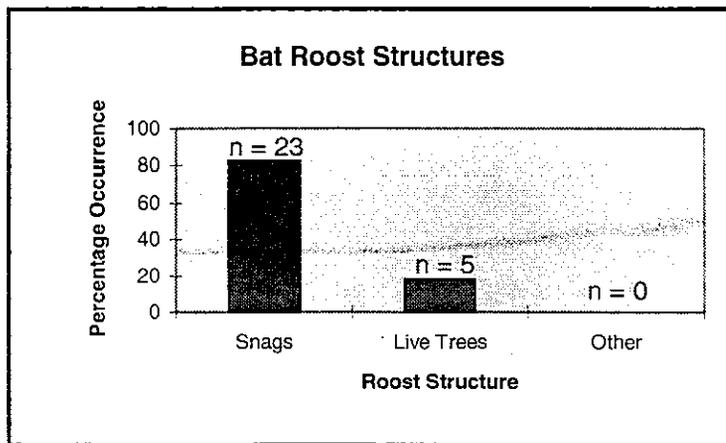


Figure 1: Bat roost structures used by *M. volans*. Teanaway River Valley, 1995

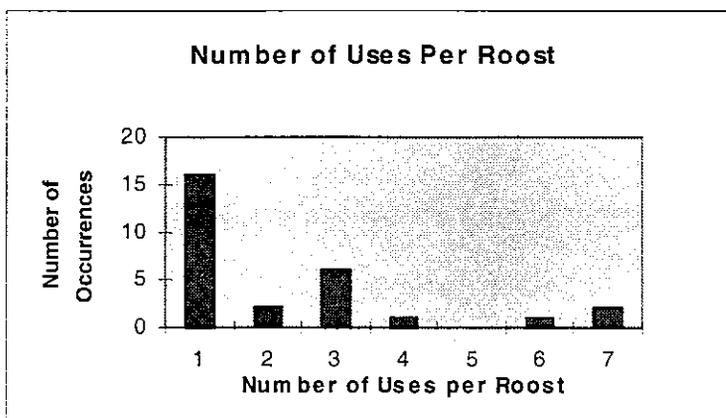


Figure 2: Number of occurrences of a single bat using a given roost. Teanaway River Valley, 1995

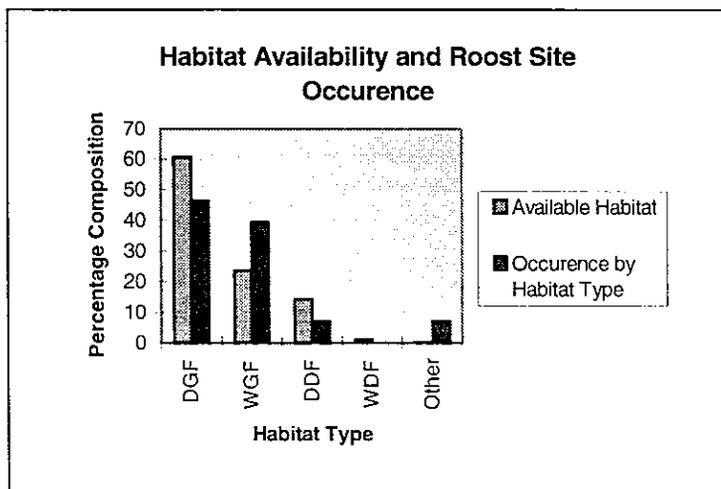


Figure 3: Comparison of habitat use and availability. Teanaway River Valley, 1995

NOTES:

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Overview of the East Side Portion of the Landscape Project

James G. Hallett and Margaret A. O'Connell

This study was designed to examine wildlife responses to varying landscape conditions in managed forests of northeastern Washington to assist resource managers in meeting the wildlife habitat objectives of the Timber Fish and Wildlife Agreement (1987). The objectives of our project were to:

- characterize the size, shape, and context of stands of different forest types in watersheds in northeastern Washington and utilize this analysis to determine the disturbance gradient for these watersheds and provide the basis for our study site selection.
- describe the species composition and abundance levels of wildlife and plant communities occurring in forest stands of varying seral stages, size-classes, and landscape configurations in watersheds managed primarily for timber production
- determine the stand- and landscape-level habitat variables that significantly influence wildlife use of managed forests, and evaluate how these relationships will affect the long-term viability of wildlife populations in managed landscapes
- develop methods for analyzing wildlife responses to landscape-level habitat conditions in managed watersheds

Old-growth coniferous forests have been replaced by second-growth, "managed" forests over large areas of the Pacific Northwest. Subsequent harvest has created a mosaic of forest patches of varying size and age within a matrix of closed-canopy forest (<90 years). To evaluate the consequences of these changes on species diversity and population dynamics, the pattern and extent of habitat fragmentation on such landscapes must be understood. The analysis of the disturbance gradient and context of stands for the watersheds was an important part of watershed and study site selection. We wished to work in watersheds that ranged from moderate to high degrees of disturbance.

We addressed this problem by using geographical information systems to map and analyze fragmentation of coniferous forests in northeastern Washington. The study area in northeastern Washington (Stevens and Pend Oreille Counties) is primarily coniferous forest. Forest composition varies with local conditions, but the principal tree species are grand fir (*Abies grandis*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Landsat imagery (1991) was classified into four broad habitat types (cleared, disturbed canopy, regeneration, and mature, closed-canopy)

that resulted from timber harvesting activities. For 20 watersheds ($\approx 2,000-7,000$ ha) representing a range of harvest intensities, we created polygon representations of forest patches and a database containing the habitat type, size, and perimeter for each patch in a watershed. We determined the number of patches and the proportion in each habitat type, and calculated dominance, contagion, and two fractal indices for each watershed. We also examined a line-transect sampling method to estimate the probabilities of encountering changes in habitat types.

The watersheds varied in size, perimeter (Table 1), and shape. From $\approx 20-50\%$ of the area in each watershed has been converted from mature, closed-canopy forest to other forest types. The number of patches and proportions of each category differed considerably among the watersheds indicating differences in the extent of fragmentation (Table 1). Dominance was highly correlated with contagion ($r = 0.94, p < 0.0001$) and the proportion of total area in mature, closed-canopy forest ($r = 0.91, p < 0.0001$). As expected with such diversity measures, different proportions of the four habitat categories provided similar measures of dominance (e.g., Ruby and Mill, Table 1). Contagion also was correlated with proportion of total area in mature, closed-canopy forest ($r = 0.88, p < 0.0001$).

The line-transect analysis indicated differences in the relative fragmentation of the watersheds. The average number of transitions per transect and the proportion of transects without transitions were highly correlated ($r = -0.82, P = 0.0001$). Transition probabilities between habitats were highly variable reflecting differences in the frequency of occurrence and spatial distribution of habitat types among watersheds. Most transitions were between mature and regeneration patches and between mature and clearcut patches (46.0 ± 4.2 and $27.9 \pm 3.6\%$ [$\bar{X} \pm 1 SE$], respectively). The transition between mature and disturbed patches accounted for another $10.1 \pm 2.2\%$. The three other types of transition accounted for about 16%.

Principal components analysis was used to examine intercorrelations among the variables and to describe patterns of fragmentation. The first component characterized the general gradient in fragmentation. Fragmentation increased with increases in the number of patches, areal proportion of disturbed and clearcut habitats, and number of transitions per transect. There were concordant reductions in dominance, areal proportion of mature forest, and the proportion of transects without transitions. The second component reflected differences in the extent of regeneration forest and thus in the length of time over which fragmentation has taken place. The third component highlighted differences in the way that fragmentation has taken place. Increasing values corresponded to increasing numbers of regenerating and clearcut patches, and decreases in the proportion of area in clearcut. Constancy in perimeter-area fractals indicated that the processes determining stand shape, primarily forest harvest, were similar across all watersheds.

In 1993, based on the above analysis to characterize the size, shape, and context of stands of different forest types in watersheds in northeastern Washington (Stevens and Pend Oreille Counties), we selected seven watersheds that ranged from moderate to high degrees of disturbance. For the seven watersheds, we mapped all stands that met our size (i.e., ≈ 16 ha and >36 ha) and forest type (i.e., basal area retention, regeneration, and mature closed canopy) criteria. Six stands of each size and forest type were selected for a total of 36 stands:

Table 1. Characteristics of the 20 watersheds.

Watershed	Area (ha)	Perimeter (km)	Number of patches				Proportion of total area				Dominance	Contagion
			^a R	M	D	C	R	M	D	C		
1. Fence	2638	22.2	18	4	9	16	10.3	75.5	2.1	12.1	0.60	9.34
2. Flume	2836	22.0	24	1	3	15	7.3	78.1	0.6	13.9	0.70	9.26
3. Sweet	2866	25.9	35	8	0	26	23.0	62.2	0.0	14.8	0.47	10.10
4. Jim Cedar	4665	41.2	43	16	15	38	25.1	59.0	2.8	13.1	0.36	9.44
5. Smackout	3418	30.2	32	11	29	23	9.4	59.4	11.3	19.9	0.29	9.41
6. Little Muddy	2937	27.3	28	21	32	39	12.6	49.9	13.9	23.5	0.16	11.12
7. Muddy	3534	34.8	38	15	42	37	9.8	66.6	10.5	13.2	0.38	9.15
8. Lost	5741	52.4	59	13	44	33	10.4	69.8	7.0	12.7	0.45	9.42
9. S Fork Lost	2383	24.9	37	6	7	14	16.6	73.3	1.3	8.7	0.59	9.47
10. Ruby	5739	33.0	85	5	21	42	9.8	72.2	3.9	14.0	0.52	9.43
11. Mill	5456	42.3	34	9	15	27	4.0	63.6	2.2	30.2	0.52	9.60
12. Upper Tacoma	5402	35.8	55	7	6	28	10.0	71.3	0.5	18.2	0.58	9.41
13. Tacoma	6275	45.5	95	6	26	52	11.7	74.9	3.0	10.4	0.58	9.31
14. S Fork Tacoma	3958	35.2	56	3	14	20	8.0	80.4	2.6	9.0	0.70	9.38
15. E Fork Small	3175	32.1	47	5	10	30	13.3	65.5	2.9	18.2	0.43	9.26
16. Small	3544	38.3	33	10	10	23	7.1	54.3	1.3	37.4	0.44	9.35
17. Winchester	4201	38.5	46	10	30	26	16.1	49.3	5.5	29.1	0.22	8.45
18. N Fork Calispell	7160	38.5	85	26	44	45	11.8	57.9	5.9	24.3	0.31	9.24
19. M Fork Calispell	5588	34.0	55	9	9	25	8.8	69.9	1.6	19.7	0.54	11.62
20. S Fork Calispell	2982	25.3	26	3	9	17	13.8	71.6	2.6	12.0	0.53	9.58

^aR = regeneration, M = mature, closed-canopy, D = disturbed canopy, C = clearcut.

Avian Survey Results: Habitat Occupancy Patterns

Deborah K. Beutler

Second-growth mixed-coniferous forests managed for timber production now cover millions of hectares of the northwestern USA. These forests are younger (<80 yr) and less structurally diverse than the forests they replaced, and because of recent harvesting have been fragmented into a mosaic of patches of various ages and sizes. We examined how size and age of forest patches affects avian community composition in managed forests of northeastern Washington.

Thirty-six sites representing the three predominant habitat types and two size classes were selected for study. Habitat types were closed-canopy forest (>60 years old), regenerating forest (15-25 years), and clearcuts. The two size classes were large (>35 hectares) and small (16-18 hectares). There were six replicates of each combination of habitat type and patch size. Dominant trees of these mixed coniferous forests are western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and grand fir (*Abies grandis*). We established transects on each patch with 3-4 and 12 point-count stations on small and large patches, respectively. Point-count stations were ca. 100 m apart and >100 m from the edge of the stand.

Point-count surveys were conducted during the breeding season (mid-May to late June) in 1993 to 1995. Surveys were conducted four times in 1993 and six times in 1994 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 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."

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. The Shannon-Weaver index of species diversity also was calculated for birds detected within the count circle. 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. For each species, two values were calculated for each patch: the percent of surveys when the species was detected and the mean number of birds detected per point. Data were analyzed using a three-way analysis of variance (ANOVA). The three factors were habitat type (closed-canopy, regenerating, or clearcut), patch size (small or large), and year. All interaction terms also were tested ($\alpha = 0.05$). For each species, two ANOVAs were run using percent of surveys and mean number per point. We also examined differences in SRA, SRB, species diversity, and mean number of birds per point.

Species richness A and B were higher in clearcuts and regenerating forests than for closed-canopy forests and they were significantly higher on large than small forest patches; however, the latter result was confounded because there were more point-count stations on large patches than on small patches. The number of birds per point was significantly higher in regenerating forest and small patches had more birds per point than larger patches. Species diversity was not significantly different for patch type, but large sites had significantly higher species diversity than small patches. There were significant effects of year. Species richness A was lower in 1993 than in the other two years, but this could be reflect lower sampling effort in 1993. Species richness B and species diversity were higher in 1995 than in either 1993 or 1994.

There were 110 species detected during the three years and ANOVAs were run for the 39 most common species (Table 1). Using the percentage data, most species showed a preference for one patch type. Thirteen species preferred closed-canopy forest while eight species preferred regenerating forests and only five species showed a preference for clearcuts. A few species showed a preference for two habitat types. Analysis of the number data showed that fewer birds preferred a particular habitat type. In two cases, the habitat preference changed. Number per point was the only parameter used to test the effect of patch size because of the differences in the number of stations between patch sizes. Few species showed a size preference; four species preferred large patches and nine species were detected more often in small stands.

Patch size and type may have an important effect on species richness and composition of a patch. These results suggest that patch type is more important than patch size in predicting avian species richness in forest patches. Species richness is higher in regenerating forests and clearcuts than in closed-canopy forest. The number of birds per point is highest in regenerating forests. Most species show a patch type preference but do not show a preference for patch size.

One could argue that because regenerating forests have higher species richness and more birds per point than the other forest types, these forests provide the best habitat for birds. However, the species found in regenerating forests and clearcuts are species, such as Warbling Vireo and MacGillivray's Warbler, that are found in a variety of habitat types throughout the west. Nevertheless, species such as the Townsend's Warbler and Chestnut-backed Chickadee prefer closed-canopy forests and have distributions that are restricted to this forest type. The species composition of a patch may be more important factor than species richness.

Table 1. Habitat and patch size preferences of avian species in northeastern Washington.

Closed-canopy		
Pileated Woodpecker	Gray Jay	Winter Wren
Chestnut-backed Chickadee Kinglet	Brown Creeper	Golden-crowned
Swainson's Thrush	Hermit Thrush	Varied Thrush
Solitary Vireo	Townsend's Warbler	Red Crossbill
Evening Grosbeak		
Closed-canopy and Regenerating		
Ruffed Grouse		
Regenerating		
Dusky Flycatcher	Warbling Vireo	Nashville Warbler
Orange-crowned Warbler Grosbeak	Wilson's Warbler	Black-headed
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 Kinglet	Brown Creeper	Golden-crowned
Solitary Vireo Warbler	Orange-crowned Warbler	Townsend's
Chipping Sparrow	Dark-eyed Junco	Pine Siskin

Small Mammal Survey Results: Habitat Occupancy and Population Patterns

Margaret A. O'Connell and James G. Hallett

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 in forests managed for timber harvest.

Research was conducted in the Selkirk Mountains of northeastern Washington. The forests of this region are a mosaic of habitat types resulting from differences in slope, aspect, edaphic factors, fire history, and timber management practices. We used pitfall trapping to sample small mammal populations in three upland forest types (closed canopy, >60 yr; regeneration, 15-20 yr; and recent clearcuts) and two stand sizes (~12 and ≥ 36 ha) for a total of 36 sites. At each site a 6 by 6 grid was established 10-m spacing between trap stations. Grids were placed in areas considered representative of each stand and were ≥ 50 m from riparian areas. 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/yr and 54,432 trap nights total. Animals were weighed and measured upon capture and frozen. Specimens were later autopsied to determine reproductive condition. 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. Determination of male reproductive condition was based on size of testes and epididymis.

We captured a total of 3,739 individuals of 18 species. Six species were not adequately sampled with pitfall traps or were quite rare and are not considered further: *Spermophilus columbiana* (12 captures), *Lepus americanus* (8), *Tamias amoenus* (6), *Tamias ruficaudus* (2), *Microtus richardsoni* (1), and *Sorex palustris* (1). For the remaining species, number of captures and the distribution among different patch types and sizes varied substantially among years. Sex ratios and proportion of reproductive individuals also varied between years and habitat types and sizes.

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 ($F = 23.55$, $df = 2$, $P < 0.001$). There was no difference in species diversity between different-sized stands ($F = 0.64$, $df = 1$, $P > 0.4$). All but one species were found on ≥ 1 site in all years; *Microtus pennsylvanicus* was not captured on any site in 1993.

Nine of the twelve species were captured on more sites in 1994 than in either 1993 or 1995. In contrast, *Sorex hoyi* and *Thomomys talpoides* were captured on more sites in 1993 and *Sorex cinereus* was found on more sites in 1995.

The total number of captures in 1994 (2,248) was about three times those of 1993 (743) and 1995 (718). *Clethrionomys gapperi*, *Peromyscus maniculatus*, *Sorex cinereus*, *Sorex monticolus*, and *Sorex vagrans* were captured significantly more frequently in 1994 than in other years. *Phenacomys intermedius* was uncommon in 1993 (19 captures), increased in 1994 (108 captures), and remained relatively high in 1995 (77 captures). Sex ratios of two species differed significantly between years. Male *Microtus longicaudus* significantly outnumbered females in 1994 as compared to 1993 or 1995 ($X^2 = 9.64$). Twice as many male as female *Sorex vagrans* (163 vs. 82) were captured in 1995, whereas sex ratios were equal during the previous two years. Interyear variation in the proportion of reproductive animals was more pronounced in males than in females.

Two species, *Clethrionomys gapperi* and *Sorex cinereus* were captured more frequently in closed-canopy stands ($\bar{X} = 35.2$, $F = 10.6$, $df = 2$, $p < 0.001$; $\bar{X} = 63.7$, $F = 12.7$, $p < 0.002$, respectively) than in either the clearcuts (16.2, 16.8) or regenerating stands (11.8, 22.2). The proportion of reproductive to nonreproductive female *C. gapperi* was 2x greater in closed-canopy stands (56:21) but equal in the other stand types. Although overall captures did not differ with stand size for either species, the number of male vs. female captures of *Sorex cinereus* did. Males were more common than females in the smaller stands (213:97) but were equally abundant to females in the larger stands (191:120) ($X^2 = 3.84$).

Two species were captured more frequently in clearcuts. The mean number of captures of *Peromyscus maniculatus* and *Thomomys talpoides* was greater in clearcuts ($\bar{X} = 36.2$, 12.5, respectively), but did not differ between closed-canopy ($\bar{X} = 11.5$, 1.7) or regenerating ($\bar{X} = 12.8$, 4) stands ($F = 7.86$, $df = 2$, $p < 0.009$; $F = 4.67$, $df = 2$, $p < 0.051$). The mean number of captures of *Zapus princeps* differed between all three habitats (clearcut = 15, regeneration = 8.3, closed canopy = 1; $F = 15.32$, $df = 2$, $p < 0.01$). *Z. princeps* was more common in the smaller stands ($\bar{X} = 15.3$) than larger stands ($\bar{X} = 3.5$) ($F = 38.5$, $df = 1$, $p < 0.002$); 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; $X^2 = 8.89$).

Three species avoided closed-canopy stands but were equally abundant in clearcuts and regenerating stands. The mean number of captures of *Sorex vagrans* and *Phenacomys intermedius* in the closed-canopy stands was 46 and 2.5, respectively, 99.5 and 15.2 in the clearcuts, respectively, and 106.3 and 17, respectively in the regenerating stands ($F = 7.6$, $df = 2$, $p < 0.01$; $F = 7.86$, $df = 2$, $p < 0.009$). The mean number of captures of *Microtus montanus* was greatest in the clearcuts ($\bar{X} = 4.5$), which did not differ from the mean number of captures in regenerating stands ($\bar{X} = 2.7$) but was different from the number in the closed-canopy stands ($\bar{X} = 1.5$). 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 ($X^2 = 6.67$).

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) ($X^2 = 5.39$). *Sorex vagrans* was more common in the larger ($\bar{X} = 99.3$) than the smaller stands ($\bar{X} = 68.6$; $F = 4.95$, $df = 1$, $p < 0.05$).

The 12 small mammal species varied in their distribution and occurrence across these landscapes managed for timber harvest. Captures varied more due to habitat type than stand size; captures of eight species were associated with specific habitat types, whereas overall captures of only three species varied with patch size. Numbers of captures, distribution across sites, and population parameters varied between years. This pronounced temporal variation highlights the importance of multiyear population sampling.

Bat Survey Results: Habitat Occupancy Patterns and Roost Use by Silver-haired Bats, *Lasionycteris noctivagans*

Lori A. Campbell, James G. Hallett, and Margaret A. O'Connell

In large regions of the Pacific Northwest of the United States, forest harvest has converted old-growth coniferous forests into a mosaic of young patches (<90 years old) of differing size and age. We examined the consequences of these changes on the roosting habits of the silver-haired bat, *Lasionycteris noctivagans*, which preferentially uses older forests in other parts of its range in the Pacific Northwest. Our objectives were to locate roost sites of *L. noctivagans*, to describe the roost sites and associated habitat, and to examine the use of these habitats relative to their availability.

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*). Bats were captured using mist nets and harp traps at stream, pond, and road sites in 1992 and 1993. *L. noctivagans* was captured only over water. Fifteen of 30 *L. noctivagans* captured were equipped with radiotransmitters. Radiotagged 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 (DBH), height, and decay class of the trees were recorded. Approximate location of bats on the roost trees was determined. 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. We described the habitat of the area immediately surrounding the roost within a 15-m radius plot. For each plot, we tallied the number, species, DBH, and decay class of all trees >4 cm DBH. Based on DBH, each tree was placed into one of four size classes: 1) >4 and ≤10 cm, 2) >10 and ≤25 cm, 3) >25 and ≤50 cm, and 4) >50 cm. We determined the species, DBH, decay class, distance from the center, and height for the five nearest neighbors of the roost tree. Canopy closure was measured once at the plot center and in each of four quadrants with a convex densiometer. Total cover and average height of vegetative understory were estimated. To evaluate habitat use versus availability, characteristics of the roost plots were compared to those of 45 randomly selected plots. The species, DBH, decay class, and height were recorded for all plot centers, and habitat characteristics of the plots were measured as for roost plots.

Of the 15 bats with radiotransmitters, 13 bats including three juveniles were relocated and 15 roost sites were identified. All three 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 one roost site for the duration of the monitoring period. All but one of the roost sites were in snags. Fourteen of 15 roost sites were located in trees with DBH >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 one of the roost sites were located in gaps in otherwise closed-canopy patches. Height of roost trees 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 $\leq 50\%$ 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. All roost sites were >100 m from the nearest riparian area with a permanent water source.

Seven species of trees were used as roosts (Table 1). Twenty-six percent of roosts were in ponderosa pine (*Pinus ponderosa*), and white pine (*Pinus monticola*) was the next most frequent species at 20%. Although these two 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. 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. The roost tree was often one 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. 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. Roost trees were significantly taller than random plot centers. Roost sites had significantly more size class 3 trees belonging to decay classes 4 and 5. As this is the grouping to which most roost trees belonged, roost plots had more roost-type trees than did random plots. Canopy closure was significantly less at roosts than at random-plots. Overall, roost plots exhibited significantly less canopy closure than random plots. Height of understory vegetation was greater on random plots than on roost plots, as was understory cover.

Roost sites are a critical resource for bat populations. 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. 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 two 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 one roost each. 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.

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

Species	DBH (cm)		
	<i>n</i>	\bar{X}	Range
Grand fir— <i>Abies grandis</i>	1	54	54
Western larch— <i>Larix occidentalis</i>	2	48	31-64
Lodgepole pine— <i>Pinus contorta</i>	2	26	20-31
White pine— <i>Pinus monticola</i>	3	48	37-55
Ponderosa pine— <i>Pinus ponderosa</i>	4	49	32-74
Douglas fir— <i>Pseudotsuga menziesii</i>	1	36	36
Western redcedar— <i>Thuja plicata</i>	2	52	37-68

Patterns of Shrew Community Composition

Robert E. Griffith

A central goal of much ecological research has been to explain and predict patterns of community structure in animals. Diamond introduced assembly rules in 1975 and stated that competitive interaction and degree of niche overlap will determine the probability that a given species is represented in a species assemblage. This idea was criticized because it did not take into account the random vs. observed assemblages possible. The assembly rule for functional groups of species rather than individual species was introduced by Fox in 1987. The functional groups in this study were comprised of three trophic groups, insectivore, herbivore, and omnivore. Fox and Kirkland examined the structure of eastern North American shrew communities using functional groups based on body size and found that shrews were separated into specific assemblages, and that the random assemblages were different from the observed. Recent arguments suggest that shrew assemblages in eastern North America are structured following rules based on relative body size. Because of their high metabolic rate, they must feed quite often, with smaller individuals feeding more periodically than the larger. They can show high species richness with as many as six species inhabiting one given area.

The assembly rule operates in the following manner. Suppose that six species inhabit an area and that they can be grouped into three different size classes: small, medium, and large. For this example, two of the six species occur in each size class. The rule predicts that there should be one species in each size class before a second species can be added to a class. An assemblage with two small, zero medium, and one large species would be considered an unfavored state because one group is empty. An example of a favored state would be an assemblage with two small, one medium, and one large species present.

I examined the composition of shrew assemblages in the Selkirk mountains of northeastern Washington. The forests of this region are a mosaic of habitat types resulting from differences in slope, aspect, edaphic factors, fire history, and timber management practices. Shrew populations were sampled from a total of 72 sites representing different habitat types and forest stand sizes in 1994 and 1995. Pitfall (18,144 trap nights/yr) and snap-traps (41,472 trap nights/yr) were used to sample shrew populations from 18 closed-canopy riparian and adjacent upland sites. Pitfall traps (18,144 trap nights/yr) were used to sample shrew populations in three upland forest types (mature, >60 yr; regeneration, 15-20 yr; and recent clear cuts) and two stand sizes (~12 and ≥36 ha). Specimens were weighed and measured upon capture. Species identification was based on dental characteristics, relative body measurements, and pelage. Five species of shrews were present in the study area.

Preliminary work by O'Connell and Hallett divided the five shrew species into three functional groups based on body mass. These groups were: small, *Sorex hoyi*, medium, *S. cinereus*, *S. monticolus*, and large, *S. vagrans*, *S. palustris*. I refined this analysis by also examining differences in jaw and cranial measurements, which might be better indicators of the feeding niches of these species. Principal components analysis of 15 jaw and cranial measurements and body mass suggested that the following groupings were more appropriate: small, *S. cinereus*, *S. hoyi*; medium, *S. vagrans*, *S. monticolus*; large, *S. palustris*.

To determine whether shrew assemblages followed an assembly rule, I compared the frequency distribution of the actual assemblages with that generated by a random model. Random species assemblages were generated based on the three groups. Constraints placed on the model were: 1) the number of random communities generated must equal the number of observed sites for each level of species richness, 2) the maximum number of species entering a group could not exceed the observed number, 3) sites must be considered in order of species richness. For example, consider 15 assemblages observed to contain three species. A random number is drawn to determine which group the first species should belong, a second random number is drawn independently to determine to which group the second species belongs, and again for the third. From this simulation there are seven possible outcomes, described in terms of the number of small, medium, and large species present: 210, 120, 201, 111, 021, 102, and 012 (unfavored states underlined).

A total of 3,224 individuals of the five *Sorex* species were captured in 1994. The species and their number of captures were: *S. palustris* (12 captures), *S. vagrans* (1,981), *S. monticolus* (173), *S. cinereus* (1,024), and *S. hoyi* (34). In 1995, the total was 1,389 with the number of captures as follows: *S. palustris* (3 captures), *S. vagrans* (803), *S. monticolus* (46), *S. cinereus* (510), and *S. hoyi* (27). Eleven of 17 and 10 of 17 possible assemblages of small, medium, and large species were observed for the 72 sites in 1994 and 1995, respectively. The distribution of observed assemblages differed from that based on random assembly in 1994 ($X^2 = 43.22$, $df = 16$, $P \leq 0.05$), but not for 1995 ($X^2 = 21.88$, $df = 16$, $P \geq 0.05$; Table 1). In 1994, observed frequencies of unfavored states were greater than expected from random. This was especially true for assemblages of 1 small, 2 medium, and 0 large species. The addition of a second medium-sized species to the assemblage before a large-sized species is most likely because even though shrew densities were high, the number of sites at which the large species, *S. palustris*, was present did not increase due to its habitat specificity. Yearly variation of shrew assemblages was observed on all 72 sites sampled for two years (Tables 2 and 3). The reduction in the number of sites at which a species occurred was 2 for *S. hoyi*, 8 for *S. cinereus* and *S. vagrans*, 34 for *S. monticolus*, and 5 for *S. palustris*.

Species assemblages in the interior Pacific Northwest may exhibit high interyear variation and also reflect the habitat requirements of the species. Future analyses will incorporate these habitat requirements and resource use. For example, assemblages may be influenced by availability of food resources in the area. I am in the process of analyzing stomach contents of shrews from the 1995 field season. These contents will be compared with invertebrates collected in the field to compare prey size and availability.

Table 1. The observed vs. random species assemblages for five soricid species (unfavored states in bold).

State	1994		1995	
	Random	Observed	Random	Observed
0 0 1	0.15	0	0.17	0
0 1 0	2.33	2	4.73	6
0 1 1	0.43	0	0.48	0
1 0 0	1.52	2	4.11	3
1 0 1	0.31	0	0.45	0
1 1 0	4.32	6	13.51	25
1 1 1	1.47	1	0.61	2
1 2 1	1.89	3	0.15	0
2 1 1	0.88	2	0.12	0
2 2 1	3.00	2	1.00	1
0 2 0	3.47	4	6.97	3
0 2 1	1.48	0	0.49	0
1 2 0	16.12	37	12.99	15
2 0 0	1.47	0	6.73	1
2 0 1	1.13	0	0.42	0
2 1 0	19.18	1	12.32	9
2 2 0	12.85	12	2.75	3

1994: $X^2 = 43.22$, $df = 16$, $P \leq 0.05$

1995: $X^2 = 21.88$, $df = 16$, $P \geq 0.05$

Table 2. The presence (+) or absence (-) of the five soricid species and number of sites at which species combinations were found in 1994 (unfavored states in bold).

Small		Medium		Large	No. of Sites
<i>S. hoyi</i>	<i>S. cinereus</i>	<i>S. vagrans</i>	<i>S. monticolus</i>	<i>S. palustris</i>	
-	-	+	-	-	2
-	+	-	-	-	2
-	+	+	-	-	6
-	+	+	-	+	1
-	+	+	+	+	3
+	+	+	-	+	2
+	+	+	+	+	2
-	-	+	+	-	4
-	+	+	+	-	37
+	+	+	-	-	1
+	+	+	+	-	12

Table 3. The presence (+) or absence (-) of the five soricid species and number of sites at which species combinations were found in 1995 (unfavored states in bold).

Small		Medium		Large	No. of Sites
<i>S. hoyi</i>	<i>S. cinereus</i>	<i>S. vagrans</i>	<i>S. monticolus</i>	<i>S. palustris</i>	
-	-	+	-	-	5
-	-	-	+	-	1
-	+	-	-	-	3
-	+	+	-	-	24
-	+	-	+	-	1
-	+	+	-	+	2
+	+	+	+	+	1
-	-	+	+	-	3
-	+	+	+	-	14
+	-	+	+	-	1
+	+	-	-	-	1
+	+	+	-	-	9
+	+	+	+	-	3

Predation on Artificial Nests: Effects of Patch Type and Size

James G. Hallett and Margaret A. O'Connell

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. 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. The decline or local extinction of many bird populations has been attributed to habitat fragmentation, nest predation, and nest parasitism. Nest predation is considered a major influence on the population dynamics and community relationships of many bird species, and can increase with habitat fragmentation. The creation of open-canopy patches and edge habitats can allow predators to invade the landscape and forest interiors, respectively. 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. We hypothesized that predation rates would decrease with increasing habitat area, and be higher in open-canopy habitats.

The study was conducted on seven watersheds managed primarily for timber production in NE Washington (Stevens and Pend Oreille counties). Second-growth mixed-coniferous forest of <90 yr is the predominant habitat type. We selected 5 replicate patches of two size classes (small: 16-20 ha; large: >35 ha) and three forest types (closed canopy, regeneration, and clearcut) for a total of 30 patches. The smaller size class is representative of the minimum patch size typically resulting from harvest. The three forest types comprise 82% of the total area and represent the most common habitat classes.

Beginning in late May 1994, 20 artificial nests were placed at each of the 30 sites for a total of 600 nests. Nests were placed throughout each forest stand with >25-m spacing between nests. Nests were >100 m from the edge of each stand to reduce edge effects. Nest locations were unmarked to prevent predator recognition. 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. Three quail eggs were placed in each nest and the nests were checked and removed after 7 days. This corresponds to typical egg-laying or incubation times for small passerine birds. The experiment was repeated 21 days after completion of the first trial. This replication 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 one 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. Consequently, nests found with eggs that were scratched by the incisors or

claws of small mammals were considered to be depredated. We categorized the type of predator at each disturbed nest by noting how the nest had been disturbed. Relative abundance of red squirrels (*Tamiasciurus hudsonicus*) was determined by tallying the number of individuals calling during each point count survey of birds.

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 four quadrants along the cardinal directions. Presence of logs >6 cm in diameter, saplings >4 and <10 cm diameter at breast height (DBH), trees ≥ 10 cm DBH, stumps >16 cm DBH, 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 two size classes (4 to <10 cm DBH and ≥ 10 cm DBH) was tallied in the circle. Horizontal cover was measured at the nest with a 25 by 25-cm coverboard divided into 5-cm squares. Cover was estimated as the percent of squares that were >50% obstructed by vegetation when viewed at a distance of 5 m. Measurements were taken from the four 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 by 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 seven classes: 0, no cover; 1, >0-5%; 2, >5-25%; 3, >25-50%; 4, >50-75%; 5, >75-95%; 6, >95-100%.

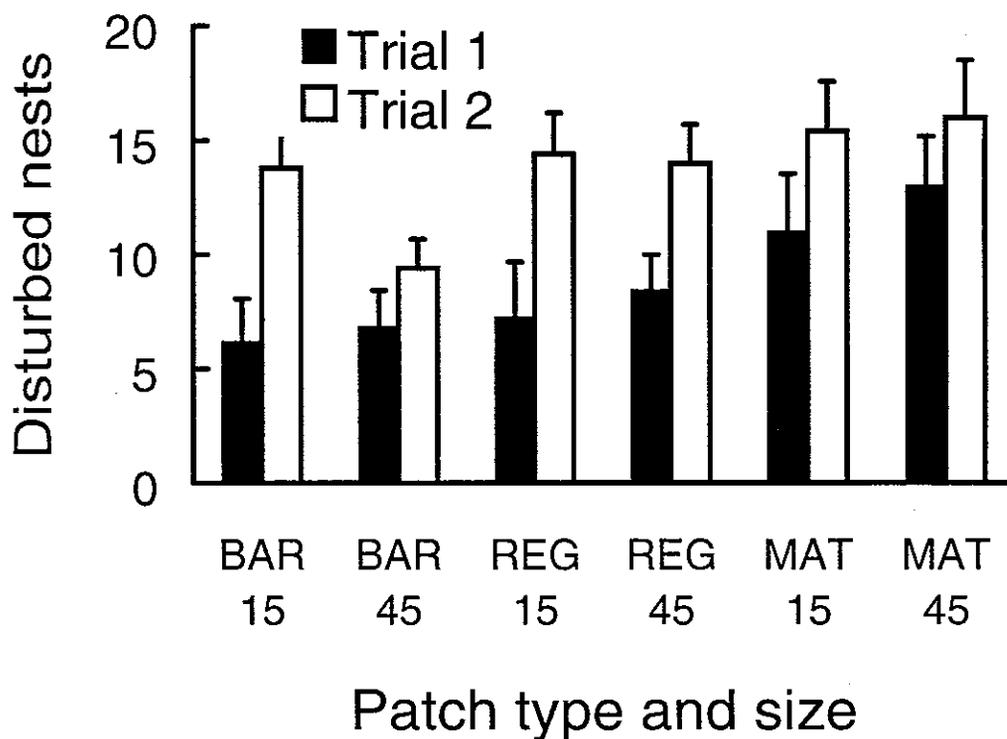
Two statistical approaches are appropriate for examining differences in degree of predation with patch size and habitat type, and time. Using repeated measures analysis of variance (ANOVAR), the dependent variable is the number of disturbed nests per site repeated on site for the two trials. Patch size and type are independent classification variables. Alternatively, the problem can be viewed as one of resource selection in which differences in used versus unused nests are examined. Under logistic regression, the dependent variable is the state of each nest, designated as 1 if disturbed and 0 otherwise. The independent variables are 0 or 1 "dummy" variables that represent the size class (e.g., 1 if small and 0 if large), habitat classes, and time period. Additional model building is possible with logistic regression to examine the effects of variables describing the nest locations.

Totals of 262 and 412 of the 600 nests available were disturbed during the first and second trials, respectively. The mean number of disturbed nests varied significantly across the 30 sites during the first trial ($F = 2.3$, $df = 3,26$, $p < 0.05$; Fig. 1), but not the second ($F = 1.9$, $df = 3,26$, $p > 0.15$). Differences during the first trial were associated with habitat type ($F = 4.1$, $df = 2,26$, $p < 0.03$), but not with patch size ($F = 0.6$, $df = 1,26$, $p > 0.4$). The number of disturbed nests increased significantly during the second trial ($F = 94.4$, $df = 1,26$, $p < 0.001$; Fig. 1).

Patch size did not contribute to the likelihood that a nest would be preyed upon. This was somewhat surprising because other studies have found higher rates of predation in smaller patches. It is possible that our small patch size was above a critical threshold below which predation might increase because of a higher ratio of edge to total area. The minimum

distance from the edge of a patch to a nest was >100 m in our study might prevent differences due to predation at the edge from being observed. Significantly greater predation occurred in closed-canopy than in regeneration or clearcut patches during the first trial. This pattern corresponds to the greater abundance of red squirrels in the closed-canopy patches. The lack of differences in the second trial are likely due to the development of a search image by the predators. Most predation appeared to be due to mammalian predators. Red squirrel abundance varied considerably between years, which suggests that the results of artificial nest predation studies might vary depending on when they are conducted.

Fig. 1. Mean number of nests ($\pm 1 SE$) that were disturbed during the two experimental trials for the three habitat and two size classes.



Analyzing Movement Patterns of Vertebrates on Fragmented Landscapes

Stephen Mech and Douglas Call

Forest harvest activities produce a mosaic of different habitat types which influence interactions between populations and viability of individual populations. At a local scale harvest activities can destroy populations that are dependent on mature forest structure, and at a larger scale, logging units may impede or enhance movement between discrete populations. Smaller populations are not as likely to persist for extended periods of isolation because of negative demographic and genetic events. Loss of connectivity between discrete populations can increase rates of local extinction and reduce colonization of suitable habitat leading to the regional decline of a species.

There are few empirical data from managed forests that allow us to evaluate the validity of many of the problems described above. This is mainly due to the logistic difficulty of conducting the required large scale research. For instance, radiotelemetry provides an ideal means of tracking the fate of individual animals, but it can be very expensive for large sample sizes. We also could tag individual animals within a patch and then trap outside that patch in the hope of detecting movements. This approach also is expensive because the area that needs sampling increases exponentially with patch size. A removal study would involve eliminating all members of a population and then resampling to detect colonization. This approach can be logistically challenging as well as ethically questionable in many circumstances. We could try genetic approaches including introducing novel alleles, measuring genetic distances and detecting changes in genotypic frequencies. The novel allele approach has similar problems and expense as marking and following individual animals.

The genetic distance approach is based on the premise that populations that are genetically similar have less migration between them or were recently separated compared with populations that are genetically dissimilar. If we can measure genetic distance for a series of populations we might be able to correlate these values with contemporary changes in landscape structure to identify areas where gene flow is restricted or enhanced. This approach allows us to collect samples from a number of populations in a short period of time, thus reducing field costs and allowing us to replicate samples from certain disturbance regimes.

We chose this approach using the spotted frog (*Rana pretiosa*), Pacific chorus frog (*Pseudacris regilla*) and red-backed vole (*Clethrionomys gapperi*) as our study organisms. We began searching for variable markers by examining a short sequence of mitochondrial DNA (330 bp) from spotted frogs, but found no variation between the northern and southern extremes of the Landscape study area. We then investigated multilocus DNA fingerprinting and found that frog populations exhibited little differentiation (65% similar) compared with much larger differences between vole populations (45% similar). The multilocus fingerprints were not variable enough to provide useful information for the frogs, but were too variable for the voles.

Our next approach was to develop microsatellite markers that might provide the necessary variation to detect differences between frog populations. Once we have these markers it is possible to determine genotypes of individuals using minute quantities of DNA. We have developed three such markers for the spotted frog and 4-10 for the chorus frog (development is ongoing). Sequences have already been published for five *Clethrionomys* microsatellites.

We also initiated a simulation study to determine under what conditions genetic distance data would be informative. The simulations show a great deal of variation surrounding mean estimates of differentiation. We can reduce this variation by sampling more individuals and more genes within individuals. For isolated populations, however, the rate of differentiation is entirely dependent upon population size. That is, smaller populations will diverge very rapidly compared with larger populations. If we estimate mean differentiation between a group of isolated populations compared with a group of semi-isolated populations, we find very little power to discriminate between them. Under ideal circumstances, with two loci there is only a 65% chance that we will correctly discriminate between these two groups after 75 years ($n = 100$ individuals/population). In this case, forest succession should erase the effects of the original disturbance before any pattern of isolation can be detected based on genetic differentiation. Even without reconnection, it appears that genetic drift decouples genetic differentiation from historical gene flow so it may be impossible to infer the biological processes that led to the observed patterns of differentiation.

Another genetic approach involves testing for departures from the Hardy-Weinberg equilibrium model. There are a number of underlying assumptions to this model which, if satisfied, allow us to predict genotypic ratios for a population. If we find differences between predicted and observed ratios, we know that one or more of the underlying assumptions have been violated. One important assumption is that our data are collected from the same population. Thus, if genotypic frequencies are pooled from two populations (e.g., two habitat patches) and these data do not depart from expected values, then we can conclude that the two populations are linked by significant migration because the genotype data "behave" as a single population. If the pooled data depart from expected values then we know that one or more of the assumptions for this model have been violated. We are using computer simulations to explore the sensitivity of this method to the number of individuals moving between populations and to the number of individuals sampled and loci surveyed.

We propose to monitor genotypic frequencies for isolated habitat patches and continuous forest areas inhabited by the red-backed vole. We plan to establish live-trapping grids and collect blood samples at the beginning and end of the breeding season in case genotypic frequencies are biased from winter mortality. If the spring data are biased, the population can return to Hardy-Weinberg equilibrium by the end of the breeding season. We can estimate differences in relative population sizes using mark-recapture estimators and allele frequency data. We also propose to use a limited number of radio-tagged animals to monitor movement behavior in isolated and continuous forest areas. These data would be particularly useful if they confirm migration between isolated and continuous patches.

Once we have collected the genetic data, we can pool these data from the isolated and continuous populations and determine if the observed genotypic ratios concur with expected values. That is, if we find that the pooled data are at Hardy-Weinberg equilibrium we can conclude that clearcuts are not impeding demographically and genetically significant movement of individuals between populations. If the pooled data do not concur with the expected values for Hardy-Weinberg equilibrium, this suggests possible separation of the two populations, but it will be very difficult to identify all factors that contribute to this pattern. Population size estimates and radiotelemetry data will help us narrow the range of factors that contribute to the observed ratios. Thus, by sampling isolated and continuous habitat and using basic population genetics, we should be able to determine if an isolated patch contains a portion of a demographically continuous population. Departures from Hardy-Weinberg equilibrium will be more difficult to interpret, but may suggest that clearcuts do isolate *C. gapperi* populations.

Spatial Dynamics of Snowshoe Hares in Managed Forests

Jason A. Thomas

Understanding the spatial and temporal dynamics of wildlife populations is becoming increasingly important to conservation efforts. It is especially applicable to populations of animals that use ephemeral or patchy habitats. The snowshoe hare fits this model and it also is a critical food source for more than a dozen predator species. In Washington State, hares are particularly important as a winter food supply for lynx (*Lynx canadensis*). Several raptor and owl species as well as fisher, marten, and mink also are known to prey on snowshoe hares. Due to the large home range of these predators, it becomes even more important to understand their foraging requirements from a landscape perspective. The habitat preferences and requirements of snowshoe hares makes them particularly suited to study of habitat dynamics at a landscape scale.

Snowshoe hares are typically associated with regenerating coniferous forests that are from 10 to 28 years old and have dense understory cover. The landscapes that snowshoe hares inhabit are characterized by patches of this habitat interspersed among a mosaic of clearcuts and mature, closed-canopy forest. These mosaics change in the quantity of young regeneration stands and their relationships to one another as succession proceeds and forest management activities take place.

If a forest was managed for sustainable yield on a 100 year rotation, the amount of young regeneration stands (10-28 years of age) would occupy 16% of the entire management area (excluding reserves). The time during which nearby pairs of patches are both suitable for hares may be minimal. Thus, it is evident that the spatio-temporal relationships of these patches may play an important role in determining the population dynamics of a species that depends on new patch colonization.

Other forest management activities can degrade patch quality or change the temporal dynamics of the system. For instance, pre-commercial thinning as early as 14 years after replanting could reduce the amount of preferred habitat in a management area in the above example to as little as 4% (forest stands would be suitable for 4, rather than 16 years of a hypothetical 100 year rotation). Similarly, failure to successfully and quickly regenerate forest on recent clearcuts will decrease the relative amount of the forest's successional timeline that is occupied by forest of the age selected by hares.

To study the interaction of landscape structure (spatial and temporal) and snowshoe hare population dynamics, we have initiated both a field study of snowshoe hare habitat use and the development of a spatially-explicit, individual-based model of snowshoe hare populations on the Colville National Forest. Our spatially-explicit model tracks populations on a lattice of square "cells". Each cell is classified by successional habitat type and stand age. The simulation area can represent hypothetical landscapes or be derived from a GIS database.

Our model is individual-based because it stores information for each individual organism rather than composite values for entire populations. This modeling strategy allows us to incorporate the effects of patch edge/area ratio on dispersal success, and an additional element of demographic stochasticity. Reproduction, mortality, and dispersal are controlled by habitat specific probability functions.

Succession and harvesting activity also can be incorporated by the simulation model, and allows the user to specify different harvest regimes. Models that correlate static landscape metrics with wildlife population data are simpler to use than our dynamic model. However, simulating populations through time concurrent with the processes of succession and disturbance gives us a unique opportunity to assess both spatial and temporal effects of habitat management on hare populations. The field component of our study has provided detailed information on habitat use and the temporal variance of hare activity within stands. Along with demographic data from the literature this information is being used to parameterize the simulation model.

Our field data includes monthly counts of hare pellets collected over two summers (1995, 1996) which will be used as an indication of habitat use and relative density of hares. Twenty-seven regenerating forest patches as well as two clearcuts and two mature forest stands were surveyed in 1995 to study the relationship between local habitat and landscape qualities on hare use. To separate the effects of landscape quality and local habitat quality (on hare use), vegetation surveys (visual cover, summer vegetation species composition, plant association) were conducted on all sites as well. Preliminary data analysis suggests a positive relationship between patch size and density of pellets. A regression analysis indicated that mean pellet counts for September 1995 increase significantly ($r^2 = 0.57$) with patch size ($P = 0.003$) and horizontal cover at 2 m ($P = 0.006$).

In summer 1996, 15 additional young forest patches were sampled specifically to begin a validation process of the simulation model. Of these 15 stands, five were selected randomly from each of three watersheds. After simulation of the last 20 years for each of these watersheds is completed (using several sets of demographic parameters), the predicted relative hare densities for each set of five young forest patches will be compared to the relative hare densities estimated from the field data. It will then be possible to test whether the simulation model is valuable in predicting the effects of spatial configuration and habitat context on hare densities in sets of young forest stands. Also the value of predictions from the simulation model can be compared to static analytical models that utilize landscape metrics, stand context, and local habitat quality.

Using these tests to better refine the model, we propose to then conduct additional field sampling which would allow us to test the predictive capability for hare populations on a watershed scale. This would allow us to continue to develop the model as a tool to study the effects of alternative harvesting plans on hare populations. Further study also would allow us to get a better understanding of annual variance in regional hare populations.

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