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TFW-WL4-98-002

WILDLIFE USE OF MANAGED FORESTS:

A LANDSCAPE PERSPECTIVE

Volume 2

West-Side Studies
Research Results

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December 19, 1997

TIMBER/FISH
&WILDLIFE

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SAMPLING AND ANALYSIS OF VEGETATION

WEST-SIDE STUDIES

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We measured structural and vegetational components of stands to (1) describe wildlife habitats at the stand scale, (2) correlate habitat features at the stand scale with wildlife population parameters, and (3) identify stand components altered by harvest that affect wildlife species. We sampled vegetation at three scales. At each bird sampling point and within each pitfall grid, 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 (2,025 m2; Fig. 1).

VEGETATION VARIABLES MEASURED

For logs we used 3 decay classes: 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 in[act, sapwood firm); moderately decayed (limbs either stubs or absent, sapwood soft);

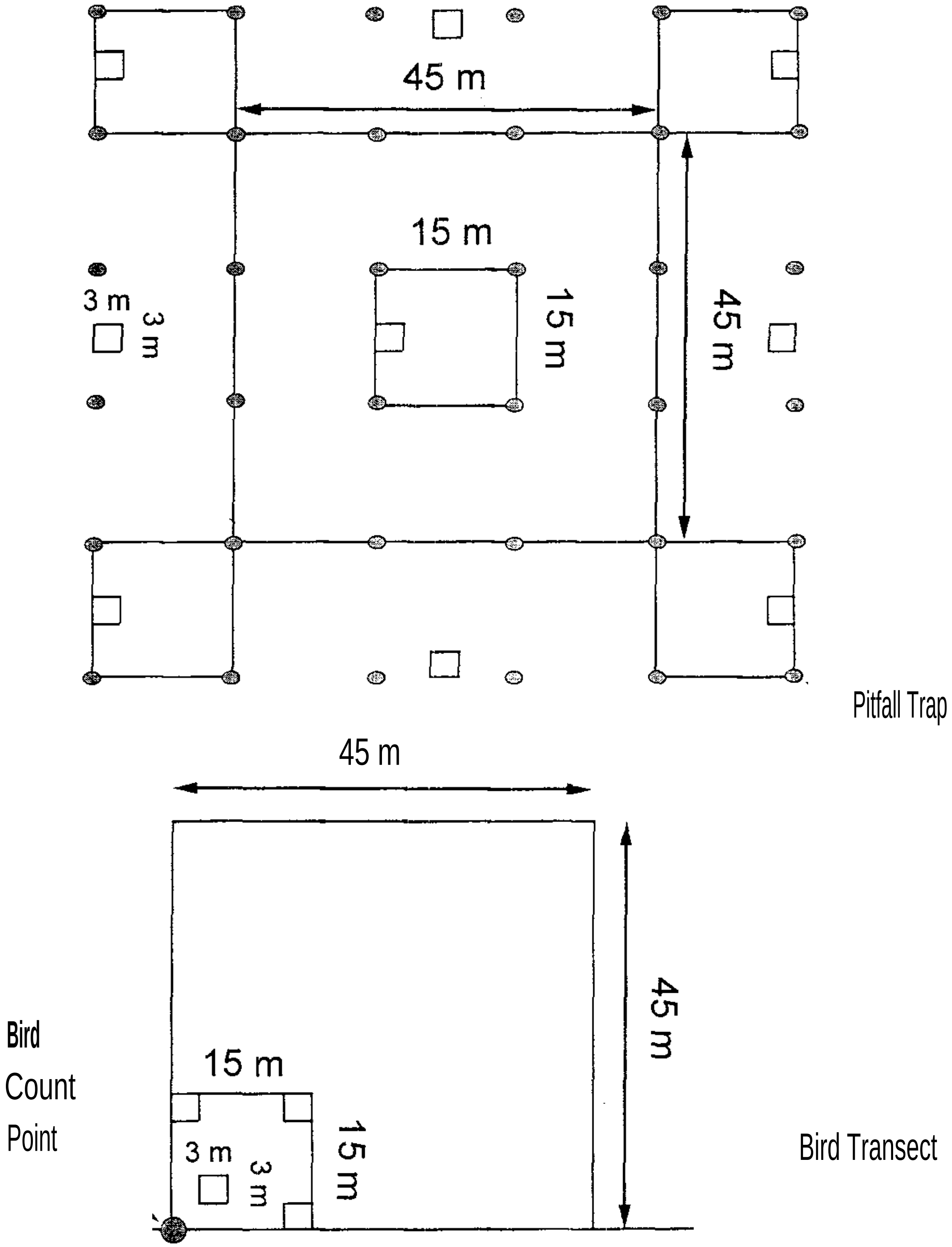


Figure 1. Diagram of 3- x 3-m, 15- x 15-m, and 45-. x 45-m vegetation sampling plots located at each bird sampling point and within each pitfall grid.

and well-decayed (all wood soft, bark and sapwood usually sloughed). Fine woody debris was defined as logs (or leaning snags at < 45° angle) < 10 cm in diameter on average; coarse woody debris is .>_ 10 cm on average. We sampled the following vegetation variables:

Within Each 3 x 3-m Plot (Herb/Low Shrub Plots)

Percent Cover Variables

- Berry-producing deciduous shrubs *(Vaccinium, Rubus)* < 1 m tall
- Broad-leaved evergreen shrubs < 1 m tall
- Other deciduous shrubs < 1 m tall
- Tree seedlings < 1 m tall
- Ferns
- Leaf litter
- Moss
- Bare soil
- Rock
- Forbs
- Grass
- *Lobaria* lichen
- Fine woody debris
- Coarse woody debris
- All stumps
- Other (saprophytes, above-ground roots, tree and snag boles, fungi, etc.)

Within Each 15 x 15 m Plot £Small and Medium Tree, Snag; and Log Plots)

Percent Cover Variables

- Trees 1-3 m tall by species
- Berry-producing deciduous shrubs *(Vaccinium, Rubus)* > 1 m tall
- Broad-leaved evergreen shrubs > 1 m tall
- Other deciduous shrubs > 1 m tall
- Small logs (10-30 cm dia.) by species and decay class

Large logs (> 30 cm dia.) by species and decay class ________________

Density Variables

Small (< 10 cm d.b.h.) live trees > 3 m tall by species and canopy position ____________

Medium (10-50 cm d.b.h.) live trees > 3 m tall by species and canopy position ____________

Small (< 10 cm d.b.h.) snags by species and decay class ________________

Medium (10~50 cm d.b.h.) snags < 1.5 m tall b v species and decay class _____

Medium (10-50 cm d.b.h.) snags 1.5-15 m tall by species and decay class ____________

Medium (10-50 cm d.b.h.) snags > 15 m tall by species and decay class ________

Within Each 45 x 45 m Plot (Large Tree and Snag Plots)

Presence/absence Variables

Talus

Intermittent stream

Permanent stream

Bog/Marsh

Pond

Tree pit

Riparian zone

Density Variables

Large (50-100 cm d.b.h.) live trees by species and canopy position ________________

Very large (>100 cm d.b.h.) live trees by species and canopy position ____________

Large (> 50 cm d.b.h.) snags and stumps < 1.5 m tall by species and decay class _______

Large (> 50 cm d.b.h.) snags 1.5-15 m tall by species and decay class ___________

Large (> 50 cm d.b.h.) snags > 15 m tall by species and decay class ____________

Deciduous trees in the canopy by species .

VARIATION IN VEGETATIVE CONDITIONS AMONG THE 4 STRUCTURE CLASSES

The four structure classes we sampled represent habitat conditions that typically occur in intensively managed landscapes, but which represent strikingly different stand structures (see Figs. 5ab and 6ab in Introduction and Technical Approach). These differences result partly from stand age and partly from management history. By studying differences in the composition and structure of vertebrate communities occurring in each of these 4 distinct structure classes, we can gain insights into the major structural and vegetative characteristics that influence the distribution and abundance of wildlife in intensively managed Douglas-fir forests west of the Cascade Crest. Some of the major vegetative and structural differences among the 4 classes we sampled are depicted in graphical form in the following pages.

The herb layer was described from sampling conducted in 3 x 3 m plots. Harvest stands contained substantially greater litter depths than any of the other 3 classes, but had the lowest cover percentage of fine woody debris (<10 cm dia.). The latter cover type, however, was relatively common in all 3 younger structure classes (Figs. 2a and 2b). This may be because this material is removed in commercial thinning operations or that it decomposes into the litter by the time stands reach harvest age. Both grass cover and cover of *Lobaria* lichen, which are both typical components of old-growth forests, were highest in the harvest class, but virtually absent from closed-canopy stands (Figs. 2c and 2d).

The shrub and tree layers were sampled in 15 x 15 and 45 x 45 m plots. Shrubs, including berry-producing shrubs, were most abundant in pre-canopy stands, virtually absent in closed-canopy stands, and important in harvest stands. Shrub presence in harvest stands was due to thinning, which allowed increased light to reach the forest floor and stimulate their growth (Fig. 3a). Deciduous trees were common in closed-canopy stands, but relatively uncommon in harvest stands, presumably because most were removed during commercial thinning operations (Fig. 3b). In general, closed-canopy stands were composed of coniferous trees 10~50 cm in d.b.h., whereas harvest stands were dominated by trees 50-100 cm d.b.h., reflecting both increasing tree ages in the harvest stands and increased diameter growth from competitive release following commercial thinning (Fig. 3c and 3d).

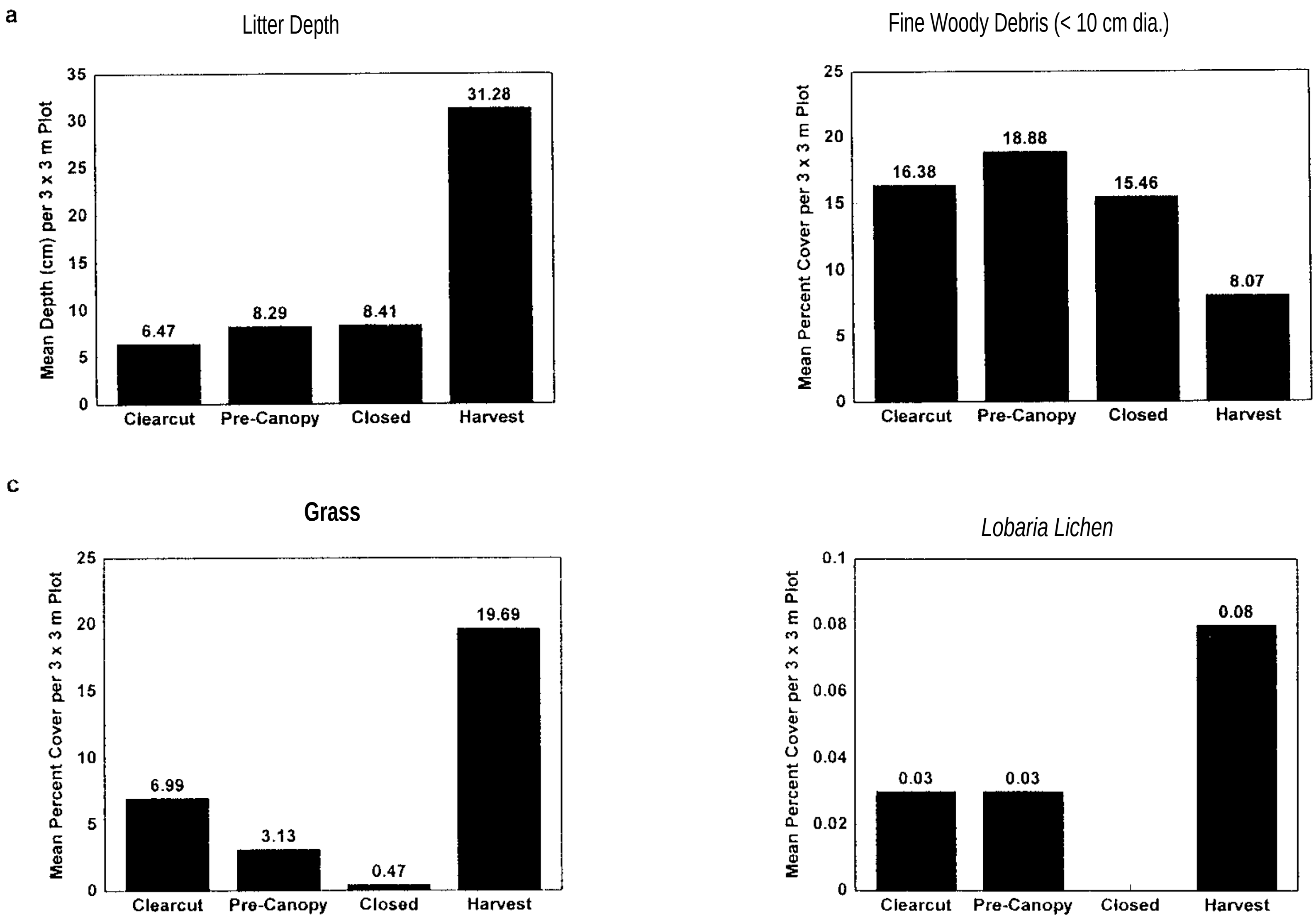
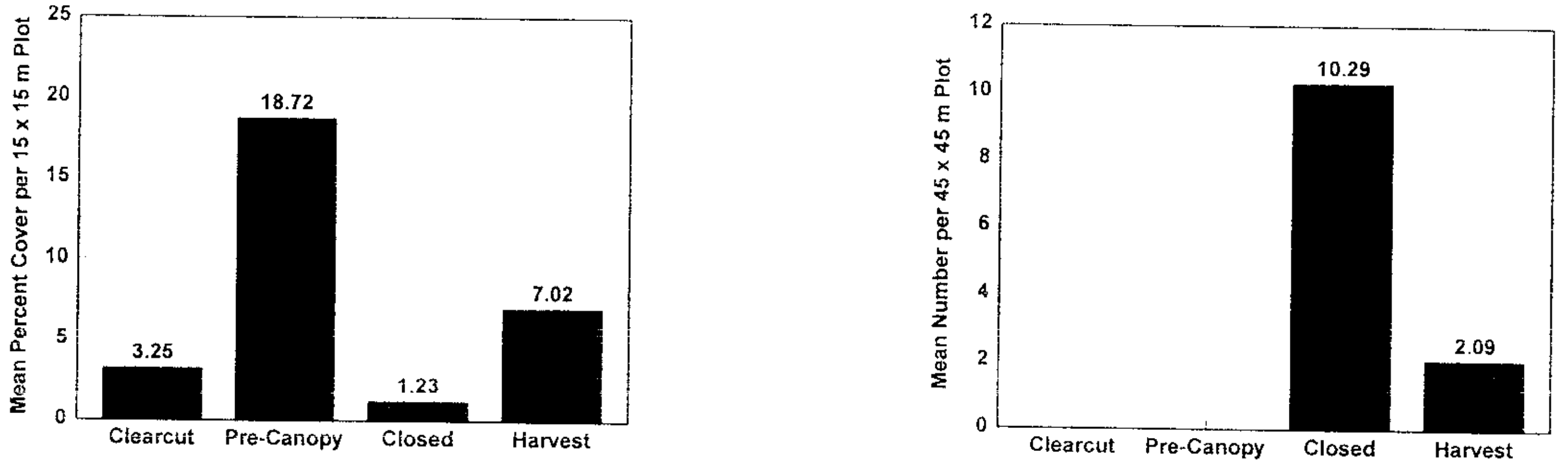
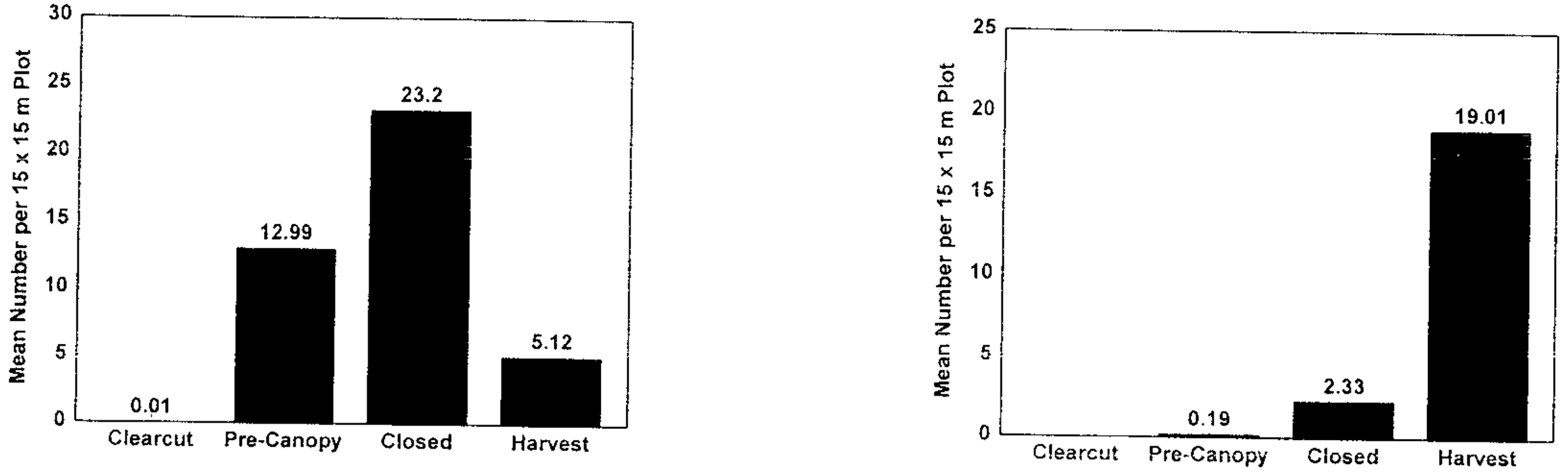


Figure 2. Histograms depicting major differences among stand structures for key cover variables sampled in 3 x 3 m plots,


All Shrubs

Deciduous Trees in the Canopy


Trees 10-50 cm d.b.h, and > 3 m Tall

Trees 50-100 cm d.b.h.

Figure 3. Histograms depicting major differences among stand structures for key live vegetation variables sampled in 15 x 15 and 45 x 45 m plots.

Woody debris, both as snags and as logs, was sampled in the 15- x 15- and 45~ x 45-m plots. Small (< 10 cm d.b.h.) snags representing both competition and suppression mortality were common in pre-canopy and closed-canopy stands (Fig. 4a). As expected, medium-sized snags (10-50 cm d.b.h, and > 15 m tall) were relatively uncommon in all structure classes, but occurred most often in closed-canopy and harvest stands (Fig. 4b). Snags larger than 50 cm d.b.h, were rare and were found only in the harvest class (Fig. 4c). Relatively large logs (> 30 cm in mean dia.) were typical of both pre-canopy and closed-canopy stands but occurred at much lower densities in clearcut and harvest stands (Fig. 4d).

A list of mean values for each variable (pooled across species) sampled in each stand is presented in Tables 1-3.

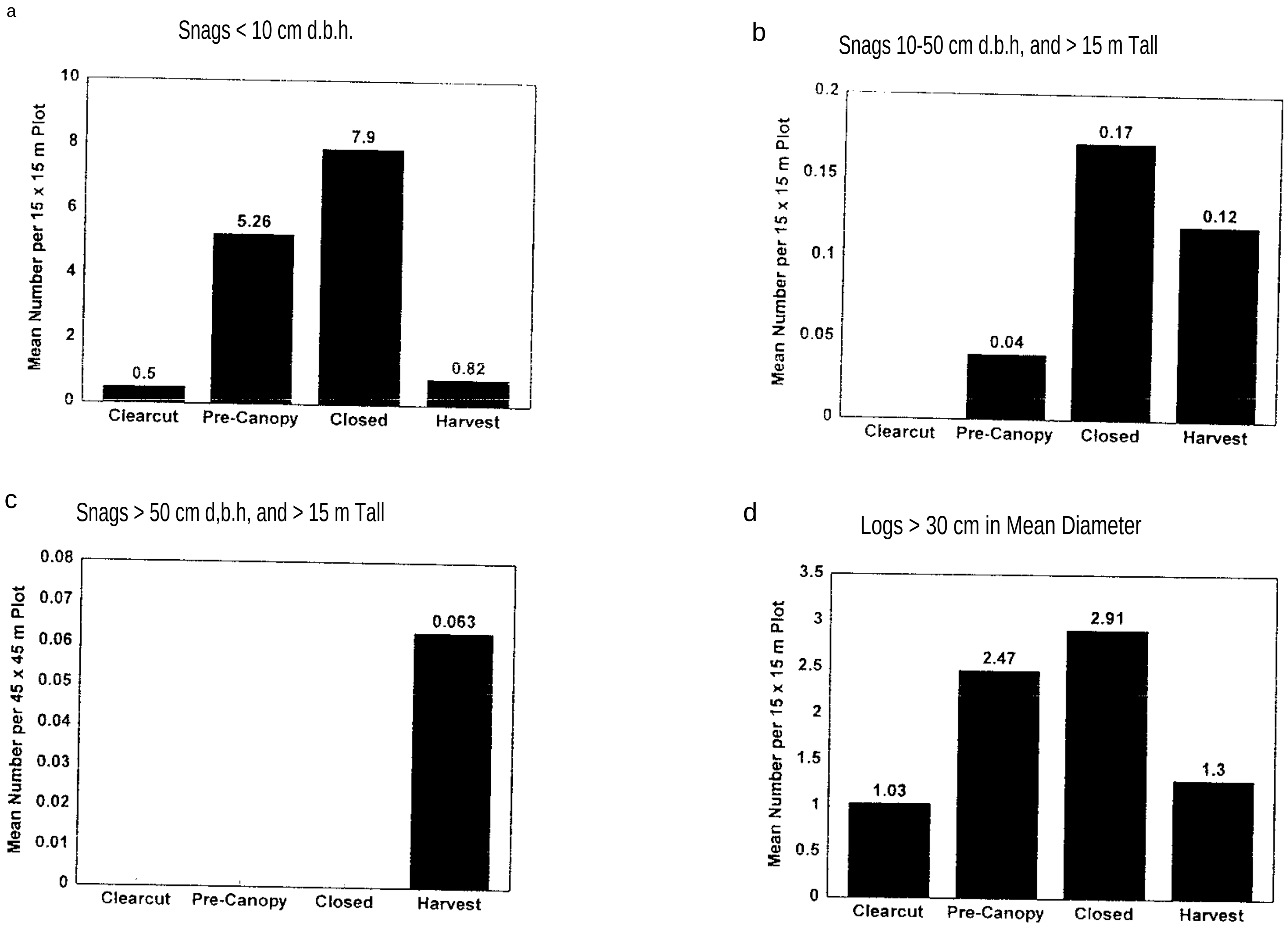


Figure 4. Histograms depicting major differences among stand structures for key snag and log variables sampled in 15 x 15 and 45 x 45 m plots.

Table 1. Vegetation and habitat sampled within 3 x 3 m plots.

Site		depth	bpshr	evshr	odshr	fern	litter	moss	soil	rock	forb	grass	lobaria	FWD	CWD	stump	other
A1	mean	3.56	23.86	28.18	1.07	28.75	81.05	8.70	0.39	1.11	16.02	4.26	0.00	17.37	5.60	2.98	0.00
A1	stdev	1.51	16.49	17.88	3.78	22.18	13.34	10.45	2.07	3.14	13.03	6.59	0.00	8.99	6.13	5.58	0.00
A1	min	1	**5**	**0**	O	0	30	O	O	0	1	0	0	5	0	O	0
A1	max	7	80	70	25	70	100	60	15	20	50	40	0	50	20	25	0
A2	mean	8.54	15.54	27.56	0.61	25.46	70,62	11,53	2.53	2.14	23.88	2.61	0.00	10.25	5.89	2.89	0,14
A2	stdev	20.28	14.59	14.75	1,79	17.07	22.62	10.83	10.79	3.38	17.20	7.46	0.00	6.38	8.40	5.42	0.69
A2	rain	1	**0**	**0**	0	0	3	0	0	0	0	0	0	1	0	O	0
A2	max	100	70	70	10	80	100	40	70	15	70	50	0	30	40	30	**5**
A3	mean	5.37	6.75	0.53	1.49	37,39	75.46	8.65	2.37	0.04	32.47	22.56	0.11	18.26	13.23	1,86	2.32
A3	stdev	2.07	7.18	2.23	3.04	30.44	18.19	10,02	7.71	0.18	19.40	25,85	0.67	14.62	14.10	3.40	9.48
A3	mm	1	O	0	O	0	1	0	0	0	1	0	0	1	0	0	0
A3	max	12	25	10	15	90	100	60	50	1	90	90	**5**	**80**	**70**	**15**	60
A4	mean	11.96	14.77	5.75	6.72	23.05	45.91	I0.58	6.07	3.04	37.23	3.68	0.00	12.72	12.04	3.05	1.46
A4	stdev	23.49	15.89	11.97	9.04	26.63	28.27	11.66	10.60	8.46	24.33	5.24	6.00	14,77	11.32	6.31	9.21
A4	mm	1	O	O	0	O	2	0	O	0	0	0	0	1	0	0	0
A4	max	60	60	60	40	100	90	50	50	40	90	20	0	70	50	30	70
A5	mean	3.91	20.18	36.07	0.96	16.77	72,46	15.77	0.23	2.60	12,23	0.89	0.07	14.56	8.60	4.68	3.67
A5	stdev	1.51	19.61	19.76	4.19	20.67	15.25	11.43	1.32	4.34	10.16	2.60	0.26	14.89	8.37	7.26	12.40
A5	min	1	O	O	0	0	30	O	0	0	0	0	0	1	O	0	0
A5	max	7	100	80	30	70	100	50	10	20	40	15	1	80	40	40	70
A6	mean	5.47	8.65	21.74	6.49	17.56	73.77	3.63	2.30	0.89	46.67	7.75	0.00	25.II	9.72	2.98	1.35
A6	stdev	8.91	9.91	18.09	12.32	18.83	18.74	6,97	6.04	2.92	21.61	11.30	0.00	17.68	10.40	6.03	9.20
A6	min	1	0	0	0	0	20	0	0	0	10	0	0	1	O	0	0
A6	max	70	50	70	50	90	90	50	30	20	90	50	0	80	50	25	70
B1	mean	5.16	10.63	7.07	0.72	20.42	82.46	11.67	1.51	1.35	4.84	8.60	0.00	7.47	3.11	0.96	1.56
B1	stdev	1.58	11.66	I1.34	2.48	17.89	16.04	13.78	4.45	3.06	8.35	16.19	0.00	12.95	5.81	4.19	2.58
B1	min	2	0	0	0	0	10	0	0	0	0	O	O	O	O	O	0
B1	max	9	60	60	15	90	100	80	25	20	40	80	O	80	30	30	15
B2	mean	7.57	6.00	0.06	0.93	5.58	6658	26.84	0.00	0.02	1.33	0.09	0.00	39.82	11.82	3.81	1.77
B2	stdev	2.39	8.28	0.00	2.42	8.27	18.76	17.88	0.00	0.13	3.94	0.28	0.60	25.18	12.80	7.06	2.14
B2	min	3	0	0	0	0	5	5	0	O	O	O	0	O	0	0	0
B2	max	12	40	0	10	40	90	90	0	1	20	1	0	90	70	40	5
B3	mean	5.54	5.53	0.02	0.04	9.98	59.56	39,75	0.53	0.11	5.14	0.16	0.00	28.56	8.89	3.26	3.35

Site		depth	bpshr	evshr	odshr	fern	litter	moss	soil	rock	forb	grass	lobaria	FWD	CWD	stump	other
B3	stdev	2.68	6.94	0.13	0.18	12.95	23.51	25.08	2.76	0.67	9,96	0.70	0.00	23.78	11.17	5.06	7.87
B3	Bin	1	0	0	0	0	10	1	0	0	0	0	0	1	0	0	0
B3	max	14	30	1	1	80	100	80	20	5	50	5	0	90	70	30	40
B4	mean	4.82	18.44	15.12	0.12	21.12	81.32	10.95	0.89	0.11	8.51	6.32	0.18	11.54	4.67	2.02	3.16
B4	stdev	1.73	15.03	21.54	0.68	15.68	13.78	11.47	4.16	0.67	13.07	13.53	1.31	14.92	6.86	5.55	7.16
B4	mln	1	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0
B4	max	10	60	90	5	60	100	50	30	5	80	70	10	60	25	25	40
B5	mean	4.65	2.02	9.33	0.14	26.40	82.11	9.82	0.28	0.19	3.37	0,60	0.00	6.86	5.77	3.51	2.84
B5	stdev	1.66	4.26	18.97	0.69	24.07	13.98	10,81	0.95	1.32	7.60	1.54	0.O0	9.65	6.50	9.14	2.75
B5	min	2	0	0	0	1	30	0	0	0	0	0	0	0	0	0	0
B5	max	9	20	90	5	90	100	40	5	10	40	7	0	60	25	60	10
B6	mean	22.00	7.09	12.63	0.61	8.05	49.37	15.84	1.54	0.32	4.42	3.04	0.02	19.04	13.79	2.79	1.46
B6	stdev	32.87	7.72	18.51	1.79	11,94	29.41	18.42	4.28	1.13	7.74	8.39	0.13	19.26	13.73	5.49	1.88
B6	min	2	0	0	0	0	3	0	0	0	0	0	0	0	0	O	0
B6	max	100	40	90	10	70	90	80	20	5	30	40	1	80	50	20	5
C1	mean	6.95	0.00	0.23	0.00	2.42	78.95	5.93	0.00	0.02	0.30	0.00	0.00	13.40	6.44	2.32	3.95
C1	stdev	1.78	0.00	0.94	0.00	10.13	16.62	7.41	0.00	0.13	1.46	0.00	0.00	10.93	8.83	6.68	3.69
C1	min	3	0	0	0	0	20	0	0	0	0	0	0	1	0	0	0
C1	max	1!	0	5	0	70	100	40	0	|	10	0	0	60	40	40	20
C2	mean	6.05	0.42	6.65	0.00	19.49	83.33	7.37	0.12	0.70	0.28	0.02	0.00	15,19	5.56	1.58	2.44
C2	stdev	1.87	1.14	11.79	O.00	24.61	11.75	8.16	0.68	2.02	0,95	0.13	0.00	12.94	8.88	4.86	3.38
C2	min	3	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0
C2	max	12	5	60	0	90	90	40	5	10	5	1	0	60	30	30	10
C3	mean	6.30	0.07	0.5!	0.02	4.23	67.72	15.11	0.00	0.16	1.30	0.00	0.00	9,46	11.86	2.67	3.65
C3	stdev	1,91	0.26	1.70	0.13	10.40	19.91	17.87	0.00	0.70	3.40	0.00	0.00	7.74	12.38	5.09	3.58
C3	mill	3	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0
C3	max	11	1	10	1	60	100	80	0	5	15	0	0	30	60	25	15
C4	mean	8,12	042	0.56	0.00	1,65	79.39	9.60	0.00	0.04	1.30	1.42	0.02	26.86	12.14	1.49	4.49
C4	stdev	2.48	1.59	1.80	0,00	3.86	15.73	14.17	0.00	0.18	663	10.50	0.13	23.07	11,96	2.68	4.46
C4	min	4	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0
C4	max	15	10	10	0	25	100	80	0	1	50	80	1	80	60	10	15
C5	mean	16,61	033	1.39	0.02	2.44	70.00	6.61	146	0.46	0.12	1.37	0.00	16.28	8.93	4.23	2.16
C5	stdev	26.80	1.47	4.08	0.13	5.88	29.81	7.60	4.52	1.29	0.33	6.17	0.00	17.61	10.95	11.91	2,25

Table 1. Continued

Site		depth	bpshr	evshr	odshr	fern	litter	moss	soil	rock	forb	grass	Iobaria	FWD	CWD	stump	other
C5	rain	3	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
C5	max	90	10	25	1	40	100	30	25	5	1	40	O	90	60	80	10
C6	mean	6,44	0,40	1,40	0.04	5.23	81.58	10.00	0.60	0,91	0.70	0.02	0,00	11.60	10.05	1.58	3.35
C6	stdev	2.93	1.59	5,46	0.18	10.87	14.12	13.42	2.76	3,59	2.48	0.13	0,00	10.85	13.44	4.75	5.67
C6	rain	2	0	0	0	0	40	0	0	0	0	0	O	1	0	0	0
C6	max	15	10	40	1	60	100	60	20	25	15	1	0	50	60	25	30
D1	mean	52.56	2.44	44,35	0.79	0.02	5.30	6.02	27.68	3.91	0.04	36,86	0,14	3.84	2.95	1.11	1.35
D1	stdev	25,43	5.64	31.85	2.37	0.13	4.99	0.13	24.78	12.20	0.18	25,86	0,69	4.47	5.32	2.70	3.51
D1	rain	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
D1	max	90	40	90	10	1	40	1	90	60	1	90	5	20	25	10	20
D2	mean	64.04	0.65	56.77	0.04	0.09	5.11	O.OO	16.07	2.28	0.09	27.53	0.04	5.79	3.47	1.35	1.33
D2	stdev	21.93	2.63	22,35	0.18	0.66	4.25	0.00	13.63	4.48	0.66	23.73	0,18	6.77	9.84	3.25	3.12
D2	min	5	0	1	0	0	2	0	0	0	O	0	0	0	0	0	0
D2	max	90	20	90	1	5	30	0	70	25	5	90	1	30	70	20	15
D3	mean	5.18	6.00	36.32	1.74	23.75	57.98	34.30	0.02	0.95	3.68	0.12	0.04	14,44	8.28	1.60	3.47
D3	stdev	1.59	8.54	30.02	6.39	2819	21.78	23.55	0.13	4.19	7.76	0.33	0.18	10.86	9.86	3,74	4.43
D3	min	3	0	0	0	0	10	0	0	0	0	0	0	!	0	0	0
D3	max	11	50	90	25	90	90	90	1	30	40	1	1	60	40	20	20
D4	mean	33.54	3.70	1.81	0.04	11.07	30.07	15.63	10.18	9.67	8.04	21.18	0.05	7,65	7.09	2.07	1.49
D4	stdev	29.44	5.74	4.81	0.18	18.41	29.90	22.84	15.15	16.65	15.81	23.63	0.22	4.81	7.83	5.53	3.04
D4	rain	2	0	0	0	0	2	0	0	0	0	0	0	1	O	0	0
D4	max	90	30	20	1	70	90	90	60	70	80	80	1	20	30	25	15
D5	mean	6.60	1.91	0.44	1.18	36.68	72.28	18.07	0.00	0.00	9.56	0.02	0.02	8.88	7.11	2.40	3,88
D5	stdev	2.02	6.62	1.94	3.70	26.56	20.18	18.88	0.00	0.00	17.21	0.13	0.13	10.08	7.10	5.74	4.78
D5	mIn	2	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0
D5	max	12	40	10	25	90	100	80	O	0	80	1	1	70	25	30	15
D6	mean	55.79	4.00	0.26	0.19	0.02	6.96	0,02	14.46	4.44	0.07	32.42	0.16	7.81	9,51	1,19	2.40
D6	stdev	22.34	8.53	1.46	0.71	0.13	2.53	0.13	17.00	9.31	0.26	22.89	0.70	5,64	12.76	3.18	4.35
D6	mIn	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D6	max	90	50	10	5	1	15	1	70	50	1	80	5	25	80	1,5	20

Table 1. Continued

Definitions for column headings:

Depth, the vertical depth (in cm) of litter from the surface to the soil.
Bpshr, percent cover of berry-producing deciduous shrubs <1 m in height.
Evshr, percent cover of evergreen shrubs <1 m in height.
Odshr, percent cover of other deciduous shrubs <1 m in height.
Fern, percent cover of ferns.
Litter, percent cover of ground litter.
Moss, percent cover of moss.
Soil, percent cover of bare soil.
Rock, percent cover of exposed rock.
Forb, percent cover of forbs.
Grass, percent cover of grass.
Lobaria, percent cover of *Lobaria* lichen.
FWD, percent cover of fine woody debris (<10 cm in diameter).
CWD, percent cover of coarse woody debris (>10 cm in diameter).
Stump, percent cover of stumps occurring within the subplot.
Other, percent cover of object(s) not accounted for in the above categories.

Table 2. Vegetation and habitat sampled within 15 x 15 m plots.

Site	Stat	SUMShr	SUMTr	SUMSs	SUMSd	SUMMs	SUMMd	SUMS1	SUMS2	SUMS3	SUMMs1	SUMMs2	SUMMs3	SUMMm1	SUMMm2	SUMMm3	SUMMt1	SUMMt2	SUMMt3	SUMS1Log	SUMS2Log	SUMS3Log	SUMI1Log	SUMI2Log	SUMI3Log
A	Mean	3,25	444	009	0.08	0.01	0.01	0.77	0.69	0.04	2.14	3,38	0.60	0,03	0.03	004	000	001	0.00	1.45	5.36	0,61	0.47	1.58	1.03
A	Var	45.57	63.83	0.12	0.37	0.01	0.01	7.54	2.40	0.04	9.96	10.30	1.07	0,05	003	0.06	000	0.01	0.00	9.33	3246	1.27	1,35	7.24	302
A1	Mean	2.35	1.50	0.18	0.00	0.06	0.06	0.00	094	008	0.71	2.65	0.75	000	0.00	000	0.00	000	0.00	0.12	4,38	0.24	0.32	0.47	0.71
A1	Vat	7.68	6,75	0.28	0,00	0.06	0.06	000	1.81	006	1.47	3.37	1.07	000	0.00	0.00	000	000	0.00	0.11	6.30	010	0,22	0.36	1.38
A2	Mean	050	1.71	0.00	0.06	0.00	000	0.12	071	006	0.47	588	094	0.00	0.00	000	0.00	0.00	0.00	0.03	2.88	1.15	0.00	0.59	1.62
A2	Var	1.53	3.66	0.00	006	0.00	000	011	222	006	0.64	14.36	1.31	0,00	000	0.00	0.00	000	000	0.01	1570	2.31	0.00	1.51	3.92
A3	Mean	3.53	4.97	0.12	0.00	0.00	000	0.00	065	000	1.47	471	0.35	000	000	000	0.00	000	0.00	0.68	9.65	0.56	1.06	203	1.00
A3	Vat	91.76	48,36	011	000	0.00	0,00	0.00	067	000	564	1047	0.24	000	000	000	000	0.00	000	2.72	19.52	0.18	675	14.64	269
A4	Mean	6.26	3.44	000	000	000	0.00	0,59	0.29	0.00	335	1.86	0,06	0.18	0.00	000	0.00	0.00	0.00	3.86	3.09	0.18	0.50	3,68	147
A4	Var	12350	39.28	0.00	0.00	000	0.00	063	0.60	0.00	10.62	10.99	0.06	028	0.00	0,00	0.00	0.00	0.00	17,15	8.69	012	0.38	11.40	7.33
A5	Mean	3.91	14,12	0.24	0.41	0.00	0.00	3.59	1.18	0,12	3.94	4.18	1.18	0.00	0.12	0.18	0.00	0.00	0.00	0.94	7.03	1.29	0,44	1.62	0.74
A5	Var	35.35	172.20	0.32	2.13	0.00	0.00	3601	8,28	0.11	22.93	5.90	278	0.00	0.11	0.28	0.00	0,00	0.00	2.25	32.45	3.85	018	3.61	1.38
A6	Mean	2.97	0.91	0.00	0.00	0.00	0.00	0,35	035	0.00	2.88	100	0.29	0.00	0.06	006	000	0.06	0.00	3.09	5.15	0,24	0.47	1,12	0.68
A6	Var	8.67	1.44	0,00	0,00	0.00	0.00	0.49	0.74	000	10.36	1.75	0.35	000	0.06	006	0.00	0.06	0,00	22.73	86.68	0.13	0.33	670	1.44
B	Mean	18.72	2.74	15.15	1.44	1.16	12.99	8.87	5.79	1.12	2.26	200	1.50	0.34	0.06	0.00	010	0.03	0.00	1.67	2.58	2.84	0.00	1.88	5.53
B	Var	318.65	9,69	1173.67	18.09	7.10	3809	12481	10462	10.26	12.18	8.28	5.16	062	008	0.00	0,11	0.09	0,00	6.41	715	11.94	000	9.50	45.98
61	Mean	!7,25	291	22.06	0.94	259	10.65	2.12	124	059	1.65	1.29	176	041	006	000	000	0.00	000	155	262	097	000	1.21	1.35
61	Vat	259,19	10.54	177993	3.18	3251	23.49	4.99	307	101	2,74	6.97	11.82	1.38	006	000	0.00	0,00	0.00	3.09	7.61	1.36	000	397	399
62	Mean	25.38	0.76	1.88	053	0.94	14.41	15.24	16.12	0.59	2.35	3.71	1,41	041	0 12	0,00	0.35	0.18	0.00	1.50	2.56	4.12	0.00	2.94	800
62	Var	452.11	1.41	2.61	2,14	143	52.01	125.69	290.36	1.51	6.37	985	4.26	1 01	0 11	000	037	0,53	0.00	4.31	518	24.39	0.00	8.31	27,38
63	Mean	24.29	168	1059	0.35	1.29	10,65	8.35	12.65	1.35	1.53	1,65	2.53	0.18	0.00	0.00	0.06	0.00	000	1.24	3.26	2.82	000	185	397
63	Vat	571.85	6,94	67201	149	3.85	2149	9924	92.49	449	1001	4.87	926	0,15	000	0.00	006	0.00	0.00	366	8.16	715	0,00	768	12.58
64	Mean	2285	3.50	14.59	041	0.76	11.82	2,35	0.12	0.00	2.76	0.65	0.65	024	000	0.00	000	0.00	0.00	3,62	0.71	0.82	000	109	2,00
64	Var	292,59	1341	1151.13	1,51	1.82	19.53	4.99	0.11	0,00	9.32	099	1.87	0.32	000	000	000	000	000	820	025	134	000	426	8.50
65	Mean	8.24	4.09	38.53	5.29	0.88	13,12	1288	1.94	347	035	1.06	147	041	006	000	0.18	0.00	000	0.15	2.88	6.94	000	2.18	5.12
65	Vat	63.53	11.60	2798.01	78,60	1.74	15.86	275.99	21.43	47.51	0.74	2.31	0.76	0.26	006	0.00	0.15	0.00	0.00	0.12	8.08	1568	000	24.78	26.99
66	Mean	14.29	347	3.24	1.12	0.47	17.29	12.29	2.71	0,71	4.94	3.65	1.18	041	0.12	0.00	0,00	000	000	1.94	3,44	2.38	0.00	2.00	12.76
66	Var	134.03	880	1457	7.86	051	73,10	11047	760	2,22	34.93	17,74	2.53	076	0.24	000	0.00	0.00	0.00	14.25	10,75	5.24	0.00	850	114.19
C	Mean	123	154	13,59	069	1.25	23.20	19.80	386	049	0.28	0.56	1.31	132	095	0.14	0,39	0.11	0.00	0.36	1,79	1.96	0.00	204	6.68
C	Var	10,37	6.42	2774.58	2.68	3.35	135.68	42285	4000	5.91	1,41	1.36	2.26	396	4.90	0,22	076	0.18	0.00	1,13	5.39	7.13	0.00	1681	37.87
C1	Mean	0.38	0.12	3.47	0.12	0.47	25.65	2482	659	0.12	0,12	0.24	1.53	1.35	071	035	024	006	000	053	135	2.50	000	0.29	7.32
C1	Vat	2.11	0.11	5.26	0,11	0.51	104,37	76390	79.01	024	0.11	019	2.89	399	110	0.62	032	006	000	1.51	3.24	8.47	000	1.47	24,65
C2	Mean	1.32	1.41,	1329	0.18	065	14.41	618	1.35	0.00	0,12	0.00	053	0.65	0,24	012	024	0.24	0.00	0,06	0.26	1.15	003	0,12	782
C2	Vat	4.53	3.98	477.55	0.53	0.87	52.01	47.03	4.74	0.00	024	000	0.51	162	032	024	019	0.32	0.00	0.06	0.19	5.68	001	0.11	35.28

Table 2, Continued

Site	Stat	SUMShr	SUMTr	SUMSs	SUMSd	SUMMs	SUMMd	SUMS1	SUMS2	SUMS3	SUMMs1	SUMMs2	SUMMs3	SUMMm1	SUMMm2	SUMMm3	SUMMt1	SUMMt2	SUMMt3	SUMS1Log	SUMS2Log	SUMS3Log	SUMI1Log	SUMI2Log	SUMI3Log
C3	Mean	1.91	074	629	229	1.18	33.71	2982	382	0.18	076	059	2.12	082	041	006	0.00	0.00	0.00	053	2.62	2.65	0.00	1.97	826
C3	Vat	24.66	1.53	34.72	1060	4.90	218.22	551.65	60.78	0.l5	7.19	2.26	261	1.90	076	0.06	0.00	0.00	0.00	1.61	830	4.90	0.00	11.70	2432
C4	Mean	1.06	2.62	2265	0.41	124	29.94	14.12	582	2.00	012	071	188	1.94	335	024	071	0.29	0.00	0.76	247	2.t5	0.00	2.74	9.24
C4	Var	1490	17.99	597174	101	507	96.56	114.11	17.65	39.38	024	172	324	5.18	2012	0.32	1.72	0.60	0.00	3.28	595	4.87	000	2057	6732
C5	Mean	176	203	3.53	0!2	1 4!	!900	26 47	247	035	04!	0.53	0 59	1.47	0.41	'~	086	006	0.00	018	174	138	000	1.2i	268
C5	Var	1475	4.76	1401	0.11	263	12.50	56539	5.39	0.62	063	064	0 63	6.76	0 51	0 06	t 61	0.06	0.00	0.15	344	7.52	000	3.44	5.45
C6	Mean	094	232	3229	041	2.56	16.47	1741	3.12	0.29	018	1.29	1.24	1.71	059	0.00	029	000	0.00	009	229	191	0.00	5.91	4.53
C6	Vat	284	719	10279.72	0.76	4.25	52.01	20876	63.61	022	0.15	285	2.07	422	063	000	035	000	000	0.07	875	10.66	0.00	4444	47.36
D	Mean	703	769	6.93	006	1.79	512	096	1.01	049	0.24	290	1.30	044	052	024	030	005	001	0.18	236	157	0.02	112	2.76
D	Vat	88.38	141.35	232.98	011	7.25	19.35	1192	353	085	0.44	959	229	261	110	042	061	007	0.01	0.38	811	671	0.01	796	15.06
D1	Mean	1224	185	529	012	141	4.47	0.35	100	04t	016	200	153	000	012	012	000	006	000	006	056	103	0.00	053	288
DI	Var	20310	427	7660	0.24	151	901	0.37	175	0.51	028	600	364	000	0il	0tl	000	0.06	0.00	0.03	0.40	298	0.00	164	1855
D2	Mean	4.06	1,85	241	024	0.82	2,53	059	0.24	006	041	176	0.59	0.00	024	006	012	000	000	003	041	050	0.00	032	176
D2	Vat	2287	5.84	2151	032	1.90	5.76	1.26	019	006	O38	432	0.88	000	0.32	006	O24	000	0.00	001	013	013	000	178	14.13
D3	Mean	1065	10.16	1918	000	1.88	9.47	3.35	2.94	065	018	559	129	0.35	047	000	024	006	0O0	0.41	282	091	000	256	250
D3	Vat	74.15	187,34	922..5	000	14.74	1351	5987	11.43	0,74	028	2188	1.22	074	0.51	000	0.19	0.06	000	1.51	487	2.54	000	2009	781
D4	Mean	4.91	17.32	6.47	006	276	2.35	065	071	024	0.00	276	218	0.12	041	005	0.06	000	0.00	0.06	212	238	0.06	0.24	215
D4	Var	12.44	291.59	83.14	006	669	274	4.74	1 /0	019	000	607	4!5	0!!	!0!	006	006	0.00	000	0.06	449	864	0.06	019	7.98
D5	Mean	435	706	665	006	212	376	012	029	0.59	006	276	I24	1 24	071	0.65	059	0.06	000	0.24	506	1 32	003	0.41	2.09
D5	Vat	3431	54.03	14699	006	11,36	8.69	0.11	0.22	088	006	619	182	1294	1 10	1.49	088	006	0.00	032	1803	247	001	041	5.69
D6	Mean	597	785	159	000	1.76	8.12	071	0.88	1.00	059	253	1.00	094	118	053	082	012	006	026	318	329	003	265	5.18
D,6	Var	145.39	171.15	5.76	000	732	35.11	135	2.36	238	151	601	1.25	118	3.15	0.51	3.15	024	006	0.38	706	1969	0.01	1906	3269

Definitions for column headings:

Shr, all shrubs

Tr, trees between 1-3 m

as, small subdominant tree

Sd, small dominant tree

Ms, medium subdominant tree

Md, medium dominant tree

Table 2. Continued

S1, decay-class 1 small snag
S2, decay-class 2 small snag
S3, decay-class 3 small snag
Ms1, decay-class 1 medium shod snag
Ms2, decay-class 2 medium short snag
Ms3, decay-class 3 medium short snag
Mml, decay-class 1 medium mid-height snag
Mm2, decay-class 2 medium mid-height snag
Mm3, decay-class 3 medium mid-height snag
Mr1, decay-class 1 medium tall snag
Mt2, decay-class 2 medium tall snag
Mr3, decay-class 3 medium tall snag
S1log, decay-class 1 small log
S21og, decay-class 2 small log
S3log, decay-class 3 small log
L1log, decay-class 1 large log
L21og, decay-class 2 large log
L31og, decay-class 3 large log

Table 3, Vegetation and habitat sampled within 45 x 45 m plots

				UMLs2	SUMLs3	SUMDd	SUMLm1	Lm2	Lm3				m1+	UMLm2+	m3+
A	Mean	0.0	14.6	6.0	4.1	0.O	0.0	0.6	1.8	0.0	0.0	0.0	0.0	0.6	1.8
A	Var	0.0	72.5	54.8	!4.5	0.0	0.0	5.8	100	OO	0.0	0.0	0.0	5.8	10.0
A1	Mean	0.0	16.0	1.8	4.5	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.3
A1	Var	0.0	52.7	3,8	ii.3	0.0	0.0	0.0	0.2	0,0	0.0	0.0	0.0	0.0	0.2
A2	Mean	0.0	6.5	7.1	7.4	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	1.2
A2	Vat	0.0	21.6	30.1	11.8	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	2.0
A3	Mean	0.0	15.5	9.2	1.0	0.0	0.1	0.1	0.5	0.0	0.0	0.0	0.1	0.1	0.5
A3	Var	0.0	66.1	38.5	0.8	0.0	0.1	0.1	0.6	0.0	0.0	0.0	0.1	0.1	0.6
A4	Mean	OO	13.9	!1.5	3.3	0.0	OO	3!	05	0.0	0.0	0.0	0.0	3.1	0.5
A4	Var	0.0	153.1	160.8	2t.9	0.0	0.0	28.6	0.4	0.0	0.0	0.0	0.0	28.6	0.4
A5	Mean	0.0	16.9	5.1	6.2	0.0	0.0	0.2	7.5	0.0	0.0	0.0	0.0	0.2	7.5
A5	Vat	0.0	44.7	25.1	12.3	0.0	0.0	0.2	15,6	0.0	6.0	0.0	0.0	0.2	15.6
A6	Mean	0.0	18.8	1.4	2.1	0.0	0.0	0.2	1.1	0.0	0.0	0.0	0.0	0.2	1.1
A6	Var	0.0	27.0	6.1	3.1	0.0	0.0	0.3	2.1	0.0	0.0	0.0	0.0	0.3	2.l
B	Mean	0.2	OO	5.2	9.9	0.0	0.0	0.7	2.4	0.0	0.0	0.0	0.0	0.7	2.4
B	Vat	1.2	0.0	52.6	32.6	0.0	0.0	1.4	6.6	0.0	0.0	0,0	0.0	1.5	6.6
B1	Mean	0.0	0.0	2.8	5.2	0.0	0.0	0.9	3.3	O.0	0.0	0.0	0.0	0.9	3.3
B1	Vat	0.0	0.0	9.5	3.8	0.0	0.0	2.1	6.2	0.0	0.0	0.0	0.0	2.1	6.2
B2	Mean	11	0.0	2.8	11.8	0.0	0.0	0.6	2.2	0.0	0.0	0.0	0.0	0.6	2.2
B2	Vat	6.6	0.0	19.6	17.8	0.0	0.0	0.4	3.9	0.0	0.0	0,0	0.0	0.4	3.9
B3	Mean	0.0	0.0	3.7	15.2	0.0	0.1	0.8	2.9	0.0	0.0	0.0	0.1	0.8	2.9
B3	Var	0.0	0.0	t2.2	44.5	0.0	0.1	4.3	6.2	0.0	0.0	0.0	0.1	4.3	6.2
B4	Mean	0.0	0.2	0.6	6.9	0.0	0.0	1.3	4.7	0.0	0.1	0.0	0.0	1.4	4.7
B4	Var	0.0	0.1	2.8	11.2	0.0	0.0	0.7	9.7	0.0	0.1	0.0	0.0	1.1	9.7
B5	Mean	0.1	0.1	16.1	7.3	0.0	0.0	0.5	0.1	O.0	0.0	0.0	0.0	0.5	0.1
B5	Vat	0.1	0.1	113.7	15.7	0.0	0.0	0.6	0.1	OO	0.0	0.0	0.0	0.6	0.1
B6	Mean	0.0	0.0	4.9	13.0	0.0	0.0	0.1	1.3	0.0	0.0	0.0	0.0	0.1	1.3
B6	Var	0.0	0.0	138	29.7	0.0	0.0	0.1	2.1	0.0	0.0	0.0	0.0	0.1	2.1

Table 3. Continued

Site	Stat	SUMLd	SUMLs1	SUMLs2	SUMLs3	SUMDd	SUMLm1	SUMLm2	SUMLm3	SUMLt1	SUMLt2	SUMLt3	SUMLm1+	SUMLm2+	SUMLm3+
c	Mean	2.3	0.0	1.3	14.4	10.3	0.0	0.2	0.9	0.0	0.0	0.0	0.0	0.2	0.9
C	Vat	7.3	0.0	7.4	42.5	391.7	0.0	0.2	1,1	0.0	0.0	0.0	0.0	0.2	1.1
C1	Mean	2.9	0.0	0.6	19.7	0.6	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.8
C1	Var	5.7	0.0	0.8	22.7	1.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5
C2	Mean	3.2	0.0	0.1	10.7	11.8	0.0	0.3	1.2	0.0	0.0	0.0	0.0	0.3	1.2
C2	Var	6.9	0.0	0.1	22.9	142.1	0.0	0.2	1.5	0.0	0.0	0.0	0.0	0.2	1.5
C3	Mean	0.2	0.1	0.2	20.2	8.6	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4
C3	Vat	0.7	0.1	0.2	36.0	389.6	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4
C4	Mean	4.0	0.0	0.0	15.7	3.2	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5
C4	Vat	10.3	0.0	0.0	25.1	33.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4
C5	Mean	2.4	0.0	4.2	7.9	26.5	0.0	0.5	1.2	0.0	0.0	0.0	0.0	0.5	1.2
C5	Vat	10.3	0.0	14.9	17.7	1226.1	0.0	0.6	1.5	0.0	0.0	0.0	0.0	0.6	1.5
C6	Mean	1.2	0.0	2.5	12.4	11.0	0.0	0.1	1.3	0.0	0.0	0.0	0.0	0.1	1.3
C6	Vat	2.7	0.0	15.8	14.6	275.8	0.0	0.1	1.9	0.0	0.0	0.0	0.0	0.1	1.9
D	Mean	1g.0	0.0	0.4	I0.6	2.1	0.0	0.2	1.0	0.1	0.0	0.1	0.1	0.2	1.1
D	Var	106.9	0.0	0.5	42.6	66.7	0.0	0.2	2.9	0.1	0.0	0.6	0.1	0.2	3.3
D1	Mean	11.8	0.0	0.5	9.6	0.5	0.0	0.2	0.5	0.0	0.0	0.0	0.0	0.2	0.5
D1	Var	42.3	0.0	0.9	17.8	1.3	0.0	0.2	0.9	0.0	0.0	0.0	0.0	0.2	0.9
D2	Mean	15.9	0.1	0.2	8.0	0.3	0.1	0.2	0.8	0.3	0.0	Q0	0.4	02	0.8
D2	Var	15.2	0.1	0.4	16.5	0.4	0.1	0.3	2.4	0.4	0.0	0.0	0.4	0.3	2.4
D3	Mean	5.5	0.0	0.2	15.7	6.2	0.0	0.5	0.5	0.0	0.1	0.1	0.0	0.5	0.6
D3	Var	33.4	0.0	0.2	32.9	188.1	0.0	0.3	0.9	0.0	0.1	0.1	0.0	0.3	0.9
D4	Mean	28.2	0.1	0.4	18.8	3.8	0.0	0.2	2.8	0.0	0.0	0.5	0.0	0.2	3.4
D4	Vat	40.0	0.1	0.4	15.9	I92.3	0.0	0.1	7.8	0.0	0.0	3.8	0.0	0.1	8.3
D5	Mean	29.2	0.0	0.2	4.2	0.3	0.0	0.1	1.1	0.1	0.0	0.0	0.1	0.1	1.1
D5	Var	27.2	0.0	0.4	9.8	1.2	0.0	0.1	1 7	0.1	0.0	0.0	0.1	0.1	1.7
D6	Mean	23.4	0.0	0.6	7.2	1.5	0.2	0.2	0.5	0.1	0.0	0.0	0.2	0.2	0.5
D6	Var	40.6	0.0	0.8	13.6	12.9	0.1	0.1	0.4	0.1	0.0	0.0	0.2	0.1	0.4

Table 3 Continued

Definitions for column headings:

Ld, large dominant tree
Ls1, decay-class I large short snag
Ls2, decay-class 2 large short snag
Ls3, decay-class 3 large short snag
Dd, dominant deciduous tree
Lm1, decay-class 1 large mid-height snag
Lm2, decay-class 2 large mid-height snag
Lm3, decay-class 3 large mid-height snag
Lt1, decay-class 1 large tall snag
Lt2, decay-class 2 large tall snag
Lt3, decay-class 3 large tall snag
LM1+, decay-class I Very large mid-height snag
LM2+, decay-class 2 Very large mid-height snag
LM3+, decay-class 3 Very large mid-height snag

INFLUENCE OF STAND STRUCTURE AND LANDSCAPE COMPOSITION ON TERRESTRIAL AMPHIBIANS

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INTRODUCTION

The habitat relationships of amphibians in managed forest landscapes in the Pacific Northwest have received relatively little attention from researchers (Irwin and others 1989). An extensive program of research on wildlife communities in late-seral, unmanaged forests was conducted by the USDA Forest Service in the mid-1980's (Ruggiero and others 1991), but the applicability of these studies in managed forests was limited. Although stand ages surveyed varied from 30-900 yr, all stands had resulted from catastrophic wildfires and all contained residual structures from the previous stand, such as large decadent trees and large logs and snags. Consequently, for species such as terrestrial salamanders that are closely associated with these structures, abundances did not vary substantially among age classes (Bury and Corn 1988a, Bury and others 1991a). Accordingly, one of the most common recommendations for future research made by the biologists who conducted these studies was the need to initiate similar community studies in intensively managed forests. Others (deMaynadier and Hunter 1995) have stressed the need to design studies that compare amphibian communities in managed forest stands having identifiably different characteristics, and to initiate studies on the effects of landscape structure and composition in managed forests on both abiotic and biotic components of amphibian habitat quality. The TFW Landscape Studies address all of these concerns.

METHODS

AMPHIBIAN SAMPLING

Sampling of amphibians was based on protocols developed during the USDA Forest Service's Old-Growth Wildlife Habitat Research Program (Ruggiero and others 1991). Amphibians were sampled with pitfall traps in each stand after the onset of fall rains from 1992-1994. Pitfall traps were constructed in accordance with descriptions provided in Corn and Bury (1990); 36 traps were installed in each stand in a 6 x 6 grid array with 15-m spacing between traps and at least a 50-m buffer to the edge of the week. During the first 2 weeks of sampling in 1992, all amphibians captured were collected and preserved to obtain voucher specimens and to ensure that field crews were proficient at species identification. After that, amphibians captured alive were marked or held until the end of the trapping period and released at the capture site. All specimens found dead were collected, preserved, and deposited in the University of Washington Burke Museum in Seattle.

HABITAT VARIABLES

Including large numbers of habitat variables in statistical analyses involving relatively small sample sizes greatly increases the likelihood of obtaining biologically meaningless results, especially if the variables are linearly correlated. My sample size was 24 stands; consequently, I reduced both within-stand and landscape-scale habitat data sets to a small number of variables that were likely to be important influences on amphibian populations. I selected variables on the basis of previously described habitat associations (see deMaynadier and Hunter [1995] for a summary), lack of strong collinearity with other variables, and professional judgement.

PHYSIOGRAPHIC VARIABLES

Four physiographic variables were used in analyses of amphibian habitat relationships: elevation, slope, aspect, and the presence of permanent ponds within 500 m of the pitfall grid. Elevation and slope were analyzed as continuous variables, whereas aspect and the presence of ponds were analyzed as categorical variables. In the north-temperate zone, north-facing slopes are cooler and wetter than south-facing slopes. Cool, moist environments generally provide the most suitable habitat conditions for terrestrial amphibians (Nussbaum and others 1983). Consequently, I scored aspects between 315^{o} and 45^{o} with a value of 1, and all other aspects, a value of 0. Among the 24 stands, 8 had north-facing aspects; these 8 stands occurred in all structure classes except closed-canopy stands. If permanant ponds occurred within 500 m of the pitfall grid, I scored this variable as 1, if they weren’t present, as 0. Permanent ponds occurred within 500 m of the pitfall grid in 13 of the 24 stands, and in all 4 structure classes.

WITHIN-STAND VARIABLES

Live and dead vegetation was sampled at three spatial scales within each pitfall grid (see Fig. 1 in Sampling and Analysis of Vegetation - West-side Studies). Ocular estimates of percent cover for habitat variables occurring at ground level were made in the 3 x 3 m plots (9 plots evenly spaced throughout each grid); densities of tall shrubs, small to medium-sized trees and snags (<50 cm d.b.h.), and coarse woody debris (_>10 cm dia.) were measured in the 15 x 15 m plots (5 plots evenly spaced throughout each grid); and densities of large trees, snags, and stumps (>50 cm d.b.h.) were measured in the 45 x 45 m plots (1 plot located in the center of each grid).

I selected 13 variables from the within-stand data set, including 6 variables collected in the 3 x 3 m plots (% cover of moss, fern, litter, fine woody debris [<10 cm dia.], coarse woody debris [>_10 cm dia.], and rook), 5 variables collected in the 15 x 15 m plots (percent cover of shrubs >1 m in height, small [10-30 cm dia.] and large [>30 cm dia.] Jogs of decay class 2, large logs of decay class 3, and the density of medium-diameter [10-50 cm d.b.h.] snags of decay class 3) and 2 variables collected in the 45 x 45 m plots (densities of large-diameter [>50 cm d.b.h.] snags of decay class 3 and large dominant live conifers). I emphasized decay-class 2 logs and decay-class 3 snags because previous studies in unmanaged forests in the Washington Cascades showed that plethodontid salamanders were most often found under moderately decayed logs (decay class 2) 10-30 cm in diameter and sloughed pieces of bark (which typically do not begin to accumulate around snags prior to decay class 3) (Aubry and others 1988).

LANDSCAPE VARIABLES

The landscape structure surrounding each pitfall grid was described within 100-ha (564-m radius) and 1,000-ha (1,784-m radius) circles having the pitfall grid at their centers. Because of the relatively small home range size and low vagility of amphibians (Ovaska 1988, Sinisch 1990), I considered larger areas to be beyond the geographic scope of landscape-scale influences on forest-dwelling amphibians. The landscape database consisted of 25-m pixel Landsat satellite imagery classified into 5 habitat types: clearcuts (3-8 yr), young pre-canopy forests (10-20 yr), mature closed-canopy forests

(50-80 yr), old multi-storied forests (>80 yr), and other (Young and others 1993). A complete description of the GIS database used in these analyses is presented in the chapter entitled Introduction and Technical Approach presented in Volume 1 of this report. I used the FRAGSTATS computer program (McGarigal and Marks 1995) to quantify landscape structure in each circle. Because FRAGSTATS generates a large number of highly correlated variables, I reduced the data set to include only those metrics that seemed likely to influence the distribution and abundance of amphibians, and that could be interpreted in relation to their life history characteristics. I selected the same 7 variables from both the 100-ha and 1,000-ha data sets, resulting in a total of 14 landscape variables analyzed (percentage of the 4 forested habitat types within the landscape, Shannon's diversity index, mean patch size, and total edge). A complete list of variables used in statistical analyses is presented in Table 1.

DATA ANALYSIS

AMPHIBIAN SPECIES RICHNESS

Total captures varied considerably among structure classes; consequently, I used rarefaction analysis to adjust unequal sample sizes for comparisons of species richness among structure classes (Ludwig and Reynolds 1988).

AMPHIBIAN COMMUNITY ORGANIZATION

I examined differences in the organization of amphibian communities among stands with detrended correspondence analysis (DCA) using the DECORANA computer program (Hill 1979). DCA is an ordination technique that creates multi-dimensional metrics based on the species composition and abundance values occurring in each stand. I compared community composition among stands by plotting out stand scores on the first 2 axes and visually examining how stands clustered together.

Table 1. Physiographic, within-stand, and landscape variables used in analyses of amphibian habitat relationships. All variables, except the categorical variables ASPECT and PERPONDS, were used in correlation analyses; variables used in logistic regression analyses are shown in bold text.

	Physiographic Variables
ELEV	Elevation
ASPECT	Aspect
SLOPE	Percent slope
PERPONDS	Permanent ponds within 500 m of grid
	Within-stand Variables
Percent cover variables	
MOSS	Moss
FERN	Ferns
LITTER	Ground litter
FWD	Fine woody debris (<10 cm in diameter)
CWD	Coarse woody debris (>_10 cm in diameter)
ROCK	Exposed rock
SHRUBS	All shrubs >1 m in height
SMLLOG_2	Logs 10-30 cm in diameter, decay class 2
LARLOG_2	Logs >30 cm in diameter, decay class 2
LARLOG_3	Logs >30 cm in diameter, decay class 3
	Density variables
MEDSNG_3	Snags 10-50 cm in d.b.h., decay class 3
LRGSNG_3	Snags >50 cm in d.b.h., decay class 3
LDOMCONF	Live canopy-dominant conifers >50 cm in d.b.h.
	Landscape variables
l O0-ha circles, centered on pitfall grid	
PCTCC_H	Percent of landscape in clearcut (3-8 yr)
PCTPRC_H	Percent of landscape in pre-canopy forest (10-20 yr)
PCTMAT_H	Percent of landscape in mature closed-canopy forest (50-80 yr)
PCTOG_H	Percent of landscape in old multi*storied forest (>80 yr)

Table 1. Continued

SHNDIV_H	Shannon's diversity index
MEANPS_H	Mean patch size
TOTEDG H	Total edge
1000-ha circles, centered on pitfall grid	
PCTCC T	Percent of landscape in clearcut (3-8 yr)
PCTPRC_T	Percent of landscape in pre-canopy forest (10-20 yr)
PCTMAT_T	Percent of landscape in mature closed-canopy forest (50-80 yr)
PCTOG_T	Percent of landscape in old multi-storied forest (>80 yr)
SHNDIV_T	Shannon's diversity index
MEANPS_T	Mean patch size
TOTEDG T	Total edge

VARIATION IN AMPHIBIAN ABUNDANCES AND HABITAT QUALITY AMONG STRUCTURE CLASSES

Because amphibian and habitat data I collected generally failed to meet one or more of the assumptions of parametric statistics, I used only nonparametric statistical methods. I conducted all analyses with SPSS for Windows 6.1 (Norusis 1993). Preliminary analyses of data for species with sufficient captures to evaluate year-to-year variation in abundance values (>200 captures), showed that patterns of abundance did not vary significantly from year to year; i.e., there were no significant year X structure class interactions. Consequently, I used total captures of each species over the 3 years of sampling in all statistical analyses; only species with >20 total captures were included. I used Kruskal-Wallis tests to evaluate the null hypothesis of equal abundance values among the 4 structure classes. For those species showing significant ($P < 0.05$) differences among structure classes, I used nonparametric Tukey-type multiple comparison tests to identify significant differences between structure classes (Zar 1984).

To estimate differences in habitat quality among structure classes, I calculated a condition index for western redback salamanders and ensatinas (Dupuis and others 1995). I assumed that a measure of physical condition for woodland salamanders, which are independent of aquatic habitats for breeding, would best reflect differences in terrestrial habitat quality among structure classes. I calculated the index by dividing expected weights by observed weights; expected weights were derived from a linear regression equation of weight against snout-vent length (SVL) for all individuals used in the analyses. Thus, condition index values less than 1 were lower than expected, and values greater than 1 were higher than expected. Specimens found dead and bloated or with missing limbs or regenerating tails were excluded from this analysis. For western redback salamanders, only adults >35 mm SVL were included; for ensatinas, only adults >40 mm SVL were included (Dupuis and others 1995, Nussbaum and others 1983, Ovaska and Gregory 1989, Peacock and Nussbaum 1973).

SPECIES-HABITAT RELATIONSHIPS

Associations between amphibian abundance values and physiographic, within-stand, and landscape variables were examined in two ways. For continuous habitat variables, I used Spearman rank correlations to identify potentially important associations between total captures for each species and individual habitat variables ($P < 0.1$). For categorical habitat variables (aspect and the presence of ponds), I used chi-square analysis of contingency tables (P _< 0.1) for the categorical amphibian occurrence values (high abundance vs. low abundance and captures vs. no captures) I used in logistic regression analyses (see below).

To identify the most discriminating habitat variables and to derive predictive models, I then used stepwise logistic regression analyses (P to enter = 0.10, P to remove = 0.15). For species with >200 captures (northwestern salamander, western redback salamander, and ensatina), I separated stands into those with high captures vs. those with low captures. For species with >20 and <200 captures (roughskin newt and red-legged frog), I separated stands into those where the species was captured vs. those where it was not captured. I removed up to 1 stand from each regression analysis if the studentized residual was greater than 2.0, and if removing the outlier substantially improved model fit or interpretability. I used the same 16 variables, including 3 physiographic variables, 7 within-stand variables, and 6 landscape variables (see Table 1), in all regression analyses; thus, the resulting models can be directly compared among species. In addition, the inclusion of variables at a variety of spatial scales provides insights about the scale at which important influences on amphibian abundances are occurring I did not include elevation as a variable in logistic regression analyses because its inclusion resulted in the complete separation of groups at step 1 for several species. The importance of elevation in the structuring of amphibian communities in this region is well documented (Aubry and Hall 1991; Bury and others 1991a; Lehmkuhl and others 1991, this study). Because they share the same center, 100-ha and 1,000-ha landscape data sets are highly correlated. Consequently, the set of landscape variables I used in regression analysis for each species was based on either the '100-ha circle or the 1,000-ha circle, depending on which scale was most useful in discriminating between groups for that species.

RESULTS

CAPTURES

I captured 842 amphibians of 11 species (Table 2), including 6 salamanders (caudates) and 5 frogs and toads (anurans). Three distinct reproductive strategies were represented in the sample; there were 7 pond-breeders, 2 headwater stream-breeders, and 2 woodland salamanders (plethodontids). Three species dominated the terrestrial amphibian communities in all 4 structure classes: the northwestern salamander, western redback salamander, and ensatina. These 3 species each accounted for over 200 captures, whereas no other species had more than 34 captures. Each of the 4 structure classes was unique in community composition (Fig. 1). Clearcut stands were dominated by western redback salamanders and had relatively low captures of northwestern salamanders and ensatinas; roughskin newts were captured most frequently in this structure 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 structure 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 structure class was the only class in which all 11 species were captured at least once;

Table 2. Total amphibian captures by species and structure class from 1992-1994 in the TFW West-side Landscape Study.

Species	Clearcut	Pre-canopy	Closed-canopy	Harvest	Totals
Northwestern salamander	37	85	95	60	277
Western redback 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
Totals	195	154	171	322	842

western toads and long-toed salamanders were only captured in this structure 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 structure class than in any other. Total captures of amphibians in this structure class was almost twice as high as in any other class (Table 2).

COMPARISON OF SPECIES RICHNESS AMONG STRUCTURE CLASSES

Expected species richness differed among structure classes (Fig. 2). Rarefaction analysis revealed that the higher species richness found in harvest-age stands was an artifact of sample size. When sample sizes were adjusted among structure classes, pre-canopy stands showed the highest expected species richness; harvest-age stands had a similar but lower species richness. Clearcut stands were intermediate in expected species richness, whereas closed-canopy stands were depauperate.

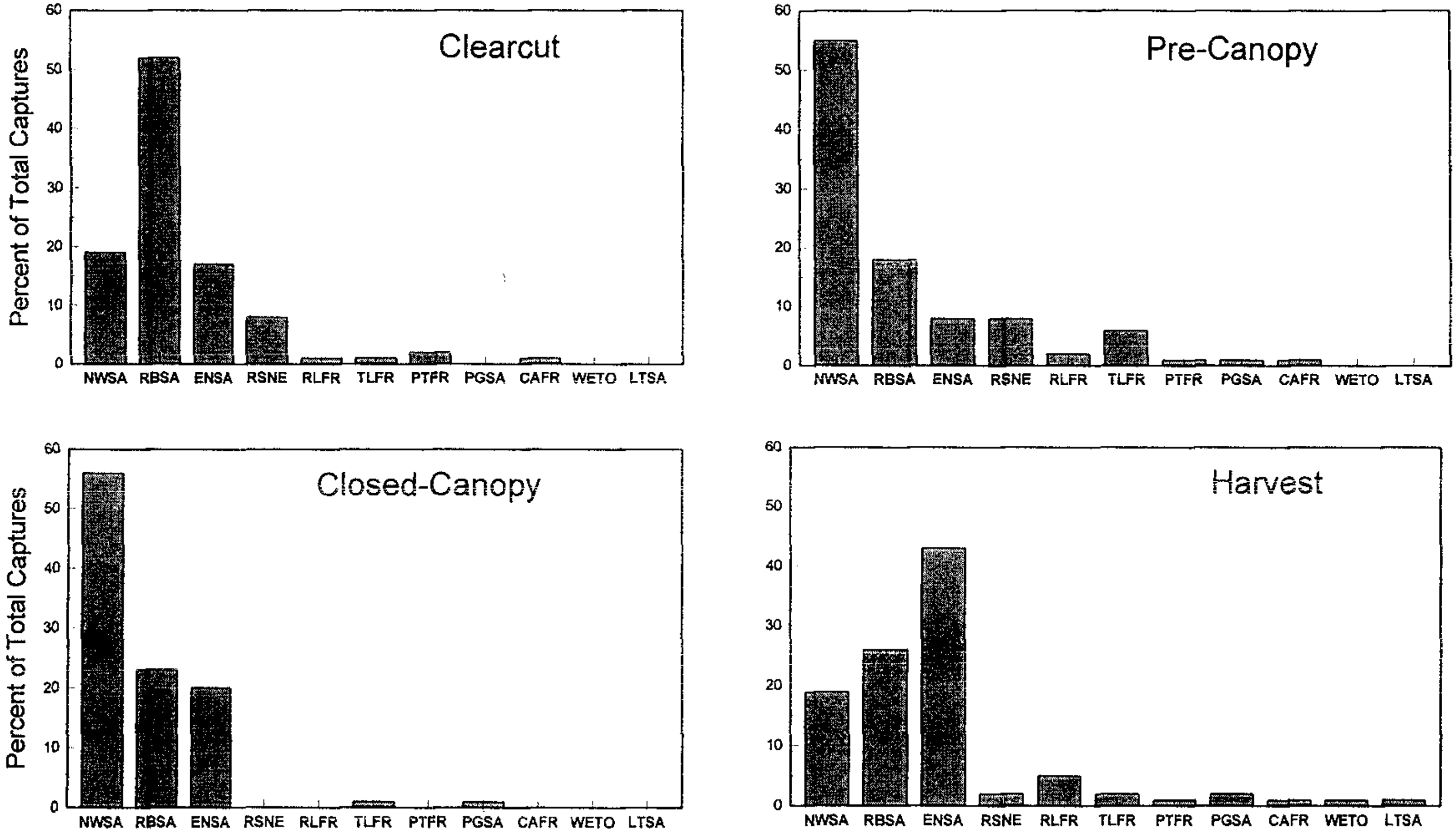

Amphibian Community Composition

Figure 1. Histograms showing the percent contribution of each species to total captures within each structure class.
Species abbreviations: NWSA=northwestern salamander, RBSA=western redback salamander, ENSA=ensatina, RSNE=roughskin newt, RLFR=red-legged frog, TLFR=tailed frog, PTFR=Pacific treefrog, PGSA=Pacific giant salamander, CAFR=Cascades frog, WETO=western toad, LTSA=long-toed salamander.

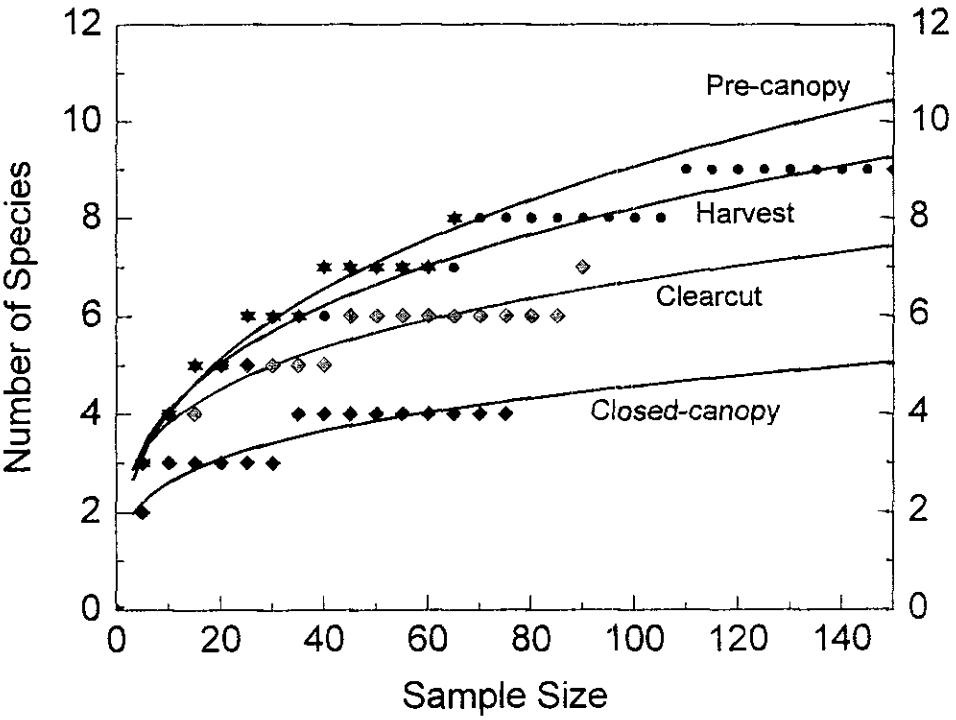


Figure 2. Species richness curves for each structure class derived from rarefaction analysis. Power curves gave the best fit to the data; all r values are >_0.92.

AMPHIBIAN COMMUNITY ORGANIZATION

Ordination analysis of amphibian communities occurring in each stand revealed patterns of community organization operating at the scale of major river basins. In the upper graph in Fig. 3, stand scores are depicted according to the WAU (Watershed Administrative Unit; about 4,000-12,000 ha in size) each occurs in; but no clustering of stands is evident. In the lower graph in Fig. 3, the same data are depicted according to the WRIA (Water Resource Inventory Area; about 60,000-81,000 ha) in which stands occur. In the lower graph, clustering of stands is evident for stands in WRIA 1005 and 1004. This similarity in community composition among stands within WRIAs is independent of geographic proximity. Four of the stands in WRIA 1004 lie just over the ridge from several stands in 1005, but are as far as '12 km away from the other 2 stands in 1004 (See Fig. 4 in Introduction and Technical Approach). The only stand in 1002 is located by itself near the top of the graph. Stands in WRIA 1102 are the only stands that do not form a distinct cluster; this WRIA contains stands that are similar to those occurring in both 1004 and 1005. However, 20 of the 24 stands sampled occur in

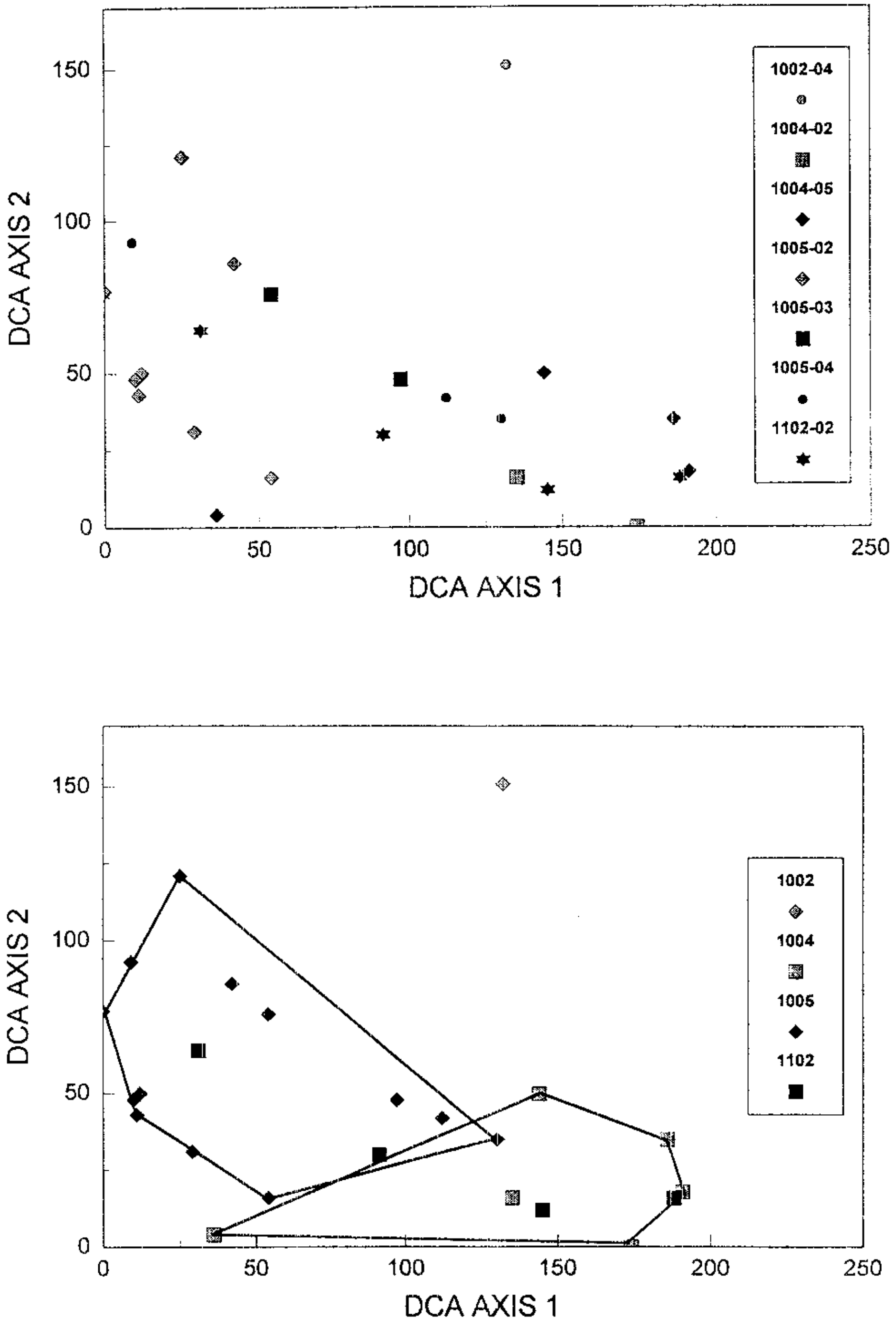


Figure 3. Ordination of amphibian species abundances in the 24 stands sampled. In the upper graph, each stand is identified by the WAU in which it occurs; in the lower graph, by the WRIA in which it occurs.

distinct clusters that reflect the WRIA they occur in, indicating that different WRIAs have different terrestrial amphibian assemblages.

In the upper graph in Fig. 4, the same data are depicted according to the structure class in which each occurs. For ease of interpretation, I have eliminated 1 outlier from each structure class and connected the outer boundaries of distinct clusters. Harvest-age stands contain amphibian communities that are substantially different from those in other structure classes (see also Fig. 1). Clearcut and closed-canopy stands also contain distinct communities, but ones that are more similar to each another than to harvest-age stands. As is evident in Figs. 1 and 4, pre-canopy stands contain components of both clearcut and closed-canopy stands, interestingly, although closed-canopy stands are more similar in age and stand structure to harvest~age stands, amphibian communities occurring there more closely resemble those found in pre-canopy and clearcut stands.

VARIATION IN AMPHIBIAN ABUNDANCES AMONG STRUCTURE CLASSES

Of the 11 species captured, only 5 had >20 total captures: northwestern salamander, western redback salamander, ensatina, roughskin newt, and red-legged frog (Table 3). Northwestern salamanders were captured most frequently in pre-canopy and closed-canopy stands, but there were no significant differences among structure classes (Tables 3 and 4, Fig. 5). Captures for western redback salamanders exhibited almost the reverse pattern, with most captures occurring in clearcut and harvest-age classes (Table 3). As with northwestern salamanders, however, none of the differences among structure classes was significant (Tables 3 and 4, Fig. 5). Captures for ensatinas were significantly higher in harvest-age stands than in pre-canopy stands, but neither clearcut nor closed-canopy stands differed significantly from any other structure class (Tables 3 and 4, Fig. 6). Roughskin newts and red-legged frogs were captured significantly less often in closed-canopy stands than in clearcut or harvest stands, respectively (Tables 3 and 4, Figs. 6 and 7). As with ensatinas, none of the stands with intermediate rankings differed significantly from any other structure class (Table 4).

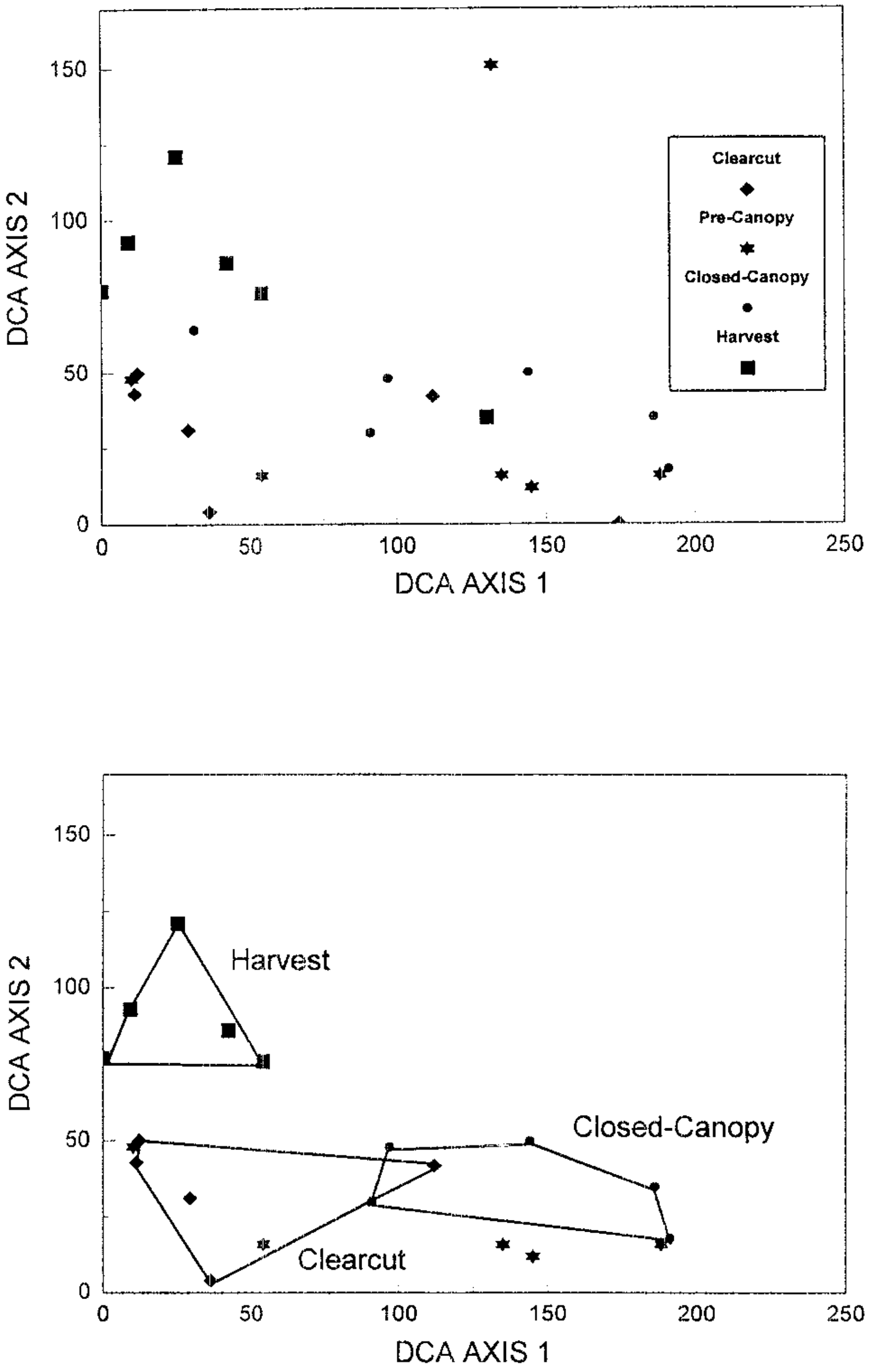


Figure 4. Ordination of amphibian species abundances in the 24 stands sampled by structure class (upper). In the lower graph, one outlier was removed from each structure class to facilitate interpretation of the clusters. Lines connect extrailimital records for harvest, closed-canopy, and clearcut stands; pre-canopy stands are indicated by stars.

Table 3, Distribution of captures among the 24 study sites for species with >20 total captures; species codes are defined in Figure 1. Groups used in logistic regression analyses are indicated by bold vs. normal text; outliers eliminated from the final analyses are underlined.

Study site	NWSA	RBSA	ENSA	RSNE	RLFR
Clearcut I	7	32	11	5	0
Clearcut 2	0	11	8	3	1
Clearcut 3	8	0	0	2	0
Clearcut 4	12	3	4	0	1
Clearcut 5	9	38	1	2	0
Clearcut 6	I	18	9	3	0
Pre-canopy 1	1	14	4	0	1
Pre-canopy 2	7	0	3	I	1
Pre-canopy 3	13	3	3	0	0
Pre-canopy 4	2	5	0	2	1
Pre-canopy 5	34	6	2	8	0
Pre-canopy 6	28	0	0	I	0
Closed-canopy 1	30	0	0	0	0
Closed-canopy 2	17	9	7	0	0
Closed-canopy 3	9	0	0	0	0
Closed-canopy 4	19	0	6	0	0
Closed-canopy 5	11	10	2	0	0
Closed-canopy 6	9	20	19	0	0
Harvest 1	2	32	35	1	2
Harvest 2	10	2	44	I	5
Harvest 3	5	2t	32	1	7
Harvest 4	32	7	7	1	1
Harvest 5	6	18	8	1	0
Harvest 6	5	4	11	2	2
Total Clearcut	37	102	33	15	2
Total Pre-canopy	85	28	12	12	3
Total Closed-canopy	95	39	34	0	0
Total Harvest	60	84	137	7	t7
Grand Total	277	253	216	34	22

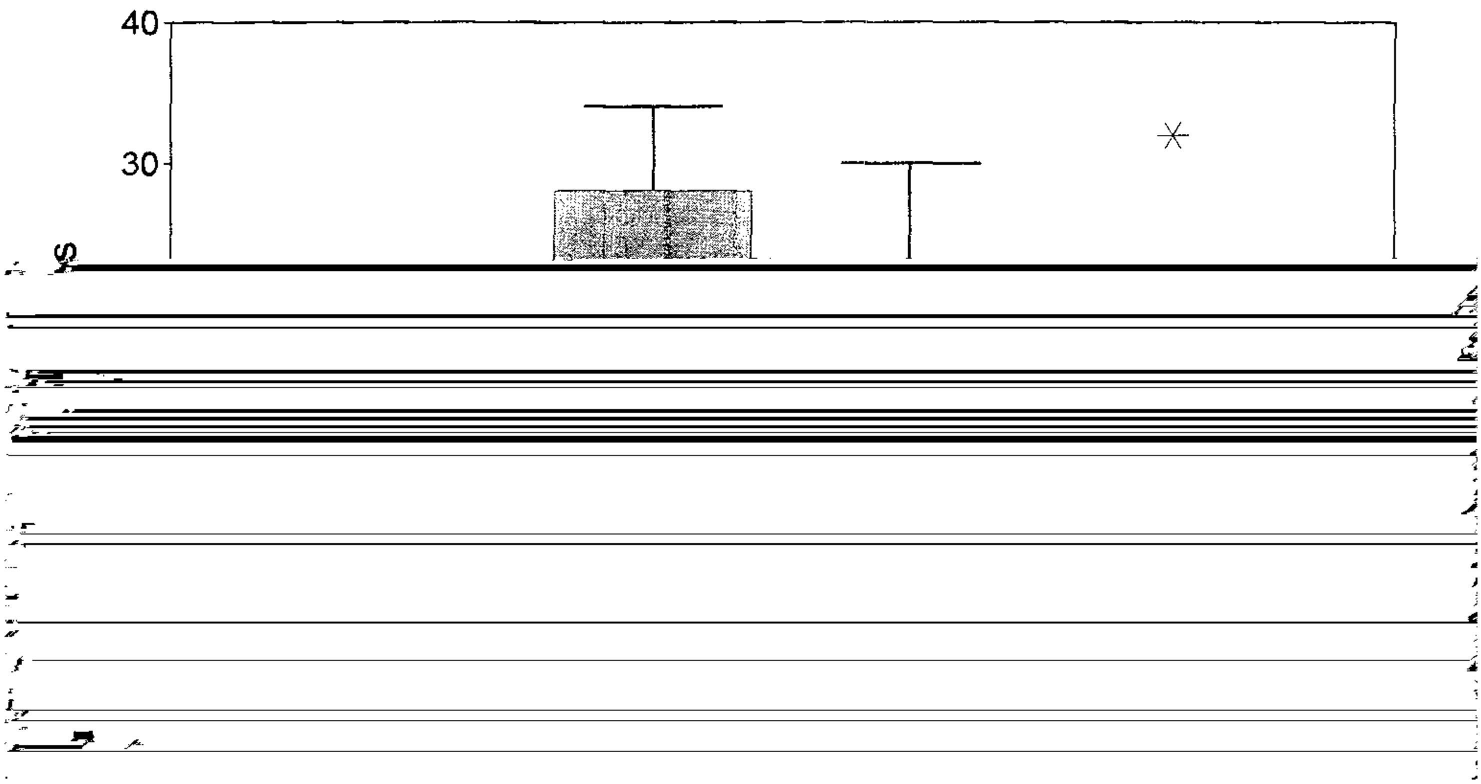
Table 4. Results of Kruskall-Wallis nonparametric 1-way ANOVA and multiple comparison tests for amphibian species with >20 captures. For each species, structure classes are arranged in ascending order of rank means; data sets that cannot be differentiated statistically ($P \_< 0.05$) are underlined.

Species	P value	Tukey-type multiple comparison tests			
Northwestern salamander	0.203	Clearcut	Harvest	Pre-canopy	Closed-canopy
Western redback salamander	0.243	Pre-canopy	Closed-canopy	Harvest	Clearcut
Ensatina	0.015	Pre-canopy	Closed-canopy	Clearcut	Harvest
Roughskin newt	0.009	Closed-canopy	Pre-canopy	Harvest	Clearcut
Red-legged frog	0.012	Closed-canopy	Clearcut	Pre-canopy	Harvest

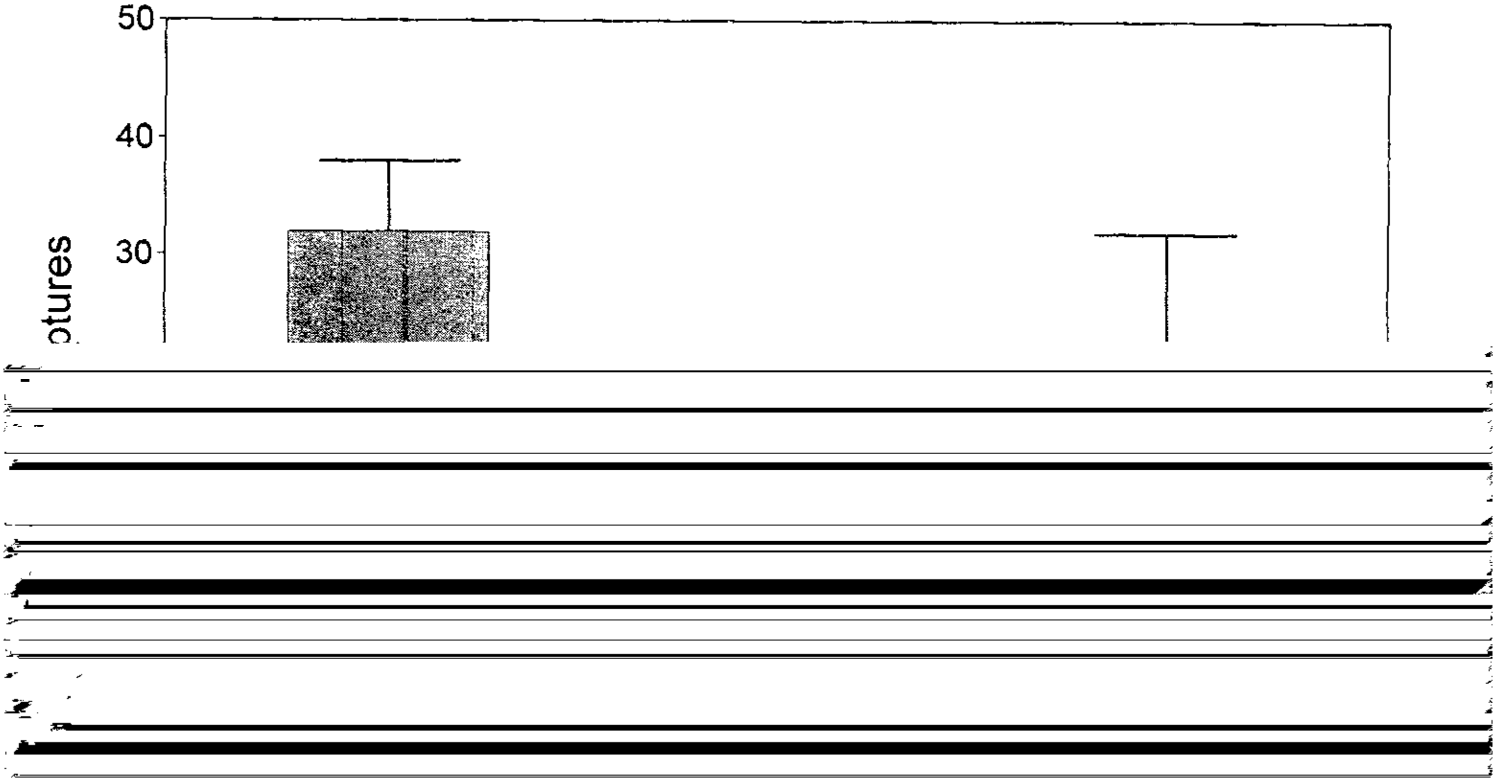
Condition index values for western redback salamanders were significantly higher in closed-canopy forests than in clearcuts, but neither harvest-age nor pre-canopy stands could be distinguished statistically from any other structure class (Table 5, Fig. 8). The order of mean rankings for ensatinas was the same as for redback salamanders, but none of the structure classes differed statistically from any other (Table 5, Fig. 8)

SPECIES-HABITAT RELATIONSHIPS

Correlation analyses showed elevation to be a consistently strong influence on amphibian abundances; correlations with abundance values were significant for all 5 species (Table 6). Elevation was the only habitat variable evaluated that significantly influenced abundance values for all 5 species but, with the exception of northwestern salamanders, all species were negatively associated with elevation. The pattern of association with elevation for northwestern salamanders was almost the inverse of that found for ensatinas and western redback salamanders (Fig. 9). Only red-legged frogs were strongly influenced by slope, with highest abundances occurring on flatter slopes (Table 6). High abundances of ensatinas and roughskin newts occurred most often in

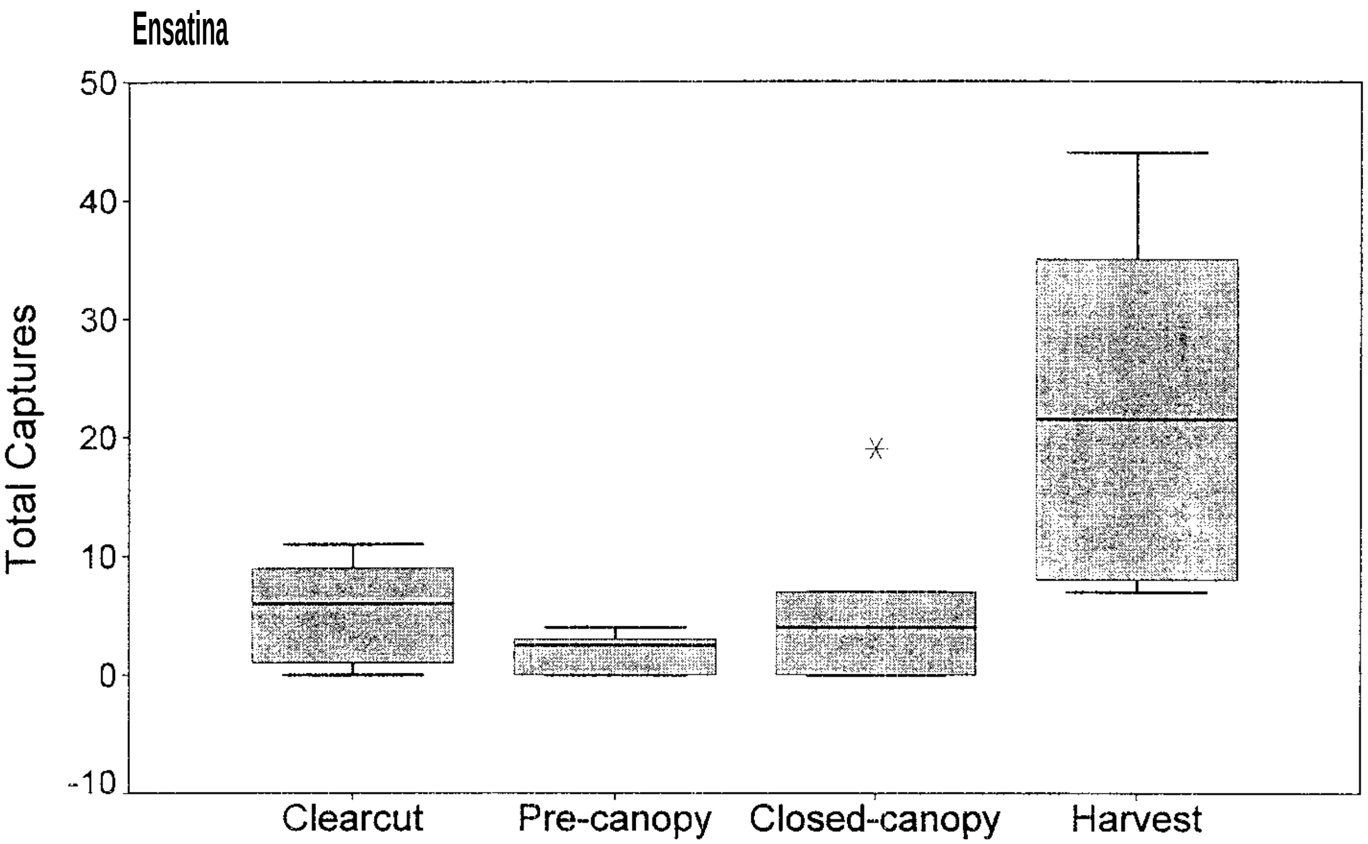


Northwestern Salamander



Western Redback Salamander

Figure 5. Boxplots of total captures of northwestern salamanders by structure class (upper graph), and boxplots of total captures of western redback salamanders by structure class (lower graph). Boxplots depict the median (line inside box) and quartiles (box shows range of middle two quartiles; horizontal bars show upper and lower quartiles); outliers (>1.5 boxlengths from upper or lower end of box) are indicated with an asterisk.



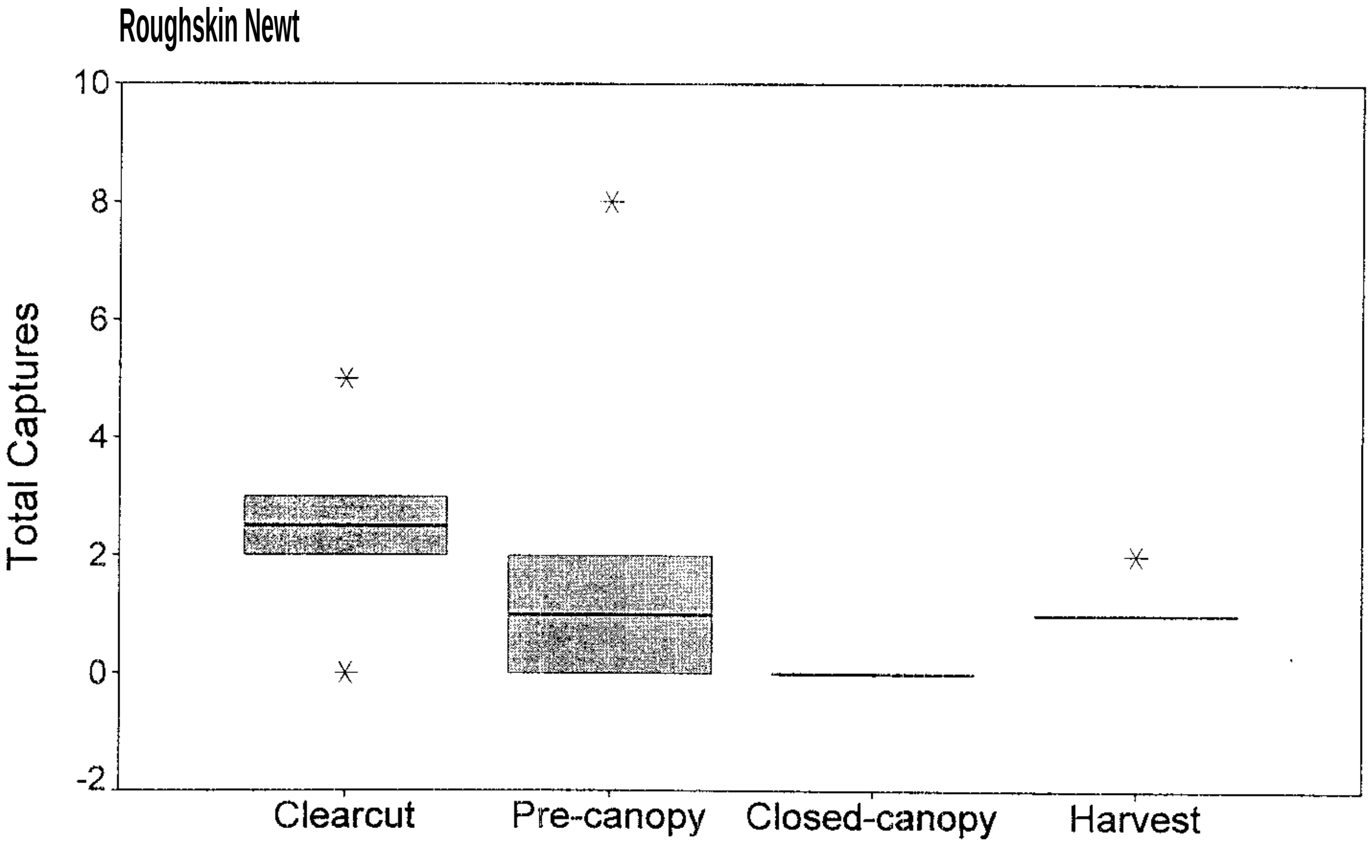
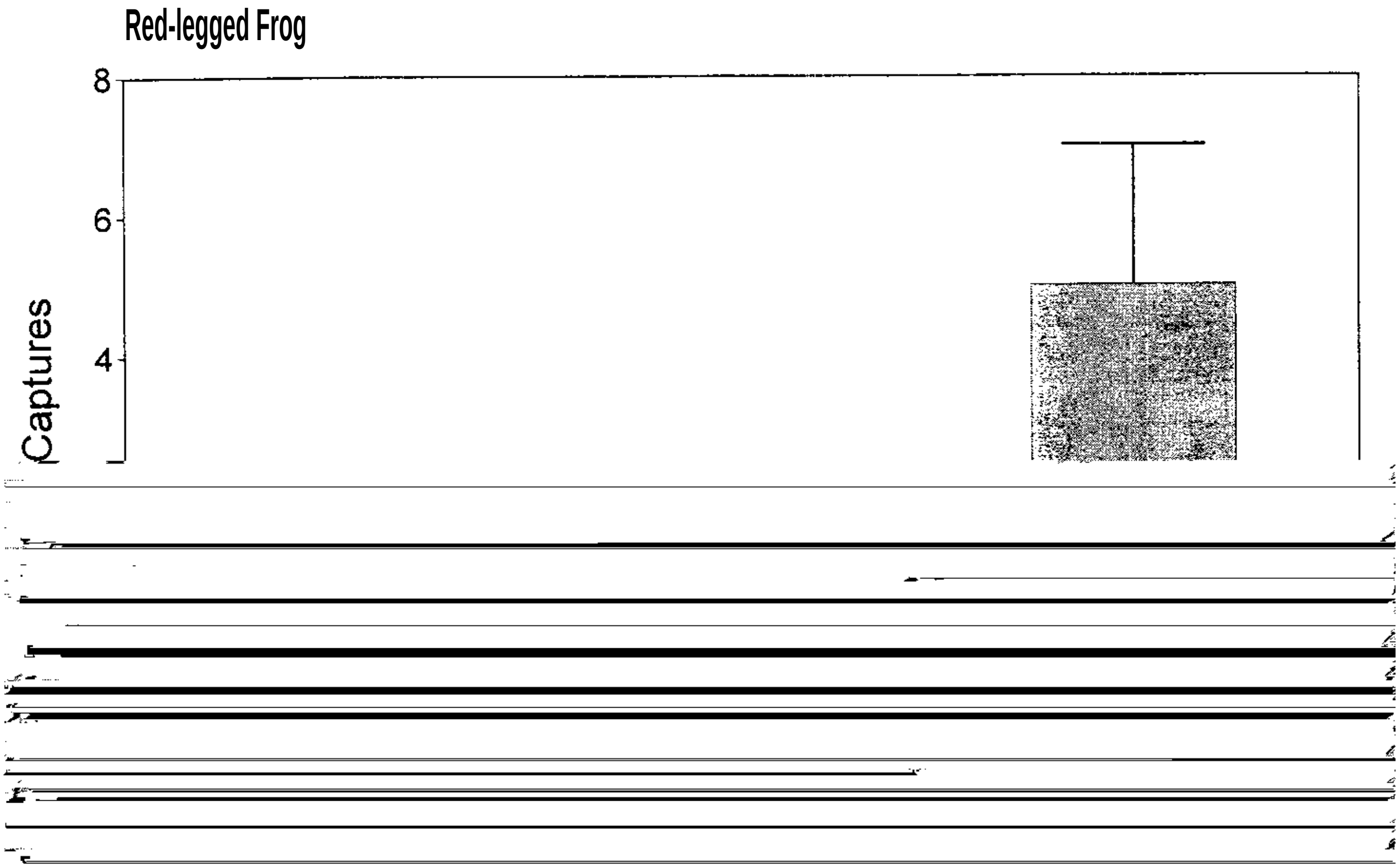


Figure 6. Boxplots of total captures of ensatinas (upper graph) and roughskin newts (Lower graph) by structure class.



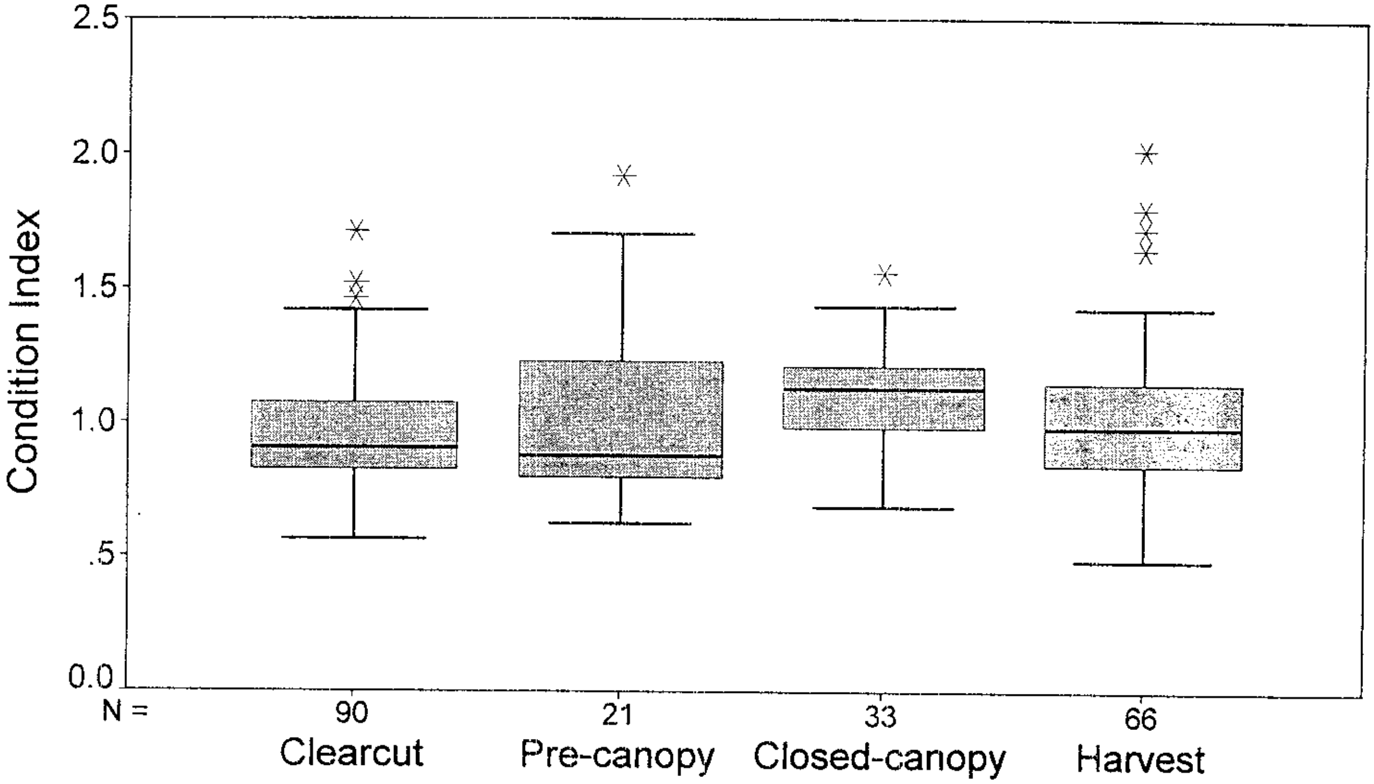
Red-legged Frog

Figure 7. Box plots of total captures of red-legged frogs by structure class.

Table 5. Results of Kruskall-Wallis nonparametric 1 -way ANOVA tests of condition index among structure classes for plethodontid salamanders. For each species, structure classes are arranged in ascending order of rank means; data sets that cannot be differentiated statistically (P < 0.05) are underlined.

Species	*P* value	Tukey-type multiple comparison tests			
Western redback salamander	0.003	Clearcut	Pre-canopy	Harvest	Closed-canopy
Ensatina	0.100	Clearcut	Pre-canopy	Harvest	Closed-canopy

Western Redback Salamander



Ensatina

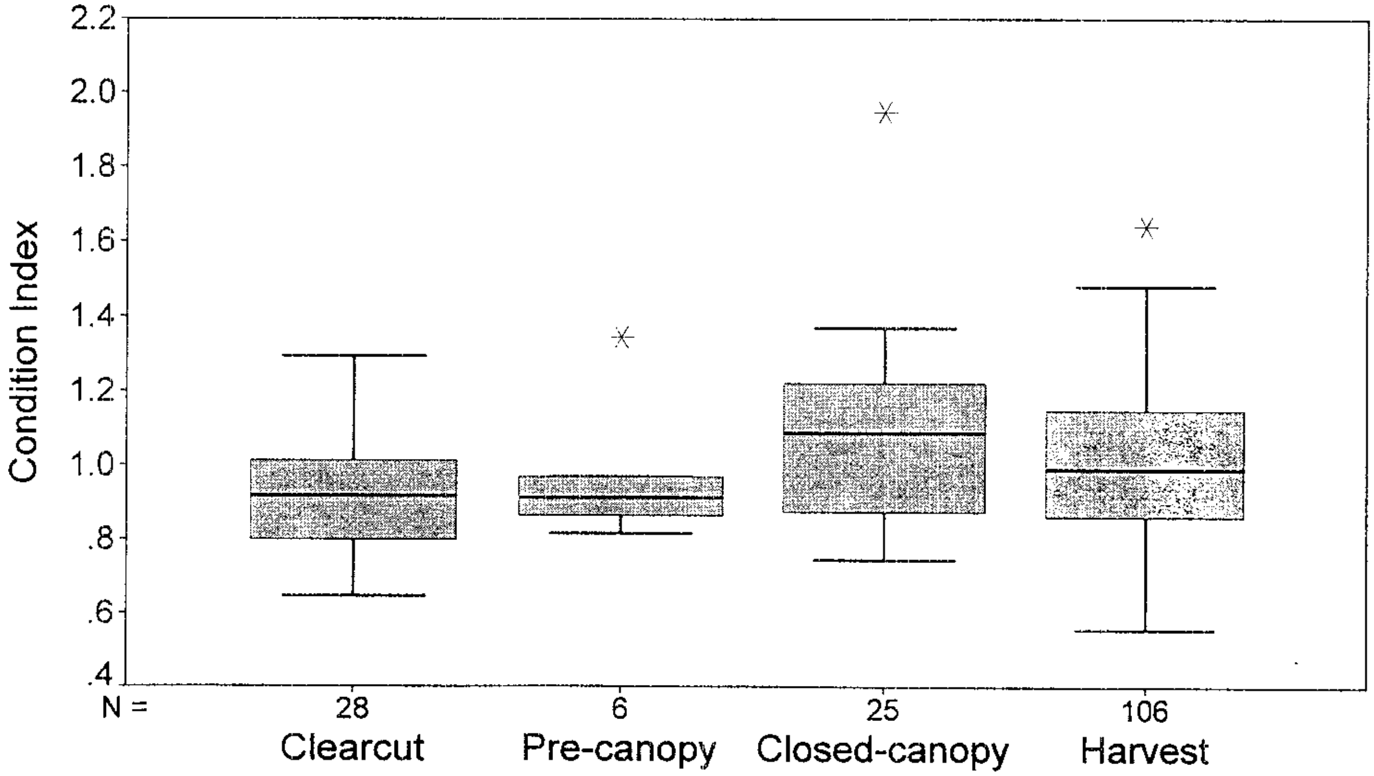


Figure 8. Boxplots of condition index values (see text) of western redback salamanders with snout-vent lengths >35 mm (upper graph) and ensatinas with snout-vent lengths >40 mm (lower graph) by structure class.

Table 6. Spearman rank correlations with P values < 0.1 between amphibian captures and habitat variables; variable names are defined in Table 1, species codes are defined in Fig. 1. Values presented are correlation coefficients (r), with the direction of the relationship indicated in parentheses. Variables used in logistic regression analyses are shown in bold text.

Habitat variables	NWSA	RBSA	ENSA	RSNE	RLFR
		Physiographic variables			
ELEV	0.66 (+)	0.68 (-)	0.40 (-)	0.46 (-)	0.43 (-)
SLOPE					O.52 ( )
		***Within-stand** variable.';*			
MOSS			0.42 (-)		
FERN					
LITTER					0.58 (-)
FWD		0.43(-)	0.42( )		0.42 ( )
CWD					
ROCK	0.36 (-)	0.48 (+)	0.38 (+)	0.34 (+)	
SHRUB					0.37 (+)
SMLLOG2					
LARLOG2					
LARLOG3	0.37 (+)	0.40 ( )			
MEDSNAG3	**0.40 (+)**				
LARSNAG3	0.42 (+)			0.41(-)	
LDOMCONF			0.47 (+)		
		***Landscape** variable..;*			
PCTCC_H				**0.38(+)**	
PCTPRC_H				0.37(-)	0.57(-)
PCTMAT_H			**0.38 (+)**		
PCTOG H					
SHNDIV_H					
MEANPS_ H					**0.41 (+)**
TOTEDG_ H					**0.41 (-)**
PCTCC_ T					

Table 6. Continued

Habitat variables	NWSA	RBSA	ENSA	RSNE	RLFR
PCTPRC_T					0.47 ( )
PCTMAT_T	0.49 (+)	0.36 ( )		0.49 (-)	
PCTOG_T				0.39 (+)	0.54 (+)
SHNDIV_T	0.60 (-)			0.59 (+)	
MEANPS_T					
TOTEDG_T		0.46 (+)			

stands with north-facing slopes; northwestern salamanders, redback salamanders, and red-legged frogs showed no pattern of association with aspect (Table 7). Northwestern salamanders were abundant in stands near permanent ponds, whereas the other 2 pond-breeders, the roughskin newt and red-legged frog, reached highest abundances in stands away from permanent ponds; neither western redback salamanders nor ensatinas showed any pattern of association with ponds (Table 7).

The northwestern salamander was the only species that was negatively associated with rocky soils (Table 6). It was positively associated with several types of coarse woody debris and the percent of mature closed-canopy forests within 1,000 ha of the pitfall grid, and negatively associated with high levels of patch diversity in those landscapes. There were relatively few associations with within-stand or landscape variables for western redback salamanders. This species was negatively associated with fine woody debris and large logs of decay class 3, and positively associated with rocky soils. At the landscape scale, redback salamanders were negatively associated with percent of mature forest and positively associated with total edge within 1,000 ha of the pitfall grid. Ensatinas were negatively associated with moss and fine woody debris and positively associated with rocky soils and large, dominant conifers in the overstory. The only important landscape-scale habitat variable found for ensatinas was the percentage of mature forest within 100 ha of the pitfall grid.

Capture totals for roughskin newts and red-legged frogs were minimal for correlation analyses (34 and 22, respectively); thus, result.'; of these analyses should be interpreted cautiously. At the stand scale, roughskin newts were positively associated

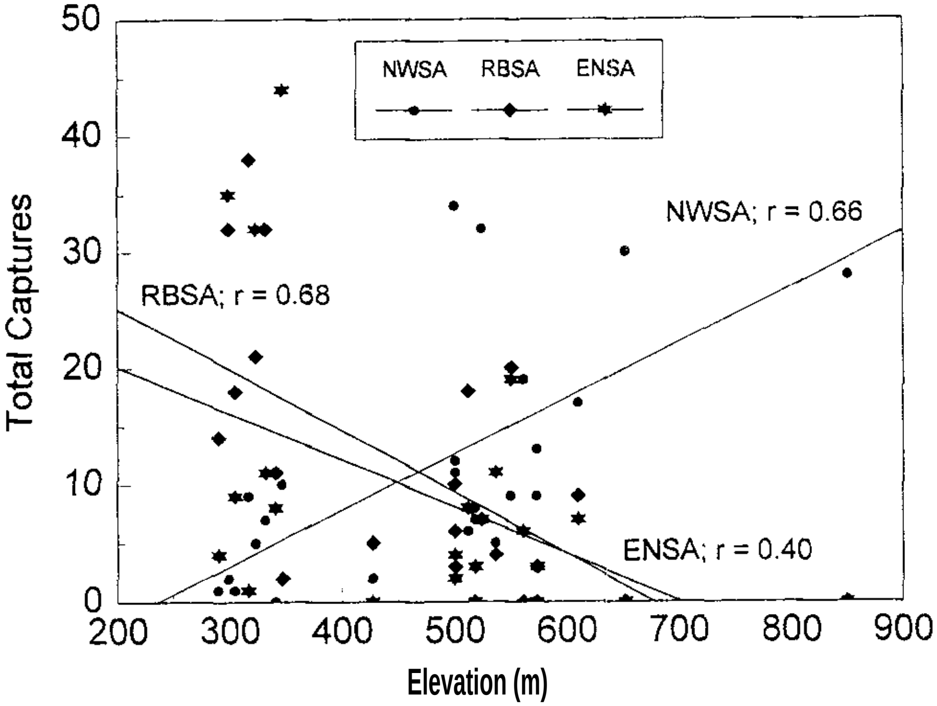


Figure 9. Scatterplot and linear regression lines for species abundances vs. elevation; species codes are defined in Fig. 1.

Table 7. Results of contingency table analyses using the Chi-square statistic for categorical physiographic variables. Both variables were used in logistic regression analyses.

	Aspect		Presence of ponds	
Species	*P* value	Relationship	*P* value	Relationship
Northwestern salamander	0.247	No pattern of association	0.015	Associated with the presence of ponds
Western redback *salamander*	0.371	No pattern of *association*	0.916	No pattern of *association*
Ensatina	0.083	Associated with N-facing slopes	0.219	No pattern of association
Roughskin newt	0.074	Associated with N-facing slopes	0.072	Associated with the absence of ponds
Red-legged frog	0.143	No pattern of association	0.044	Associated with the absence of ponds

with rocky soils and negatively associated with large (>5(3 cm d.b.h.) snags of decay class 3. At the landscape scale, results were somewhat inconsistent. Within 100-ha landscapes, newts were positively associated with clearcuts and negatively associated with young pre-canopy stands. Within 1,000-ha landscapes, they were negatively associated with mature forest and positively associated with old multi-storied forests; however, they were also associated with increasing patch diversity in those landscapes. Red-legged frogs were associated with low amounts of litter and fine woody debris and high shrub cover. Associations were negative with pre-canopy forests at both landscape scales, and positive with greater amounts of old forest within 1,000 ha. Landscape structure and diversity indices were only important at the 100-ha scale, where red-legged frogs were associated with large patch sizes and low amounts of edge (Table 6).

Logistic regression analysis produced models that resulted in at least 83% correct classifications for all 5 amphibians studied (Table 8). Models for northwestern salamanders and red-legged frogs contained only physiographic and landscape variables. High abundances of northwestern salamanders occurred near permanent ponds and where large percentages of mature closed-canopy forest occurred within 1,000 ha of the pitfall grid. Red-legged frogs were generally captured only in relatively flat stands at least 500 m from permanent ponds. Both models include variables that were also shown to be important in correlation and contingency table analyses (Tables 6 and 7).

Models for the two woodland salamanders studied contained variables occurring at a variety of spatial scales. High abundances for both species were strongly influenced by north-facing aspects. In addition, abundances of western redback *salamanders* were high in stands where small (10-30 cm dia.) moderately decayed logs were common, and in landscapes having large amounts of edge habitat within 1,000 ha of the grid. Stands where ensatinas were abundant were characterized by low amounts of moss within stands and high amounts of mature forest in close proximity to the grid. The ensatina was the only species for which the 100-ha landscape indices were better discriminators of high vs. low abundance values than the 1,000 ha indices. Important

Table 8. Results of logistic regression analyses for species with >20 captures. Model results <0,5 = low abundance values or "absence" (for roughskin newt and red-legged frog) and model results >0.5 = high abundance values or "presence". All model Chi-square values are significant at P _< 0.001.

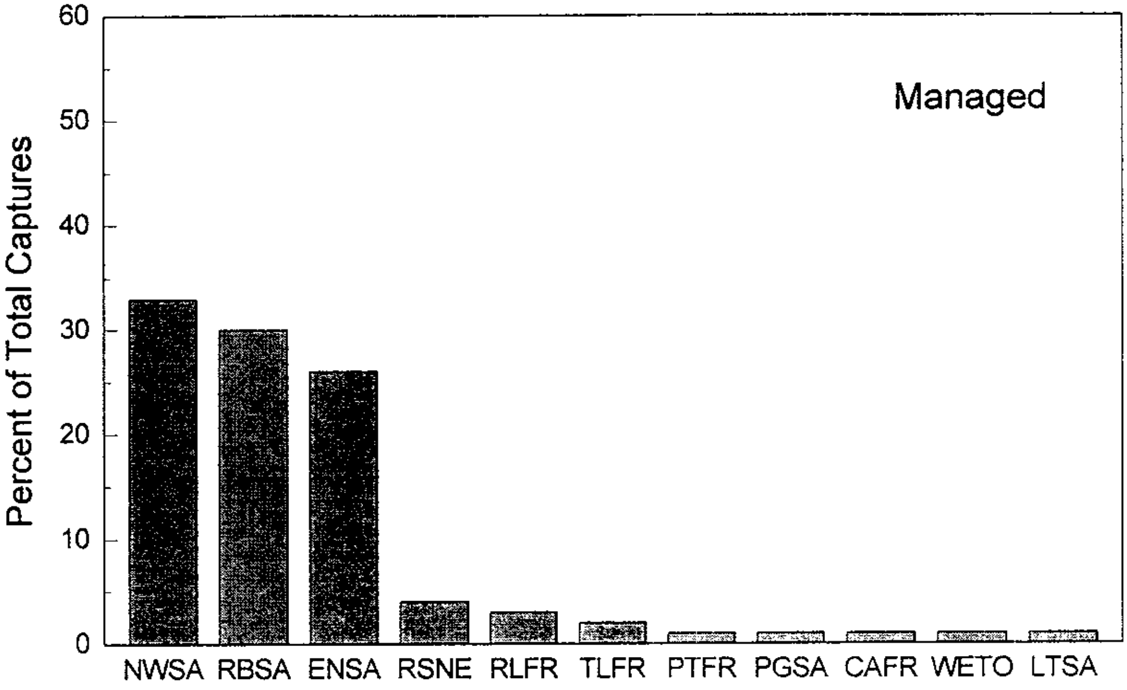
Species	Regression coefficient	Standard error	Wald statistic	P value for Wald star.	Odds ratio	Correct classification
Northwestern salamander						
PERPONDS	3.66	1.72	4.55	0.033	38.80	87%
PCTMAT_T	0.11	0.06	4.29	0.038	1.12	
Constant	--6.29	2.74				
Western Redback Salamander						
ASPECT	3.99	2.20	3.30	0.069	54.27	96%
SMLLOG_2	0.50	0.31	2.62	0.106	1.64	
TOTEDG_T	0.0002	0.0001	3,74	0.053	1.00	
Constant	-41.82	21.38				
Ensatina						
ASPECT	5.52	2.65	4.33	0.037	248.97	92%
MOSS	0.21	0.13	2.71	0.100	0.81	
PCTMAT_H	0.11	0.05	5.44	0.020	1.11	
Constant	- 3.21	1.87				
Roughskin Newt						
SMLLOG 2	0.89	0.53	2.83	0.092	2.43	83%
PCTOG T	10.53	5.42	3.78	0.052	37427.18	
Constant	3.72	1.84				
Red-legged Frog						
PERPONDS	14.05	8.23	2.91	0.088	0.00	91%
SLOPE	- 2.25	1.23	3.37	0.067	0.11	
Constant	19,84	11.26				

habitat variables for ensatinas in logistic regression models were also found to be important in univariate analyses (Tables 6 and 7). In contrast, neither north-facing aspects nor small, moderately decayed logs were shown to be associated with redback salamander abundances in univariate analyses. The importance of this size and decay class of logs and of cool, moist environmental conditions to western redback salamanders has been documented elsewhere, however (Aubry and others 1988, Dupuis and others 1995). The occurrence of roughskin newts was also best discriminated by high levels of small, moderately decayed togs; these latter two species were the only ones for which any measure of coarse woody debris was included as a variable in logistic regression models. Roughskin newts were also present most often in stands that had high levels of old multi-storied forest within 1,000 ha of the pitfall grid.

DISCUSSION

AMPHIBIAN DIVERSITY IN MANAGED FORESTS

it has been suggested that intensive forest management in the Pacific Northwest employing clearcut harvest methods is likely to result in reduced amphibian diversity, either because the loss of canopy cover will result in conditions that are too dry and warm for some amphibian populations to persist, or because the amount of coarse woody debris remaining on site will be insufficient to sustain some of the woodland forms that use such structures for cover (Blaustein and others 1995; Bury and Corn 1988a,b; papers in Ruggiero and others 1991). A comparisien of amphibian species composition in managed forests (this study) with that found in unmanaged forests (Aubry and Hail 1991), however, shows that no loss of species has occurred, even though old-growth forests have been virtually absent from the managed landscapes I studied for several decades. All species found in naturally regenerated, unmanaged forests in the south-central Cascade Range in Washington also occurred in intensively managed plantations (Fig. 10), including stream-breeding tailed frogs and Pacific giant salamanders, which are believed to be particularly sensitive to the effects of timber harvesting (Corn and Bury 1989). At present, differences between amphibian communities in these two forest conditions lie in their structure, not their composition.



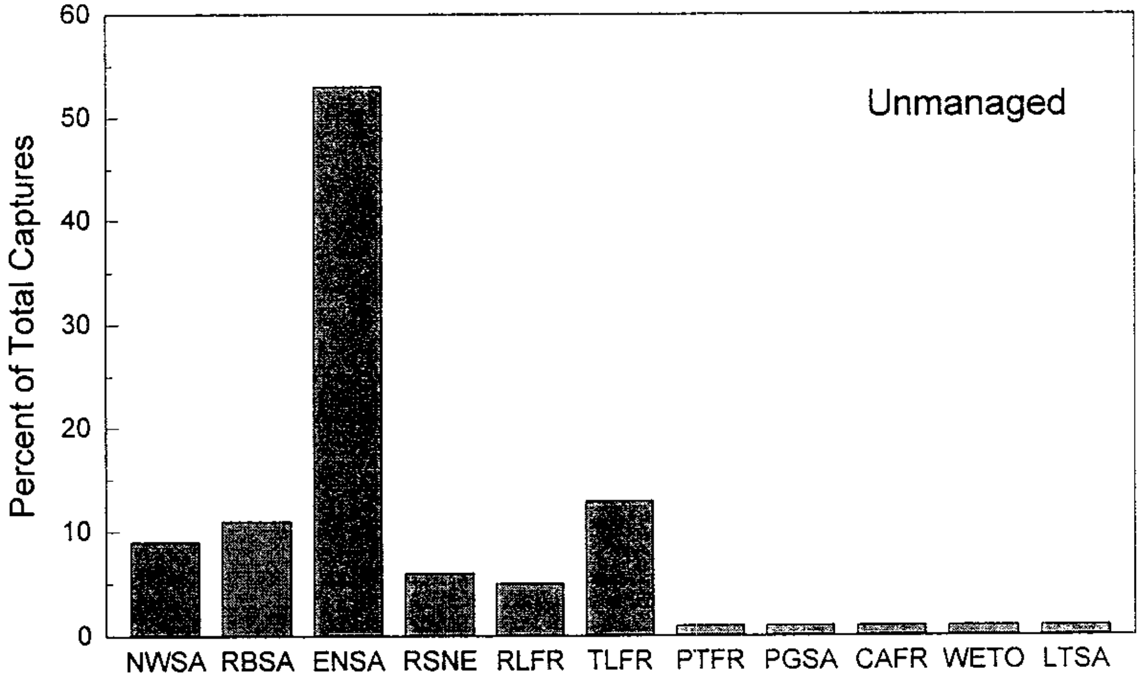


Figure 10. Histograms of the percent contribution of each species to total captures in managed forests (upper, this study) vs. unmanaged forests (lower, Aubry and Hall 1991) in the southern Washington Cascade Range; species codes are defined in Fig. 1.

Managed forests were numerically dominated by three species: northwestern salamanders, western redback salamanders, and ensatinas, with each representing about 30% of the amphibian community; all other species each represented less that 5% of the total community. In contrast, unmanaged forests were dominated by a single species, the ensatina (53% of captures), and had a broader array of other species occurring at relatively high abundances. The tailed frog, a stream-breeding species, was the second largest component of the terrestrial community, comprising 13% of captures; northwestern salamanders, redback salamanders, roughskin newts, and red-legged frogs each represented 5-11% of total captures.

Thus, although species richness is the same, amphibian community structure in unmanaged forests included twice as many species representing at least 5% of total captures than managed forests. This suggests that intensively managed forest landscapes may have a lower overall amphibian habitat diversity than unmanaged landscapes. For example, the relatively few captures of Pacific giant salamanders and tailed frogs may indicate that suitable habitat for these species is limited in forest plantations where mitigation measures for headwater creek habitats in harvest units have only recently been implemented. Terrestrial species may also be occurring at lower densities than during pre-harvest conditions. Dupuis and others (1995) found that clearcut logging reduced terrestrial amphibian populations by up to 70% in coastal old-growth forests on Vancouver Island. Rare populations are particularly susceptible to local extirpations resulting from cyclic or stochastic catastrophic disturbances (Rosenzweig 1995); consequently, the probability of this amphibian community persisting intact over the long term may be lower than in unmanaged landscapes. In addition, detrimental cumulative effects of intensive forest management on amphibian populations may only become apparent over very long time frames or additional rotations (Grant and Swanson 1991).

Among structure classes, expected amphibian species richness was highest in pre-canopy stands and lowest in closed-canopy stands (Fig. 2); there was no evidence that species richness increased with stand age. This finding is in accordance with other studies conducted in the Pacific Northwest, including those comparing managed with unmanaged stands (deMaynadier and Hunter 1995, Raphael 1991). At the stand level, the diversity of amphibian species occurring in the managed forests I surveyed appears to be largely a function of vertical foliage diversity, especially near the forest floor. The expected species richness gradient closely parallels gradients for both herb and shrub vegetation layers. Closed-canopy stands are essentially lacking in either herb or shrub layers, whereas pre-canopy stands have extensive herb and shrub communities, as well as coniferous trees of intermediate height. Although clearcut and harvest stands generally had well-developed herb layers, their shrub cover was relatively sparse and, in clearcuts, trees were non-existent.

Dense herb and shrub layers may be important components of foraging niche space for terrestrial salamanders (deMaynadier and Hunter 1995). Jaegar (1978) found that salamanders of the genus *Plethodon* foraged along the leaves and stems of understory herbs and shrubs during rainy nights and other periods of high relative humidity, ingesting more food than surface-dwelling conspecifics on the forest floor. As Dupuis and others (1995) have argued, however, the major effects of vegetation on terrestrial amphibians are probably indirect; the environmental and ecological factors that ultimately determine the composition and structure of forest amphibian communities are moisture and temperature regimes in the air and soil and associated microhabitat conditions. Pre-canopy stands were generally dense thickets, whose vertical heterogeneity probably served to buffer the forest floor from temperature and moisture extremes (Chert and others 1992, Geiger 1959). Although there was always a well-developed herb layer in harvest-age stands, the relatively open canopies resulting from commercial thinning may have resulted in less favorable (drier and warmer) conditions on the forest floor for terrestrial amphibians than in pre-canopy stands (Dupuis and others 1995, Nussbaum and others 1983).

Physiographic influences also play a role in determining amphibian diversity within forested landscapes. Four of the five species analyzed showed a negative association with elevation, and neither ensatinas nor western redback salamanders were captured in stands occurring above 610 m in elevation. This strong inverse relationship between elevation and amphibian species richness in this region has been documented by others (Aubry and Hall 1991, Bury and others 1991a, Harris 1984), and probably reflects the lowered ability of most species to survive and/or flourish as climatic conditions become progressively colder. Amphibians strongly prefer mesic forest conditions (Nussbaum and others 1983). In north-temperate latitudes, the cool, moist conditions occurring on north-facing slopes and the deep, moist soils that form in relatively flat areas would be expected to contain higher' amphibian species diversity than steeper, south-facing slopes with shallower soils. In addition, the formation of ponds and creeks is strongly influenced by these physiographic features; the presence of breeding sites for pond- and stream-breeding species within forest stands will strongly influence overall amphibian diversity. Many of the terrestrial salamanders occurring in this region breathe through their skin, however, and retreat into the soil and humus layers when they are not foraging or breeding (Nussbaum and others 1983); consequently, very wet stand conditions are poor habitat for these species. Wet old-growth stands have lower mean species richness and lower salamander abundances than either mesic or dry old growth (Aubry and Hall 1991, Aubry and others 1988, Bury and Corn 1988a).

AMPHIBIAN COMMUNITY ORGANIZATION

The similarity of amphibian community composition within WRIAs (Fig. 5) indicates that topographical, zoogeographical, or ecological influences operating at the scale of river basins (60,000-81,000 ha) are more important in the structuring of amphibian communities than those occurring at the smaller scale of sub-basins (4,000-12,000 ha). Because amphibians are strongly tied to moist environmental conditions, riparian systems probably provide the primary dispersal corridors for most species. In small watersheds, the ridges that form watershed boundaries are unlikely to significantly impede dispersal processes. In very large watersheds, however, such ridges may represent substantially different habitat conditions than those occurring in the valleys below. The similarity of amphibian communities within WRIAs (including situations where stands in adjacent WRIAs are in closer proximity than those occurring at opposite sides of a WRIA) strongly suggests that the boundaries of WRIAs create barriers to amphibian dispersal that do not occur at the smaller scale of WAUs. These findings may have implications for conducting amphibian surveys and for managing habitat at the landscape scale. Because communities within WRIAs are likely to be more similar in community composition than those occurring in different WRIAs, surveys will be most informative if field efforts are spread across as many WRIAs as possible. In addition, although prescriptions for landscape-scale management of habitat to maintain or enhance amphibian diversity and abundance do not yet exist (deMaynadier and Hunter 1995), these results suggest that they should be developed and evaluated within relatively large watersheds, such as major river basins, rather than within smaller order watersheds.

Amphibian communities in harvest-age stands were unique (Figs. 1 and 4). This stand structure had the highest overall amphibian abundance, and relatively high abundance values for a wide array of species (Table 2). The harvest-age structure class was also high in species richness, and was the only class in which all 11 species were found (Fig. 2, Table 2). In addition, unlike other structure classes sampled, amphibian community structure in harvest-age stands closely resembled that found in unmanaged forests (Figs. 1 and 10). *Lobaria* lichen, a species shown to be closely associated with old-growth forest conditions (Spies 1991), was more than 2 times as prevalent in harvest-age stands than in either clearcuts or pre-canopy stands, and was absent entirely from closed-canopy stands. Thus, harvest-age stands appear to provide habitat conditions for terrestrial amphibians that are similar in various ways to those occurring in unmanaged forests. Future analyses, in which I will combine data sets from community studies in managed forests (this study) with those from unmanaged forests (Aubry and Hall 1991), will provide further insights into this hypothesis.

SPECIES-HABITAT RELATIONSHIPS

NORTHWESTERN SALAMANDERS

Northwestern salamanders select habitat in completely different ways than the other 4 species studied. Although western redback salamanders, ensatinas, roughskin newts, and red-legged frogs exhibit varying reproductive ecologies, they showed consistent patterns of association with habitat variables, whereas patterns of association for northwestern salamanders were exactly the opposite, For each physiographic, landscape, or within-stand habitat variable for which a significant relationship was found, these 4 species was all either postively or negatively associated with that variable; northwestern salamanders always showed the opposite relationship (Table 6). This pattern of association was also reflected in their relative abundances. Abundances of northwestern salamanders were negatively associated with abundance values for all other species; in other words, northwestern salamanders were most common in habitats where the other 4 species were scarce (Table 9).

The northwestern salamander was positively associated with decay-class 3 snags and large logs of decay-class 3, and was the only species whose abundances were positively correlated with coarse woody debris (Table 6). Well-decayed logs generally do not serve as surface cover objects, however, since they are beginning to merge with the soil (Aubry and others 1988). Northwestern salamanders spend most of the summer and winter in underground retreats, often using rodent burrows to gain access to the soil column (Nussbaum and others 1983). The roots of decay-class 3 snags have decomposed, forming interconnected channels (Maser and others 1988) that may serve as access routes to such retreats. Thus, the association of northwestern salamanders with these structures may be more related to soil conditions and underground retreats than to surface cover.

The northwestern salamander was the only species of amphibian whose abundance was correlated with increasing elevation. Northwestern salamanders are common in subalpine zones and are known to occur at elevations exceeding 3,000 m, well above the etevational thresholds of the other 4 species (Nussbaum and others 1983). Although colder conditions at higher elevations may play a role in habitat quality for northwestern salamanders, the ability of this species to occupy such habitats probably enables them to reduce competitive interactions with both plethodontid salamanders and other species of pond-breeding amphibians, most of which favor lower elevations and warmer water temperatures The northwestern salamander was also the only species associated with the presence of permanent ponds within 500 m (-Fable 7). The logistic regression model distinguished stands with high abundances of northwestern salamanders on the basis of two variables: permanent ponds and high amounts of mature forest within 1,000 ha of the pitfall grid (Table 8). This strong relationship with the proximity of permanent ponds agrees closely with the findings of

Table 9. Spearman rank correlations with P values < 0.1 among amphibian species. Values presented are correlation coefficients (r); the direction of the relationship is indicated in parentheses.

Species	Western redback salamander	Ensatina	Roughskin newt	Red-legged frog
Northwestern salamander	0.46 (-)	0.37 (--)	0.35 ( )	0.42 (-)
Western redback salamander		0.55 (+)		
Ensatina				0.48 (+)
Roughskin newt				

Semlitsch (1981), who found that most adult mole salamanders *(Ambystoma talpoideum)* migrated 100-300 m between breeding ponds and non-breeding upland habitat.

These results indicate that northwestern salamanders occupy a variety of forested habitats in close proximity to permanent ponds, but reach highest abundances in landscapes having relatively high proportions of mature forest cover. Their relatively broad tolerance of environmental and ecological conditions apparently enables northwestern salamanders to seek out and successfully occupy habitats where competition from other amphibians is low. Although large and well-decayed woody material may play a role in habitat quality, within-stand management of habitat for northwestern salamanders is unlikely to result in significant benefits for this species.

WESTERN REDBACK SALAMANDERS

Western redback salamanders reached highest abundances in clearcuts, but differences among structure classes were not significant (Table 4). However, a seral gradient in habitat quality was indicated from analysis of body condition indices for both redback salamanders and ensatinas (Table 5). Only results for western redback salamanders were significant, but habitat quality indices for both species followed the same pattern: body condition indices increased as forests developed from clearcuts through pre-canopy forests to mature forests. Interestingly, closed-canopy stands appear to represent higher quality habitat than harvest-age stands. Food resources may be more plentiful in closed-canopy stands where ameliorated temperature and moisture extremes and high levels of detritus on the forest floor may result in more abundant invertebrate prey populations.

Condition index and abundance values did not exhibit the same pattern among structure classes, suggesting that density and habitat quality may not be positively correlated for redback salamanders. Most of the factors Van Home (1983) believed would increase the probability that density will be a misleading indicator of habitat quality apply to western redback salamanders in the managed landscapes I surveyed. Consequently, intensive demographic studies over the range of structure classes surveyed may be necessary to distinguish "source" from "sink" habitats. This apparent negative correlation between density and habitat quality was also observed by Dupuis and others (1995), who captured 3-6 times as many western redback salamanders in old-growth forests compared to managed stands on Vancouver Island, yet condition indices for adults >35 mm SVL were higher in managed stands in both years of their study.

Western redback salamanders were positively associated with rocky soils and total edge within 1,000 ha of the pitfall grid (Table 6). The latter variable was also included in the logistic regression model, as were north-facing aspects and small, moderately decayed logs. Western redback salamanders prefer the mesic habitat conditions occurring on north-facing aspects, but generally occupy drier habitats than other ptethodontids in this region and avoid very wet forest conditions (Aubry and others 1991, Nussbaum and others 1983). The unique value of small, moderately decayed fogs as cover’ objects to redback salamanders agrees with findings in unmanaged forests (Aubry and others 1988), and the strong association of plethodontid salamanders with rocky soils and talus is well known (Bury and others 1991a, Herrington 1988, Nussbaum and others 1983). Rocky soils provide interstices that plethodontid salamanders use as breeding sites, and where they seek refuge when they are not actively foraging on the surface of the ground. The high abundances of western redbacks in clearcuts and harvest-age stands, and their association with fragmented landscape conditions, probably reflects their association with relatively dry to mesic habitat conditions (Nussbaum and others 1983). In unmanaged forests, western redback salamanders were most common in young (55-75 yr) stands that were low in elevation, had relatively warm microclimates, and were drier and steeper than other stands (Aubry and Halt 1991). This suggests that increasing landscape diversity and changes in forest structure from thinning may result in higher abundances of this species.

ENSATINA

Ensatinas and western redback salamanders generally occupy the same habitats (Table 9, Nussbaum and others 1983), but ensatinas appear to be somewhat less tolerant of warm, dry microclimates and more closely associated with mature forest conditions. In unmanaged forests in the southern Washington Cascades, ensatinas dominated upland amphibian communities, representing over half of all individuals captured (Fig. 10). In managed landscapes, the ensatina is clearly a mature forest species; captures of ensatinas were over 4 times greater in harvest-age stands than in any other structure class (Table 2, Fig. 6). Furthermore, the ensatina was the only species associated with large, dominant conifers or the percent of mature forest within 100 ha of the pitfall grid (Table 6). Ensatinas appear to be particularly sensitive to differences in landscape composition occurring near the stand they occupied; it was the only species for which landscape metrics within 100--ha circles were better discriminators of high vs. low abundances than those in the 1,000-ha circle.

Ensatinas also favored rocky soils, but were low in abundance where moss cover was high (Table 6). Moss cover is probably indicative of relatively wet conditions. The logistic regression model was in accordance with results from other analyses; the most significant discriminators were north-facing aspects, low moss cover, and large amounts of mature forest in adjacent landscapes. Thus, mesic microhabitats, rocky soils, and mature forest conditions, at both stand and landscape scales, are important habitat components for ensatinas.

ROUGHSKIN NEWT

Due to the relatively small number of captures for roughskin newts and red-legged frogs, interpretation of results for these species should be considered preliminary.

Roughskin newts were significantly more abundant in clearcuts than in closed-canopy stands, where none were captured (Tables 2 and 4). The only within-stand variable with which this species was positively associated was rocky soils. Landscape variables showed a positive association with clearcuts within 100 ha, and with old forests and landscape patch diversity within 1,000 ha. Logistic regression analysis (based on presence/absence data, rather than abundances), however, showed an association with old multi-storied forests in the surrounding landscape, and with small, moderately decayed logs. Roughskin newts also showed an association with north-facing aspects and the absence of permanent ponds (Table 7). Thus, unlike northwestern salamanders, roughskin newts appear to move well away from ponds during the non-breeding season. Roughskin newts remain in breeding ponds longer than northwestern salamanders (Nussbaum and others 1983), possibly into the fall when pitfall trapping took place. Consequently, many captures may represent individuals that are in transit from breeding ponds to non-.breeding habitat, which may explain the lack of any consistent pattern in habitat associations.

RED-LEGGED FROG

The red-legged frog is the most forest-associated anuran in Washington, generally breeding in relatively still waters shaded by overhanging vegetation (Corkran and Thoms 1996). Red-legged frogs are commonly encountered considerable distances from water in upland forest habitats during the non-breeding season (Aubry and Hall 1981, Corkran and Thorns 1996, Leonard and others 1993, Nussbaum and others 1983). My results confirm these observations; red-legged frogs were captured significantly more often in sites that were not near permanent ponds (Table 7). In the managed landscapes I studied, red-legged frogs appeared to select habitat during the non-breeding season in much the same way as did ensatinas (Table 9). The distributional ranges of ensatinas and red-legged frogs in the Pacific Northwest are virtually identical (Nussbaum and others 1983). In addition, these two species were the only amphibians studied that reached highest abundances in harvest-age stands; red-legged frogs were captured almost exclusively in this structure class (17/22 captures), and significantly more often in harvest-age forests than in closed-canopy forests, where none was captured (Tables 2 and 4). Logistic regression classified stands containing red-legged frogs as those that were far from permanent ponds and had relatively flat slopes. This indicates that although red-legged frogs move away from ponds in the summer and fall, they remain in relatively low topographic positions.

Red-legged frogs were also associated with dense shrub layers, which they may use for protective cover. Patterns of habitat selection at the landscape scale suggest a preference for older, unfragmented forests. Red-legged frogs were negatively associated with amount of pre-canopy forests at both landscape scales, and tended to be absent in landscapes with lots of edge habitat or small patch sizes. In addition, they were most abundant in landscapes having the most remnant old-growth forest (Table 2). Thus, unlike the roughskin newt, which showed few associations with particular stand or landscape conditions, red-legged frogs appear to seek out forested habitats that provide particular moisture and temperature regimes and microhabitat conditions in much the same way as the ensatina.

IMPLICATIONS FOR FOREST MANAGEMENT

CLEARCUTTING

A number of studies have shown an overall decrease in amphibian abundances in clearcuts compared to uncut control stands (see review in deMaynadier and Hunter 1995). Although both western redback salamanders and ensatinas had the lowest condition indices in clearcuts (Table 5), there were few other indications that clearcuts represent substantially lower quality habitat for terrestrial amphibians than other structure classes. Clearcuts contained the highest abundances of western redback salamanders and roughskin newts (Table 2) and had a higher expected species richness than closed-canopy forests (Fig. 2). As Corn and Bury (1989) found in the Oregon Coast Range, however, clearcuts appear to represent relatively hostile environments for most stream-associated amphibians, especially tailed frogs. Only a single tailed frog was captured in a clearcut, and this structure class was the only one in which Pacific giant salamanders were not captured (Table 2). Furthermore, woodland salamanders, especially those in the genus *Plethodon,* commonly occur in rocky soils or talus, presumably because the large number of interstices enable them to move through the soil easily (Herrington 1988). Excessive soil compaction will affect the ability of woodland salamanders to move vertically within the soil and may result in direct mortality. Consequently, care should be taken to reduce compaction by heavy machinery and prevent removal of the upper soil and gravel layers during clearcut timber harvesting operations.

THINNING

No previous studies comparing amphibian communities in thinned vs. unthinned stands have been conducted in the Pacific Northwest. In this study, all pre.-canopy stands were pre-commercially thinned and all harvest-age stands had been commercially thinned. Both kinds of thinning typically result in increased insolation in forest stands and stimulation of vegetative growth (Oliver and Larson 1990), especially near the forest floor. As discussed previously, such changes are generally beneficial to terrestrial amphibians. The 2 thinned stand conditions had the highest expected species richness (Fig. 2), and harvest-age stands had almost twice the total captures of any other stucture class (Table 2). In contrast, unthinned closed-canopy stands had the lowest expected species richness, and was the only structure class in which roughskin newts and red-legged frogs were not captured. Thus, both pre-commercial and commercial thinning are likely to improve overall habitat conditions for terrestrial amphibians in forest plantations.

COARSE WOODY DEBRIS

Coarse woody debris has often been identified as a potentially scarce and limiting habitat component in managed forests (e.g., Maser and others 1988, Hunter 1990), and several researchers have found strong and/or statistically significant relationships between salamander captures and coarse woody debris (Aubry and others 1988, Bury and Corn 1988a, Dupuis and others 1995, Raphael 1988). There was little evidence, however, that levels of coarse woody debris had a significant influence on amphibian abundances in the managed stands I studied. Physiographic conditions and stand-structure exerted a much stronger influence on amphibian communities in managed forests than amounts of dead woody material. Closed-canopy stands had the highest levels of small (<10 cm d.b.h.) and medium-sized (10-50 cm d.b.h, and > 15 m tall) snags and logs >30 cm in diameter, yet had the lowest expected species richness and relatively low amphibian abundances compared to harvest-age stands (Fig. 2, Table 2).

Neither ensatinas nor western redback salamanders (two species that are commonly associated with coarse woody debris for surface cover) were positively correlated with any snag or log variable (Table 6). However, small (10-30 cm dia.) moderately decayed logs were included in logistic regression models for both western redback salamanders and roughskin newts. This size and decay class of log was most abundant in clearcuts and harvest-age stands, which were the structure classes having the highest abundances of western redback salamanders. In unmanaged forests, this diameter and decay class of log was used by redback salamanders more often than any other cover object (Aubry and others 1988). Thus, there is strong empirical evidence for the importance of this structural element to plethodontid salamanders in both managed and unmanaged forests in western Washington. In addition, large logs provides breeding sites for plethodontid salamanders (Jones and Aubry 1985) and are important components of nutrient cycling and water storage in unmanaged forests (Franklin and others 1981). The latter function may play an important role in creating favorable microhabitat conditions for terrestrial salamanders and providing refuges during dry conditions.

Although my findings do not indicate that levels of woody debris are currently limiting populations of terrestrial amphibians in the landscapes I studied, managed stands in this region still contain many large residual stumps and logs in advanced stages of decay from the original, unmanaged stand. Eventually, these features will disappear from the landscape. Because they are still an integral part of the humus and soil layers in these stands, their presence may partly explain why few associations were found between terrestrial amphibians and coarse woody debris. However, providing for the replacement of large logs in future stands may be important for the persistence of amphibians occurring at low population levels in managed landscapes.

HEADWATER CREEKS

Available evidence indicates that headwater creeks in undisturbed old-growth forests generally provide optimal conditions for stream-breeding amphibians in the Pacific Northwest (Bury and others 1991b). The relatively few captures of tailed frogs and Pacific giant salamanders in managed landscapes may indicate that habitat for stream-associated amphibians has been detrimentally affected by timber harvesting. Riparian management directed at improving habitat conditions along headwater creeks will be important for maintaining these species in managed landscapes, especially where large portions of the landscape were harvested prior to existing riparian management guidelines. The primary objectives of headwater management should be retention of shade to keep water temperatures low and prevention of sedimentation (Corn and Bury 1989). Budd and others (1987) speculated that buffer strips 7.6-18 m wide on each side of headwater creeks would protect wildlife habitat and water quality, although this prescription remains untested. Staggering harvest units along a stream system would also be beneficial. Corn and Bury (1989) found that logged stands had a higher amphibian diversity where there was uncut timber upstream, whereas logging upstream had little effect on amphibian populations in unharvested stands. These authors have also argued that excessive removal of coarse woody debris from stream channels during harvest operations can result in increased erosion of the streambank and increases in fine sediments (Bury and Corn 1988b). They recommend that natural coarse woody debris be retained in streams during logging cleanup, especially large pieces that are partially buried or decayed. Cull or broken trees that fall across or near streams should be left in place to enhance the structural diversity of stream habitats.

Woody debris also provides important ecosystem functions within creeks and streams. Logs form pools that trap sediments and leaf litter, providing nutrients for a wide variety of plant and animal species (Franklin and others 1981, Sedell and Swanson 1984). Such pools provide important microhabitats for larval and neotenic Pacific giant salamanders (Bury and others 1991b). For these reasons, creeks that have been cleared of woody debris during timber harvesting operations, or that have been scoured of organic debris by high levels of runoff (Sedell and Swanson 1984), should be restored to old-growth conditions by the addition of woody debris.

Examination of nearby undisturbed streams should provide the basis for determining appropriate sizes and amounts of woody debris to place within target streams.

Headwater creeks in coniferous forests west of the Cascade Crest in Washington and Oregon are often located within the upland forest canopy; riparian zones containing typical hardwood plant communities may not develop along headwaters (Swanson and others 1982). Thus, stream channels should be identified from topographic maps and forests carefully surveyed on foot for the presence of permanent headwater creeks before management prescriptions are developed. If possible, stream surveys to assess the current distribution and abundance of stream-associated amphibians (Bury and Corn 1991) and effectiveness monitoring to evaluate the success of mitigation strategies should also be conducted.

MANAGEMENT OF LANDSCAPES

Amphibian diversity and abundance in intensively managed forests was more strongly influenced by stand structure and physiographic conditions than by landscape characteristics. These findings agree closely with those of Lehmkuhl and others (1991) for unmanaged stands, who found only weak correlations between amphibian species richness and abundance and various landscape metrics within 2,025-ha circular landscapes around sampled stands. These authors found few strong landscape-scale relationships for any vertebrate group, but noted that amphibians responded less to landscape variables and more to stand characteristics than either birds or small mammals. Given the low vagility and small home range sizes of most amphibians, such results are not surprising.

Because harvest-age stands had much higher amphibian abundances and expected species richness than either closed-canopy forests or clearcuts, however, silvicultural strategies that maintain a higher percentage of harvest-age forest conditions within managed landscapes would be expected to provide substantial benefits to terrestrial amphibians. There are at least two ways to accomplish this. One would be to design silvicultural prescriptions for thinning closed-canopy stands so that the vegetative and structural conditions found in harvest-age stands are reached as soon as possible in the life of the stand. A second is to extend rotation ages so that harvest-age conditions will occur in a higher proportion of the landscape relative to clearcuts. Longer rotations in the Douglas-fir forest zone are not only ecologically desirable in many ways but can be economically viable (Curtis and Marshall 1993). Extended rotations would increase the amount of high-quality habitat in managed landscapes, reduce the frequency of entries, reduce ground-disturbing activities, and reduce the frequency of slash burning, which may be particularly detrimental to ensatinas and Pacific giant salamanders (Cole and others 1997). In addition, extended rotations would improve habitat connectivity among mature forest stands, which may reduce the susceptibility of some amphibians to local extirpations.

ACKNOWLEDGMENTS

I thank Angela Stringer for data on the presence of permanent ponds near study sites and Teresa Loo for assistance in the field during the early years of this project. Angela's dedication to this project and her hard work on stand selection, vegetation sampling, amphibian trapping, and data management made a significant contribution to the success of the TFW Landscape Studies. Scott Pearson, Janet Erickson, and Levon Yengoyen also contributed to the stand selection process and to vegetation sampling.

TERRESTRIAL SMALL MAMMALS

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INTRODUCTION ....

INTRODUCTION

The goal of the small mammal work was to compare the occupancy patterns of small mammals across the 4 structural classes identified for study and to relate the patterns for individual species and species groups to stand-level and landscape-level characteristics. 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. As detailed below we chose our sampling methods with this knowledge gap in mind. Due partly to monetary constraints and in recognition of extensive work done by others on this group (Carey and others 1992, Rosenberg and Anthony 1992, Carey 1995, Carey and Johnson 1995), arboreal rodents were not a focus of our investigation. We have included, however, some information for 2 species in our analyses (Townsend’s chipmunk and Douglas’ squirrel) that could be sampled by their vocalizations during the breeding bird surveys.

SAMPLING METHODS FOR SMALL MAMMALS

During the OGWHP studies, techniques for sampling vertebrate communities were developed and refined for conditions in Pacific Northwest forests. Based on extensive experience with amphibian and small mammal surveys gained during these studies (Bury *and* Corn 1987; 1988a, b; Aubry and others 1988; Bury 1988; *Corn* and others 1988; Aubry and others 1991; Aubry and Hall 1991; West 1991) we decided to sample terrestrial amphibians and small mammals with pitfall traps. Pitfall traps effectively capture surface-active amphibians and most small mammals, resulting in good estimates of relative abundance in forested habitats for both groups (Aubry and Hall 1991, West 1991). In addition, by capturing large numbers of individuals, this technique allows assessment of demographic structure of populations through analyses of body size-classes for *amphibians* and *age-classes* for small mammals.

Pitfall traps effectively sample small mammals that use tactile and olfactory cues for orientation more than visual cues. They therefore capture insectivores and non-jumping rodents well, but are less effective at capturing deer mice, chipmunks, and jumping mice (Briese and Smith 1974, Williams and Braun 1983, Bury and Corn 1987). We were comfortable with this known sampling bias, because the natural histories of many of the rodent species that are caught more effectively with other methods were much better understood than those species sampled well with pitfall traps. We wanted to emphasize those species that were not well sampled in previous studies. It has been our experience that many of the more common species, while not sampled effectively with pitfall traps, are still caught in sufficient numbers for statistical analyses.

FIELD SAMPLING

Pitfall traps were constructed in accordance with descriptions provided in Corn and Bury (1990). Thirty-six double deep (2 #10 cans used) 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 occurred by early November, and operated them for 4 consecutive weeks (28 days) in 1992, 1993, and 1994; traps were checked weekly. Due to funding constraints, our sampling effort was limited to 1 period per year. The timing of the trapping was set by the need to sample when amphibians were surface-active. In western Washington this occurs in late fall. Consequently, mammals were not sampled during their breeding season. Although a few individuals showed signs of reproductive activity, the populations generally had concluded reproduction at the time of sampling. Populations consisted of high proportions of juvenile and sub-adult age classes. Animals were frozen end transported to the University for later species identification and measurement. When appropriate, animals were prepared and deposited in the Burke Museum at the University of Washington.

Douglas squirrels *(Tamiasciurus douglasii}* and Townsend’s chipmunks *(Tamias townsendii)* were censussed during the spring breeding bird surveys. Both of these species were vocal during spring and their frequency of occurrence was recorded on the avian field forms and subsequently included with the small mammal data set.

STATISTICAL METHODS

TO determine the statistical significance of habitat patterns, both with respect to structural classes and years, we used repeated measures ANOVA after log-transforming the capture totals. We ran the analysis for each species with at least 20 captures. Univariate post-hoc contrasts were calculated to investigate differences between cell means. Responses to habitat patterns by taxonomic groups (e.g., Insectivores) were evaluated in the same way.

The direction and strength of correlations between selected habitat variables at stand and landscape scales and small mammal captures were assessed with univariate or multiple regression using average values for habitat variables and captures per site. Habitat variables were transformed as needed prior to regression using log and arcsine transformations. As explained in the introductory section of this report, 100- and 1000-ha circular landscapes generated from 25-m pixel landsat imagery and centered on the pitfall grids were analyzed with the FRAGSTATS Program (McGarigal and Marks 1995). The program provided a series of descriptive indices for correlation with small mammal capture data. Of the 2 scales, the 100 ha landscape seemed the most logical for small mammal work. The radius of a 100-ha circular area is just over 564 m, a good distance for investigating the effects of nearby, contrasting habitat types on the structure of small mammal communities. In addition to simple metrics such as patch richness (number of different patches) and the area of different patches, Simpson’s (1949) diversity index was used, which is a measure of proportional abundance of patch types across the landscape that varies from 0 (no diversity, that is, 1 patch type) to 1 (equal abundance of all patch types), as was an edge density measure, which indexed the amount of edge on a landscape by summing perimeter distances for selected patch types and expressing the sums on a unit area basis (ha). The basic approach was to see how closely the abundance of selected species would correlate with landscape indices calculated for individual structural classes and for entire landscapes.

Hierarchical clustering was used to show similarities in small mammal communities across structural classes and landscape units. An unweighted group pair algorithm was used, based on Pearson correlation coefficients calculated for average small mammal captures per site. Rarefaction curves using program Rarefrac. qba (Ludwig and Reynolds 1988) were calculated to compare species richness of small mammal communities in standardized samples among structural classes.

All analyses were done in SYSTAT 6.01 (Wilkinson 1996). Statistical significance was set at ((=0.05, although we discuss any trends between P=0.05 and 0.10.

RESULTS

SMALL MAMMAL CAPTURES

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). A few animals could only be identified to genus because of partial consumption by animals, decomposition, or an inability to distinguish young between the 2 species of deer mice. At least 20 individuals were captured for 13 of the 18 total species (Table 1).

Statistically significant differences among structural classes were found for 9 species: vagrant shrew (Fig. 1), montane shrew (Fig. 2), marsh shrew (Fig. 3), Trowbridge’s shrew (Fig. 4), shrew-mole (Fig. 5), coast mole (Fig. 6), creeping vole (Fig 7), forest deer mouse (Fig. 8), and ermine (Fig. 9) with strong trends (P ~ 0.08) for 2 others, the southern red-backed vole (Fig. 10) and the (Jeer mouse (Fig. 11). Statistically significant differences among years were found for 6 species: marsh shrew (Fig. 3), shrew-mole (Fig. 5), creeping vole (Fig. 7), long-tailed vole (Fig. 12), Townsend’s vole (Fig. 13), and ermine (Fig. 9).

The most common pattern was for a given species to favor either early or mature classes. Only the forest deer mouse (Fig. 8) favored the young unthinned forest (class C). 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.

Table 1. Total number of small mammals captured on all 24 sites in November 1992, 1993, and 1994.

Taxa	Number caught
Insectivores	
Vagrant shrew *(Sorex vagrans)*	161
Montane shrew *(S. montanus)*	299
Water shrew *(S. palustfis)*	1
Marsh shrew *(S. bendirii)*	57
Trowbridge's shrew *(S. trowbridgii)*	1781
Masked shrew *(S. cinereus)*	2
Unidentified shrew	31
Shrew-mole *(Neurotrichus gibbsii)*	208
Coast mole *(Scapanus orarius)*	20
Townsend's mole *(S. townsendii)*	4
Total insectivores	2564
Rodents	
Townsend's chipmunk *(Tamias townsendii)*	5
Northern flying squirrel *(Glaucomys sabrinus)*	7
Deer mouse *(Peromyscus maniculatus)*	248
Forest deer mouse *(P. keeni)*	166
Unidentified deer mouse	71
Southern red-backed vole *(Clethrionomys gappen)*	137
Creeping vole *(Microtus oregoni)*	451
Long-tailed vole *(M. longicaudus)*	28
Townsend's vole *(M. townsendii)*	20
Unidentified vole	1
Total rodents	1134
Carnivores	
Ermine *(Mustela erminea)*	22
Total mammals	3720

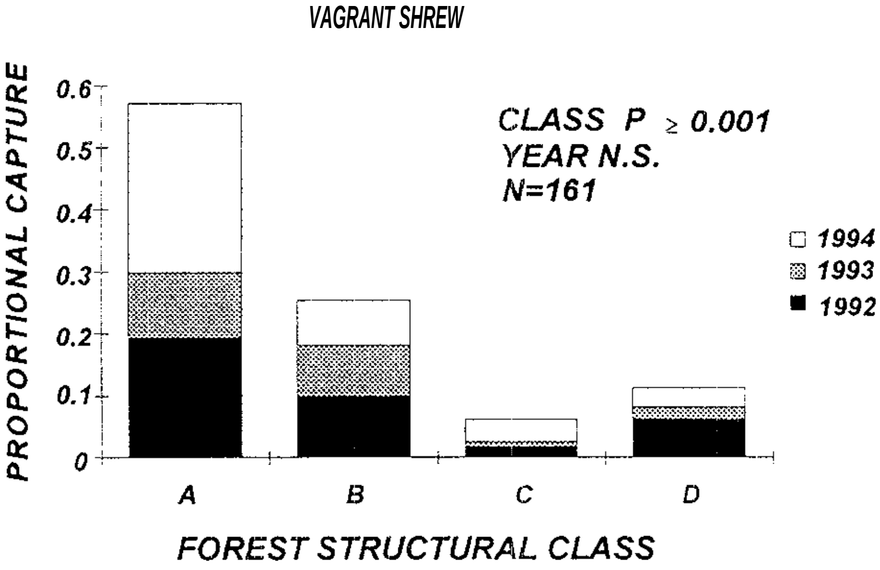

Figure 1. Proportional capture of the vagrant shrew across forest structural classes during 1992-1994. A = clearcut, B = pre-canopy, C = closed-canopy, and D = harvest-age.

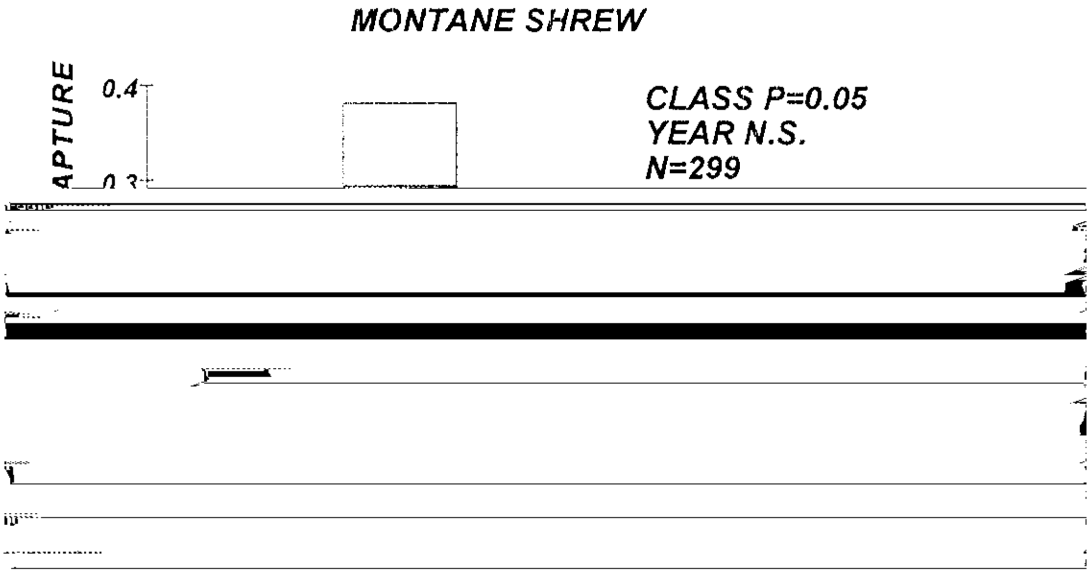

Figure 2. Proportional capture of the montane shrew across forest structural classes during 1992-1994.

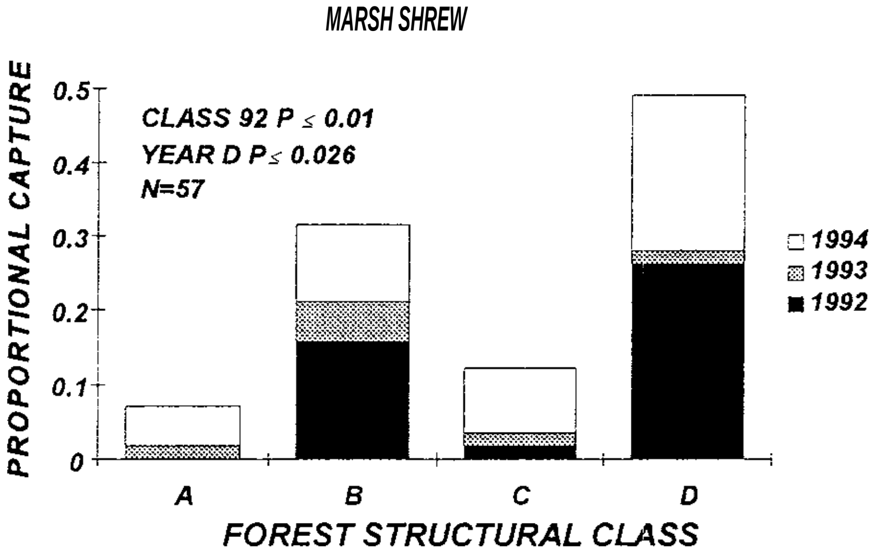
MARSH SHREW

Figure 3. Proportional capture of the marsh shrew across forest structural classes during 1992-1994.

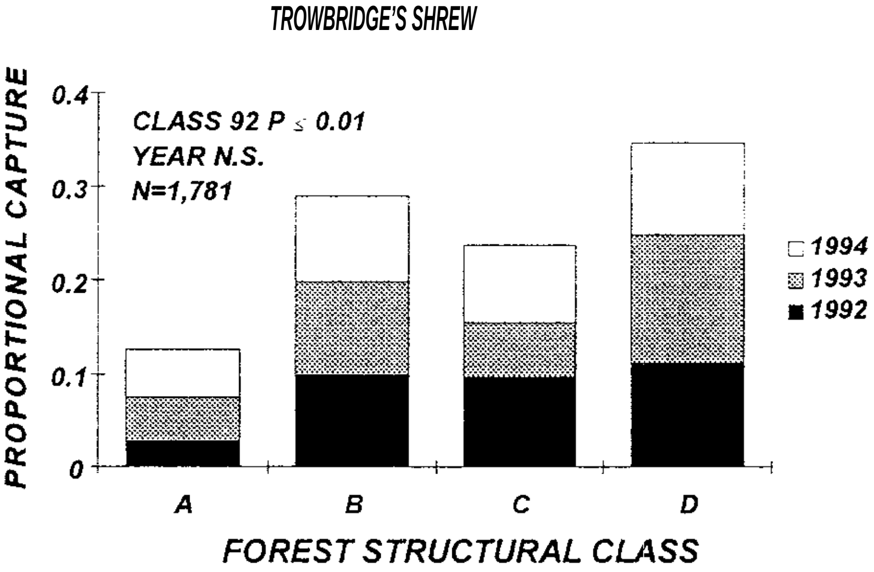
TROWBRIDGE'S SHREW

Figure 4. Proportional capture of the Trowbridge's shrew across forest structural classes during 1992-1994.

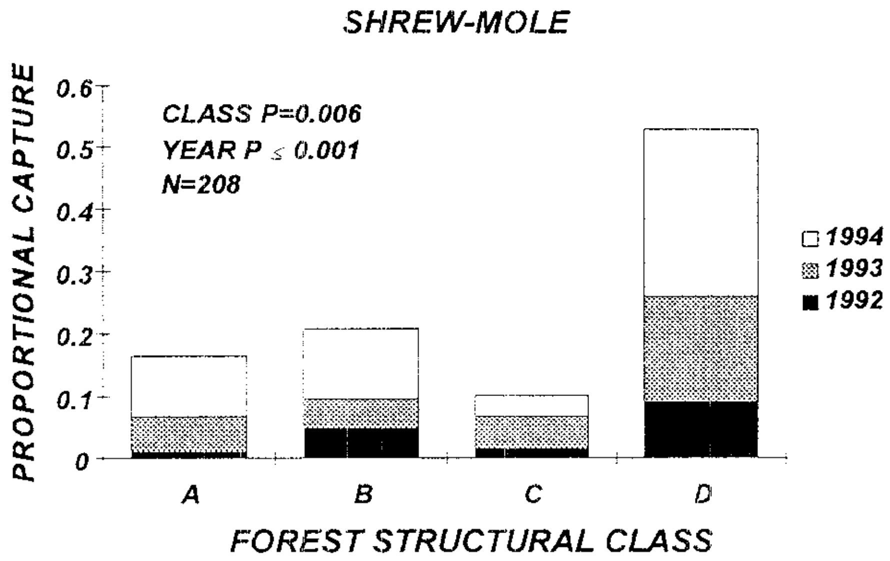

Figure 5. Proportional capture of the shrew mole across forest structural classes during '1992-1994.

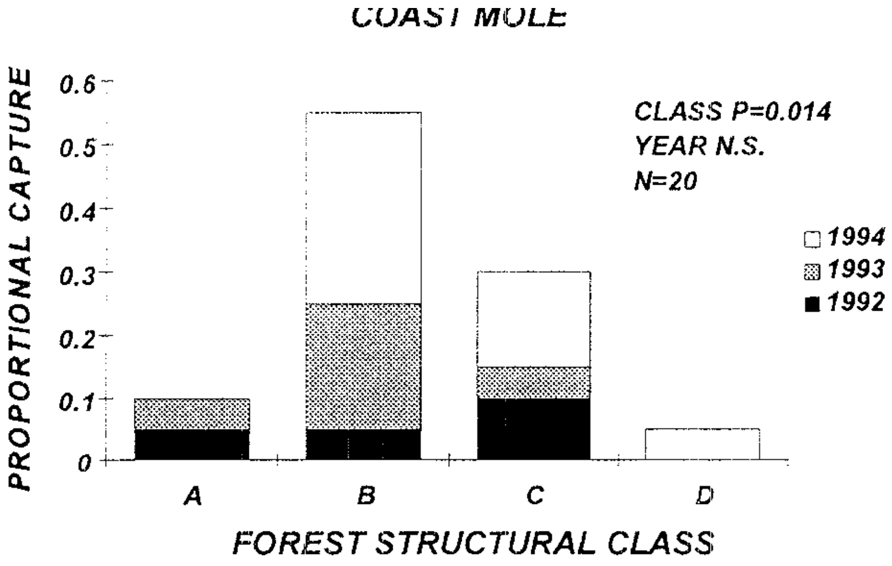

Figure 6. Proportional capture of the coast mole across forest structural classes during 1992-1994.

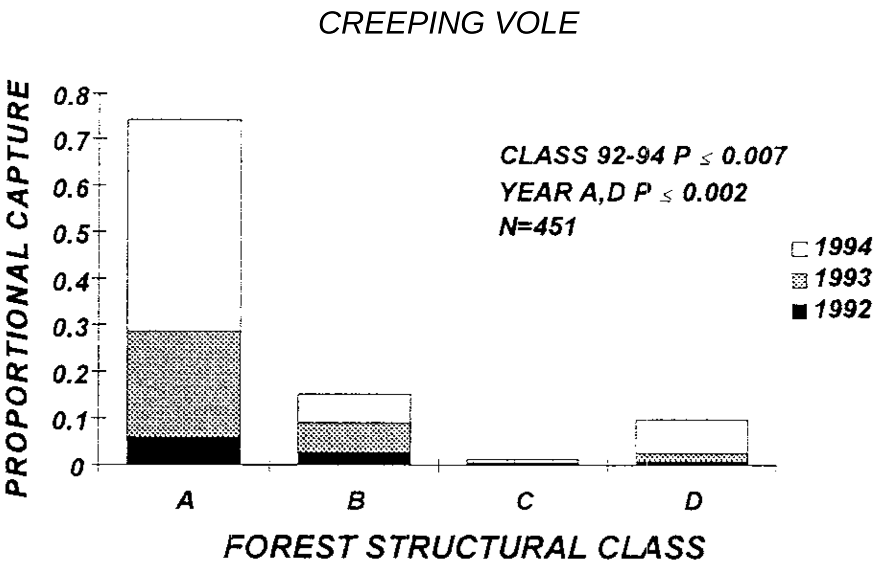

Figure 7. Proportional capture of the creeping vole across forest structural classes during 1992-1994.

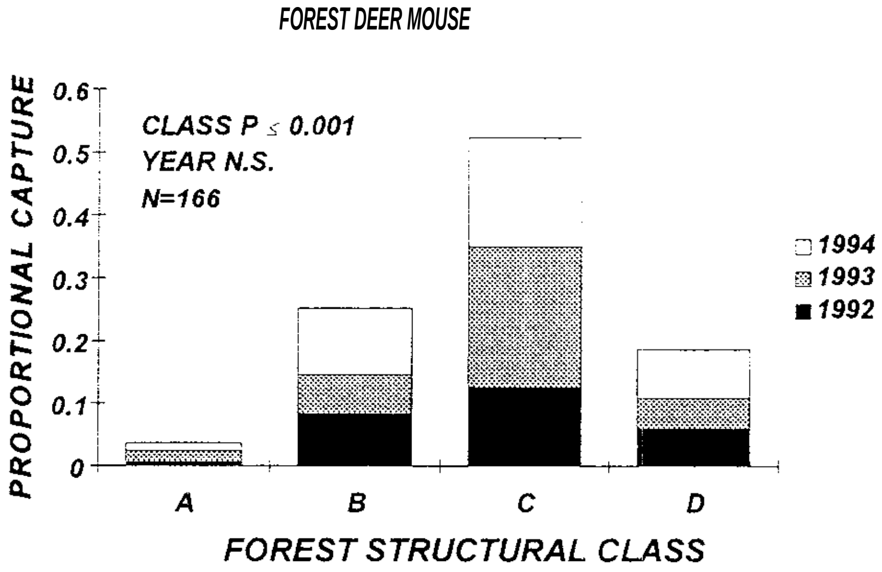

Figure 8. Proportional capture of the forest deer mouse across forest structural classes during 1992-1994.

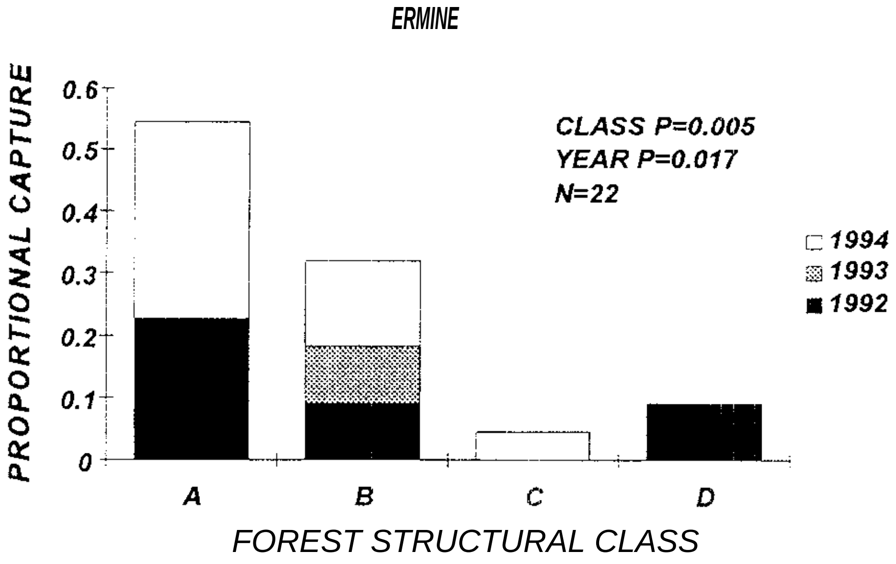

Figure 9. Proportional capture of the ermine across forest structural classes during 1992-1994.

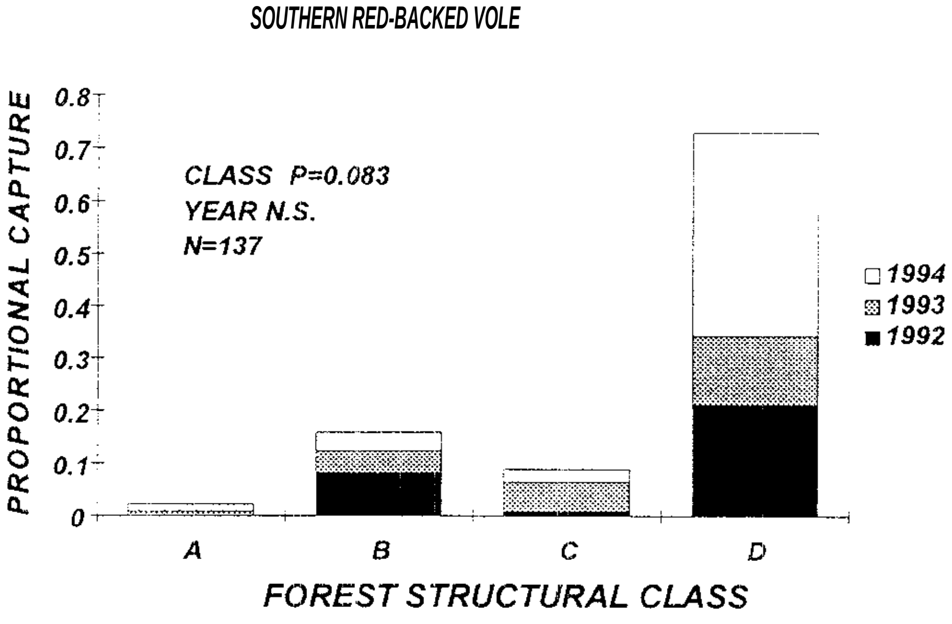

Figure 10. Proportional capture of the southern red-backed vole across forest structural classes during 1992-1994.

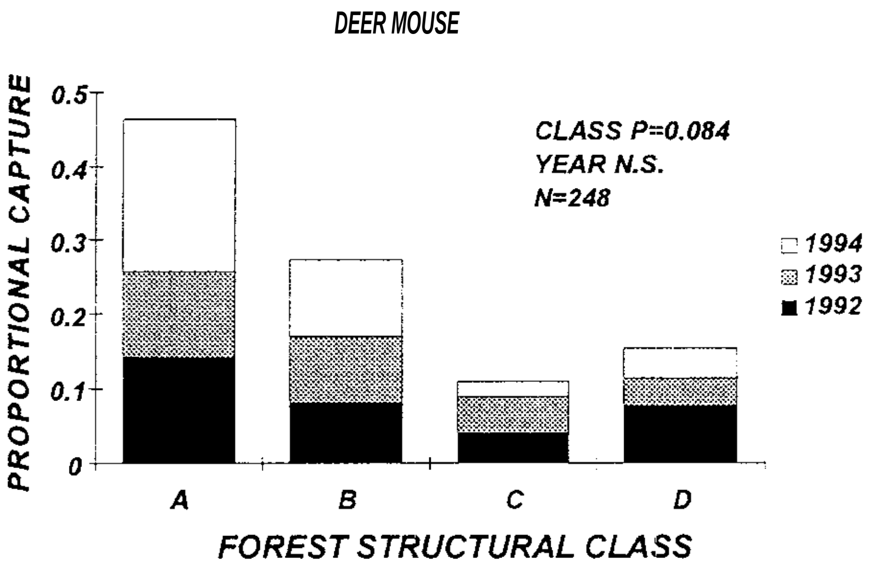

Figure 11, Proportional capture of the deer mouse across forest structural classes during 1992-1994.

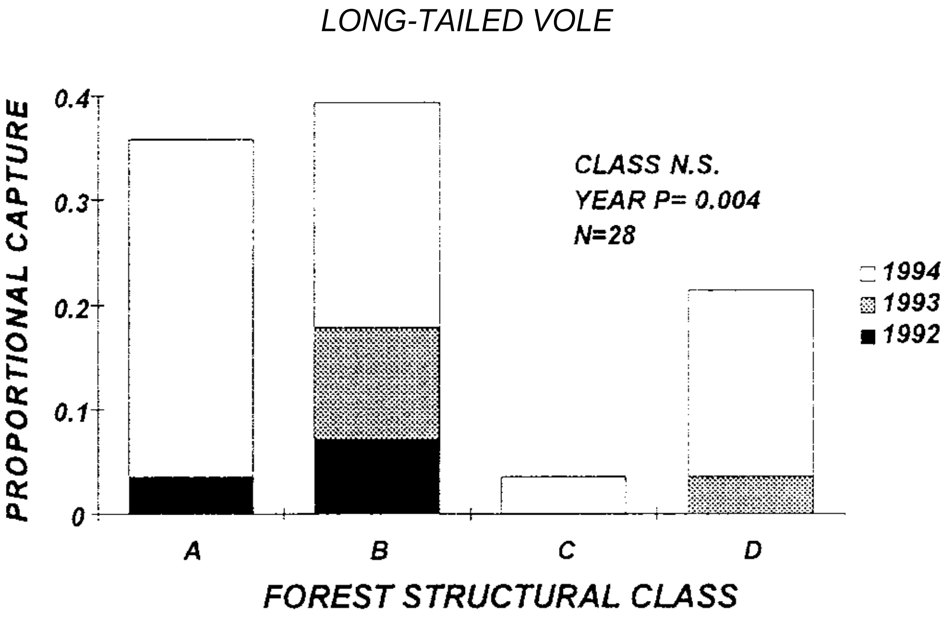

Figure 12. Proportional capture of the long-tailed vole across forest structural classes during 1992-1994.

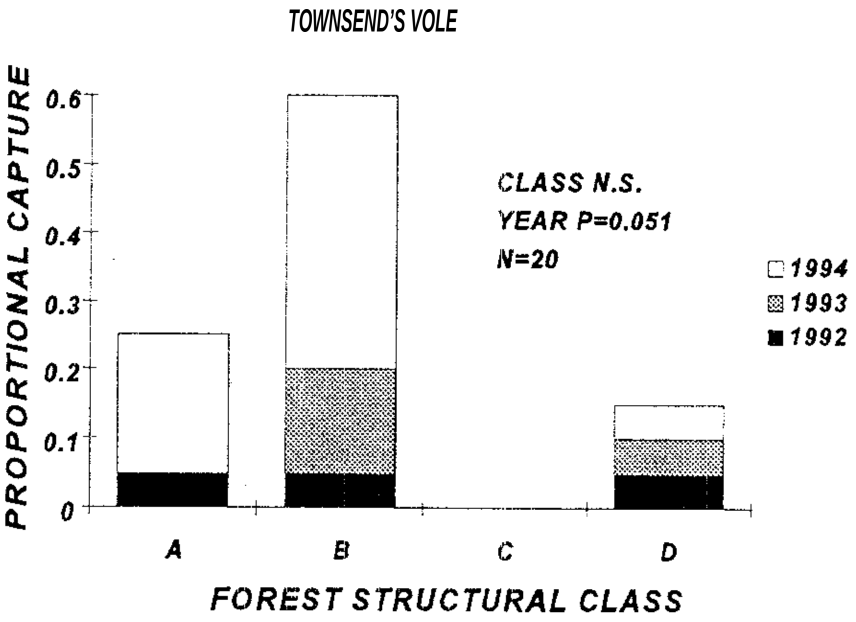

Figure 13. Proportional capture of the Townsend's vole across forest structural classes during 1992-1994.

CAPTURES OF SHREWS

Four of the 6 shrews were captured in sufficient numbers for statistical treatment. Two of the species favored early pre-canopy/edge environments and 2 favored fully developed forest. In western Washington the vagrant shrew (Fig. 1) reaches greatest abundance in open environments and does very well in managed landscapes. It showed a highly significant pattern across the 4 structural classes and no difference in the pattern between years. Another species that does well in the younger age classes is the montane shrew (Fig. 2). it is not as strongly oriented to fields as is the vagrant shrew, but reaches highest abundance in the transitional stages between fields and closed canopy forest (class B). It showed this pattern in each year. Of the common shrews in western Washington, the montane shrew exhibits the most generalized habitat use pattern. It can be found in virtually all habitats types in the region. The marsh shrew (Fig. 3) favors moist areas; generally forested. Its pattern of abundance was the most complex of the shrews, with a significant difference across the structural classes in 1992 when it favored classes B and D and a significantly lower abundance within the D class during 1993. This shrew has morphological adaptations for a semi-aquatic lifestyle, but it is much less dependent upon water than the water shrew *(Sorex palustris).* One might suspect that its abundance might be more determined by the distance to water rather than forest structure, but there is not a strong correlation between marsh shrew abundance and the presence of permanent water near the trapping grids. In work conducted primarily for the pond-breeding amphibian work (this report), the presence of permanent water within 300 and 500-m radii from the pitfall grid was noted. At 300 m permanent water was present in 17% of the class A sites, 50% of class B, 67% of class C, and 33% of class D sites. At 500 m permanent water was present in 60% of the class A sites, 50% of class B, 100% of class C, and 33% of class D sites. Viewed with the abundance patterns across structural classes the match is not very good. It is probable that these forests are sufficiently wet to allow the marsh shrew to survive in a range of structural classes, although it does not do well in clearcut areas. Trowbridge's shrew (Fig. 4) is the most abundant species of small mammal in forested habitats of western Washington. This is only realized when pitfall trapping is employed. In studies using concurrent pitfall and snap trapping the abundance of Trowbridge's shrew and both species of deer mouse is often roughly equal. Trowbridge's shrew reach high abundance across the forest structural classes, and although present in clearcuts, are less abundant there.

CAPTURES OF MOLES

Abundance of 2 of the 3 moles captured was tested for differences across structural classes. The coast mole (Fig. 6) had few captures (N = 20), but still showed statistically significant differences with most captures occurring in the middle 2 classes. Captures in clearcuts and mature forest were very low. Relatively little is known of the requirements of this species in forested habitats. It appears to be primarily an edge species, although about one-third of its total captures was in dense, closed-canopy forests (class C). The shrew-mole (Fig. 5) was caught in greater abundance and showed a clear preference for mature forest over all other classes. It also showed a difference between years with high abundance in 1994. The shrew-mole has been identified as a species associated with old-growth forest (Aubry and others t991).

While the statistical association may be real, its abundance in the mature forest classes of this study argues against a strong biological dependency. It is clear, however, that this species does best in fully developed forest.

OAPTURES OF RODENTS

Both deer mouse species, although not sampled well with pitfall traps were caught in sufficient numbers for statistical analysis. The deer mouse (Fig. 11) and the forest deer mouse (Fig. 8) show reciprocal patterns of habitat occupancy across the forest structural classes. Since its definitive separation as a distinct species (Gunn and Greenbaum 1986, Allard and others 1987, Hogan and others 1993) we are just recently beginning to understand how these species interact. One dimension appears to be some separation along habitat occupancy patterns, which are inverse between the species in clearcuts, about the same in class B, inverse in class C, and about the same in mature forest. The deer mouse is most abundant in early stages of forest succession. The opposite might be said of the forest deer mouse. The forest deer mouse was the only small mammal to show its highest abundance in class C. Its ability to use these forests, with their sparse understories, probably relates to their tree-climbing habit which allows them access to resources in the tree canopy. Both species showed similar patterns of abundance in each year. Southern red-backed voles (Fig. 10) were found more often in mature forest than any other structural class. Although the percentages caught across the structural classes would suggest a highly significant pattern, the probability level was not particularly low at 0083. Inspection of the capture totals indicates why this occurred, with most of the captures in mature forest attributable to just 2 of the 6 sites. The distribution of this species was very patchy across all structural classes. Like the shrew~mole, this species has been thought to be associated with old-growth forests, and while its association with well-developed forests (such as those in class D) seems fairly certain, its association with old-growth forest remains unclear (West 1991). Of the 3 *Microtus* species, Townsend’s vole (Fig. 4) and the long-tailed vole (Fig. 12) were not caught in very large numbers, but despite this showed significant differences between years, a feature showed by all 3 species. This genus is known for periodic fluctuations in abundance, and 1994 was a "good" year for the genus (and other species) throughout the Pacific Northwest. With additional captures of the

Townsend's vole, the pattern in Fig. 13 would be statistically significant. The habitat occupancy patterns are well known for this species, which reaches highest abundance in lowland areas of Puget Sound in open, wet field and meadow environments. Consequently, in this landscape it does best in the first 2 age classes. The long-tailed vole has not been as well studied, mainly because its distribution tends to be patchy in western Washington. As an herbivore, however, one expects it to be found in habitats with well-developed ground covers. This seems clear from Fig. 12, where the species was essentially absent from the unthinned forest that supported a very poor understory plant community. Its distribution remains somewhat enigmatic, although the TFW Riparian project is finding most captures of this species within riparian zones. The highest and most consistent captures of the long-tailed vole in this study were from a site (B4) associated with a permanent wetland. The creeping vole (Fig. 7) was caught in good numbers and showed a strong pattern favoring clearcut sites in all years. Differences between years were also seen for sites in classes A and D, again with large numbers in 1994.

CAPTURES OF CARNIVORES

Somewhat surprisingly, 22 ermine were caught in the pitfall traps (Fig. 9). The pattern of capture was distinctive and consistent enough to be statistically significant both for class and year. Ermine are specialized predators of field voles and showed highest abundance in the first 2 structural classes, just as the *Microtus* species. The difference between years was due to low abundance in 1993.

INFREQUENTLY CAPTURED SPECIES

There is always concern when species are caught in low numbers as to whether they were uncommon because of land use practices or because of an unrelated reason. Five small mammal species had very low captures: the water shrew, masked shrew, Townsend's mole, Townsend's chipmunk, and northern flying squirrel (Tables 1 and 2). The water shrew is not often found at distance from water, and the single capture of this species is incidental. The individual was captured in site B6 which had permanent water within 300 m of the pitfall array. The masked shrew is a species of the boreal

Table 2. Pitfall captures of small mammals in clearcut (A), pre-canopy (B), closed-canopy (C), and harvest-age (D) forest classes from 1992-1994.

	Forest structural classes			
Taxa	A	B	C	D
	Insectivores			
Vagrant shrew	**92**	**41**	**10**	**18**
Montane shrew	75	114	60	50
Water shrew	0	0	1	0
Marsh shrew	**4**	**18**	**7**	**28**
Trowbridge's shrew	224	517	423	617
Masked shrew	0	2	C)	0
Unidentified shrew	8	8	7	8
Shrew-mole	34.	43	21	110
Coast mole	2	11	6	1
Townsend's mole	1	2	1	0
	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	31
Unidentified deer mouse	51	9	2	9
Southern red-backed vole	3	22	12	100
Creeping vole	335	68	5	43
Long-tailed vole	10	11	1	6
Townsend's vole	5	12	0	3
Unidentified vole	1	0	0	0
	Carnivores			
Ermine	12	7	1	2

forest, with its primary distribution in northern Canada and Alaska, where it is a very common species. It is on the southwestern edge of its continental distribution in western Washington and shows rarity throughout the region. It has been captured in a wide range of habitats, including all forest successional stages. Townsend's mole is the common mole of the Puget Sound lowlands. It is elevationally replaced by the coast mole. The study area is probably at the higher end of its distribution in western Washington. The 2 rodents, the Townsend's chipmunk and the northern flying squirrel are simply not sampled well by pitfall traps, although a few of both were caught. Other techniques will be required to assess their use of structural classes, although both make use of second-growth forests.

DEMOGRAPHICS

Because of the need to operate the pitfall grids after the fall rains to capture surface-active amphibians, we did not sample actively breeding populations of mammals. This and the fact that the study was not designed to compare demographic patterns among structural classes results in a data set of limited capability for demographic analyses. Nonetheless, a concern often expressed when measures of abundance are used to compare habitat use patterns is the possibility of abundance acting as a misleading indicator of habitat quality. This is thought to be a critical problem when individuals move from high-quality habitats, with the potential to support breeding populations, into habitats that are incapable of supporting breeding populations (habitat sinks). Such a phenomenon might result in high abundance of non-reproductive individuals (typically young of the last generation) in poor habitats for some time, followed by a period of mortality and perhaps local extinction. A full documentation of such a pattern requires live-trapping and sampling of populations across years. However, if this were happening consistently across the structural classes investigated in this study, we might see consistent differences in population age classes reflected in differences in mean body mass among the 4 habitat structural classes. To get a sense of the magnitude of such differences in this data set, the mean body mass of 3 species with different patterns of abundance over time was compared among structural classes and years.

Species were chosen that had enough captures to make most if not all of the comparisons across conditions for the sexes separately.

The creeping vole, an herbivore, in common with other *Microtus* species is capable of large changes in abundance every few years, and typically reaches highest productivity and abundance in early successional habitats. Comparing the body mass of the creeping vole across structural classes and years reveals little consistent change despite large increases in abundance during the study period (Table 3). Only one instance of significantly different body mass was found: males in 1993 had lower mean body mass in clearcut sites than in the transitional sites (class B) and mature forest (class D). This difference was not seen in 1992 or 1994. Males were not caught in the unthinned forest (class C) during 1993, nor were females in '1992 or 1993.

Deer mice, generalist or omnivorous feeders, are not known to undergo regular, large changes in abundance. They are also considered habitat generalists, although they tend to favor early successional sites (this study). In 2 cases body mass was different for the deer mouse, 1 for males in 1994, where mean mass was higher in unthinned forest than all other structural classes, and for females in 1992, where body mass was lower in clearcut sites than unthinned or mature forest sites (Table 4). Neither pattern was repeated in the other 2 years. No female deer mice were caught in mature forest during 1993 or in unthinned forest in 1994.

The Trowbridge's shrew is an insectivore known to occur widely in forested habitat in the region. Although its patterns of abundance over time are less well known than the previous 2 species, it shows rather consistent, high abundance from year to year in closed-canopy forest (this study, West 1991). In 1992 males had higher body mass in transitional sites (class B) than in the other structural classes, except for similar body mass in mature forest (Table 5). In 1994 body mass was lower in the clearcut sites than all other classes. Female shrews showed only 1 difference: high body mass in transitional sites during 1992, which paralleled the pattern for males. Other differences were not statistically significant.

Table 3. Mean weights (g) of Trowbridge’s shrews (SOTR) caught during 1992-1994 across structural classes. Differences between means assessed by one-way ANOVA with Tukey’s test. Means not significantly different share superscripted letters.

	Classes							
	A		B		C		D	
Year	N	Wt	N	Wt	N	Wt	N	Wt
				Males				
1992	23	6.0^{a}	86	6.9^{b}	90	6.3^{a}	97	6.3^{ab}
1993	37	5.5^{a}	110	5.6^{a}	58	5.6^{a}	154	5.7a
1994	39	5.5^{a}	79	6.0^{b}	99	6.2^{b}	99	5.9^{b}
				Females				
1992	24	6.2’	68	7.0^{b}	76	6.3^{a}	73	6.2^{a}
1993	42	5.5"	62	5.7^{a}	42	5.6^{a}	78	5.7^{a}
1994	47	5.5^{a}	76	5.7^{a}	54	6.1a	73	5.6^{a}

COMMUNITY PATTERNS

In terms of collective captures, the Insectivores showed significant differences across structural classes in 1992 with low abundance in clearcut sites, and in 1993 with low abundance in clearcut and unthinned forest age classes (Fig. 14). Class differences were not significant in 1994. Only the vagrant shrew and the montane shrew contributed substantial numbers to capture totals for the clearcut sites. The other classes were rather similar with the exception of low captures in the unthinned sites during 1993. Overall, Trowbridge’s shrew dominated captures. Rodent species showed only 2 significant differences with clearcut sites showing higher captures than all other classes in 1994, and higher captures in the clearcuts during 1994 than in either previous years (Fig. 15). The combined picture for rodents reflects the effect of increased *Microtus* abundance in 1994, a pattern not shared by the 2 deer mice species. Fortunately, I of the 3 years was a year of high abundance for the microtines which allows a good sense of the relative importance of pre-canopy habitats for overall rodent abundance.

Table 4. Mean weights (g) of deer mice (PEMA) caught during 1992-1994 across structural classes. Differences between means assessed by one-way ANOVA with Tukey’s test. Means not significantly different share superscripted letters. Dashes indicate periods of zero capture.

	Classes							
	A		B		C		D	
Year	N	Wt	N	Wt	N	Wt	N	Wt
					Males			
1992	23	18.0^{a}	11	18.6a	6	21.5a	12	19.4a
1993	20	14.4a	9	15.3a	8	14.3^{a}	9	14.7a
1994	28	18.3^{a}	16	18.0a	5	23.6^{b}	6	18.0^{a}
					Females			
1992	13	15.7^{a}	8	18.9^{ab}	4	20.3^{b}	5	21.0^{b}
1993	8	13.8^{a}	13	15.8^{a}	4	15.0^{a}		
1994	23	18.0"	10	20.3^{a}			4	17.5a

’Table 5. Mean weights (g) of creeping voles (MIOR) caught during 1992-1994 across structural classes. Differences between means assessed by one-way ANOVA with Tukey’s test. Means not significantly different share superscripted letters. Dashes indicate periods of zero capture.

	Classes							
	A		B		C		D	
Year	N	Wt	N	Wt	N	Wt	N	Wt
					Males			
1992	13	17.8^{a}	5	20.0^{a}	2	19.0^{a}	1	15.0^{a}
1993	50	15.8^{a}	18	17.4^{b}			6	18.7^{b}
1994	89	17.7^{a}	14	17.5a	2	18.5a	18	18.1^{a}
					Females			
1992	13	16.0^{a}	5	18.8^{a}			3	16.3^{a}
’1993	51	15.5^{a}	10	16.8a			1	14.0^{a}
’1994	117	17.6^{a}	13	18.0^{a}	1	21.0^{a}	14	16.5a

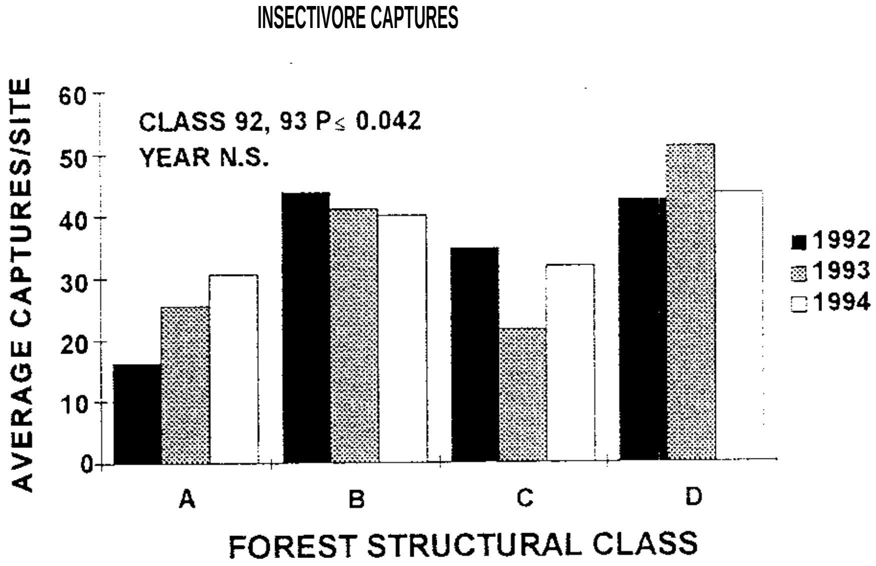

Figure 14. Average captures of insectivores per site during 1992-1994.

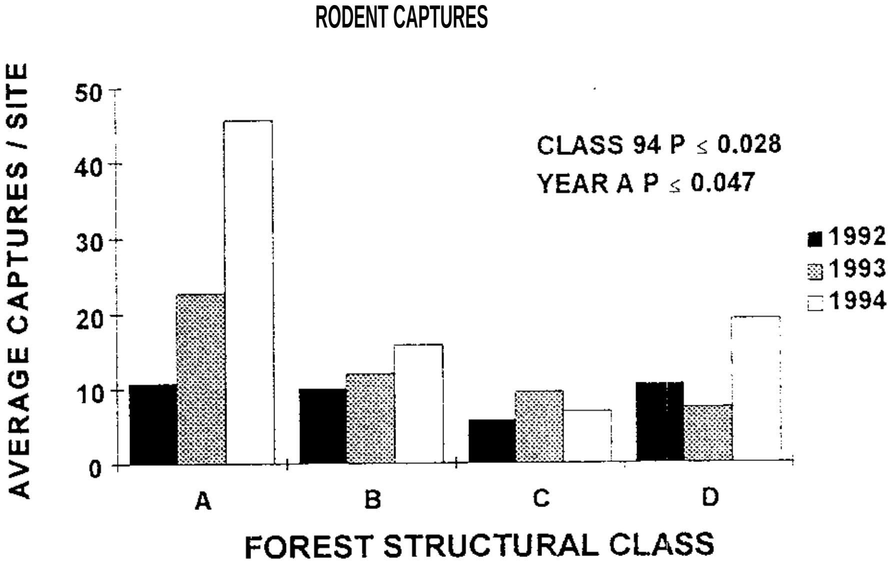

Figure 15 Average captures of rodents per site during 1992-1994

Species richness for all small mammals (Fig. 16) was consistent across the structural classes in each year, despite a considerable increase in 1994. The mean number of species per site was about the same between clearcut sites and mature forest. Of course the mammalian species composition of these most dissimilar habitats was very different. Predictably, given the foregoing pattern, species richness was highest in the transitional class (class B). This is most likely due to a simple mixing of species from either end of the habitat gradient. From unadjusted capture totals, species richness appears lowest in the unthinned forest (class C) in each year. However, when sample sizes are standardized to adjust for the low captures in the unthinned forest sites, species richness in the unthinned forest sites appears comparable to that in the clearcut and mature forest sites (Fig. 17). 'The high population abundances in 1994 drove the richness pattern between years. There was little difference in species richness between 1992 and 1993. Breaking the pooled species richness into insectivore and rodent components, the insectivore pattern is essentially the same as that for total mammals (Fig. 18). In this case the early successional species (vagrant shrew and montane shrew) and those of later stages (Trowbridge's shrew and the shrew-mole) admix in the transitional class (class B) to give the highest species number per site. Interestingly, even though differences in insectivore captures were not significant between years (Fig. 14), species richness on a per-site basis clearly was higher in 1994. Looking into this further, of the 9 species of insectivore in the area, 2 species were too rare to have an effect (water and masked shrew), 3 (montane and Trowbridge's shrews and the shrew-mole) were ubiquitous or showed little change in the number of sites occupied between years, end thus only 4 species (vagrant and marsh shrews and the coast and Townsend's moles) were responsible for the species richness increase seen in 1994. The changes were subtle with the vagrant shrew changing from 15 sites occupied in 1992 to 13 in 1993 and 17 in 1994. The pattern for the marsh shrew was 11 (1992), 5 (1993), and 16 sites occupied (1994). The coast mote was found in 4 (1992), 5 ('1993), and 8 sites (1994). Unlike the coast mole, the Townsend's mole was only caught on 3 sites, all in 1994. The pattern for rodents, although similar to the pattern for total mammals, differed in pattern strength. As expected with the high abundance in I994, species richness per site in 1994 was

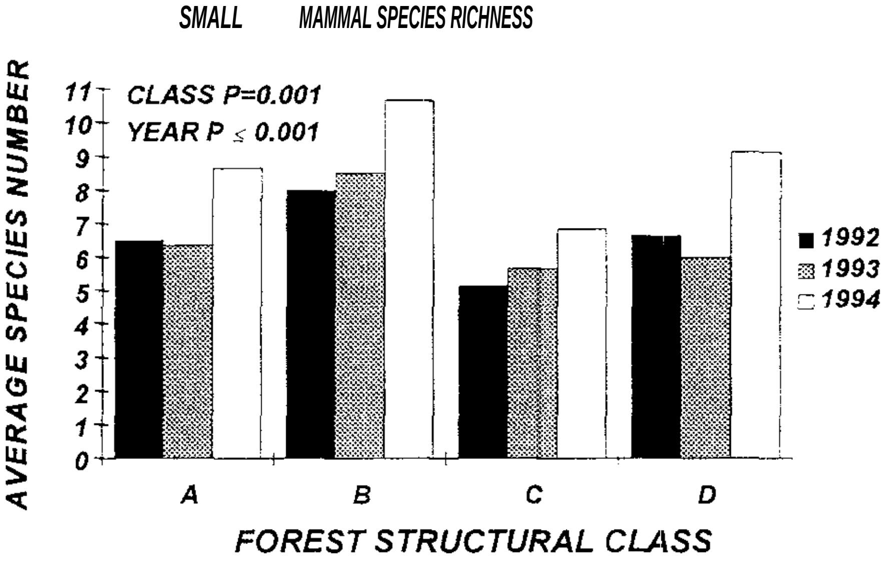

Figure 16. Average species richness of all small mammal species per site during 1992-1994.

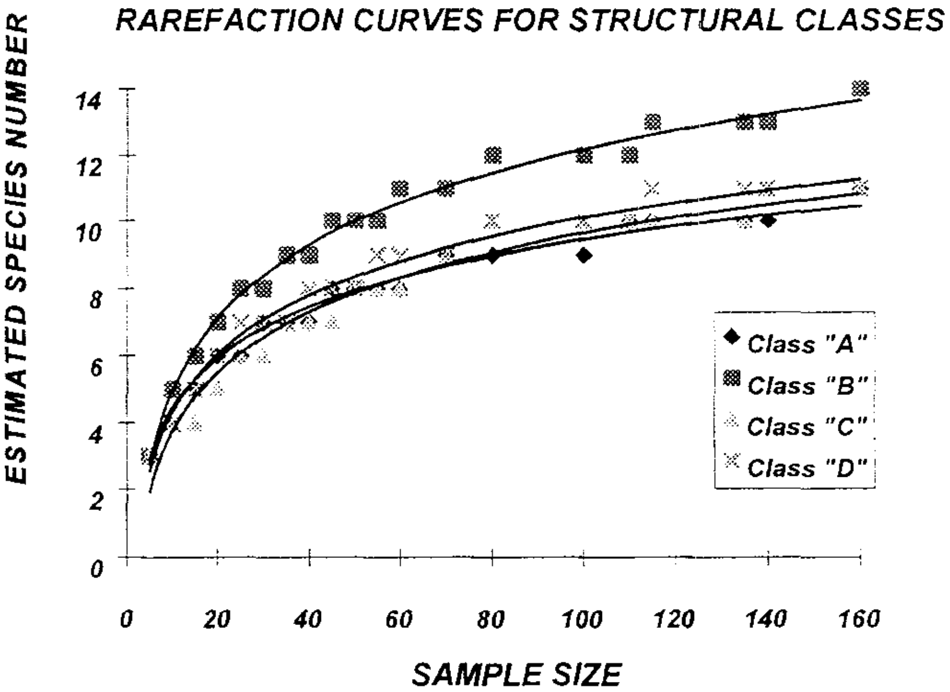

Figure 17. Estimated number of small mammal species in standardized samples for the structural classes calculated with the program Rarefrac.qba (Lugwig and Reynolds 1988).

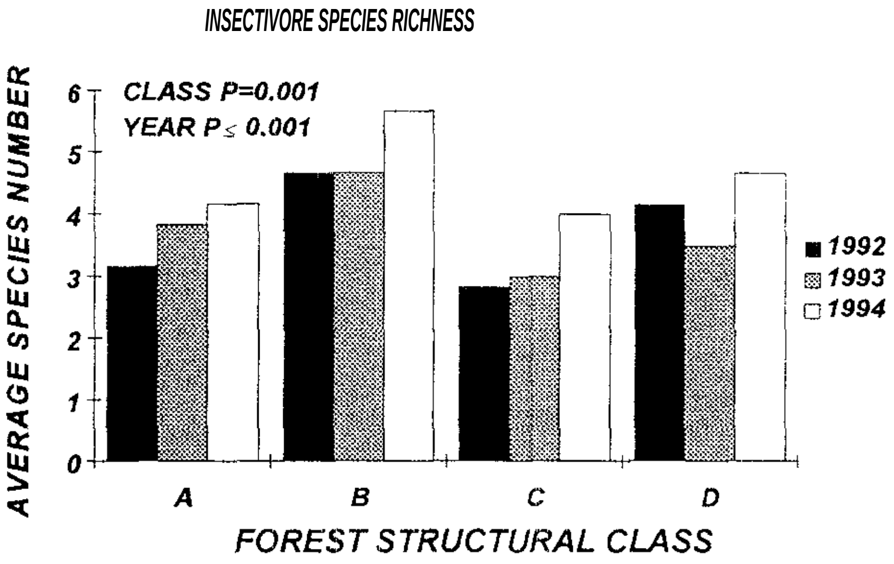

Figure 18. Average species richness of insectivore species per site during 1992-1994.

considerably higher than that seen for insectivores and helped intensify this aspect of the pattern for mammals altogether. With respect to differences between classes the probability level was close to significance (Fig. 19) with the transitional class (class B) again showing the highest species number per site. This difference, however, was weaker than seen for Insectivores.

ENVIRONMENTAL CORRELATES

STAND-LEVEL CORRELATIONS

Given the strong pattern of abundance with respect to structural classes at the stand level, we sought correlations between small mammal abundance and individual variables from the vegetation data set (Introduction, this report). Elevation of the study sites was not an important variable determining species richness, either for rodents or insectivores (Fig. 20). We focused on stand mean values for ground cover variables recorded on the 3- X 3-m vegetation sampling plots. Of the 15 variables constituting this data set, 13 variables showed statistically significant correlations with small mammal species abundance. Multiple correlation coefficients (R^2) were rather high for

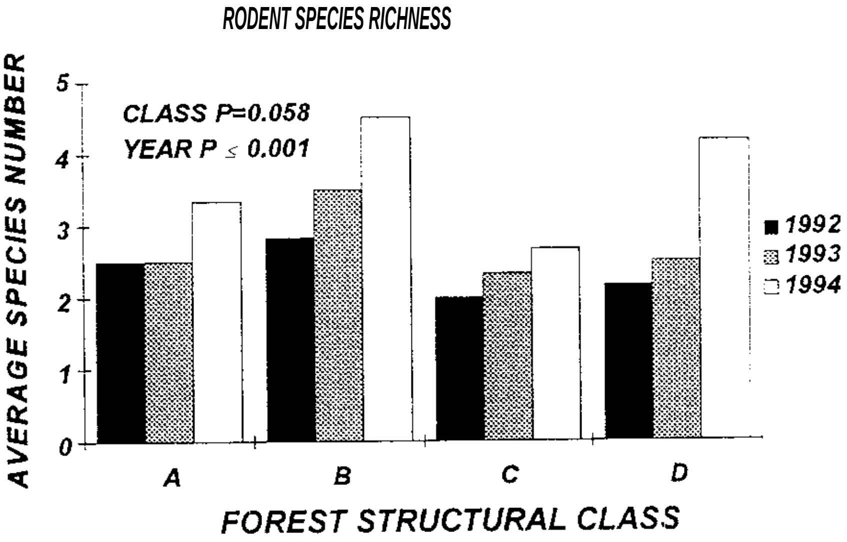

Figure 19. Average species richness of rodent species per site during 1992-1994.

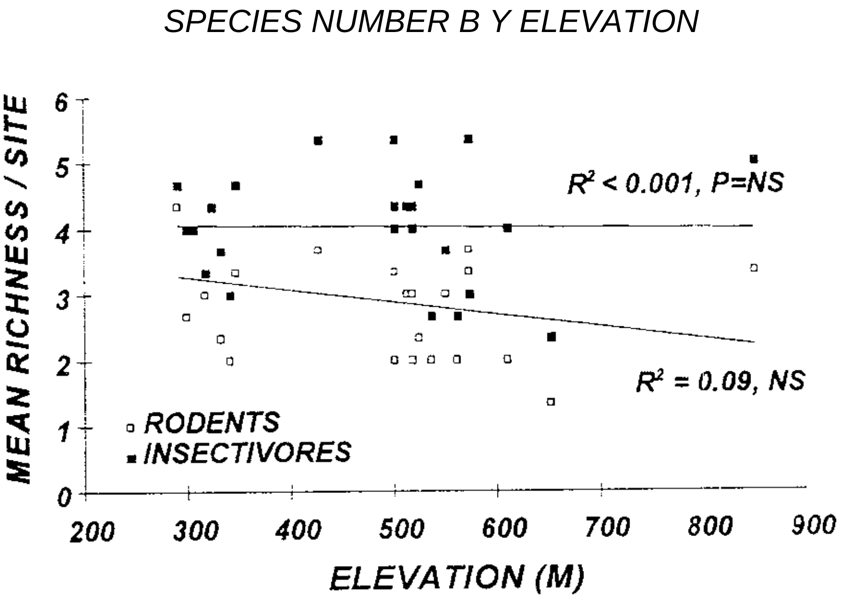

Figure 20. Mean number of insectivore and rodent species per site by elevation.

the rodents, ranging from 0.54 to 0.92 (Table 6), but lower for the insectivores, from 0.22 to 0.70 (Table 7). Partial correlations for individual vegetation variables were tow for both groups.

With strong associations between small mammal abundance and habitat variables at the stand level, one should be able to see similar small mammal communities in similar habitats. As one way of looking at the strength of such associations, we clustered small mammal capture totals for each site according to their similarity. The expectation is that the 4 structural classes would become apparent through the groupings of sites with similar small mammal communities. The hierarchical tree shows such a pattern (Fig. 21). Although not in complete conformance with expectation, the fit was rather good. The clustering indicates a primary division into non-forest (clearcut sites, class A) and forest communities (classes B, C, and D). Within the larger forest cluster, transitional sites (class B) tend to cluster together, with the exception of site B5 Five of the 6 class C sites also clustered together, with the exception of site C1 which was the greatest outlier of all 24 sites. This site had the lowest small mammal species richness and species evenness of all 24 sites. A look at the habitat structure of site C1 reveals that it was an outlier with respect to vegetational composition and structure as well (see table for C1 in Introduction section). It had essentially no shrub layer and about half the fern and forb cover as the average for the C class. Realizing that the vegetation ground cover in class C sites was low relative to the other classes makes site C1 a virtual desert at ground level. Only 40 total individuals were captured on the site, the lowest total of all sites (by a factor of 2). Over 3 years only 1 deer mouse, 11 forest deer mice, 1 coast mole, 6 montane shrews, 19 Trowbridge’s shrews, and 1 vagrant shrew were caught. Interestingly, the mature forest sites did not form a cohesive small mammal community based on the Pearson similarity measure, but were scattered throughout the block of forested sites.

LANDSCAPE-LEVEL CORRELATIONS

Landscape effects on small mammals were addressed at the species and community levels. Linear regressions were calculated for 3 species associated with clearcut sites (vagrant shrew, creeping vole, and deer mouse) and 2 species associated with

Table 6. Correlations between selected habitat variables and average abundance of rodents. Partial correlations listed for individual habitat variables. Multiple R^2 for a given rodent species and habitat variables listed at bottom of the table.

VARIABLES	PEMA	PEKE	CLGA	MIOR	MILO	MITO
B.P. Shrub	0.04	-0.05	~0.05	0.06		
O.D. Shrub	0.16				0.13	0.10
E. Shrub			.04	.02		
Forb				.05		
Fern		-.02				
Grass		-.04				-.03
Litter		-.01				
CWD					-.03	-.05
Rock		.09			-.06	
Soil		-.06				
Stump		-.19	-.21			
Multiple R^2	.55	.92	.72	.85	.54	.73

B.P. Shrub: berry-producing shrub; O.D. Shrub: other deciduous shrub; E. Shrub: evergreen shrub; PEMA: deer mouse; PEKE: forest deer mouse; CLGA: southern red-backed vole; MIOR: creeping vole; MILO: long~tailed vole; MITO: Townsend's vole

mature forest sites (Trowbridge's shrew and shrew-mole). In these cases, captures of the species were regressed on class-level indices. Both vagrant shrews (Figs. 22 and 23) and creeping voles (Figs. 24 and 25) show the same response to clearcut area and mean clearcut patch size. For each species the positive regressions are statistically significant, or close to significance, and in both cases the higher R^2 values were with clearcut area than with mean clearcut patch size. The deer mouse showed no significant relationship with clearcut area (Fig. 26) and significant or regressions close to significance for mean clearcut patch size (Fig. 27). In the latter case, however, the slope is essentially flat and the R^2 values extraordinarily low. Captures of the Trowbridge's shrew were not well correlated with either mature forest area or mean forest patch size (Figs. 28 and 29). The only significant, but weak, regressions were

Table 7. Correlations between selected habitat variables and average abundance of Insectivores. Partial correlations listed for individual habitat variables. Multiple R^2 for a given rodent species and habitat variables listed at bottom of the table.

VARIABLES	SOVA	SOMO	SOBE	SOTR	NEGI	SCOR
B.P. Shrub	0.04			0.05	0.03	
Forb	0.03					-0.01
Fern			0.02		.04	
Grass			-.02			
Moss			.02		.04	
Litter						.01
Litter Depth			.03		.03	
Stump		0.21				
Multiple R^2	.70	.22	.51	26	.60	.41

B.P. Shrub: berry-producing shrub; SOVA: vagrant shrew; SOMO: montane shrew; SOBE: marsh shrew; SOTR: Trowbridge's shrew; NEGI: shrew-mole; SCOR: coast mole

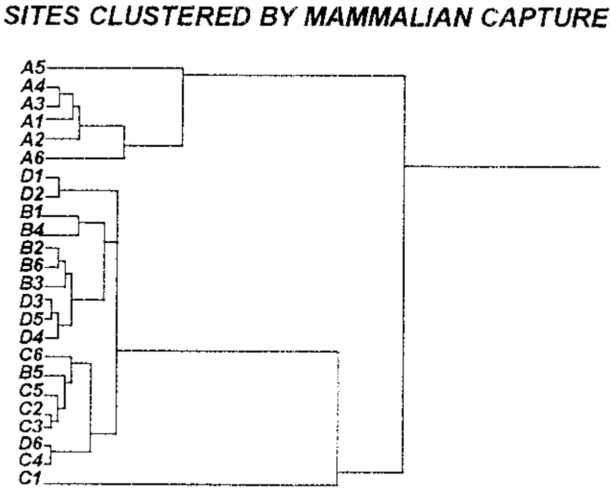

Figure 21. Small mammal community similarity clustering. Sites with similar small mammal communities join to the left of the trees; dissimilar sites join to the right. Sites labeled by forest structural class.

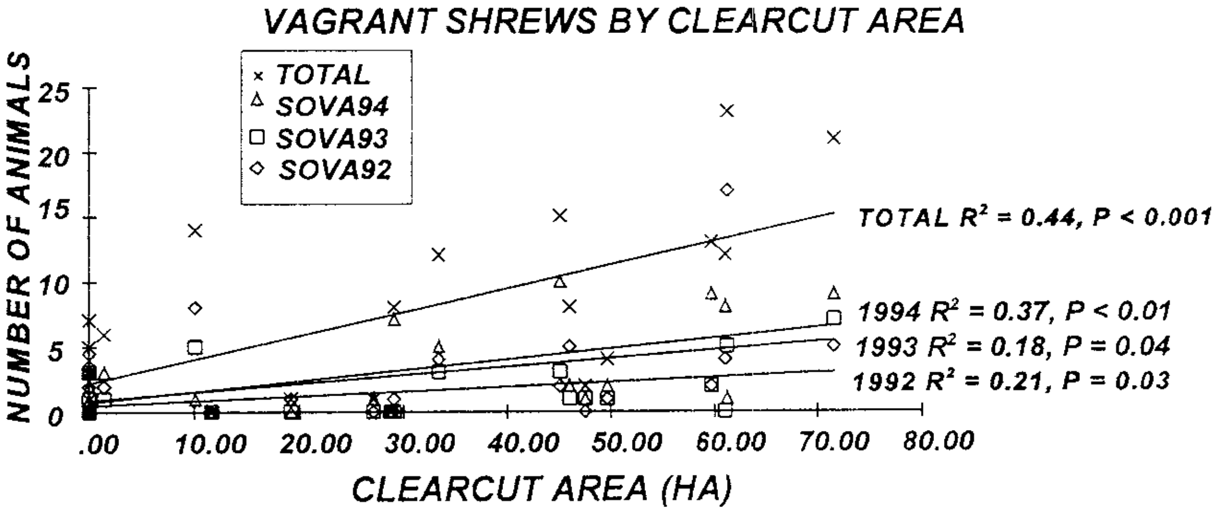

Figure 22. Number of vagrant shrews caught at the pitfall arrays during 1992-1994 on landscapes that differed in the area clearcut harvested. Pitfall arrays centered on IO0-ha circular plots.

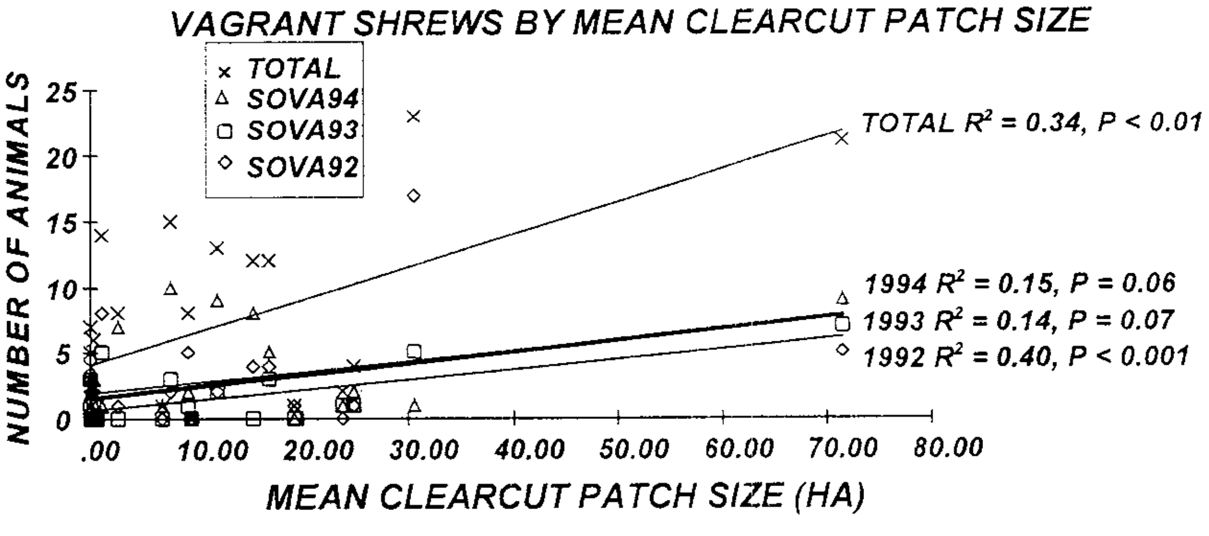

Figure 23. Number of vagrant shrews caught at the pitfall arrays during 1992-1994 on landscapes that differed in the mean size of clearcut patches. Pitfall arrays centered on IO0-ha circular plots.

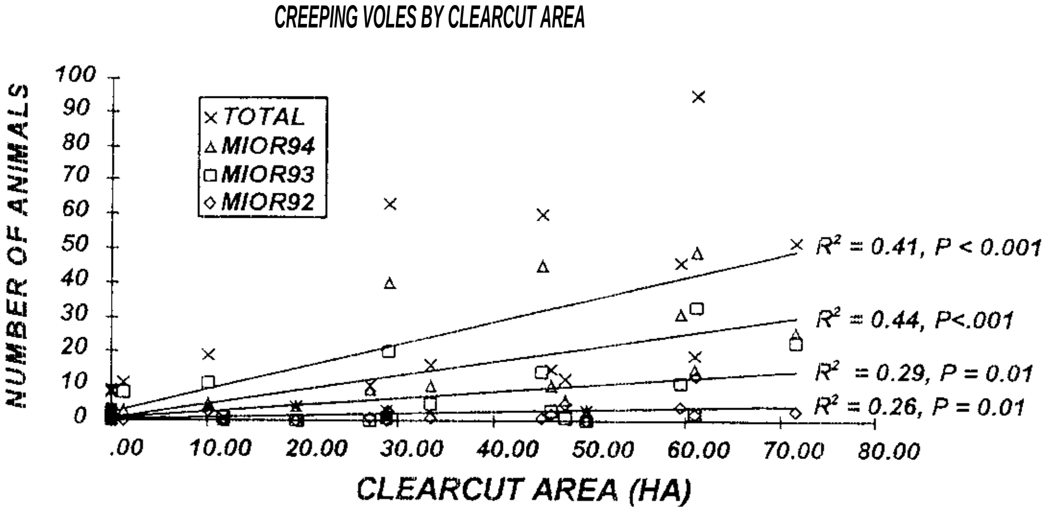

Figure 24. Number of creeping voles caught at the pitfall arrays during 1992-1994 on landscapes that differed in the area clearcut harvested. Pitfall arrays centered on IO0-ha circular plots.

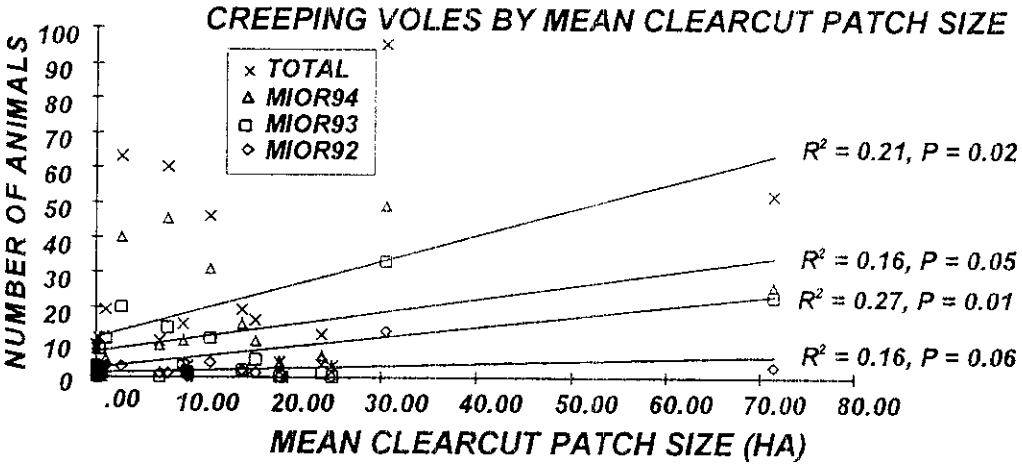

Figure 25. Number of creeping voles caught at the pitfall arrays during 1992-1994 on landscapes that differed in the mean size of clearcut patches. Pitfall arrays centered on 100.-ha circular plots.

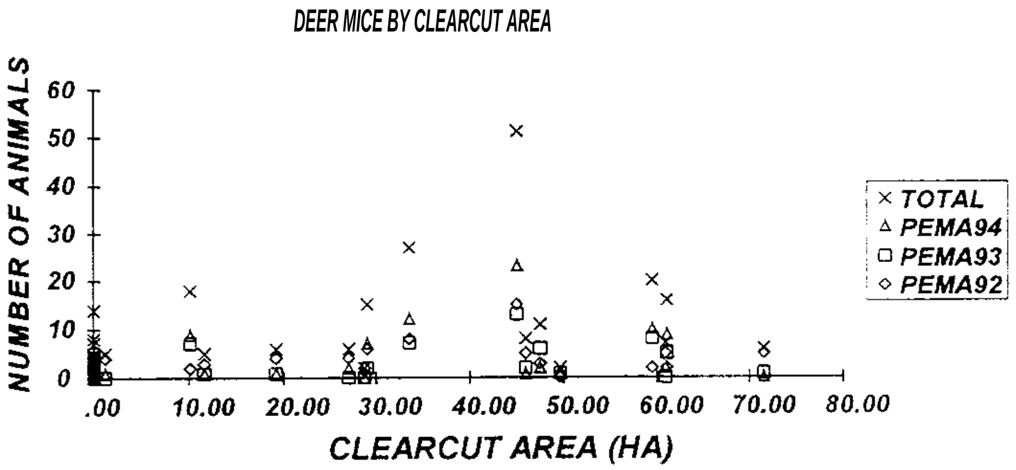

Figure 26. Number of deer mice caught at the pitfall arrays during 1992-1994 on landscapes that differed in the area clearcut harvested. Pitfall arrays centered on IO0-ha circular plots.

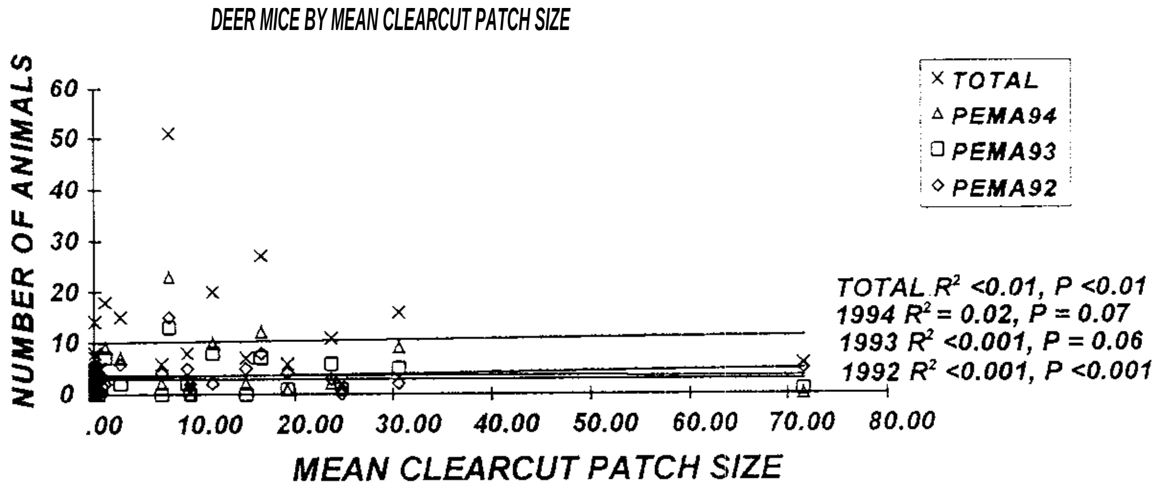

Figure 27. Number of deer mice caught at the pitfall arrays during 1992-1994 on landscapes that differed in the mean size of clearcut patches. Pitfall arrays centered on IO0-ha circular plots.

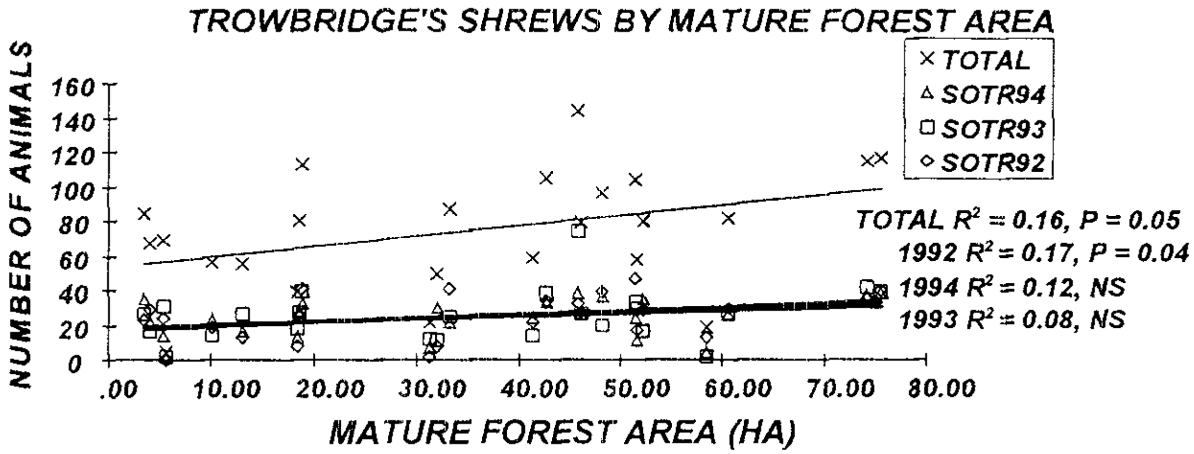

Figure 28. Number of Trowbridge's shrews caught at the pitfall arrays during 1992-94 on landscapes that differed in the proportions of mature forest area. Pitfall arrays centered on lO0-ha circular plots.

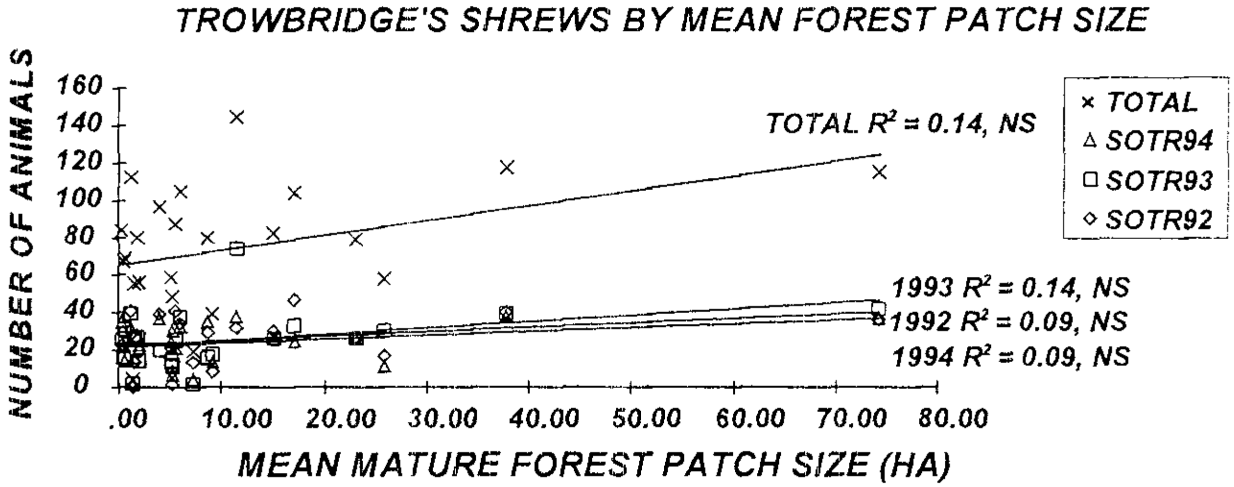

Figure 29. Number of Trowbridge's shrews caught at the pitfall arrays during 1992-94 on landscapes that differed in the mean size of mature forest patches. Pitfall arrays centered on lO0-ha circular plots.

between abundance and clearcut area in 1992 and with the cumulative captures for all 3 years (Fig. 28). Shrew-moles, which were highly associated with mature forest (Fig. 5), showed a slightly stronger regression with mature forest area than the Trowbridge's shrew (Fig. 30), and for mean mature forest patch size, the strongest relationship between abundance and a landscape metric of any species (Fig. 31).

Two other relationships were investigated at the individual species level. The montane shrew is a habitat generalist and found frequently in mixed habitat types (Fig. 2, class B). To see how it would respond to landscape habitat diversity, its captures were regressed on Simpson's index of diversity, which was calculated for all structural classes within the each landscape. No regression was significant (Fig. 32). The same regression was run for the creeping vole, a habitat specialist on clearcut areas. Again, no regression was significant (Fig. 33).

At the community level, several attempts were made to find relationships with species richness or species evenness and landscape measures. Expecting that species richness would be positively associated with the distance of the pitfall grid to an edge of a different habitat patch, species richness was regressed with distance to the edge for all 24 sites (Fig. 34), and for a look at maximum contrast between structural classes, species richness was regressed on distance to the edge for clearcut sites and mature forest sites alone (N = 12, Fig. 35). Neither set of regressions was significant. Next, expecting that species richness would be related to the diversity of habitat patches, species richness was regressed with Simpson's diversity index for all 24 sites (Fig. 36) and for the 6 clearcut and 6 mature forest sites (Fig. 37). There were no significant regressions. Similarly, the regressions between species richness and habitat edge density, a measure of habitat complexity, were all non-significant (Fig. 38). Finally, species evenness, calculated using Simpson's evenness index, was regressed on habitat diversity (Fig. 39) and mean patch size, an index calculated for all habitat classes in the landscape (Fig. 40). No regressions were significant.

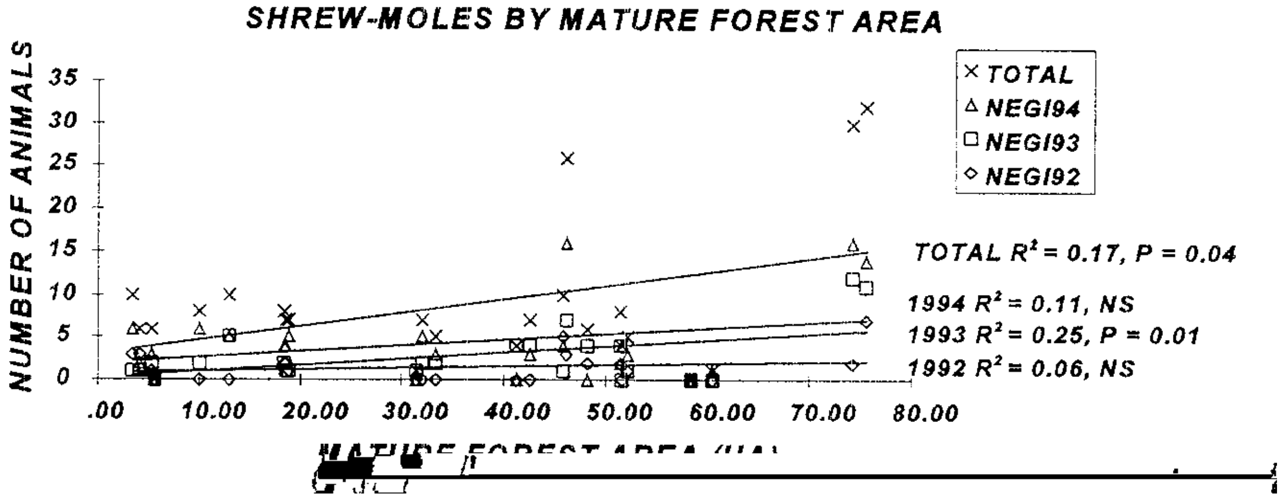

Figure 30. Number of shrew-moles caught at the pitfall arrays during 1992-94 on landscapes that differed in the proportions of mature forest area. Pitfall arrays centered on 100-ha circular plots.

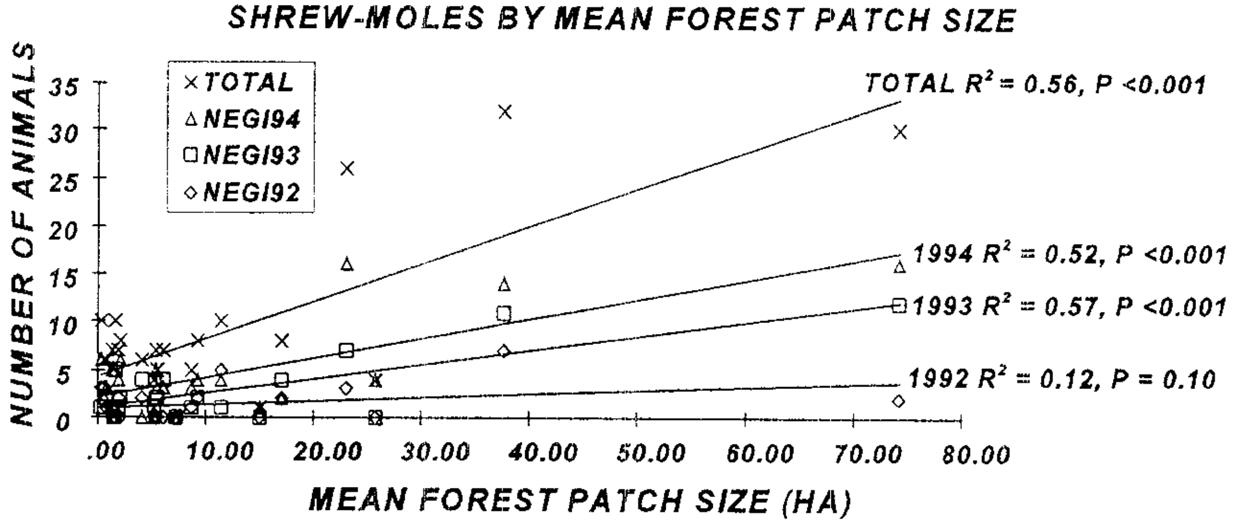

Figure 31. Number of shrew-moles caught at the pitfall arrays during 1992-94 on landscapes that differed in the mean size of mature forest patches. Pitfall arrays centered on 100-ha circular plots.

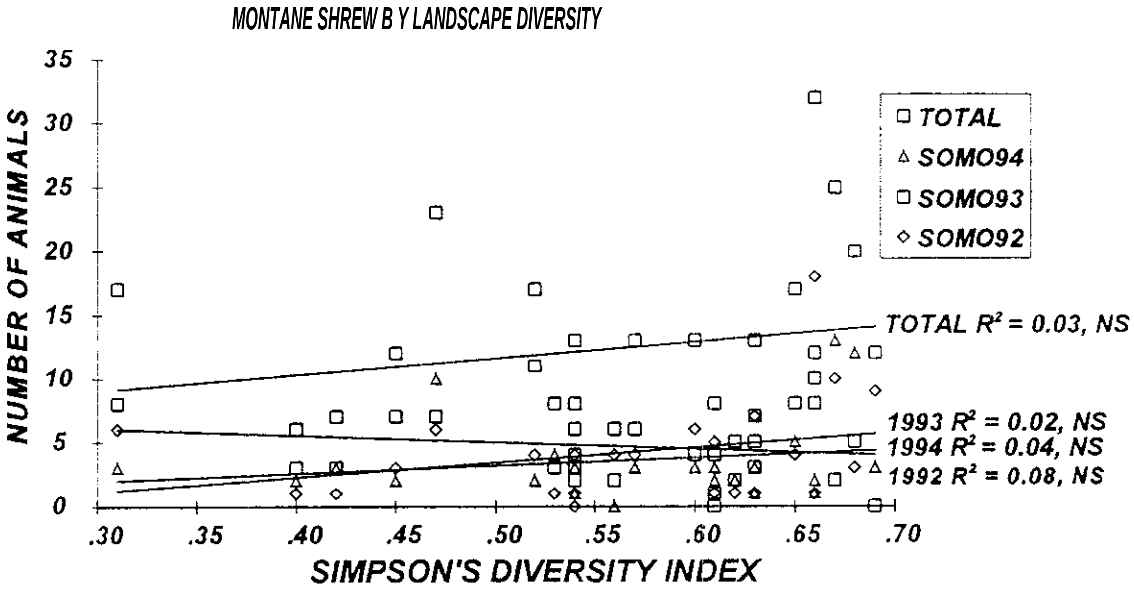
MONTANE SHREW B Y LANDSCAPE DIVERSITY

Figure 32. Captures of montane shrews for 1992-94 with respect to diversity of structural classes on 100-ha circular landscapes, Landscapes centered on pitfall grids. Diversity measured by Simpson's D.

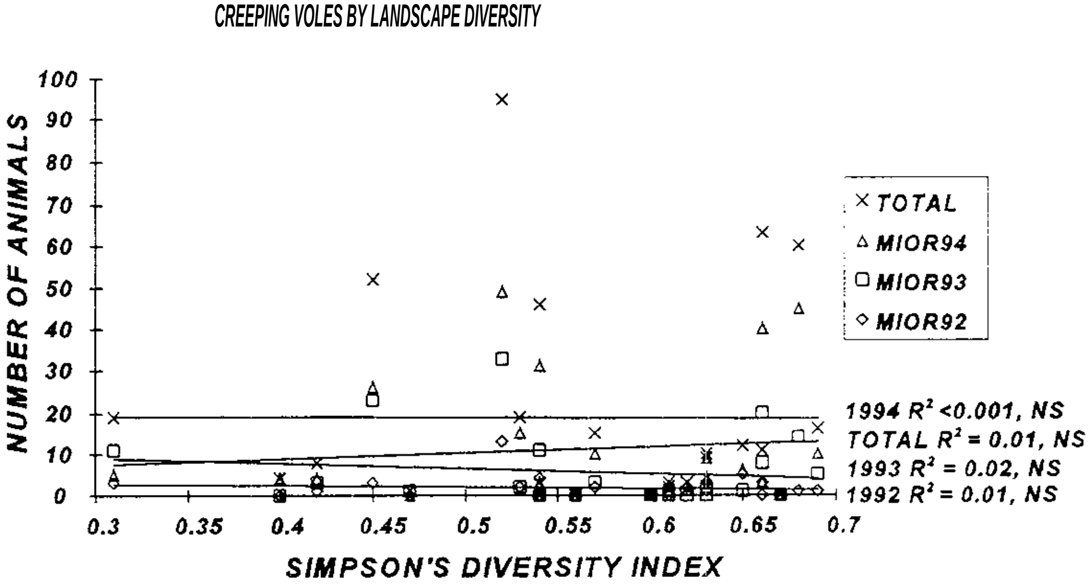
CREEPING VOLES BY LANDSCAPE DIVERSITY

Figure 33. Captures of creeping voles for 1992-94 with respect to diversity of structural classes on 100-ha circular landscapes. Landscapes centered on pitfall grids. Diversity measured by Simpson's D.

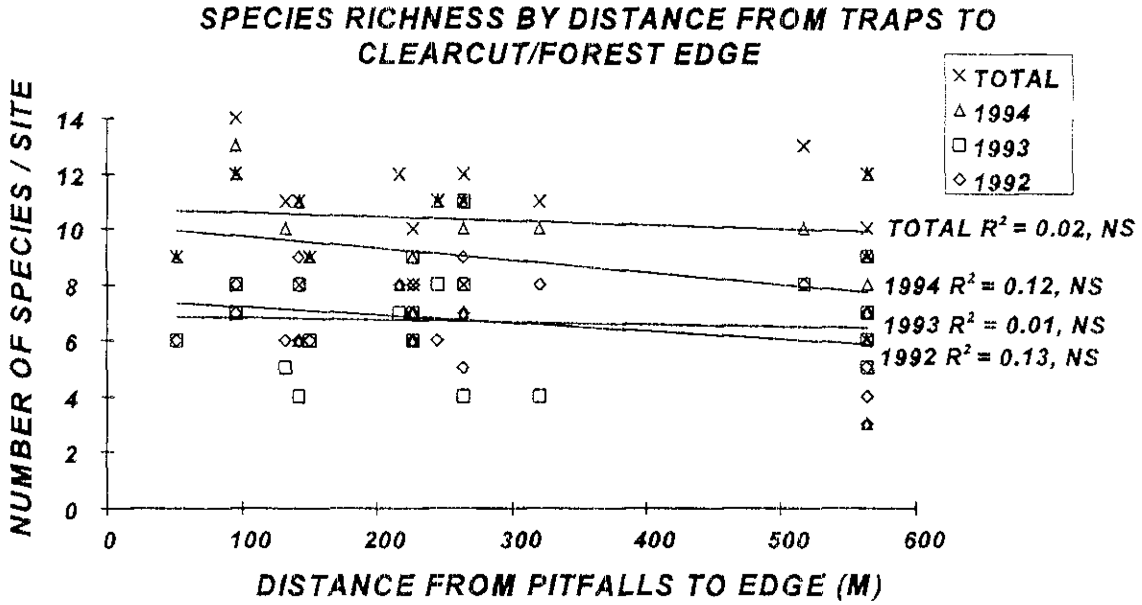

Figure 34. Species richness per site with respect to the distance from the pitfall grid to the contrasting habitat edge (forest vs. clearcut).

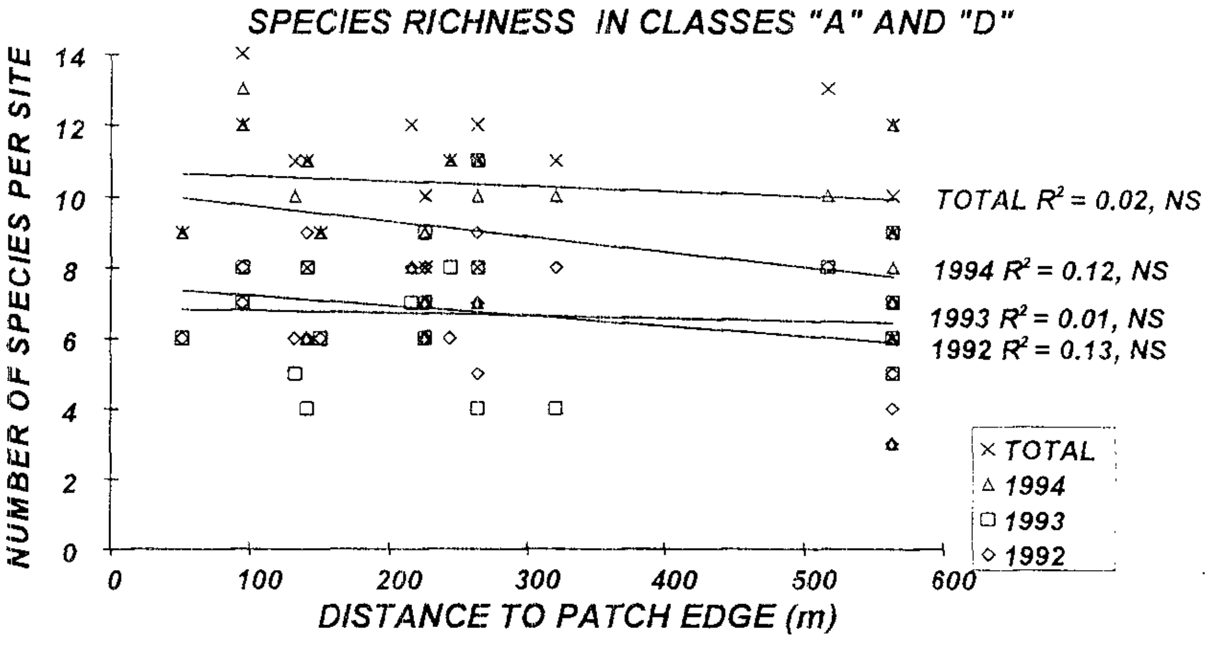

Figure 35. Species richness per site with respect to the distance from the pitfall grid to the contrasting habitat edge (forest vs. clearcut) for the "A" and "D" structural classes.

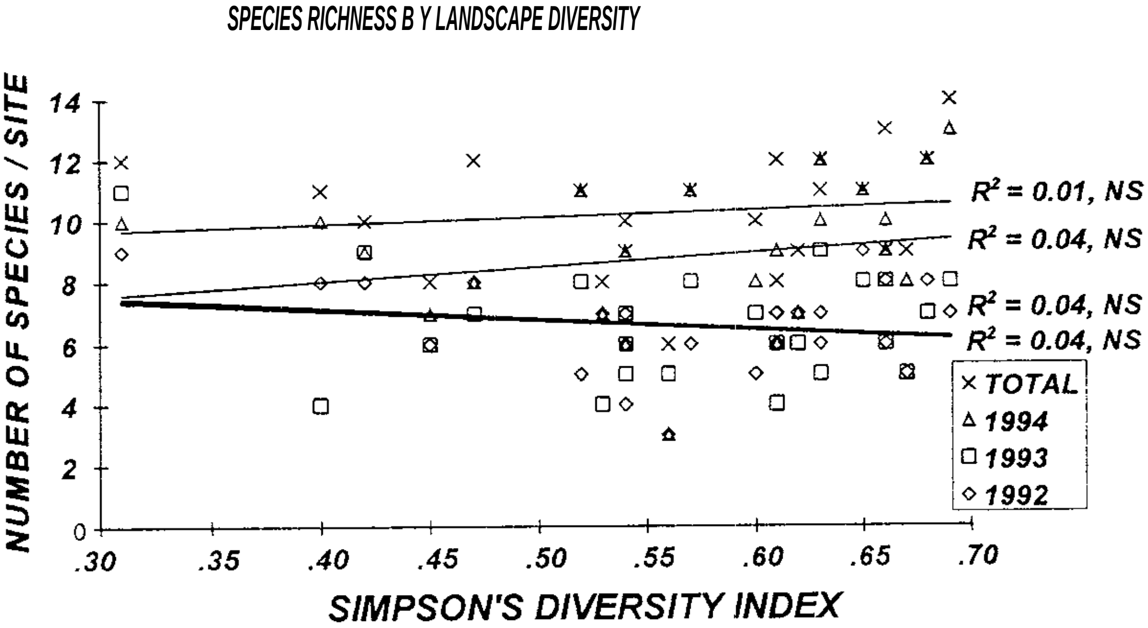

Figure 36. Small mammal species richness for 1992-94 with respect to diversity of structural classes on lO0-ha circular landscapes. Landscapes centered on pitfall grids. Diversity measured by Simpson's D.

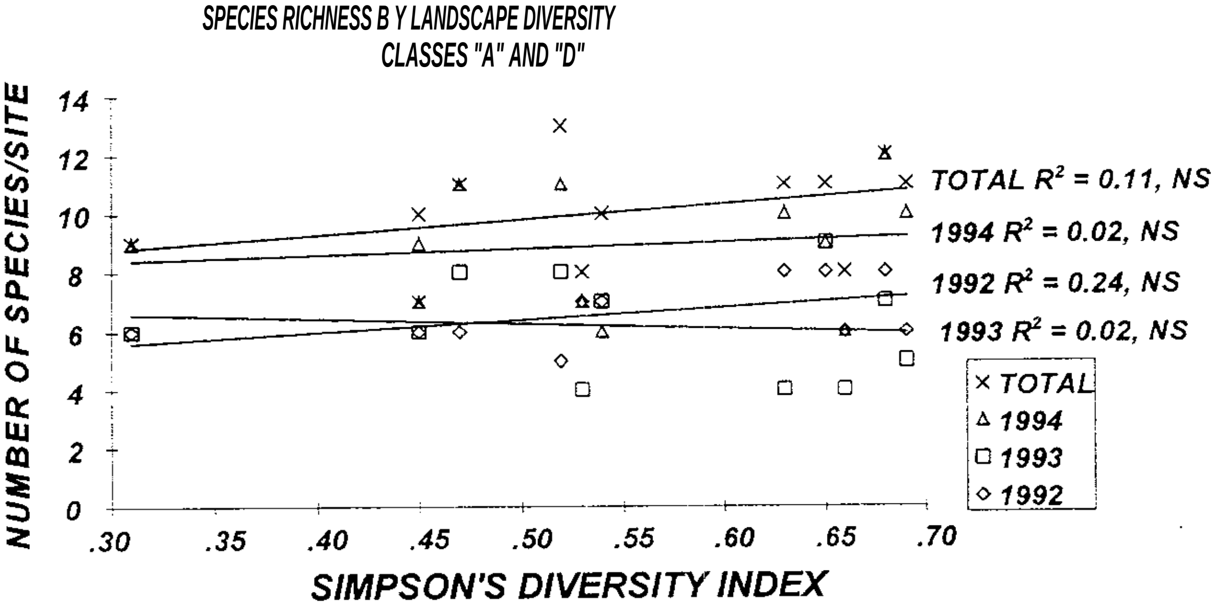

Figure 37. Small mammal species richness for 1992-94 with respect to diversity of structural classes on 100-ha circular landscapes for "A" and "D" structural classes. Landscapes centered on pitfall grids. Diversity measured by Simpson's D.

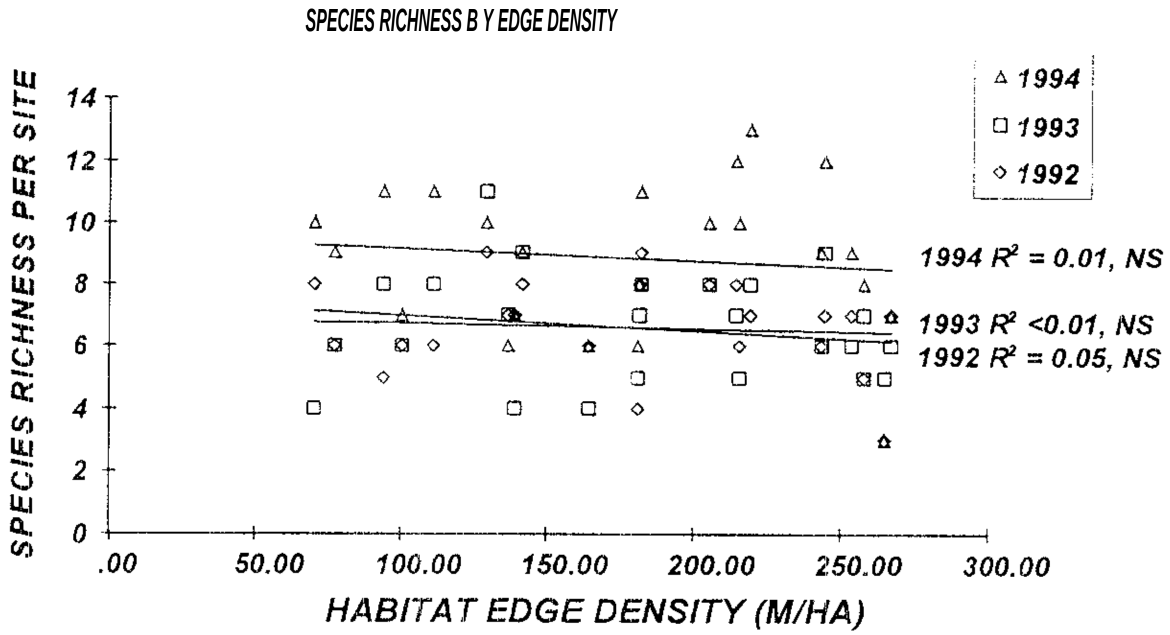

Figure 38. Species richness per site during 1992-94 with respect to total habitat edge density.

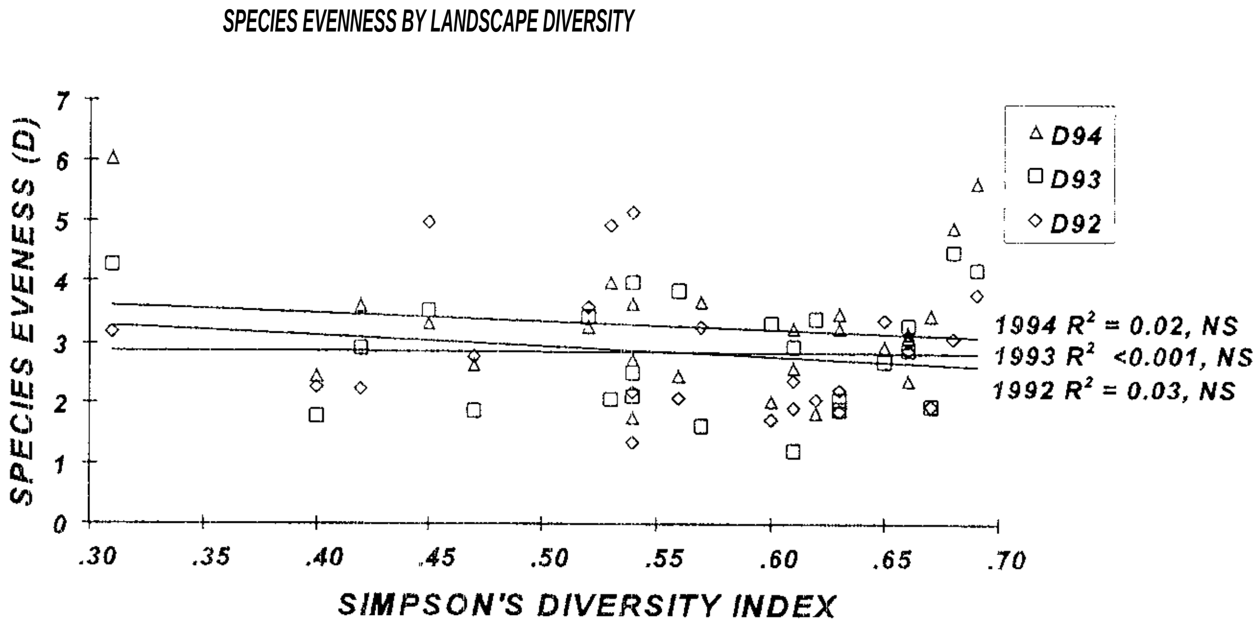

Figure 39. Small mammal species evenness per site for 1992-94 with respect to diversity of structural classes on l00-ha circular landscapes. Landscapes centered on pitfall grids. Evenness measured by Simpson's D.

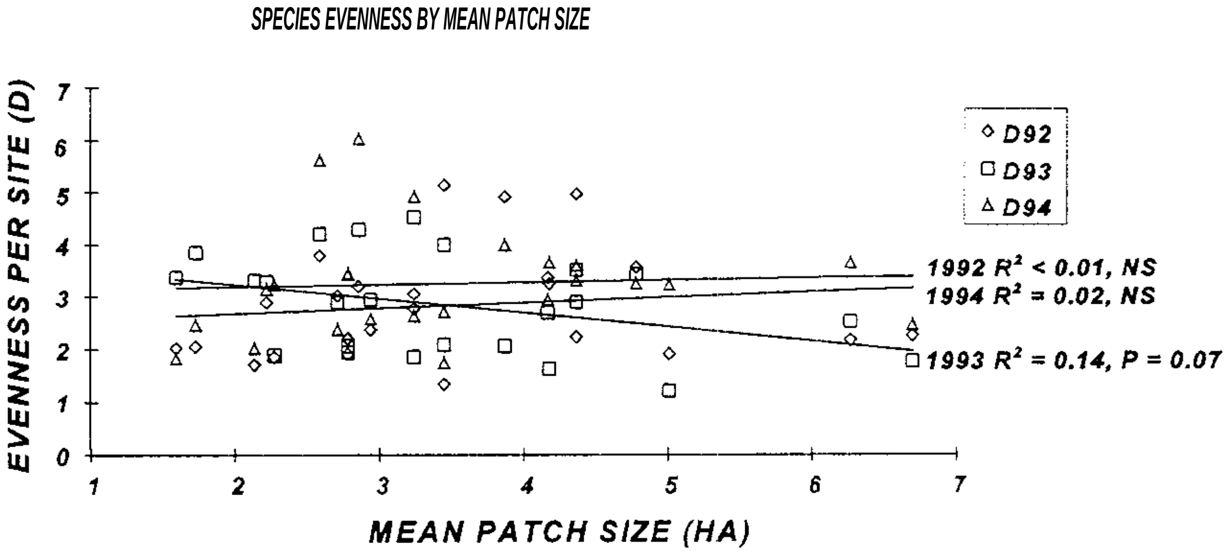

Figure 40. Small mammal species evenness per site for 1992-94 with respect to mean habitat patch size on 100-ha circular landscapes. Landscapes centered on pitfall grids. Evenness measured by Simpson's D.

DISCUSSION

PATTERNS OF ABUNDANCE

Many individual species that responded strongly to differences among structural classes sorted into species that preferred either early or late-successional classes. Only the montane shrew and the coast mole had a high proportion of total captures in the transitional class B, and the forest deer mouse was the only species with a high proportion of total captures in class C. With respect to the array of structural classes in these managed forests, 6 species favored the clearcut class and 4 favored the mature forest. Most small mammal community change in these forests takes place early in forest succession. At canopy closure there is an abundance shift that affects more than half of the species in the system. The pre-canopy period is characterized by high species richness and high rodent abundance. The abundance of insectivores tends to be higher in the period after canopy closure, although a large measure of this is due to the abundance pattern of Trowbridge's shrew, which tends to overwhelm the other species numerically.

The pre-canopy period is also characterized by large differences in abundance between years, mostly but not entirely driven by the differences in microtine rodent abundance. Several microtines showed high abundance in 1994 relative to the previous years, but so did the shrew-mole. Throughout the Pacific Northwest researchers on different projects have noted the high abundance of small mammals during 1994, so the effect is not unique to this study.

Based upon the data of this study, none of the 5 species with low capture totals appear to warrant special attention as a species compromised by forest management. Two of the 5 were out of their primary distributional range (masked shrew, Townsend's mole), 1 is a species that specializes on a habitat not sampled in the study (water shrew), and 2 species were not sampled well with pitfall traps (Townsend's chipmunk and the northern flying squirrel).

As mentioned above, this study was not designed to investigate demographic patterns, but the acquisition of body mass information does allow a glimpse of population structuring with respect to structural classes and years. In general, mean body mass was similar across most classes and years. Differences that were seen were not consistently apparent in consecutive years. At the time of year the populations were sampled, low mean body mass results from the addition of juvenile or subadult animals to the population. For the creeping vole (Table 5) and the deer mouse (Table 6) low mean body mass was found in clearcut sites, the primary habitat for the species. High body mass was found in sites with low abundance, probably indicating lower proportions of young animals in those structural classes. The pattern with the Trowbridge's shrew is more interesting because in at least 1 case (1994, Table 3) mean body mass was lower in clearcut sites, which are not primary habitat for the species. This might indicate movement of young animals into suboptimal habitat (Van Home 1983). Overall, however, the pattern of body mass was rather consistent across structural classes and years.

As one would expect from the relationships at the species level, strong patterns of association with structural classes and differences between years were also seen at the community level. Species richness varied significantly with respect to both structural classes and time (Figs. 17-19), and the differences among classes and years were very consistent. For both insectivores and rodents the highest species richness was found in the transitional sites (class B) which represent the change from a pre-canopy to a closed-canopy environment. This class supports a mix of species characteristic of both ends of the successional gradient maintained on these managed forests. Species richness is correspondingly high, varying from an average of 8 to 107 species per site between years (Fig. 16). Species richness was rather similar between early and late stages (class A vs. class D), but of course, the species composition changes dramatically as indicated in the abundance response figures (Figs. 1-13). Due to low overall mammalian abundance, the unthinned forest class (class C) showed the lowest mean values for species richness in each year. When observed using standardized samples (Fig. 17), species number for this class is not different from classes A and D. This implies that at higher capture levels the full complement of species would be present in the unthinned forest sites. Such a result is unlikely. Given the restricted resource base at ground level on these sites, large populations of diverse species are unlikely to occur. Specifically, herbivorous species that require productive ground-level vegetation layers will not inhabit these sites consistently. The heavy shading resulting from the dense canopy creates a very sparse ground cover and limits the small mammal community to insectivores and the forest deer mouse (Fig. 8) which is probably able to use these sites because of its ability to access the resources of the tree canopy. Radiotelemetry data (D. Krohne, pers. comm.) from both *Peromyscus* species shows that the forest deer mouse routinely uses the canopy of Douglas-fir forest, while the deer mouse does not.

The values for species richness in the mature forest class (class D, Fig. 16) are comparable to those obtained during the old-growth forest study for small mammals in the southern Washington Cascades (West 1991), where species richness averaged about 6.7 species per stand in young forest (aged at 55~75 years), 7.4 species per stand in mature forest (80-190 years), and 7.8 species per stand in old-growth forest (210-730 years). Further, the species capture lists are essentially the same. The species richness values for the transitional (class B) sites were of course higher (at 8-10.7 species per site) than those in old-growth forest, due to the inclusion of species favoring early successional stages.

ENVIRONMENTAL CORRELATES

Considered individually, variables from the 3- X 3-m vegetation data set were not very good predictors of small mammal abundance, although several were statistically significant. This is generally a common pattern, because it is the effect of these variables acting in concert that determines whether the habitat described will suit a given species. So it is little surprise that the R^2 values with small mammal abundance are much higher. Noting the strong associations with the structural classes any other result would have been surprising. Additional correlations could have been sought in the tree-level data set, and because of the striking differences in these variables across the structural classes, correlations with many of these variables would have been very strong as well. For most of these small mammal species, with the likely exception of the forest deer mouse, these would be of indirect importance because they would not be providing resources as directly as the 9round-level data set.

Elevation was probably of little importance in this study for small mammals because the range of elevation, roughly 560 m, was not very great relative to the ability of the species to accommodate it. This pattern was not seen for the more sensitive amphibians. Even so, the 2 species that have most of their distribution in low elevation areas, the Townsend’s vole and the Townsend’s mole, were caught sporadically.

The primary determinants of small mammal assemblages in these forests were at the stand level. This was seen in the strong associations with structural classes, the high multiple correlations with ground-level vegetation variables, and the distinctive clusters that corresponded to the structural classes formed by grouping similar small mammal assemblages. It is clear’ that these mammalian communities are best characterized as pre-canopy and closed-canopy faunas. Landscape-level effects on individual species were limited to positive associations between the percent area and patch sizes of favored habitat within landscapes (Figs. 20-31). Vagrant shrews and creeping voles showed this pattern for clearcut habitat and the shrew-mole for mature forest. The effects were not seen as strongly for the deer mouse in clearcut habitat or for the Trowbridge’s shrew for mature forest. Because of the strong associations with structural class, the weakness of these regressions underscores the importance of stand-level determination.

Configurations of adjacent habitats had little effect either on the abundance of species individually or on small mammal communities (Figs. 32-40). This result is in agreement with the findings of Lehmkuhl and others (1991) for an assessment of landscape metrics on wildlife of old-growth Douglas-.fir forests. In these forests part of the explanation for a lack of effect may be related to the patterning and scale of habitat blocks resulting from past forest management. The range of variation in patch size is very constrained with most blocks on the order of 30-80 ha. It may be that a wider range of habitat sizes is needed to have an effect with the landscape metrics related to size. As mentioned in the Introduction to the report, small patches of habitat are missing on these landscapes. Landscape metrics related to contrast between habitats or a diversity of habitats, however, should be well served in these forests. That they have little predictive power probably indicates that for these species the stand-level effects are predominant.

MANAGEMENT IMPLICATIONS OF THE PATTERNS

The management implications of the small mammal survey are rather straightforward and on balance good news. With the clear patterns of species associations among structural classes, creating habitat for desired small mammal communities seems possible. While landscape-level planning probably will be needed for species such as larger mammals and birds, it is less a concern for small mammals. Most focus can be on stand-level characteristics in forests where habitat blocks are in excess of 30 or 40 ha. Given a mix of stand ages, this area seems sufficient to allow breeding populations and species persistence.

The pitfall capture records of this study have assembled about the same species list as that resulting from the old-growth forest studies (West 1991). All species found in the old-growth forest study are present on these managed forests. Although more precise comparisons of these data sets will be made in the coming months, a preliminary assessment is that they will be similar. Because the tree farm has been intensively managed for timber production, the apparent retention of the entire small mammal fauna is very encouraging. Small mammal species not well sampled by pitfall traps of course will need information gathered for them using other techniques.

In terms of management activities that would pay immediate dividends for small mammal species, treatment of the unthinned forest structural class (class C) seems in order. This stand condition does not support a unique mammalian community, but rather is characterized by the loss of several species, which are unable to .survive the unproductive ground-level environment caused by a closed and very dense canopy. Only 1 species had a substantial proportion of its total captures in this structural class, the forest deer mouse, but it is a species that does not require these conditions and will do well in mature forests. This structural class should be moved toward the structure of a more mature class to enhance the productivity of the small mammal community. This might best be accomplished with a program of vigorous thinning.

In terms of a longer planning horizon, the provision of critical stand-level components is of paramount importance. Management must focus on elements that contribute to compositional and structural diversity within stands. A concern often expressed of wildlife in managed forests is that we are still benefitting from structural "legacies" of original forest. Even in these intensively managed forests there are old snags, large stumps from initial harvests, and very old downed woody material that plays an important role in enhancing the habitat quality of these younger stands. The replenishment of these elements must be planned. The maintenance of these elements will enhance not only the closed-canopy structural classes, but their retention during pre-canopy classes will enrich the early successional classes as well. While the results of this study suggest that old-growth levels of these elements perhaps are not needed to retain a full complement of: small mammals, attention to their provision at levels somewhat above those currently present on the landscape seems only prudent since many of these have been lost systematically in the last 100 years.

MANAGED FORESTS IN THE WESTERN CASCADES: THE EFFECTS OF SERAL STAGE AND LANDSCAPE STRUCTURE ON BAT HABITAT USE PATTERNS

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INTRODUCTION

Among mammals of their size, bats are unique in having long lives, low reproductive rates and relatively long periods of infant dependency (Findley 1993). This combination of characteristics places them at risk of population decline in the presence of habitat alteration (Soule 1986). In western Washington, where approximately 9.6 million acres of forest are 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, structure (Christy and West 1993), and fragmentation (Walsh and Harris 1996).

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, Thomas and West (1991) monitored bat activity 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+ yr) than in younger stands (35-195 yr). 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 project funded through the Washington State Timber, Fish and Wildlife Cooperative was initiated in 1992 to investigate the impact of forest management on bats and other wildlife. Here we describe results from a stand-level survey of bat activity in relation to specific vegetation and landscape-level attributes within intensively managed forests.

METHODS

STUDY AREA

To assess patterns of habitat use across a gradient of managed forest conditions, bat activity was monitored at 24 sites during the summers of 1993 and 1994. Six replicates were selected from each of 4 distinct post-harvest seral stages; clearcut (2-3 yr), pre-canopy (12-20 yr), closed-canopy (30-40 yr) and harvest-age (50-70 yr) stands for a total of 24 sites. Detailed descriptions of the environmental setting and study sites are given elsewhere.

THE BAT FAUNA

The area west of the Cascade Range crest in Washington is believed to support 11 species of bats (Barbour and Davis 1969, Thomas and West 1991). These include 7 species of *Myotis (M. califomicus, M. evotis, M. keenii, M. lucifugus, M. thysanodes, M. volans,* and *M. yumanensis),* big brown bats *(Eptesicus fuscus),* silver-haired bats *(Lasionycteris noctivagans),* Townsend's big-eared bats *(Plecotus townsendii),* and hoary bats *(Lasiurus cinereus).* At present, all of the *Myotis* species and the big brown bat are on the Washington State Priority-Habitats and Species List. In addition. Townsend's big-eared bat is designated as a species of special concern and is being considered for federal listing under the Endangered Species Act. Basic population information for many of these species, such as distribution, seasonal occurrence, and range is lacking, but all potentially occur in the study area.

ULTRASONIC DETECTION

SAMPLING DESIGN

Ultrasonic detection is a relatively simple but effective way to monitor habitat use patterns of bats. The automated detectors (Anabat II detectors and delay switches from Titley Electronics, Ballina, NS.W., Australia) consist of a divide-by-n circuit board which counts the waves in the ultrasonic signal and constructs a new wave at the rate of 1-for-n. This effectively brings the signal into the range of human hearing and is compatible with cassette tape storage. A sound-activated tape recorder stores the bat passes as they occur along with time announcements entered at the time of detection..

Following the sampling protocol developed in the OGWHP (Thomas and West 1991), a detector was left in place for 2 consecutive nights then rotated to another site. Each stand was visited at least 3 times for a minimum of 6 nights monitored in each. Samples at each site were spread over a 2-3 month period from mid-July to mid-

September. On any given night, 1 to 5 of the 24 sites were monitored. Sampling began at dusk (approximately 2045 h) and continued for 8 hr. No sites were sampled in heavy rain due to the decrease in bat activity associated with precipitation (Erkert 1982) and continual triggering of the detector system by raindrops.

Within a site, a detector was placed 1 m from the ground and oriented 30 ° from horizontal at a location greater than 100 m from the stand edge. Variation in recording conditions among heavily forested sites was minimized by placing the detector in a small gap within the stand. The same detector location was used each time a site was sampled.

ANALYTICAL PROCEDURES

A detection, or bat pass (Fenton 1970), was operationally defined as the sequence of pulses recorded as a bat flew through the airspace sampled by the microphone. To compare habitat use among seral stages, bat activity was indexed as the average number of detections per night within each site. Nightly activity patterns were evaluated as the average number of bat detections per 30-rain. interval. High repetition rate "feeding buzzes", known to be associated with prey capture, were identified as feeding activity (Griffin 1958).

The analysis of detections occurred at 2 levels. First, calls were summed regardless of species to determine the general distribution of detections among sites and trends in activity patterns. Second, calls were grouped into "call categories" using zero-crossing analysis and signal processing software (Anabat II, Titley Electronics, Ballina, N.S.W., Australia).

Because the echolocation calls of certain species were not distinguishable, *detections* were grouped into categories based *on similar* call *characteristics.* These could be associated with a particular species or group of species based on comparisons to calls of known identity. A library of known bat calls was created for this purpose using recordings made from free flying bats and from call characteristics obtained from the literature (Fenton and Bell 1981, Thomas and West 1989).

For this study, 5 categories of call types were recognized. These were associated with the following species: Type 1: big brown bat, Type 2: hoary bat, Type 3: silver-haired bat, Type 4: Townsend’s big eared bat, and Type 5: *Myotis* group (*M. californicus, M. evotis, M. keenii, M. lucifugus, M. thysanodes,* and *M. yumanensis).* Due to brevity of detection or questionable identity, a 6th category of "unknown" was also recognized.

LIMITATIONS OF ULTRASONIC DETECTION

Although ultrasonic detection has been used successfully in the field to identify bats based on species-specific call characteristics (Fenton 1970, Fenton and Bell 1981, Fenton 1982), it is important to emphasize that this technique relies on several assumptions: that species will consistently use the same call under a variety of conditions, that calls are equally detectable in different habitats, and that comparisons to reference recordings obtained from a limited geographic region are sufficient to identify field detections over broader regions. Evidence suggests that some bats may vary properties of their calls under different environmental conditions (Brigham and others 1989, Schrumm and others 1991) and across geographical regions {Thomas and others 1987) To date, variation in call structure is poorly understood, but call variability seems sufficiently high to warrant caution in species identification. Obtaining high-quality reference recordings from multiple individuals of each species under a variety of environmental conditions to determine the extent of natural variation present will facilitate future call analysis. The authors and other researchers are currently compiling such a library for’ bats of the Pacific Northwest (see Erickson and West 1996).

In spite of its limitations, ultrasonic detection is a valuable tool for surveying free-ranging bats. It is the most appropriate method for assessing patterns of distribution and activity at a large scale and eliminates many of the problems associated with extracting ecological data from trapping studies (Thomas and West 1989)

VEGETATION SAMPLING

As part of the broader research program, overstory and understory vegetation was sampled on each of the 24 sites during the summer of 1993. Live trees were tallied by species and diameter at breast height (d.b.h.) within twelve 12 m^2 plots and thirteen

45 m^2 plots on each site. Trees <10 cm and 10-50 cm d.b.h, were recorded within the 12 m^2 plot while trees 50-100 cm d.b.h, were counted within the 45 m^2 plot. Stumps and snags were counted by species, diameter-class (<10 cm, 10-50 cm, and > 50 cm d.b.h.), height class (<1.5 m, 1.5-15 m, and >15m) and decay class (1-3 from hardest to most decayed, modified from Maser and others 1979). Only stumps and snags >50 cm d.b.h, were recorded within the 45 m^2 plots. All other classes were recorded within the 12 m^2 plot. Sampling criteria conformed to standard protocols established for the OGWHP.

LANDSCAPE CHARACTERIZATION

The digital vegetation coverage maps of the study area were imported into a Geographic Information System and the program FRAGSTATS (McGarigal and Marks 1995) was used to quantify landscape structure around each study site. For a given landscape, FRAGSTATS computes several statistics for each patch type in the landscape ('patch indices') and the landscape as a whole ('landscape indices'). These various landscape and patch metrics were quantified within 3 concentric circles (100, 1000, and 5000 ha) around each of the 24 study sites. A full description of this process is given elsewhere.

STATISTICAL ANALYSIS

Mean detection rates were calculated for all species combined, all members of the genus *Myotis,* all *non-Myotis* species, and each call category. Because counts of bat echolocation calls have a strongly non-normal distribution (leptokurtic), a square root transformation was used when calculating these means. Differences between years (paired t-test) and among seral stages (ANOVA) were examined. When significant results were obtained, Tukey's pairwise comparison tests were employed to locate the differences. Mean values for relevant vegetation characteristics were also determined. for each seral stage.

Using the FRAGSTATS program, landscape indices were calculated for all 24 sites. Upon evaluation of these indices, it was decided to exclude the 6 closed-canopy sites from analysis because habitat classification from the satellite data (3-8 yr, 10-20 yr, 50-80 yr, and >80) didn’t correspond to this age class. Therefore, these stands were misclassified as either 10-20 or 50-80 yr classes rather than their actual age class of 30-40 yrs. Thus, the true homogeneity of these landscapes was not represented by the satellite data and likely resulted in misleading landscape indices.

To reduce the number of variables for the remaining 18 sites, only those variables believed to be potentially important to bats were considered for inclusion in the models (Table 1). Variables expressed as proportions were arcsine transformed (Zar 1984). Using multiple regression procedures, the independent effects of these variables on *Myotis* activity and *non-Myotis* activity were quantified. In an attempt to separate landscape-level effects from stand-level effects, seral stage was entered as the first variable in each forward stepwise regression. No regression variable was included that had $P> 0.05$ or $R^2 < 0.10$.

Principal components analysis (PCA) was used to further investigate the relationship of bat activity with landscape structure by using the ’patch indices’ produced by FRAGSTATS. By using only clearcut indices (Table 2), information about the heterogeneity of each 100-ha landscape was indirectly obtained. Unlike the landscape indices, the patch-specific indices allowed for the inclusion of all 24 sites because the clearcut habitat type was correctly classified from the satellite data. To determine whether sites grouped themselves according to a heterogeneity gradient, PCA axes were plotted within SYSTAT and examined to detect groupings. Cluster analysis was used as a complement to PCA to aid in interpretation of the axes.

RESULTS

VEGETATION

Mean densities for vegetation characteristics within each seral stage are displayed in Table 3. Closed-canopy stands had the highest mean density of trees <50 cm d.b.h., while trees >50 cm d.b.h, reached highest densities in harvest-age stands. Large snags >15 m in height were found only in pre-canopy and harvest-age stands with the latter having significantly greater densities.

Table 1. FRAGSTAT landscape indices used in regression analysis.

Index name (units)	Description*
CA (ha)	Total amount of clearcut (3-8 yrs)
CCED (m/ha)	Total amount of clearcut edge
MA (ha)	Total amount of mature forest (50-80 yr)
NP	Number of patches
ED (m/ha)	Edge density
MNN (m)	Mean nearest neighbor index
SHDI	Shannon's diversity Index
IJI (percent)	Interspersion and juxtaposition index
CONTAG (percent)	Contagion index

* See McGarigal and Marks (1995) for a complete description and definition of each index.

Table 2. FRAGSTAT patch indices used in principal components and cluster analyses.

Index name (units)	Description*
CA (ha)	Total amount of clearcut (3-8 yrs)
CCED (m/ha)	Total amount of clearcut edge
CCNP	Number of clearcut patches
CCMPS	Mean clearcut patch size (ha)
LPI	Largest clearcut patch index (percent)
PSSD	Clearcut patch size standard deviation (ha)
PSCV	Clearcut patch size coefficient of variation
MPI	Clearcut mean proximity index
IJt	Interspersion and juxtaposition index (percent)

* See McGarigal and Marks (1995) for a complete description and definition of each index.

EFFECT OF SEPAL STAGE

Over 2500 hr were monitored for bat activity during 1993 and 1994 resulting in 987 echolocation calls recorded. Each site was sampled a total of 6 nights both years with the exception of 1 pre-canopy thin stand that was not sampled in 1994.

The mean number of detections per night did not vary significantly between years ($P = 0.23$; $N = 23$; paired t-test) with an average of 3.75 (+ 0.84) detections per night in

Table 3. Vegetation characteristics (mean _+. se) for each seral stage where A = clearcut, B = pre-canopy, C = closed-canopy and D = harvest-age.

	A	B	C	D
Characteristic	X (SE)	X (SE)	X (SE)	X (SE)
Stumps				
<10 cm d.b.h.	6.697	18.222	28.987	44.36
	(0.504)	(5.375)	(5.654)	(7.016)
10-50 cm d.b.h., <1.5 m tall	5.873	6.307	5.013	2.027
	(0.347)	(0.872)	(1.244)	(0.494)
>50 cm d.b.h. < 1.5m tall	23.692	10.807	11.923	8.063
	(1.117)	(2.062)	(1.919)	(1.848)
Snags				
10-50 cm d.b.h., 1.5-15 m tall	0.057	0.318	0.582	2.585
	(0.036)	(0.089)	(0.198)	(0.661)
>50 cm d.b.h., 1.5-15 m tall	2.448	3.128	1.075	1.268
	(1.165)	(0.814)	(0.207)	(0.353)
10-50 cm d.b.h., >15m	0	0.138	0.110	0.582
		(0.068)	(0.051)	(0.218)
>50 cm d.b.h., >15 m	0	0.013	0	0.207
		(0.013)		(0.076)
Standing trees				
-Frees <10 cm d.b.h., >3m tall	0.208	14.253	16.515	5.030
	(0.148)	(6.716)	(6.298)	(1.000)
Trees 10-50 cm d.b.h., >3m tall	0.013	13.388	22.193	6.653
	(0.013)	(0.906)	(2.566)	(1.348)
Large dominant trees 50-100 cm d.b.h.	0	0.142	1.652	18.67
		(0.126)	(0.379)	(3.81)

1993 and 3.07 (+ 0.79) in 1994. Significant differences were found, however, among seral stages ($P < 0.001$; $N = 47$) (Fig. 1). Clearcuts accounted for 57% of all detections, while closed canopy stands had none. Pre-canopy and harvest-age stands had intermediate detection rates accounting for 14% and 30% of all detections respectively. Overall, activity levels were low with 46.2% of the nights having no detections.

Use of seral stages differed among species groups. Members of the genus *Myotis* were detected within all stand types except closed canopy stands but were most often detected in harvest-age stands. In contrast, detections in clearcuts accounted for the majority of *non-Myotis* detections (81%). Neither big brown bats, silver-haired bats nor

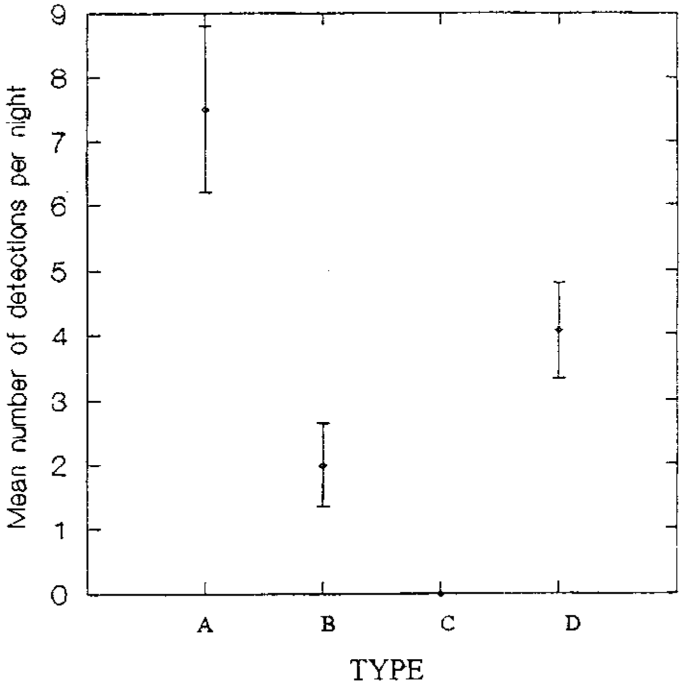

Figure 1. Mean number of detections per night where A = clearcut, B = pre-canopy, C = closed-canopy and D = harvest-age stands.

Townsend's big-eared bats were recorded in harvest-age stands. Of the 5 call categories, the *Myotis* group and hoary bat were the only ones detected in all 3 seral stages where bat use was recorded. However, the 14 hoary bat detections within the harvest-age seral stage were all recorded at t site on the same night (Table 4).

ACTIVITY PATTERNS

Bat activity was not uniformly distributed throughout the night with activity peaking during the first 2 hours following sunset. Within clearcuts, *non-Myotis* species demonstrated a gradual increase in activity that peaked between 2215 h and 2245 h followed by variable but consistently low activity (Fig. 2a). This pattern was largely driven by detections attributed to the silver-haired bat. *Myotis* spp. followed a similar pattern but peaked between 2145 h and 2215 h (Fig. 2b). Harvest-age stands had elevated activity during the first hour after dusk (2045.-2115 h) with a smaller secondary peak near sunrise (0515 h), while activity in pre-canopy stands was more evenly distributed throughout the night (Fig. 3).

Table 4. Detection rates for bats (mean + SE) in clearcut (A), pre-canopy (B), closed-canopy (C), and harvest-age (D) stands. Where ANOVA was significant, means not significantly different from each other are indicated with letters; cx =0.05).

Species	A $\bar{X}$ (SE)	B $\bar{X}$ (SE)	C $\bar{X}$ (SE)	D $\bar{X}$ (SE)
Big brown bat	0.808	0.031a	0^{a}	0a
	(0.185)	(0.021)		
Silver-haired bat	2.327	0.407^{a}	0a	0a
	(0.627)	(0.164)		
Townsend's big-eared bat	0.113^{a}	0.031^{a}	0a	0"
	(0.056)	(0.021)		
Hoary bat	0.587^{a}	0.150 a	0^{a}	0.194^{a}
	(0.267)	(0.080)		(0.194)
Myotis group	3.321 ab	1.223^{ac}	0°	3.808 b
	(2.719)	(1.598)		(2.582)
All *non-Myotis*	0.834	0.154^{a}	0^{a}	0.053^{a}
	(0.200)	(0.061)		(0.039)
TOTAL	7.504^{a}	1.989^{b,c}	0	4.058^{c}
	(1.300)	(0.652)		(0.738)

Feeding activity was very low within all stands. Of the 967 detections, only 13 were identified as feeding activity. Clearcut stands had the highest number of feeding buzzes (N = 10) which were recorded for both *non-Myotis* and *Myotis* spp. The 3 feeding buzzes detected in harvest-age stands were all identified as *Myotis* spp

EFFECTS OF LANDSCAPE-LEVEL ATTRIBUTES

MULTIPLE REGRESSION

A summary of the significant results from the multiple linear regressions of bat activity against landscape indices is given in Table 5. Within the 100-ha landscapes, *Myotis* activity was most strongly influenced by Mean Nearest Neighbor (MNN, R^2 = 0.840, Table 5). Models explaining a significant amount of variation could not be constructed for *Myotis* activity patterns at the larger scales. No significant factors influencing non-*Myofis* activity were identified at the 100-ha or 5000-ha scale, but within the 1000-ha landscape, activity was negatively influenced by the amount of mature forest (R^2 = 0.818, Table 5).

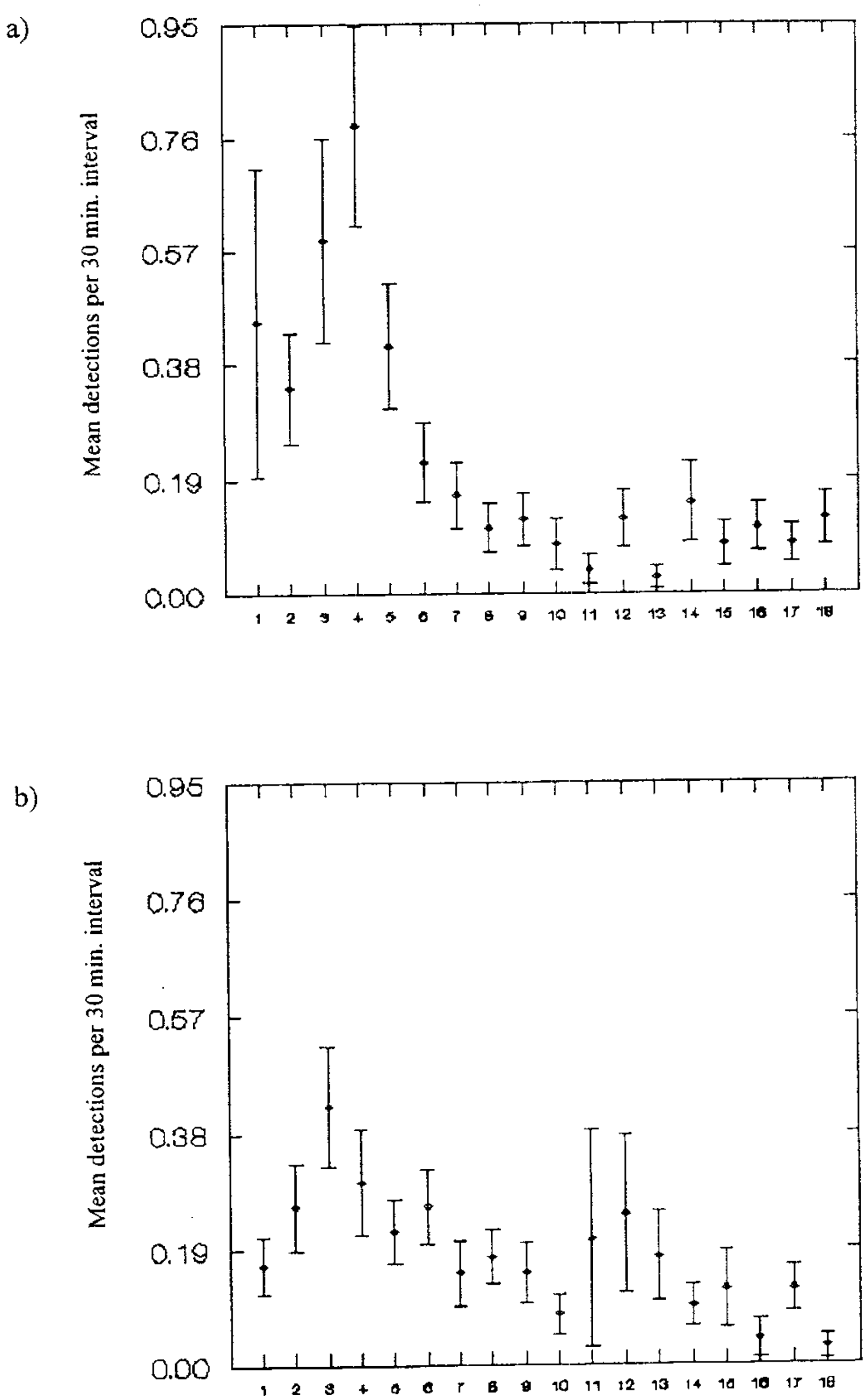

Figure 2. Mean number of detections per interval in clearcut stands for a) all non-*Myotis* bats and b) all members of the genus *Myotis.*

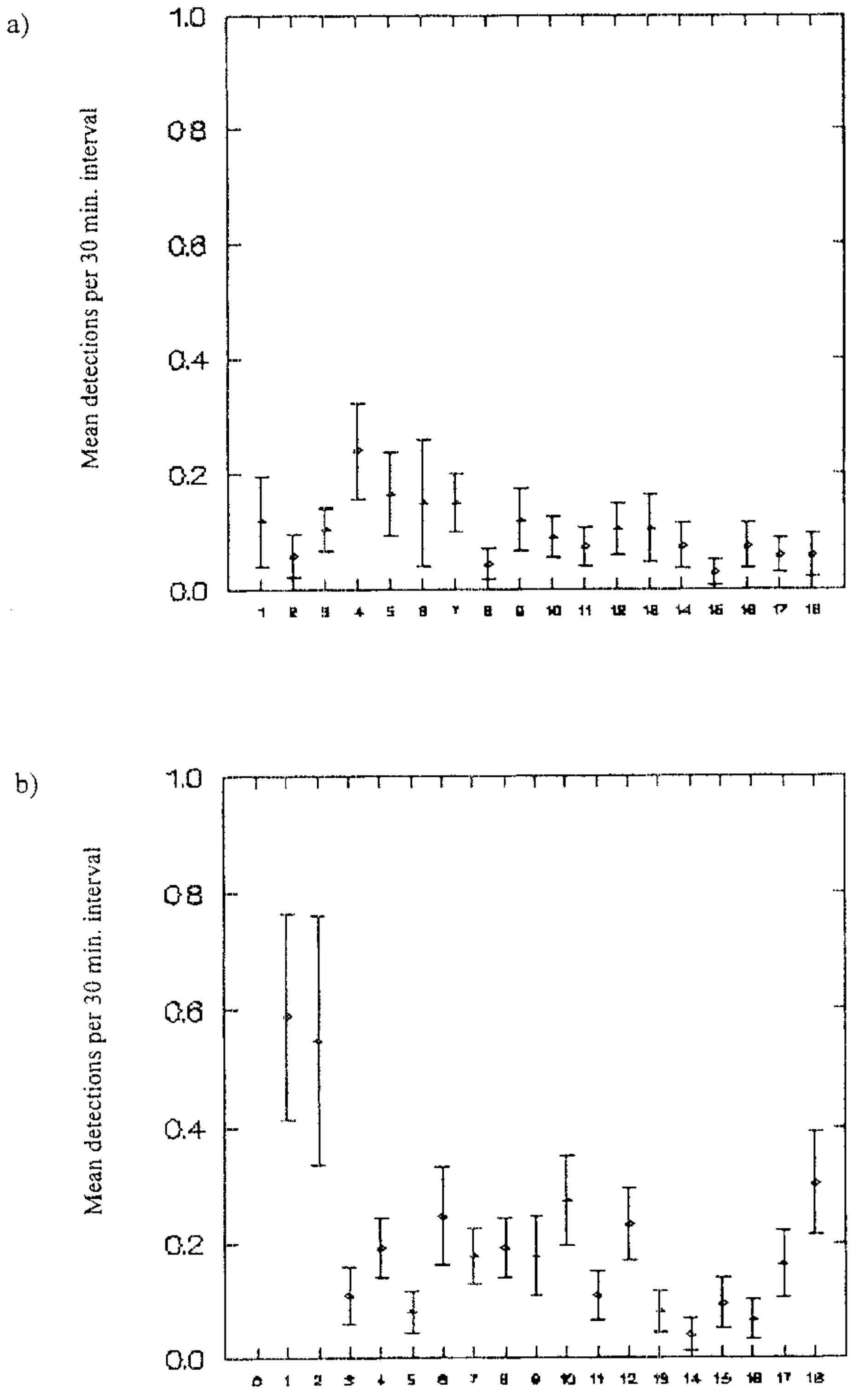

Figure 3. Mean number of detections per interval in a) pre-canopy and b) harvest-age stands.

Table 5. Summary of significant results from multiple linear regressions of bat activity against landscape indices.

Source	Partial correlation	Sum-of-squares	DF	Mean-square	F-ratio	P
		Myotis group, lO0-ha circle				
Seral stage	-0.084	2.121	2	1.061	8.801	0.004
MNN	0.791	4.774	1	4.774	39.610	0.000
MA	-0.601	0.887	1	0.887	7.356	0.018
Error		1.567	13	0.121		
		Non-Myotis group, 1000-ha circle				
Seral Stage	-0.705	6.533	2	3.267	18.315	0.000
MA	-0.448	2.624	1	2.624	14.712	0.002
Error		2.497	14	0.178		

PRINCIPAL COMPONENT ANALYSIS

The first principal component (PC1) is interpreted as a gradient of landscape heterogeneity (Fig. 4). Sites negatively associated with PC1 (C1-C6, B5 and D3) had little or no clearcut within the surrounding landscape while those positively associated with PC1 were characterized by greater amounts of this patch type. When these sites are categorized as having either low or high bat activity, the separation among sites is distinct. Those landscapes consisting of contiguous forest have low activity while those with a mix of clearcut and forest have high activity levels.

The cluster analysis classified sites into 3 main groups (Fig. 5). The top group (A1, A6, A2 and D1) is composed of the 4 sites with the highest amount of clearcut edge in the surrounding landscape. Each of these landscapes has over 10,000 m of high-contrast edge. The middle group has moderate levels of clearcut edge with an average of 5513 m while the bottom group has <90 m of clearcut edge.

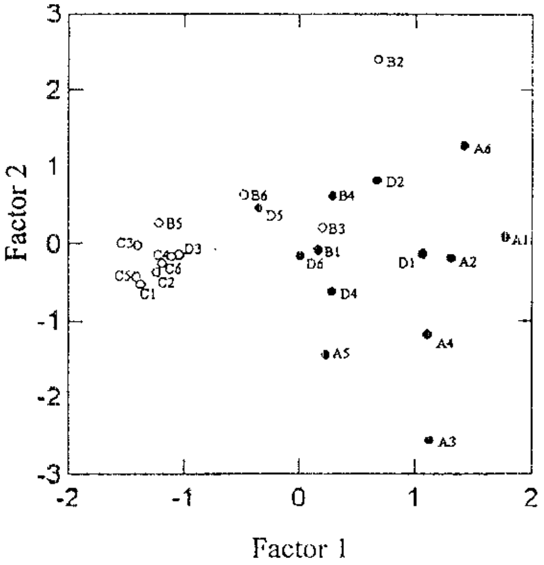

Figure 4. Principal component factors of the 24 study sites where A = clearcut, B = pre-canopy, C = closed-canopy, and D = harvest-age stands. Empty circles indicate low bat activity and solid circles indicate high bat activity.

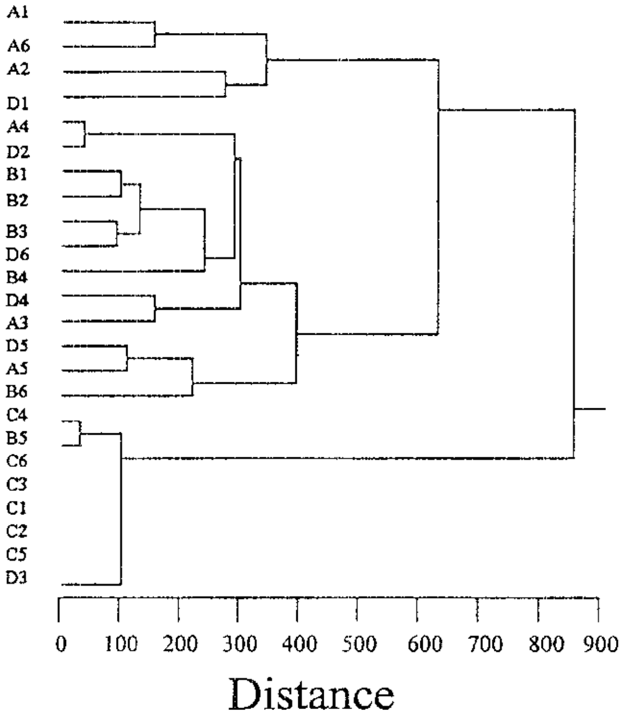

Figure 5. Cluster analysis dendogram for the 24 sites. Sites with similar landscape structure join to the left of the figure; increasingly dissimilar sites join farther to the right.

DISCUSSION

PATTERNS OF HABITAT USE AMONG SEPAL STAGES

Factors that may influence bat activity in a particular habitat include the physical structure of the habitat, microclimate, proximity to roosting or foraging sites, exposure to predators, and competition (Findley 1993). In this study, the primary differences in habitat use were likely related to the differential availability of foraging and roosting resources among sites.

Activity patterns of insectivorous bats have often been interpreted in relation to the availability of prey (Kunz 1973, Erkert 1982). Several studies have documented insect abundance to be higher in clearings than surrounding habitats (Lunde and Harestad 1986, de Jong 1994). Within this context, the high detection rate, presence of feeding buzzes, and low abundance of roosting structures within clearcut stands suggest these sites were used to some degree for foraging. The fact that the majority of *non-Myotis* calls were recorded in this seral stage suggests that these larger species are more effective foragers in these open habitats. However, clearcuts are not primary feeding areas for most bats. Numerous studies have shown bats to prefer woodland edge and water bodies as primary foraging habitat (Lunde and Harestad 1986, Thomas and West 1991, Grindal 1996, Walsh and Harris 1996). Not surprisingly, feeding rates were dramatically higher over water resources in this study area as compared to clearcut sites (Erickson, unpublished data).

The pre-canopy and closed-canopy seral stages had little or no activity. The absence of activity in closed-canopy sites indicates that these stands are unsuitable habitat for forest-dwelling bats. Although high densities of snags were present, these were typically small-diameter Douglas-fir whose lack of crevices and hollows make them unlikely roost sites. In addition, the high tree density within these stands (see Table 3) may be too dense for most bat species to negotiate given the physical limitations of their sonar systems and flight capabilities. Such impediments to flight may be particularly challenging to newly volant bats (Constantine 1966).

Harvest-age sites had the second highest detection rates and were the only seral stage to have a secondary peak in activity near sunrise. This activity pattern is similar to that described by Thomas and West (1991) for old-growth stands (185-200+ yr) of the southern Washington Cascades. They concluded that these peaks of activity after sunset and before sunrise coupled with low foraging rates indicated bats were dispersing away from roosts located in old growth and commuting elsewhere to feed. If their interpretation of the observed activity patterns is accurate, it appears at least some *Myotis* species can roost in harvest-age 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" structures for certain species in Washington State (Campbell 1993, Christy 1993), were most abundant in these stands. However, suitable roosting conditions within harvest-age stands may not be present for all forest-dwelling species, as inferred by the absence of calls for the big brown bat and silver-haired bat.

Unfortunately, specific roost characteristics of forest-dwelling bats are poorly known and it is currently impossible to measure roost availability within the harvest-age stands for most species (but see Campbell 1993; Frazier, this volume). With recent advances in the miniaturization of radio transmitters, however, radio-tracking of small bats has become feasible and presents the only practical means of gathering information on roost site characteristics. Results from recent radio-telemetry studies in the Pacific Northwest (Campbell 1993; Christy 1993; Betts 1996; Ormsbee 1996; and Frazier, this volume) concur with findings in other regions of the world, with bats preferentially roosting in the largest live and dead trees available (Lunney and others 1988, Taylor and Savva 1988). These results suggest that retention and recruitment of appropriate trees in managed forests may prove effective in encouraging bat presence in otherwise unsuitable habitat. However, further study of species-specific roosting requirements is needed to provide additional information on roost site characteristics and the availability of appropriate roosts in second-growth forests.

Because bats are highly mobile animals, restricting interpretation of habitat selection to only the stand level will limit our understanding of bat habitat associations. Consideration must also be given to the potential influence of the surrounding landscape. The landscape regression models from this analysis indicate that *Myotis* and *non-Myotis* bats may respond differently to landscape structure and that these patterns vary at different spatial scales (Table 5). These differences may be related to each group’s ecomorphology. Ecomorphology can be defined as aspects of an organism’s ecology that may be dictated by certain morphological features (Findley 1993). Morphological characteristics affecting flight (wing loading and aspect ratio) and attributes of echolocation calls (frequency, intensity, duration, and shape) may influence habitat use. In general, species with long, narrow wings, such as the non-*Myotis* bats, tend to be fast flyers with low maneuverability and long-range detection abilities. Those bats with broad, short wings, such as the *Myotis* spp., are more adapted to an agile, fluttering flight and have echolocation calls that permit fine resolution of the environment but at a short range.

At the smallest scale of investigation (100 ha), the activity patterns of *Myotis* bats were positively related to Mean Nearest Neighbor. Nearest neighbor distance is defined as the distance from a patch to the nearest neighboring patch of the same type (McGarigal and Marks 1995). As the distance between similar patches increased activity levels increased. Because small insectivorous bats tend to travel short distances between roosting and foraging sites (Lunney and others 1988) they may prefer landscapes where dissimilar patches (foraging vs. roosting sites) are within close proximity to one another, reflecting their limited travel distance.

Non-Myotis bats are larger and have echolocation and wing morphologies suited for open habitats and long-distance flight. Big brown bats are known to travel up to 4 km between roosting and foraging habitat (Brigham and Fenton 1988). Because of the greater distances traveled to foraging areas, the 100-ha landscape, with a radius of less than 570 m, may have been too small to detect any landscape-level effects. A more appropriate scale of investigation may be at the larger landscape sizes. Within the 1000-ha landscape, a significant amount of variation in activity could be explained by the amount of mature forest. The negative relationship between activity and amount of forest may reflect a preference by these bats for commuting and foraging within open habitats.

The results of the principal components and cluster analysis suggest that bats prefer landscapes which are heterogeneous resulting in greater amounts of "high-contrast edge" (forest-clearcut edge). Similar results were found from field studies in the Netherlands where most bat species preferred to fly along ’linear landscape elements' like hedgerows, tree lanes, wood edges, and canals rather than crossing open areas (Limpens and others 1989). Limpens and Kapteyn (1991) proposed that small bats, particularly *Myotis* spp., prefer flying along linear landscape elements either because of the availability of insects, shelter from wind and predation, or a reliance on these features for orientation within the landscape.

These interpretations of landscape-level effects on bat activity must be considered within the scope and limitations of this study. First, this analysis was limited to groups of species rather than to individual species. Further studies quantifying the habitat requirements of target species are required if we are to identify the specific responses of each species to landscape structure. Second, this study was specifically designed as a stand-level survey. Landscape level analysis of these data, therefore, has many limitations. This analysis did not try to address all of these but rather attempted to demonstrate that such an approach is possible and that it can produce significant results of conservation value.

MANAGEMENT IMPLICATIONS

As forested landscapes of the Pacific Northwest are rapidly being altered by timber harvest, it is becoming increasingly important to determine how bats use the forest ecosystem. Stand structure affects the availability of roosting and foraging resources and therefore influences the type of activity patterns found therein. It may be possible to increase or maintain the abundance of these resources via direct silvicultural manipulation.

In terms of their impact on bat populations, current timber harvest has its greatest influence by reducing the number of large, (iiseased, or dead trees in forest stands (Thomas and West 1991). While this study cannot be used to precisely define the structural features used by roosting bats, it suggests that stands with the greatest abundance of large live and dead trees were used predominantly as roosting sites. The retention and recruitment of a range of diseased, damaged, and dead tree species, sizes, and decay states within a given region may prove effective in maintaining appropriate roost sites. Selective harvesting may be a suitable approach to integrate forestry and bat habitat in closed-canopy stands. Prescriptions that retain dominant trees while removing smaller ones could reduce the level of clutter in these dense second-growth stands making them more appealing to bats.

Given appropriate roosts, the presence of high-contrast edges also seems important. The disturbance associated with timber harvest creates open areas used to some degree as foraging sites, especially for large bats which may be restricted to open habitat, while the edges resulting from clearcutting may provide travel corridors or foraging habitat for smaller species. Therefore, in planning the size of clearcuts, the ratio of edge to open area should be considered. Landscapes with greater amounts of edge are likely to provide better bat habitat.

Although interpretation of bat activity patterns in the context of resource availability is hindered by the lack of information on the ecology of these species, maintenance of structurally diverse mature stands within heterogeneous landscapes may provide suitable habitats for many of the forest-dwelling bats.

BIRD POPULATIONS IN MANAGED FORESTS IN THE WESTERN CASCADE MOUNTAINS, WASHINGTON

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INTRODUCTION

There are few studies of birds in the Pacific Northwest that have been directed at assessing the response of birds to the managed forests. A significant amount of the landscape in western Washington consists of commercial timberland in early successional stages. How birds respond to this mosaic of mixed-aged but largely young and often highly manipulated stands is unknown. This study attempted to document major patterns of habitat occupancy of diurnal landbirds using sites that range from clearcuts to harvest age of 50-70 years on managed forests in the southern Washington Cascades from 1993-1995. Our analysis was primarily oriented at stand-level responses of birds since current bird survey approaches are most effective at that level.

METHODS

BIRD SURVEYS

Birds were surveyed by using the point-count method (Verner 1985, Manuwal 1991): observers counted all birds detected during an 8-minute count period within a 50-m radius circle of each of 12 count stations at each study site. Count stations were spaced 100 m apart. Counts were usually started within 30 min. of official dawn and completed within 2 hours. Birds were not surveyed during periods of rain, snow or strong winds. Each study site was visited 6 times from the first week of May until 30 June in 1993, 1994, and 1995. Observers were rotated among the various study sites so as to avoid potential bias. The abilities of observers to identify birds by sight and sound and conduct point counts were tested before the field season commenced.

DATA ANALYSIS

Since birds were surveyed in the same manner at all study sites, we used 2 measures of abundance: the number of detections to compare species richness among treatments and a detection rate (the number of birds detected per visit) for comparisons among treatments and with habitat variables.

Comparisons of species richness and overall abundance among stands was tested by using one-way analysis of variance (ANOVA). This analysis was based on birds detected within 50 m of a count station, except the following wide-ranging bird species or groups: raptors, swallows, and Vaux's swift. Birds detected only once at a study site were omitted from analysis since they were probably not typical of the sampled habitat. Spearman rank correlation (rs) analysis was used to test relationship between species richness and abundance with certain environmental variables. The Mann-Whitney U test (Siegel 1956) was used to compare differences between 2 means of small samples.

We used similarity indices to compare the similarity of bird species among the 4 different forest structural age classes. We calculated the Sorenson index of species similarity (Ss) (Able and Noon 1976) by the following equation: Ss = 2C/(A + B) where C represented the number of bird species common to 2 forest age classes, and A and B the total number of bird species found with at least 2 detections in each of the 2 forest age classes being compared. Values >0.50 indicated that the 2 age classes were more alike than different.

Species evenness (E) was calculated lay the formula H/Hma$_{x}$ where the values range from 0 to 1 (Pielou 1969, Krebs 1972). Where H = index of species diversity [- (p1)(log10P1)]; p1 is the proportion of total sample belonging to ith species; S is the number of species detected in the age class; Hma× is the maximum species diversity (logl0S); and E = H/Hmax.

Individual sites or stands served as the experimental units for statistical analyses of the response of individual species to the effects of sample years and treatment type (i.e., stand type). An abundance index for each common (>30 detections/year) breeding bird species was calculated by averaging detections over 6 site visits for each treatment type in each season. Abundance estimates were log (x+l) transformed. Repeated-measures ANOVA was used to compare species abundance by year and treatment. Treatment effects were evaluated using a separate ANOVA for each year and Bonferroni tests were used to identify differences among treatments. Using these procedures, we omitted from this analysis species with significant interactions between year and treatment. For species without treatment-by-year interactions, estimates were combined between years and Bonferroni tests were used to identify differences among treatments.

To explore habitat attributes important to breeding birds, we related the abundance of each common bird species using stepwise regression (forward selection). Habitat variables having tolerance factors <0.70 were excluded from the model to reduce multicollinearity. Habitat variables not meeting the assumptions of normality were either log (x+l), arcsine or square-root transformed as appropriate. Pearson correlation matrix was used to eliminate positively correlated habitat variables.

RESULTS AND DISCUSSION

SPECIES COMPOSITION AND RICHNESS

We recorded over 51,000 birds of 73 species during this 3-year study. This total included birds within 75 m of point count stations but not species recorded only once or birds flying over. Wide-ranging species such as raptors, some species of owls, and cavity-nesting ducks were either absent from the data set or were rare since these species are not adequately sampled using the point count technique. In this analysis we used 20,435 detections of 73 species that were detected within 50 m of the count station so as to avoid potential overlap in detections among point counts as well as to omit birds that may not have actually been associated with the study site.

There was a clear pattern to bird species composition along the structural gradient. In the clearcut stage, there are many species that specialize on early successional stages and are either absent or rare later in forest succession when a canopy develops. Birds that readily pioneer clearcuts include common yellowthroat, MacGilivray’s warbler, western bluebird, northern flicker, willow flycatcher, song sparrow, white-crowned sparrow, rufous-sided towhee, and American goldfinch. As the new forest develops into the pre-canopy stand, at about 12-20 years of age, there is a mix of species that includes some of the early colonists in the clearcut, but also some true forest birds such as the chestnut-backed chickadee, golden-crowned kinglet, and winter wren. Once the forest canopy develops after 20 years, most of the birds found in the earlier stages have disappeared. A few may find pockets of suitable habitat and persist in small numbers. Assessing only birds that are found in sites that were at least 12 years old and had a developing canopy (stages B-D), we found that 8 bird species comprised over 75% of all birds detected (Table 1, Fig. 1). The winter wren is the most widespread and commonly detected species in managed forests.

A small number of species, particularly raptors, were not detected every year in a particular forest structure class. The following species were recorded in every stand type during every year: American robin, Swainson's thrush, dark-eyed junco, rufous-sided towhee, western tanager, Wilson's warbler and winter wren. A complete list of species detected is presented in Appendix Table A-2.

Annual variation

Species richness among all stand types did not vary significantly among years (F = 2.29, p = 0.11). There were also no significant differences among years when each structure class was tested (1-way ANOVA) separately. There was a slight increase in the mean in 1995 (18.8 species per stand).

Effects of elevation

Study sites varied in elevation from 290 to 850 m (mean = 508 m, SD = 137 m) above sea level. Species richness in forested stand types (B-D) decreased with gain in elevation during 1994 (rs =-0.556, p = 0.017) and 1995 (rs = -0.575, p = 0.013) but not in 1993 (rs = -0.395, p = 0.105). A similar significant trend was noted if all stand types are included in the analysis. The analysis of the relationship between species richness and elevation was confounded because only pre-canopy (B) and closed-canopy (C) stands occurred at high elevation. The following species tended to be less frequently encountered at the high-elevation sites: American crow, tree swallow, violet-green swallow, house wren, band-tailed pigeon, hermit-Townsend's warbler, common yellowthroat, bushtit, American goldfinch, and song sparrow.

Table 1. Species comprising 75 percent of all observations in 18 forested stands[1] in 1993-95 in the Washington Cascade Range.

	1993		1994		1995		Overall 1993-95	
Species	Rank	Percent	Rank	Percent	Rank	Percent	Rank	Percent
Winter wren	1	18.5	1	20.9	1	23.2	1	21.1
Pacific-slope flycatcher	3	12.5	3	11.4	2	13.7	2	12.6
Golden-crowned kinglet	2	14.1	2	13.9	3	10.0	3	12.4
Chestnut-backed chickadee	4	11.3	4	9.3	4	8.4	4	9.5
Wilson’s warbler	5	6.3	5	6.9	7	5.5	5	6.1
Hermit-Townsend’s warbler	7	5.1	6	59	6	5.6	6	5.6
Swainson’s thrush	6	6.0	7	3.9	5	5.7	7	5.2
Hutton’s vireo	8	2.0	8	2.0	8	4.0	8	2.8

Only forest types B, C, and D are included; clearcuts omitted.

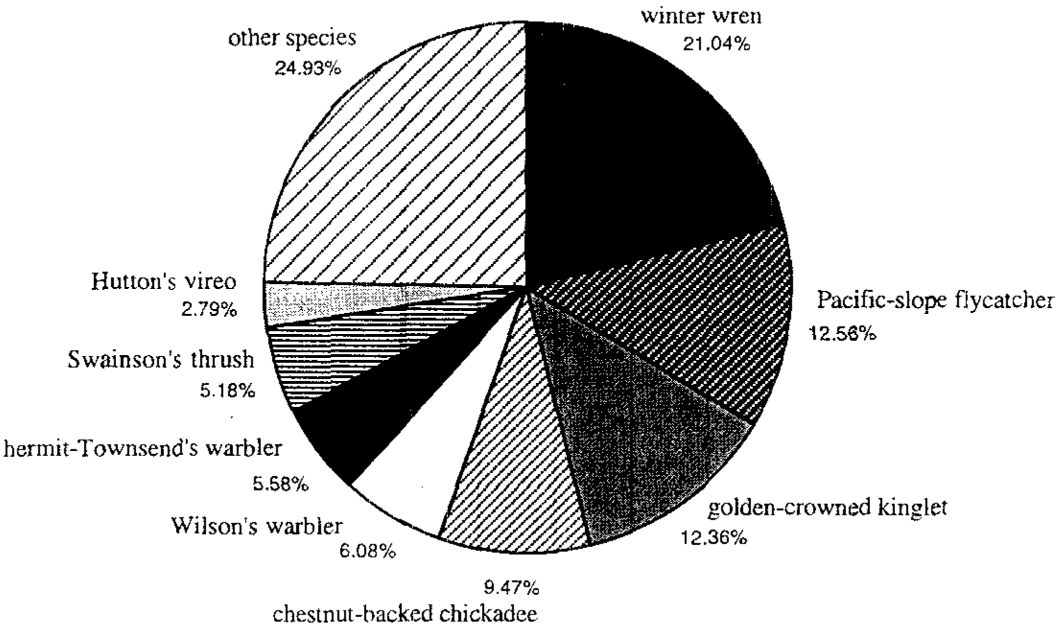


Figure 1. Species comprising the top 75 percent of the avifauna detected in Stand Types B, C, and D in 1993, 1994, and 1995. Structure types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Neotropical migrants and permanent residents

Over 50% of birds detected in this study were permanent residents. Another 34% were birds that spend the winter in the Neotropics and the remaining 11% winter somewhere south of Washington in the United States. There were noticeable differences in the percentages of birds in different migratory categories in the various forest structure classes (Fig. 2). The percentage of permanent resident species increased with forest development, whereas the percentage of birds that spend the winter in North America south of Washington decreased with forest age. Permanent residents such as the chestnut-backed chickadee were very common in the older stands. North American winter residents such as the white-crowned sparrow, song sparrow and American goldfinch were abundant in clearcuts (A). Neotropical migrants were most abundant in pre-canopy stands (B). This was due largely to the large numbers of Swainson's thrushes and Wilson's warblers in B stands.

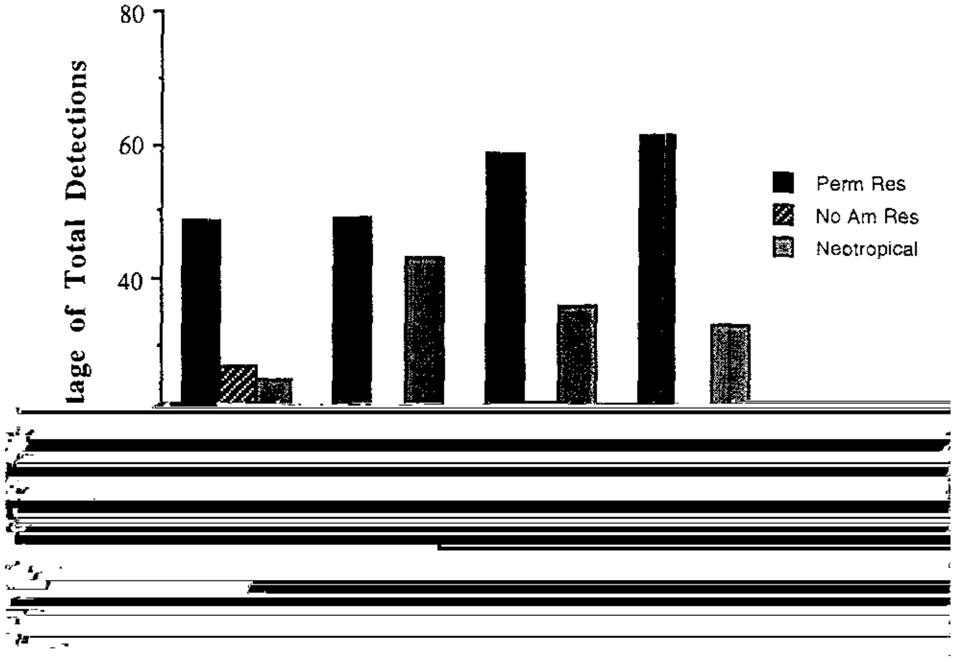


Figure 2. Residency status of birds detected in each of 4 forest structural classes in 1993-95. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

NESTING GUILD STRUCTURE

Birds were divided into 4 nesting guilds based on location of the nest in the forest environment. Some species occupied more than 1 guild but for purposes of this study, they were placed in the most typical guild for this part of their distribution. The percentage of the avifauna in each guild varied with structure class. It is apparent that ground nesters such as the song sparrow and dark-eyed junco were more prevalent in the open clearcuts (Fig. 3) and became less common as the forest develops. Shrub nesters such as the white-crowned sparrow and willow flycatcher were also common in clearcuts. However, once the tree canopy began to develop, there was a dramatic decline in these species since shrub growth declined. On the other hand, cavity-nesting species became more prevalent as the stand matured Species that nest in trees were most prevalent in stages B and C when tree density and canopy foliage volume were high.

There was a close association between cavity-nesting birds and forest structure class. The majority of cavity-nesting bird species detected in this study were most abundant in the harvest-age class (Table 2). The percentage of cavity-nesting birds increased with stand age (Fig. 4): 2,5% in A stands; 35.4% in B; 42.8% in C; and 62.7%

Figure 3. Changes in nesting guilds across a gradient of forest structure class.

in D sites. The most abundant species in the study sites in structure classes B-D were in decreasing order: winter wren, Pacific-slope flycatcher and chestnut-backed chickadee. The chickadee was the typical cavity-nester of snags and dying trees. The Pacific-slope flycatcher nested in a variety of places, including cavities, but also in cup nests on the side of tree trunks, ledges, and other objects. Not all winter wrens nested in cavities but they often used deadwood on the forest floor as both nesting and foraging substrates. Since these 3 species were often the most abundant species, they had a large influence on the percentage of cavity-nesters. We found that woodpeckers were uncommon and we failed to detect a red-breasted sapsucker in this study. The tree swallow and violet-green swallow both nested in tree cavities excavated by primary cavity-nesters. Although some birds may have nested on the study sites, we believe most detections were of birds either feeding over clearcut sites or traveling to or from distant nesting sites.

Table 2. Cavity-nesting bird species in detected during 1993-1995 in managed coniferous forests.

Species and category	Highest abundance (forest age class)
Primary cavity-nesting	
Northern flicker	Clearcut
Pileated woodpecker	Harvest age
Hairy woodpecker	Harvest age
Downy woodpecker	(Riparian areas)
Primary or secondary cavity-.nesting	
Black-capped chickadee	(Riparian areas)
Chestnut-backed chickadee	Harvest age
Red-breasted nuthatch	Harvest age
Secondary cavity-nesting	
Pacific-slope flycatcher	Harvest age
Violet-green swallow	Clearcut
Tree swallow	Clearcut
Brown creeper	Harvest age
Winter wren	Harvest age
Western bluebird	Clearcut

Effects of forest structure classes

The mean species richness at the stand level for all years was 17.4 and varied from 16.3 (1994) to 18.8 (1995) and did not vary significantly ($p < 0.05$) among stand types (Fig. 5, Table 3). The largest number of species detected was in pre-canopy stands where 57 species were detected during the 3-year study. The mean values underrepresent the total species present because of the truncation of the data to include only birds found within 50 m of count stations. Wide-ranging species such as ravens, raptors, jays, and woodpeckers were often either not detected at all or were

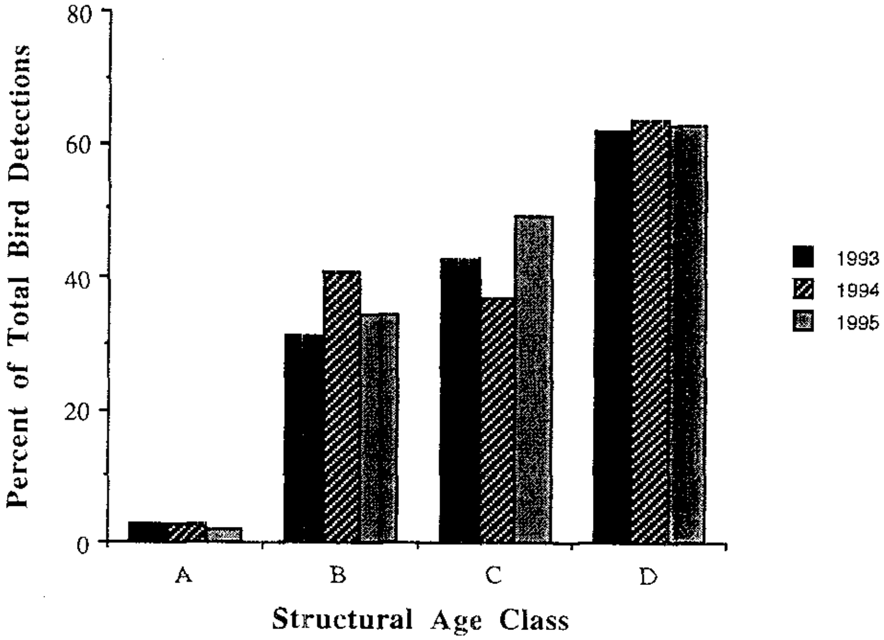


Figure 4. Cavity-nesting bird species as a percentage of total number of birds detected in 1993-1995 in managed coniferous forests. Structure classes: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

detected beyond 50 or 75 m from the count station. Some species such as gray jays or red-breasted sapsuckers are typically very quiet so are not often detected.

The pattern of bird species similarity was very similar among years (Table 4). The bird community was least similar between clearcuts and closed-canopy stands. Stages with the most similar species were closed-canopy and harvest age, but pre-canopy and harvest age were very similar. The presence or absence of forest canopy-dwelling and bark-foraging species accounted for these patterns of similarity.

SPECIES TURNOVER

As forest succession proceeded from 1 developmental stage to the next, bird species occupying these stages also changed. We calculated species composition changes from 1 forest structure class to another (Table 5). Species turnover was remarkably similar in the 3 years, with 1994 being the most different from the other 2 years. It is clear that species composition changed the most from pre-canopy to closed-canopy stands, when an average of 12 species were lost. Table 6 summarizes the species that

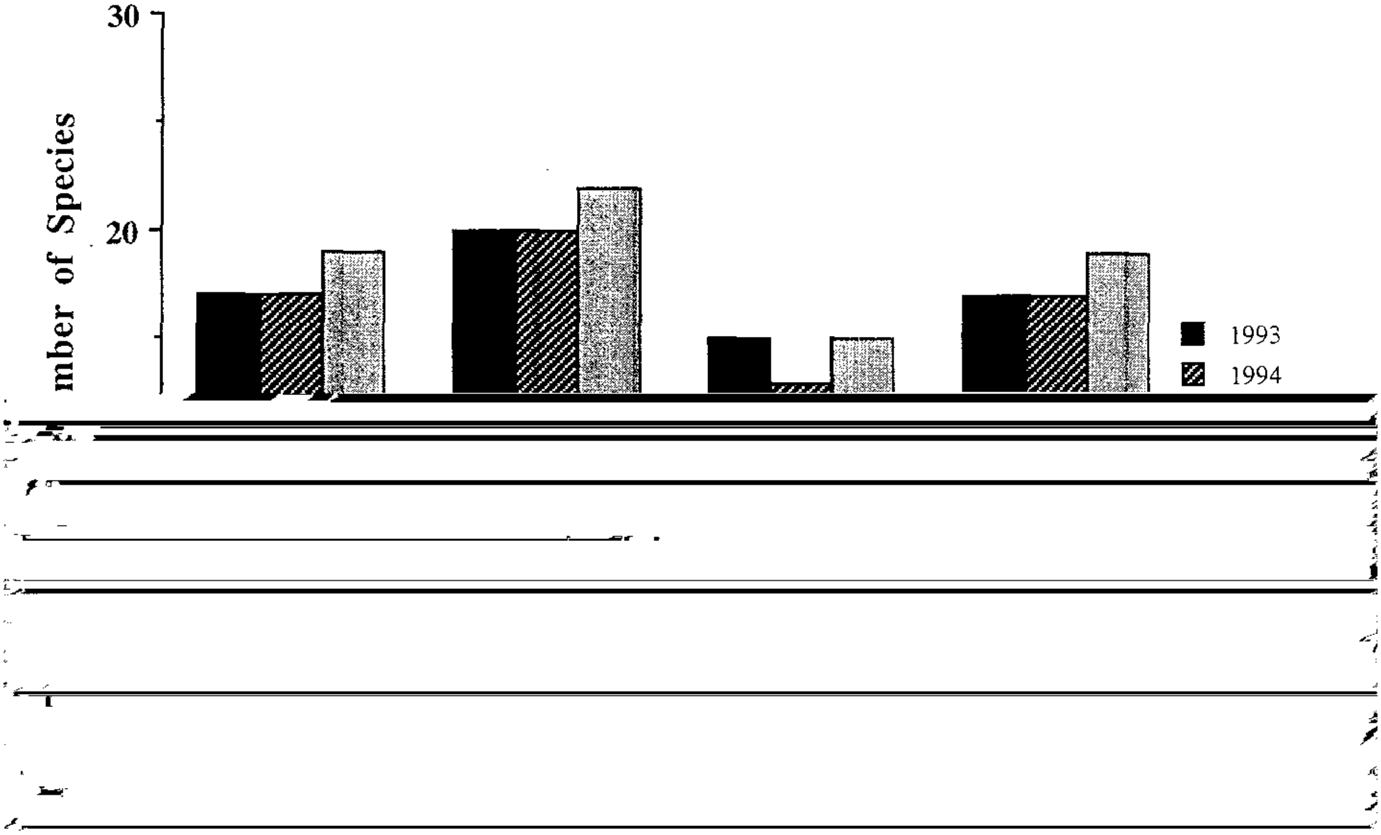


Figure 5. Mean number of bird species detected in each of 5 stand structural-age classes, 1993-1995. Birds detected within 50 m of count station. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

were most likely to either disappear or appear during a transition from 1 forest structure class to another.

CLUSTER ANALYSIS

We conducted a hierarchical cluster analysis of bird abundance to evaluate degrees of similarity or differences among birds in the 4 structural classes (Fig. 6). Results of this analysis agree well with general knowledge of habitat preferences of most birds that were clustered. Species such as winter wren (WIWR), golden-crowned kinglet (GCKI), Pacific-slope flycatcher (PSFL), and chestnut-backed chickadee (CBCH) normally associated with older age forests with relatively unbroken canopy were clustered together. The Swainson's thrush (SVVTH) and Wilson's warbler (WIWA) that are known to be associated with shrub and small-tree understory were clustered together. The black-throated gray warbler (BYWA), Hutton's vireo (HUVI), and varied thrush (VATH)

Table 3. Avian species richness in 4 different age and structural forest types in western Washington during 1993-,1995. Includes detections within 50 m of point count station.

	1993	1994	1995	1993-1995
		Clearcut (A)		
Total species	35	28	36	47
Mean per stand	17.3	16.5	19.0	17.6
Standard deviation				27
		Pre-canopy (B)		
Total species	42	35	41	57
Mean per stand	19.8	19.7	22.2	20.6
Standard deviation				5.8
		Closed-canopy(C)		
Total species	28	27	29	37
Mean per stand	14.8	12.7	15.2	14.2
Standard deviation				2.2
		Harvestage(D)		
Total species	32	32	31	37
Mean per stand	17.3	16.5	19.0	17.6
Standard deviation				23
Overall mean	17.3	16.3	18.8	17.7
Total species observed				73

were clustered together. The Wilson's warbler and Hutton's vireo often nested in deciduous trees and the varied thrush tended to be more common in older forests where deciduous trees and shrubs were likely to be present because of successional dynamics. The evening grosbeak (EVGR), hairy woodpecker (HAWO), red-breasted nuthatch (RBNU), brown creeper (BRCR), and Steller's jay (STJA) were grouped together. All but the jay were associated with older forests where the birds fed on bark insects or insects and seeds in the canopy. Another obvious grouping consists of the

Table 4. Similarity coefficients of bird species similarity among 4 different forest age classes in western Washington managed Douglas-fir forests. Coefficients are averages for 1993, 1994 and 1995.

	Forest age class			
	Clearcut	Pre-canopy	Closed-canopy	Harvest age
Clearcut		0.69	0.45	0.55
Pre-canopy			0.65	O75
Closed-canopy				0.79
Harvest age				

black-headed grosbeak (BHGR), rufous hummingbird (RUHU), cedar waxwing (CEWA), Bewick's wren (BEWR), orange-crowned warbler (OCWA) and American robin (AMRO) which occupy open-canopied early successional forests which also have a high percentage of deciduous vegetation. The final distinguishable grouping consisted of species that occupied recent clearcuts where there were deciduous shrubs and conifer reproduction. These bird species included the white-crowned sparrow (WCSP), dark-eyed junco (DEJU), song sparrow (SOSP), rufous-sided towhee (RSTO), American goldfinch (AMGO), common yellow-throat (COYE), willow flycatcher (WIFL), and MacGillivray's warbler (MGWA).

EVENNESS

Species evenness (E) or the proportion of individuals among species is a major component of species diversity. The highest diversity a bird community could have is if all species comprised an equal number of the total number of individuals present in the community.

Bird species diversity and evenness were highest in the pre-canopy stage (B) and lowest in the harvest age (D) (Table 7). Evenness showed substantial variation among years which probably reflects population fluctuations (or change in detectability) among the various species in the community. The relatively large drop in E for pre-canopy, closed-canopy, and harvest age stands in 1995 appeared to be related to the large

Table 5. Changes in species composition among the 4 forest structure classes during 1993, 1994 and 1995.

Age class transition	Species lost	Species gained	Turnover (+/-)
f993			
Clearcut to pre-canopy	9	13	+4
Pre-canopy to closed-canopy	17	4	-13
Closed-canopy to harvest age	4	7	+4
1994			
Clearcut to pre-canopy	6	13	+7
Pre-canopy to closed-canopy	15	6	-9
Closed-canopy to harvest age	4	8	+4
1995			
Clearcut to pre-canopy	9	13	+4
Pre-canopy to closed-canopy	19	5	-14
Closed-canopy to harvest age	4	8	+4
MEANS 1993-1995			
Clearcut to pre-canopy	8	13	+5
Pre-canopy to closed-canopy	17	5	-12
Closed-canopy to harvest age	4	8	+4

increase in detections of the winter wren, the most abundant species. This would reduce evenness because that species would comprise a large percentage of the total population.

EXOTIC SPECIES

The European starling and housE; sparrow are the only 2 exotic species that might be of concern to forest managers and wildlife biologists. Neither of these species were detected during this study. Rock doves, starlings, and house sparrows can be found in low abundance (see Appendix) in clearcut sites near farms or other human dwellings and appeared to avoid environments away from human settlements.

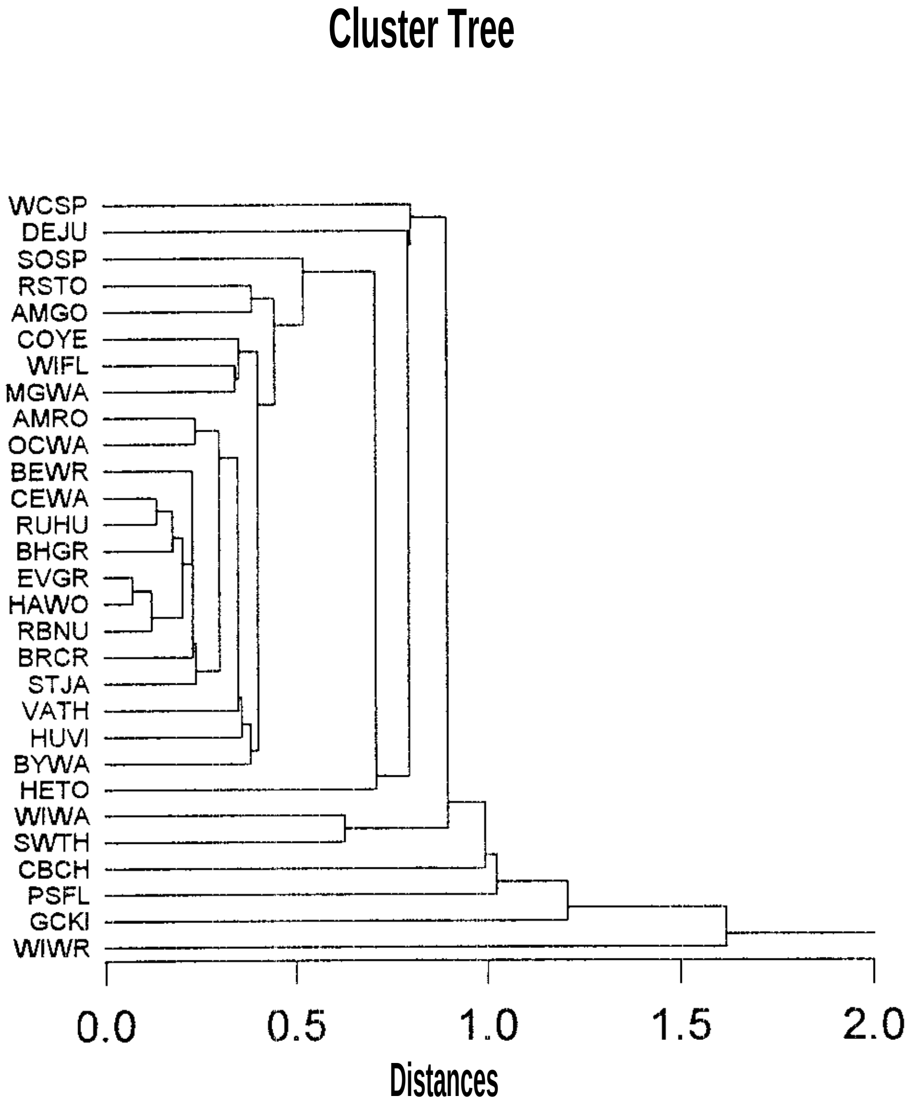
Table 6. Bird species most likely either lost or gained during a transition from 1 forest structural age class to another during 1993 to 1995.

Clearcut to pre-canopy		Pre-canopy to closed-canopy		Closed-canopy to harvest age	
Species lost	Species gained	Species lost	Species gained	Species lost	Species gained
Bushtit	Chestnut-backed chickadee	Brown creeper	Band-tailed pigeon	Hermit thrush	Brown creeper
Cedar waxwing	Evening grosbeak	Gray jay	Warbling vireo	Hammond’s flycatcher	
House wren	Golden-crowned kinglet	Common yellowthroat	Red crossbill	Northern flicker	
Red-winged blackbird	Gray jay	MacGillivray’s warbler			
Tree swallow	Hermit-Townsend’s warbler	Northern flicker			
Violet-green swallow	Hutton’s vireo	Orange-crowned warbler			
Western bluebird	Pine siskin	Olive-sided flycatcher			
Yellow warbler	Purple finch	Purple finch			
	Red-breasted nuthatch	Ruffed grouse			
	Solitary vireo	Rufous hummingbird			
	Varied thrush	Solitary vireo			
	Western tanager	Song sparrow			
		White-cr sparrow			
		Willow flycatcher			

AVIAN ABUNDANCE

Effects of elevation

In 2 of the 3 years, bird abundance did not vary significantly with elevation, but in 1994 there was a significant decline with elevation (rs = -0.663, p = 0.003). As with species richness, the relationship between abundance and elevation is confounded by the preponderance of C stands at high elevation, and abundance tends to be lowest in C stands.



Cluster Tree

Figure 6. Hierarchical cluster analysis of bird abundance by stand on managed forests in the southern Cascades o.r Washington from 1993-1995. Species within the same cluster are generally highly correlated. Clusters distantly separated are more dissimilar than closer together.

Table 7. Bird species evenness (E) across forest structure classes.

Year	H value	S	Hma$_{X}$	E
		Clearcut(A)		
1993	-1.099	35	1.544	0.712
1994	**-1.054**	**34**	**1.531**	**0.688**
1995	-1.157	44	1.643	0.704
Mean	-1.103	38	1.573	0.701
		Pre-canopy(B)		
1993	-1.269	41	1.613	0.787
1994	-1.387	45	1.653	0.839
1995	-1.255	49	1.690	0.743
Mean	-1.304	45	1.652	0.790
		Closed-canopy (C)		
1993	-1.040	28	1.447	0.719
1994	-1.107	33	1.519	0.729
1995	-1.008	35	1.544	0.653
Mean	-1.052	32	1.503	0.700
		Harvest age(D)		
1993	-1.053	32	1.505	0.700
1994	-1.062	39	1.591	0.668
1995	-0.867	33	1.519	0.571
Mean	-0.994	35	1.538	0.646

Annual variation

Total avian abundance varied significantly among years for all forest structure classes (Table 8). The most between-year variation occurred in forest structure classes A and D. These differences may be due to either observer bias, changes in survey conditions, Or actual changes in bird number's. There was no evidence that weather was substantially different between years to influence results of surveys. Observer bias was difficult to measure and we cannot rule this factor out. It was also likely that bird numbers changed between years. There were substantially more winter wrens and chestnut-backed chickadees detected in 1995 than in other years in most stands. Since these species are 2 of the most abundant, this could have accounted for the differences between years.

Effects of structure class

Total avian abundance was significantly different among structure classes in 1994 and 1995, but not in 1993 (Table 9, Fig. 7). There was a substantial amount of within-structure class variation in 1993 compared with the other 2 years. This undoubtedly affected the significance of the ANOVA test. There were consistently fewer birds detected in closed-canopy stands than the other structure classes. Table 10 ranks the most abundant bird species as well as those having the highest frequency of occurrence.

Table 8. Results of 1-way Analysis of Variance tests on avian abundance (species with at least 2 detections) across years.

Stand age class	F	p-value
Clearcut	15.741	0.000
Pre-canopy	3.991	0.041
Closed-canopy	6.643	0.009
Harvest age	13.810	O000

Table 9. Results of 1-way ANOVA tests comparing avian abundance across the forest structure classes for 1993, 1994, and 1995.

Year	F value	p-value
1993	1.63	0.21
1994	8.82	0.00
1995	4.15	0.02

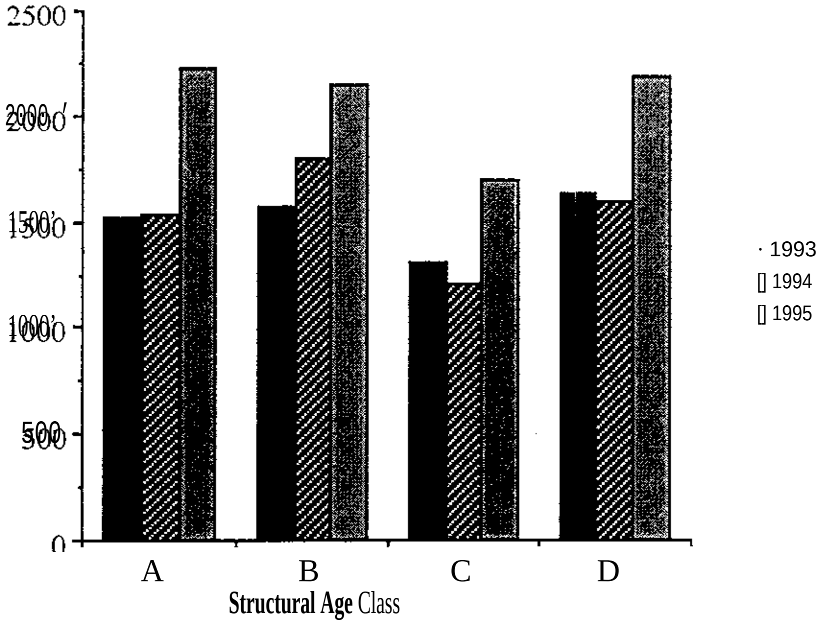


Figure 7. Bird abundance across the 4 forest structure classes in 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Table 10. Bird species most typical of 4 structure classes of managed Douglas-fir forests in the western Cascade Mountains. Birds were grouped and ranked by Habitat Occupancy Index (HOI) values from Appendix tables[1].

Clearcut (Stage A, 2-4 years old)

White-crowned sparrow
Song sparrow
Willow flycatcher
MacGillivray's warbler
Dark-eyed junco
Rufous-sided towhee
Common yellowthroat
American goldfinch

Pre-canopy (Stage B, 12-20 years old)

Winter wren
Wilson's warbler
Pacific-slope flycatcher
Swainson's thrush
Golden-crowned kinglet
Chestnut-backed chickadee

Closed-canopy (Stage C, 30-40 years old)

Golden-crowned kinglet
Winter wren
Pacific-slope flycatcher
Chestnut-backed chickadee

Harvest age (Stage D, 50-70 years old)

Winter wren
Golden-crowned kinglet
Pacific-slope flycatcher
Chestnut-backed chickadee

[1] All birds ranked by HOI values are found in Appendix tables.

Comparisons between individual species abundance and forest structural classes

At the species level, however, the abundance of only 8 species did not vary among years so we tested their response to treatment effects using the combined data over the 3 years (Table 11). Golden-crowned kinglet abundance did not differ between pre-canopy (B) and harvest-age (D) stand types but was different in clearcuts (A) and closed-canopy (C) stands. As expected, white-crowned sparrow, common yellowthroat, and American goldfinch abundance in clearcuts was different from other stand types. The abundance of hermit-Townsend's warblers did not differ' between closed-canopy forests and harvest-age forests but was different in clearcuts and pre-canopy stands

Table 11. Mean (SD) numbers of detections (abundance) of common (>30 total detections/year) breeding birds in clearcut, pre-canopy, closed-canopy and harvest-age stands (N = 6 sites/treatment) on managed forests in the southern Cascades of Washington. All species had significant treatment effects ($p < 0.05$) but no year effects, thus abundance was pooled between years by averaging total counts for each species at each site across 6 visits in each breeding season. Means sharing the same letters do not differ (ANOVA, Bonferroni test, $p < 0.05$).

	Stand structure			
Species	Clearcut	Pre-canopy	Closed-canopy	Harvest age
GCKI	0.0(0.0)A	4.9(1.9)B	8.1(1.5)C	4.2(1.6)B
WCSP	10.4(3.1)A	0.1(0.2)B	0.0(0.0)B	0.0(0.0)B
HETO	0.0(0.0)A	1.2(1.4)B	3.8(1.9)C	2.8(2.2)C
COYE	3.3(2.5)A	0.9(1.5)B	0.0(0.0)t3	0.1(0.1)B
MGWA	2.8(1.4)A	0.7(0.8)B	0.1(0.1)C	0.2(0.2)C
AMGO	2.8(1.9)A	0.2(0.3)B	0.0(O1)B	0.0(0.1)B
STJA	0.2(0.3)A	0.8(0.5)B	0.6(0.8)B	0.7(0.7)B
RUHU	O6(O7)A	O4(0.5)AB	0.0(0.0)C	0.2(0.2)BC

MacGillivray's warbler abundance was highest in clearcuts and differed between clearcuts and pre-canopy sites. It showed similar abundance in closed-canopy and harvest-age stand types. Steller's jay abundance was the same in all stand types except clearcuts. The abundance pattern of the rufous hummingbird showed a more complex pattern than the other 7 species. Abundance was similar in clearcuts and pre-canopy stands as was pre-canopy and harvest age although abundance levels were very low and there was a relatively large standard deviation from the mean number of detections. The low abundance was also similar between closed-canopy and harvest age. With more detections, the habitat affinities of the rufous hummingbird might become more recognizable.

Many bird species showed significant differences in abundance among years. To test their response to forest structure class, we treated each year separately (Table 12). There were significant differences in abundance between years and between

Table 12. Mean^{a} (SD) numbers of detections (abundance) of common (>30 total detections/year) breeding birds in clearcut, pre-canopy, closed canopy and harvest aged stands (N = 6 sites/treatment) on managed forests in the southern Cascades of Washington, 1993-1995. All species had significant year and treatment effects ($p < 0.05$). Means sharing the same letters do not differ (ANOVA, Bonferroni test, $p < 0.05$).

	1993				1994				1995			
Species*	Clearcut	Pre-canopy	Closed-canopy	Harvest	Clearcut	Pre-canopy	Closed-canopy	Harvest	Clearcut	Pre-canopy	Closed-canopy	Harvest
WIWR	0,1(01)A	62(3.2)BC	4.3(2.3)B	126(3,4)C	01(01)A	9.5(4.5)B	4.4(2.4)C	12.5(2.0)B	0.1(0.3)A	11 8(6,1)B	9.4(2.9)B	17.3(1.7)B
PSFL	0.1(0 I)A	3 I(I 5)B	59(2.8)B	86(I 5)B	00(00)A	32(1.9)8	44(29)B	88(1.8)B	0,1(0 I)A	4 I(27)B	8.3(4.1)BC	10.3(3.4)C
CBCH	0.0(00)A	34(15)B	47(I 2)8C	59(15)C	0 I(0.1)A	3.5(14)B	30(10)B	5,3(2.1)8	0.1(0.2)A	46(18)B	4 6(1,e)B	5.8(2 I)B
DEJU	6.2(2.8)A	1.0(09)AS	0.8(0.7)AB	0.6(06)B	6.6(3.9)A	1.6(1.3)B	1.0(0.8)B	07(0.6)B	10.3(4.6)A	16(0.7}B	1.1(0.8)B	1.1(03)B
SWTH	0,3(0,3)A	58(2.2)B	0.6(0.6)AC	1.1(0.5)C	04(0.5)A	3.9(1.8)B	0.5(0.4)AC	06(0.3)AC	1.3(0.9)A	89(3.2}B	1.1(0.8)AC	1.4(0.8)AC
RSTO	3.3(t.8)A	03(0.3)B	0.1(0.1)B	02(03)B	35(1.3)A	0,3(0,5)B	0,1(0,1)B	0.4(0,6)B	5,7(2.2)A	04(0.5)B	0,I(0.2)B	0.8('i.2)B
AMRO	1.5(1,0)A	13(12)A	0.4(05)A	03(03)A	07(05)A	1.3(I.5)A	0.1(0.1)A	04(0.3)A	I 5(0.4)A	13(1.4)A	0.3(0.3)B	0.9(07)AS
BYVVA	01(0. I)A	04(06)AB	1.3(1.5)B	0.2(02)AB	00(0.0)A	1.3(1,5)B	18(09)B	06(0.5)B	02(0,1)A	1.3(11)A	1.2(1.0)A	0.6(05)A
OCWA	1.2(0.8)A	I.t(1.7)A	0 I(0,1)AB	0.0(0.0)B	04(0.5)AB	I 3(1,3)B	00(00)AC	0.0(0.1)AC	1,8(1,6)A	1.8(20)AB	0.2(0.2)AB	0.2(02)B
BHGR	0.3(0.3)ABC	08(0,6)B	0.I(0.2)C	0.2(0.2)ABC	0t(0.2)ABC	0.6(0,7)B	00(00)c	01(0.1)ABC	0.7(0.3)A	09(0.6)A	0.1(0.2)B	0,5(05)AB
HAWO	01(01)A	04(05)A	0,3(0.4)A	07(04)A	01(0.1)A	0.1(02)A	00(01)A	06(0.4)B	0.1(0.1)A	0 I(0.I)AB	0.0(0.0)A	0.3(0.2)B
EVGR	0.1(0.2)A	03(0.3)A	06(0.5)A	08(05)A	00(00)A	01(0. I)A	0.0(01)A	01(0.1)A	0.0(0.1)A	01(0.2)AS	0.2(0.2)AB	0.3(0.3)B

aAveraging total counts for each species across 6 sites per treatment and across 6 visits.

*Species with significant interaction between treatment and year were not included (WIWA, HUVI, VATH, BRCR, RBNU, BEWR, CEWA, SOSP, WIFL) treatments for all 12 common species (Table 12). A review of the specific responses of these species to the forest structure classes is given in the species accounts.

HABITAT CHARACTERISTICS ASSOCIATED WITH SELECTED BIRD SPECIES

To better understand the abundance patterns of birds using particular forest structure classes, we correlated habitat variables with the abundance of individual species. Table 13 lists specific variables used in these analyses (refer to Table 14).

Variables that seemed to be positively correlated with the most bird species included: counts of dominant Douglas-fir or true fir (PSABMD), counts of sub-dominant coniferous trees, counts of sub-dominant coniferous trees 10-50 cm d.b.h, and >3 m tall (CONIFMS), and counts of dominant or sub-dominant deciduous trees (DECIDLD). Some of these variables were related to other variables in that they were common to specific successional structures associated with forest development. For example, several bird species such as the winter wren, Pacific-slope flycatcher, golden-crowned kinglet, and chestnut-backed chickadee that were usually most abundant in older forest were highly correlated with both counts of dominant Douglas-fir and true fir and counts of sub-dominant coniferous trees 10-50 cm d.b.h, and >3 m tall. These 2 sets of variables reflect the greater structural complexity of a forest stand as it matures. Canopy gaps, pre-canopy conifers, deciduous trees, and shrubs in the understory all contributed to this complexity.

In some cases, there was insufficient knowledge of particular bird species' ecology to allow a meaningful interpretation of the significance of a bird's abundance and a specific habitat variable. Interpretation of these variables on the abundance of specific bird species is given in the species accounts.

It is important to note that these correlations are between species abundance and habitat variables at the stand level. The significant correlations indicate which habitat variables were associated with the stand(s) where any given species was detected most frequently, and therefore, did not necessarily identify the habitat variables critical to the life history of a species.

Table 13. Description of variables used in statistical tests of bird abundance and habitat variables.

Variable	Description
BPSHR	Percent cover of berry-producing shrubs (15 m x 15 m plots).
EVSHR	Percent cover of evergreen shrubs (15 m x 15 m plots).
ODSHR	Percent cover of other deciduous shrubs (15 m x 15 m plots)
STUMP	Percent cover of stumps (15 m x 15 m plot)
LRGSTUM	Count of stump/snags >50 cm d.b.h, and < 1.5 m tall (45 m x 45 m plot)
LOGS	Count of logs >10 cm diameter (15 m x 15 m plot)
SNAG	Count of snags >10 cm d.b.h. (15 m x 15 m plot)
CONIFTR	Percent cover of conifer trees between 1-3 m tall (15 m x 15 m plot)
DECIDTR	Percent cover of deciduous trees between 1-3 m tall (15 m x 15 m plot)
DECIDMD	Count of dominant deciduous trees 10-50 cm d.b.h. and >3 m tall (15 m x 15 m plot)
TSTHMD	Count of dominant w. hemlock/redcedar/Sitka spruce and yew (15 m x 15 m plot)
PSABMD	Count of dominant Douglas-fir and true fir (15 m x 15 m plot)
DECIDMS	Count of sub-dominant deciduous trees 10-50 cm d.b.h. & >3 m tall (15 m x 15 m plot)
CONIFMS	Count of sub-dominant coniferous trees 10-50 cm d.b.h. & >3 m tall (15 m x 15 m plot)
DECIDS	Count of sub-dominant deciduous trees < 10 cm d.b.h. & >3 m tall (15 m x 15 m plot)
CONIFS	Count of sub-dominant coniferous trees < 10 cm d.b.h. & >3 m tall (15 m x 15 m plot)
DECIDDD	Counts of dominant deciduous trees of any d.b.h. (45 m x 45 m plot)
DECIDLD	Counts of dominant or sub-dominant deciduous trees >50 cm d.b.h. (45 m x 45 m plots)
TSTHPILD	Counts of dominant or sub-dominant w. hemlock/redcedar/Sitka spruce trees >50 cm d.b.h (45 m x 45 m plots)
PSABLD	Counts of dominant or sub-dominant Douglas-fir true fir trees >50 cm d.b.h. (45 m x 45 m plots)

Table 14. Relationship between each habitat variable per stand and bird abundance per stand over all 3 ’years of the study for common species (>30 detections per year) on managed forests in the southern Washington Cascades from 1993 - 1995. Significance levels for habitat variable ($p < 0.05$) are given.

	Habitat variables																					
Species	BPSHR	EVSHR	ODSHR	STUMP	LRGSTUM	LOGS	SNAG	LRGSNAG	CONIFTR	DECIDTR	DECIDMD	TSTHMD	PSABMD	DECIDMS	CONIFMS	DECIDS	CONIFS	DECIDDD	DECIDLD	TSTHPILD	PSABLD	R^2
WIWR													<.001		<.001							.85
PSFL	.006												<.001		<.001							.91
GCKI					.04												<.001		.02			.83
CBCH						.02							<.001		<.001							.92
DEJU													.002		<.001							.69
WCSP															<.001			.05	<.001			.85
WIWA							.02						<.001									
SWTH	.002												.001									.56
HETO																	<.001	.008	.006		.02	.86
SOSP	.02														<.001							.68
RSTO												.004	.002						.01			.82
WIFL																	<.001		.006			.87
COYE																	<.001				.03	.67
HUVI									.04				<.001		<.001							.93
VATH																	<.001		.01		.025	.85
MGWA																	<.001	.001			.014	.86
AMRO	.03											.02										.55
BYWA	.004												<.001									.68
AMGO																	<.001	.03	<.001			.84
OCWA	.008														.006							.57

Table 14. Continued.

Habitat variables

Species	BPSHR	EVSHR	ODSHR	STUMP	LRGSTUM	LOGS	SNAG	LRGSNAG	CONIFTR	DECIDTR	DECIDMD	TSTHMD	PSABMD	DECIDMS	CONIFMS	DECIDS	CONIFS	DECIDDD	DECIDLD	TSTHPILD	PSABLD	R^2
BRCR													.009						.02		<.001	.89
STJA													.001							.003		.52
BHGR						.03						<.001	.001									.77
RBNU																					<.001	.74
RUHU	.04											.001										.66
BEWR							.02								<.001							.68
CEWA												<.001										.47
HAWO																				<.001		.65
EVGR															<.001							.57

SPECIES ACCOUNTS

The following section covers selected species of birds found during this study. The 1st section covers the more common species. The 2nd section includes some uncommon species and those species in which previous information has indicated that there is some concern for the long-term health of the population or are threats to other species. In both sections, birds are treated in alphabetical order.

COMMON SPECIES

Chestnut-backed chickadee

This species is a cavity-nester that feeds in a variety of locations in and below the canopy. It primarily forages on insects that it gleans either from foliage or on the bark and branches of trees. It is typically associated with coniferous forests (Sturman 1968) and reaches maximum abundance in older natural forests (Manuwal 1991). The closely related black-capped chickadee prefers forests and riparian areas dominated by deciduous vegetation. Chestnut-backed abundance in the managed forests in this study varied among years and among structure classes. I1: was the 4th most abundant species, comprising 9.5% of all bird detections over the 3 years. This species was noticeably lower in abundance in closed-canopy sites in preference for either younger or older forest age classes (see Table 12) (Fig. 8). Its maximum recorded abundance was an average of 17.3 birds per stand per year in the harvest-age class in 1995. The abundance of chestnut-backed chickadees was significantly and positively correlated with logs, counts of dominant Douglas-fir and true fir as well as counts of sub-dominant conifers (combined $R^2 = 0.92$).

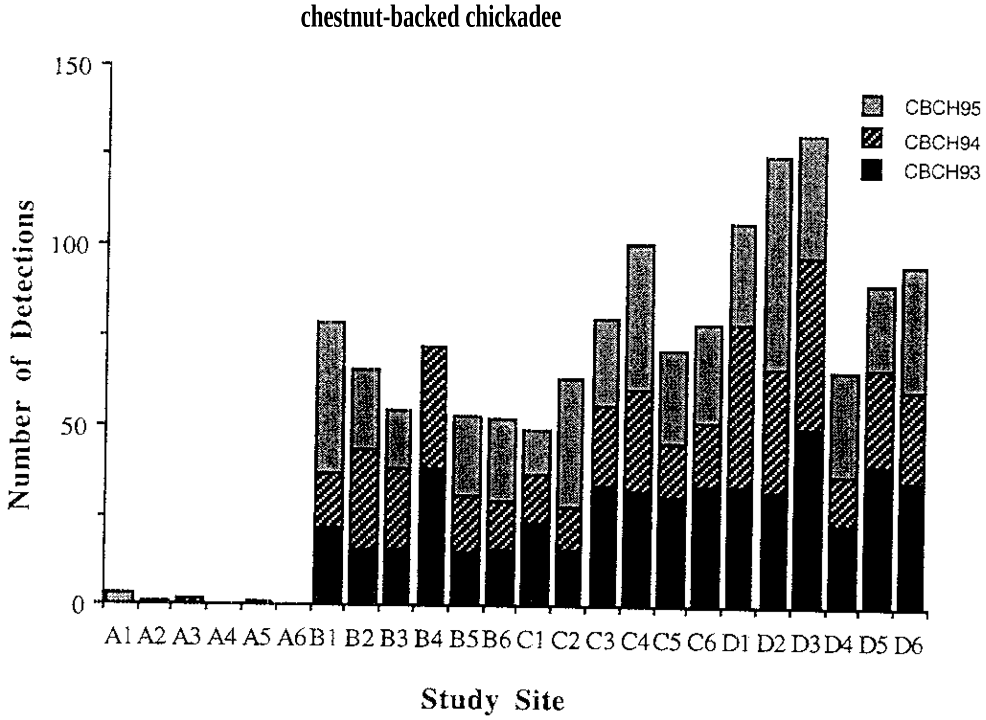


Figure 8. Number of detections of the chestnut-backed chickadee among 4 forest structural age classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Dark-eyed junco

The dark-eyed junco is a ground nester that feeds on seeds and insects on the ground as well as on shrubs and low branches of trees. In this study, juncos comprised 5.7% of over 20,000 detections. This species was clearly most associated with early regeneration sites (Fig. 9). The number of detections was 5-7 times greater in clearcuts than other forest structure classes (Table 12). Numbers of juncos were most clearly correlated with dominant Douglas-fir and true fir, and counts of sub-dominant coniferous trees 10-50 cm d.b.h, and >3 m tall.

We do not envision any *management* problems with juncos except where there is intensive use of *herbicides* to control broad-leafed plants. Being *a ground-nester,* this species depends on ground cover for protection and would likely incur *reproductive* failures or direct mortality if spraying occurred during nesting.

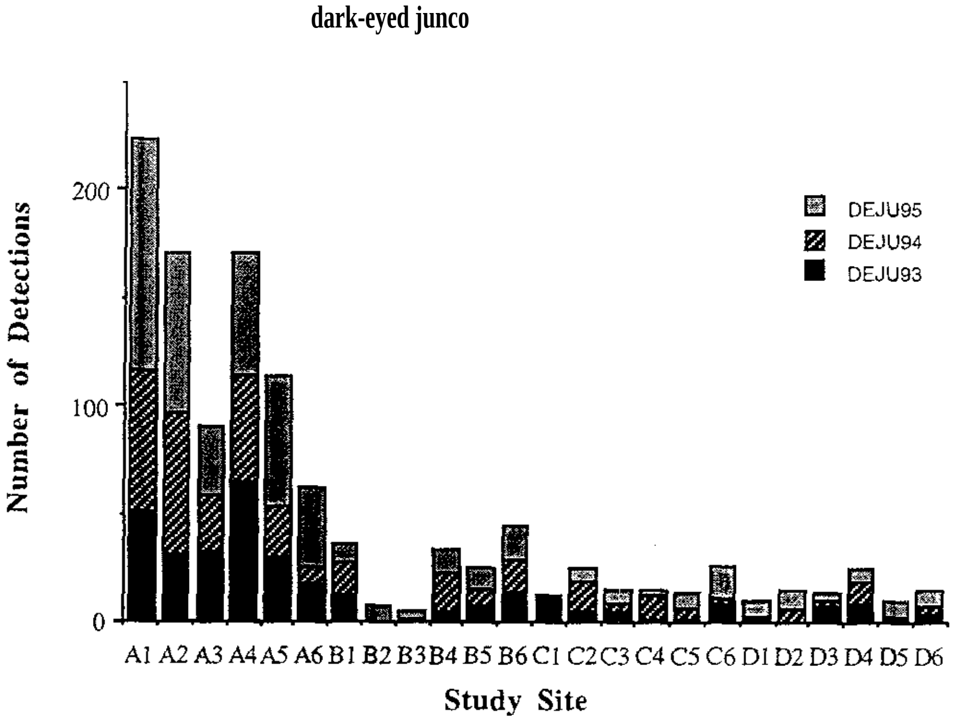


Figure 9. Number of detections of the dark-eyed junco among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Golden-crowned kinglet

The golden-crowned kinglet is a foliage-gleaning insectivore that nests in the canopy of coniferous forests. During the spring and summer this species spends most of its time in the upper canopy. During fall and winter it ventures to lower canopy levels for part of its foraging activity (Manuwal, pers. obs.). It comprised 9.2% of all bird detections in this study. Highest detections were found in the closed-canopy stands. Kinglets were one of the few species reaching highest abundance in closed-canopy stands. It was less common in pre-canopy and harvest-age stands, and absent in clearcuts (Table 11, Fig. 10). This may be because of its very small size and it being more efficient to forage in a continuous canopy with prey in closer proximity and more safety from predators. Only 3 habitat variables were significantly correlated with kinglet abundance: large stumps, abundance of sub-dominant coniferous trees <10 cm d.b.h and >3 m tall, and counts of dominant and sub-dominant deciduous trees >50 cm d.b.h. This species was probably selecting sites with large dominant conifers. It just happened that these sites also had large deciduous trees and stumps. The biological significance of these associations is not apparent.

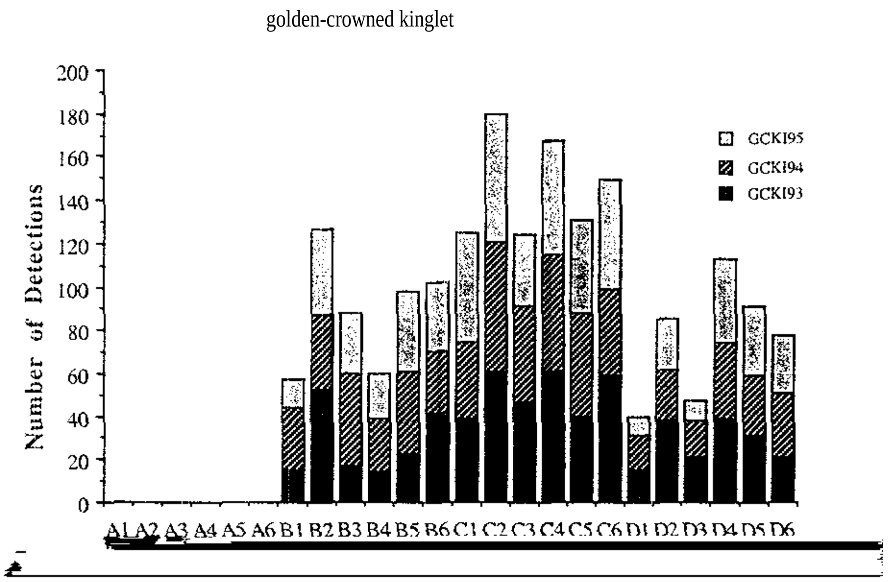


Figure 10. Number of detections of the golden-crowned kinglet among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Hermit- Townsend's warbler

The hermit-Townsend's warbler complex (designated as HETO) contains 2 currently recognized species of canopy-dwelling warblers and their hybrids. The study area lies within the area of hybridization and it is virtually impossible to distinguish the different forms by song. Many of the birds occupying our study area were hybrids (Pearson, unpubl. M.S. thesis). Both species glean insects from tree foliage and construct cup nests in the upper canopy of coniferous forests. TherE; was much among-stand variation in abundance (Fig. 11). These 2 species comprised about 4% of all detections. There was no difference in abundance between closed-canopy and harvest-age stands (Table 11). There were no detections in clearcuts and few in pre-canopy stands. HETO abundance was significantly correlated with 4 variables: counts of sub-dominant coniferous trees 10-50 cm and >3 m tall, counts of dominant and sub-dominant deciduous trees (DEClDDD and DECIDLD; Table 13), and counts of dominant and sub-dominant Douglas-fir >50 cm d.b.h. These 4 variables accounted for 86% of the variation in abundance.

Since these species are closely associated with closed-canopy and harvest-age managed forests, no conservation problems are anticipated.

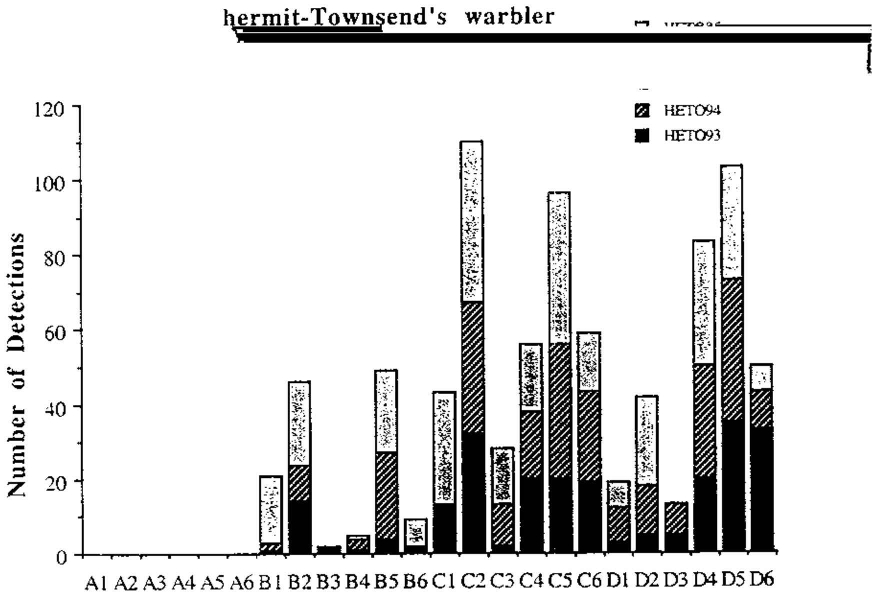


Figure 11. Number of detections of hermit-Townsend's warblers among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Pacific-slope flycatcher

This species captures insects in the air space in and below the tree canopy. It nests in a variety of locations ranging from cavities to cup nests between exfoliated bark and red alder coppice. Abundance differed among years and among stand types (Table 12). In this study, the Pacific-slope flycatcher made up 9.4% of all detections, making it 1 of the most abundant species. It was clearly associated with closed-canopy and harvest- age stand types (Fig. 12). In all years, abundancE; was highest in harvest-age stands where it comprised almost 16% of total bird detections. Over 91% of the variation in abundance was explained by the following habitat variables: berry-producing shrubs (BPSHR), abundance of dominant Douglas-fir and true fir (PSABMD), and abundance of sub-dominant coniferous trees 10-50 cm d.b.h, and >3 m tall (CONIFS) (Table 13).

No special management is required for this species.

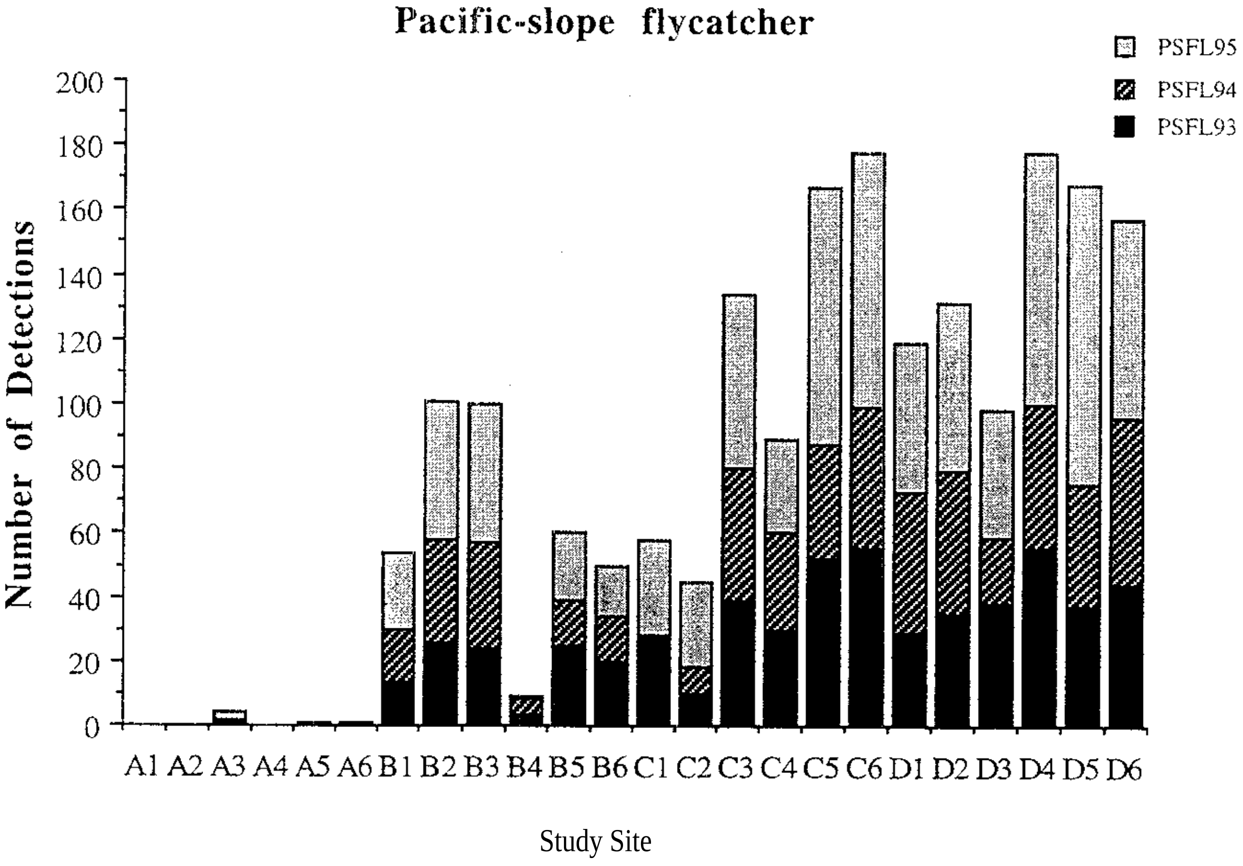


Figure 12. Number of detections of the Pacific-slope flycatcher among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Steller's jay

The Steller's jay is omnivorous and acts as a nest predator of other birds. Nesting usually occurs in shrubs, understory conifers, or in the lower branches of conifers. Although widespread and easily detected at times, the Steller's jay only comprised 1.3% Of all bird detections. This species was found in all habitat types and no pattern of abundance and distribution could be detected because of extreme variation in abundance among stands (Fig. 13).

No special management is necessary for this species.

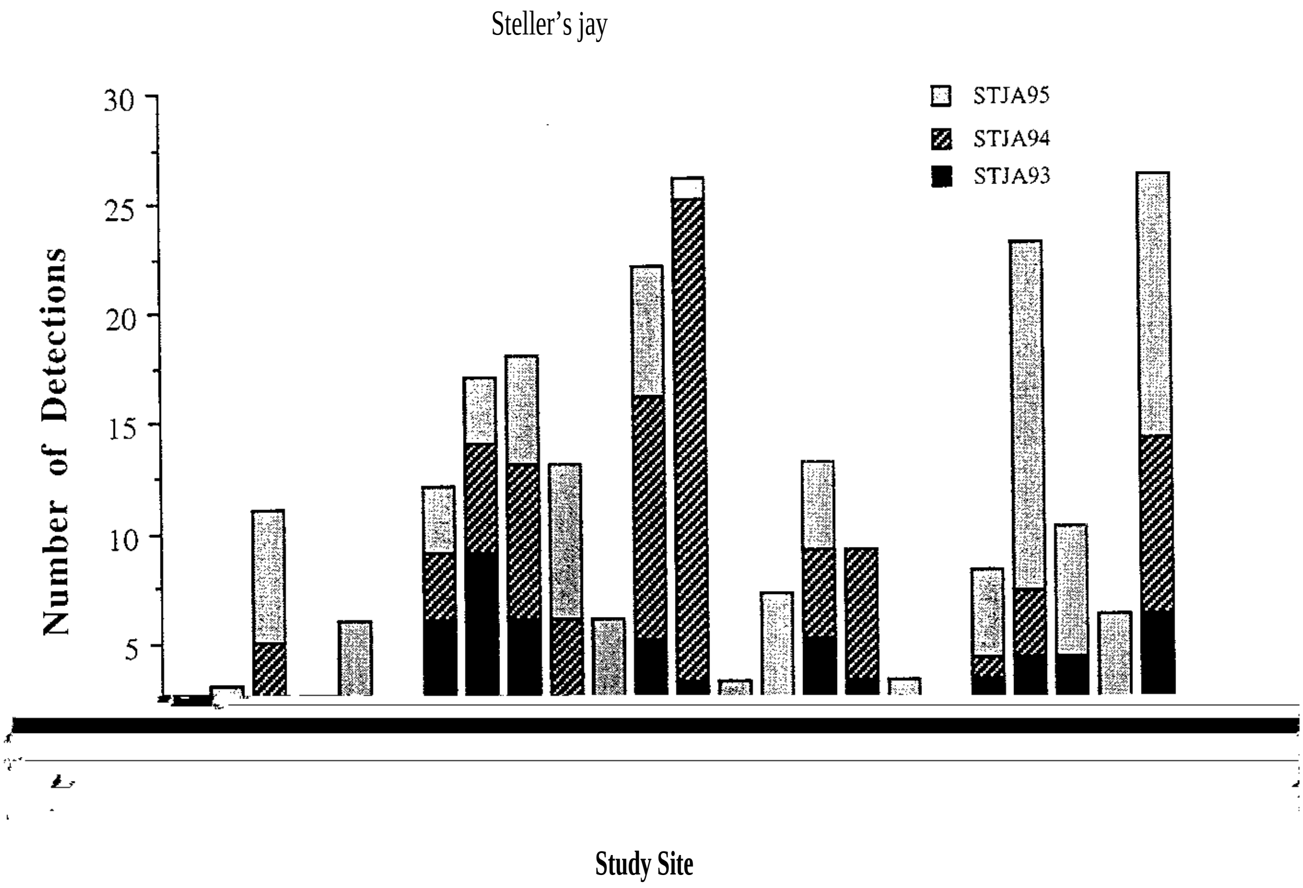


Figure 13. Number of detections of Steller's jay among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Varied thrush

This thrush forages on seeds, berries, and insects that it obtains on or near the forest floor. In this study, only about 2% of all detections were of the varied thrush. There were substantial differences in abundance between years and among stands (Fig. 14). Wells and Rosenberg (1996) showed that since 1988, varied thrush abundance levels show a biennial cycle, that is, they alternate high and low abundance years. The reason for this apparent cyclic pattern is unclear but is probably food-related. Because of low sample size and high variation, no statistical tests were possible. With the exception of stand B6, the varied thrush seemed to be more abundant in older age classes (Fig. 14).

No special management efforts are needed for this species.

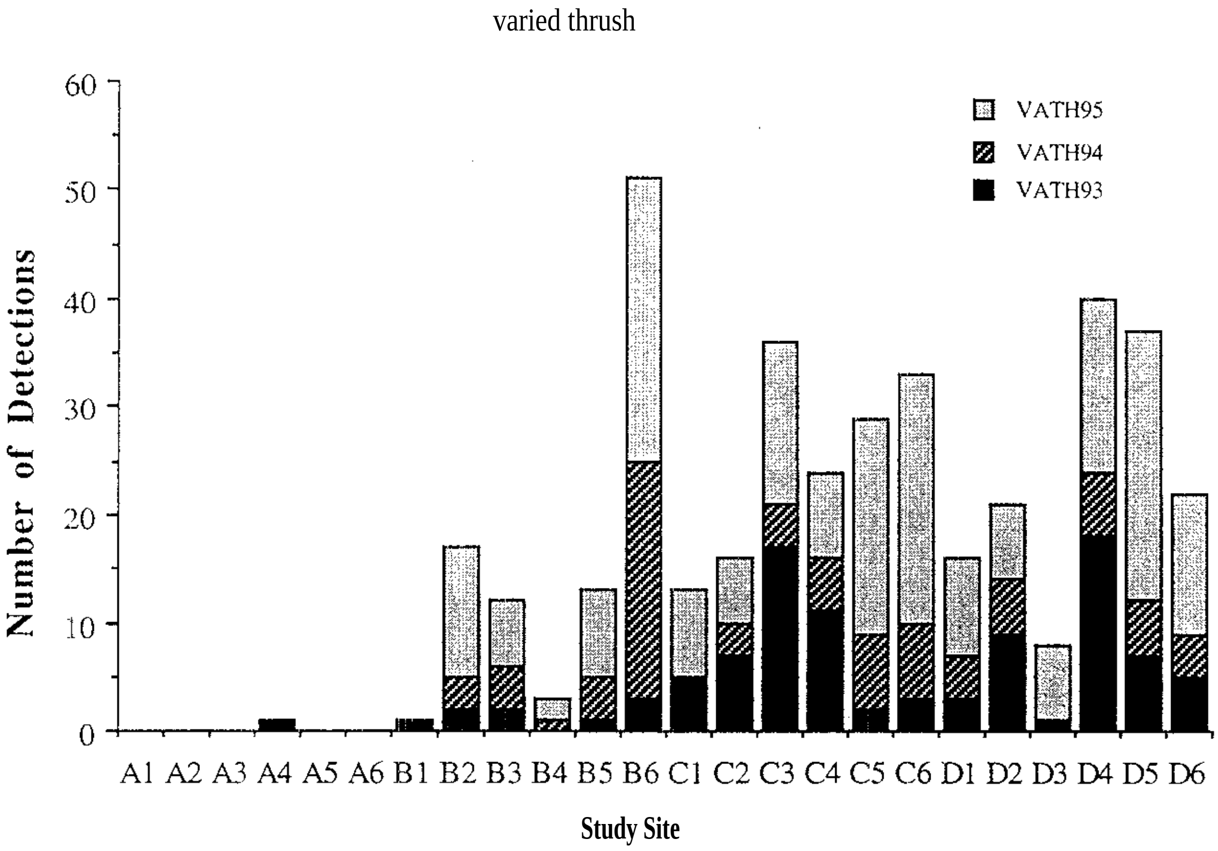


Figure 14. Number of detections of the varied thrush among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

White-crowned sparrow

This sparrow feeds on insects and seeds that it obtains from the ground or low shrubs. It nests primarily on the ground. This species made up 5.6% of all bird detections and among these, 98.7% were in clearcuts (Fig. 15). The primary and almost exclusive habitat was the clearcut sites that were characterized by open habitat dominated by small shrubs and herbaceous vegetation. Over 85% of the variation in abundance was explained by 3 variables (Table 14): counts of sub-dominant coniferous trees 10-50 cm d.b.h, and >3 m tall (CONIFS), counts of dominant deciduous trees of any d.b.h. (DECIDDD), and counts of dominant and sub-dominant deciduous trees >50 cm d.b.h. (DECIDLD) (Table 13).

No conservation problems are anticipated with this species with the exception of its potential vulnerability to the use of herbicides during the nesting season.

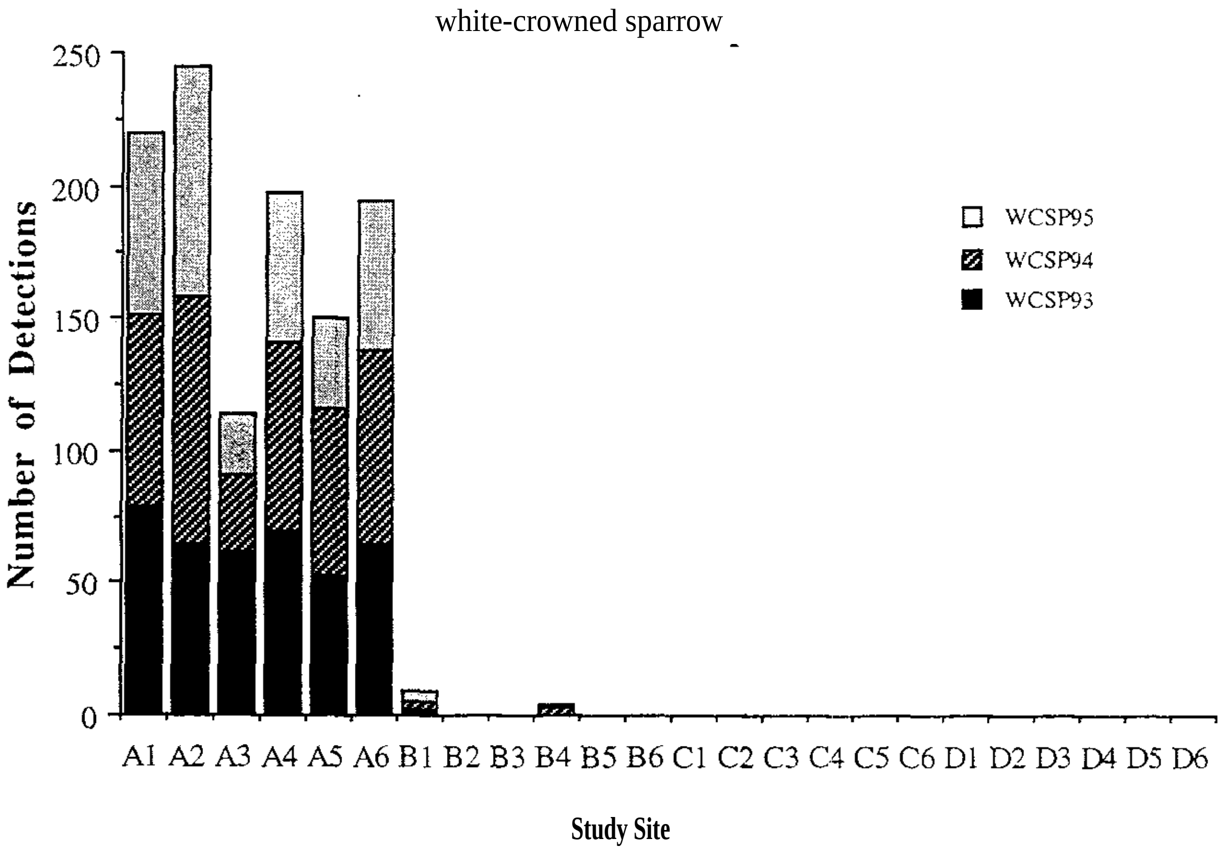


Figure 15. Number of detections of the white-crowned sparrow among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Wilson's warbler

The Wilson's warbler is a foliage-gleaning insectivore that feeds and nests primarily in the low- to mid-canopy of coniferous forests. It made up 4.7% of all bird detections. It clearly preferred pre-canopy and harvest-age stand types where there was the strongest chance of finding an abundance of shrubs and small trees below the canopy (Fig. 16). In pre-canopy sites it typically comprised over 10% of all bird detections, whereas in harvest-age stands it made up 5.5% of total detections. Only 2 habitat variables were significantly related to Wilson's warbler abundance: number of snags >10 cm d.b.h, and counts of dominant Douglas-fir and true fir. These 2 variables, however, accounted for only 45% of the variation (Table 14).

No management concerns are anticipated with this species unless there is a substantial amount of thinning of both coniferous and deciduous trees. Excessive thinning sometimes results in very open stand conditions with little understory foliage volume. Stand structural complexity, particularly in the understory, appears to be important for this species.

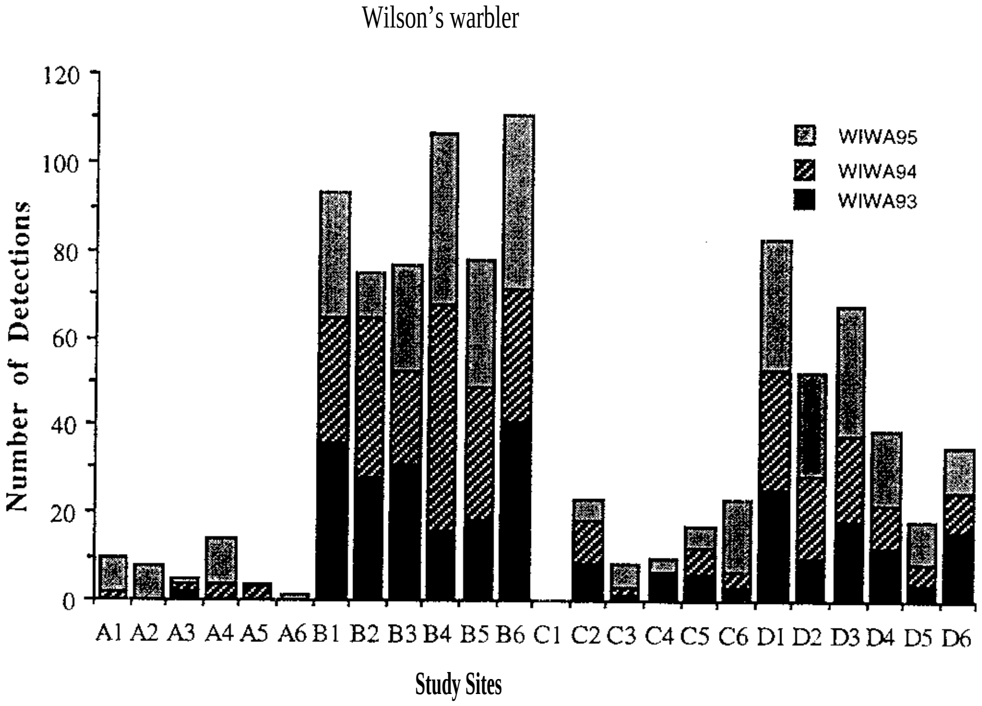


Figure 16. Number of detections of the Wilson's warbler among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Winter wren

The winter wren feeds almost exclusively on insects on the ground. Nests are often found among forest-floor woody debris. The winter wren was the most abundant bird in the surveyed managed Douglas-fir forests. Highest abundance occurred in harvest-age stands where it made up 28.2% of all detections (Fig. 17). It comprised 18% in pre-canopy and 15% in closed-canopy stands. Abundance varied significantly among years (Table 12). Such annual variations were also recorded in southeast Alaska by Dellasala and others (1996). Only 2 habitat variables were significantly correlated with wren abundance (but accounted for 85% of the variation; Table 14): counts of dominant Douglas-fir and true fir, and counts of sub-dominant coniferous trees 10-50 cm d.b.h. and >3 m tall.

No conservation problems are anticipated for this species.

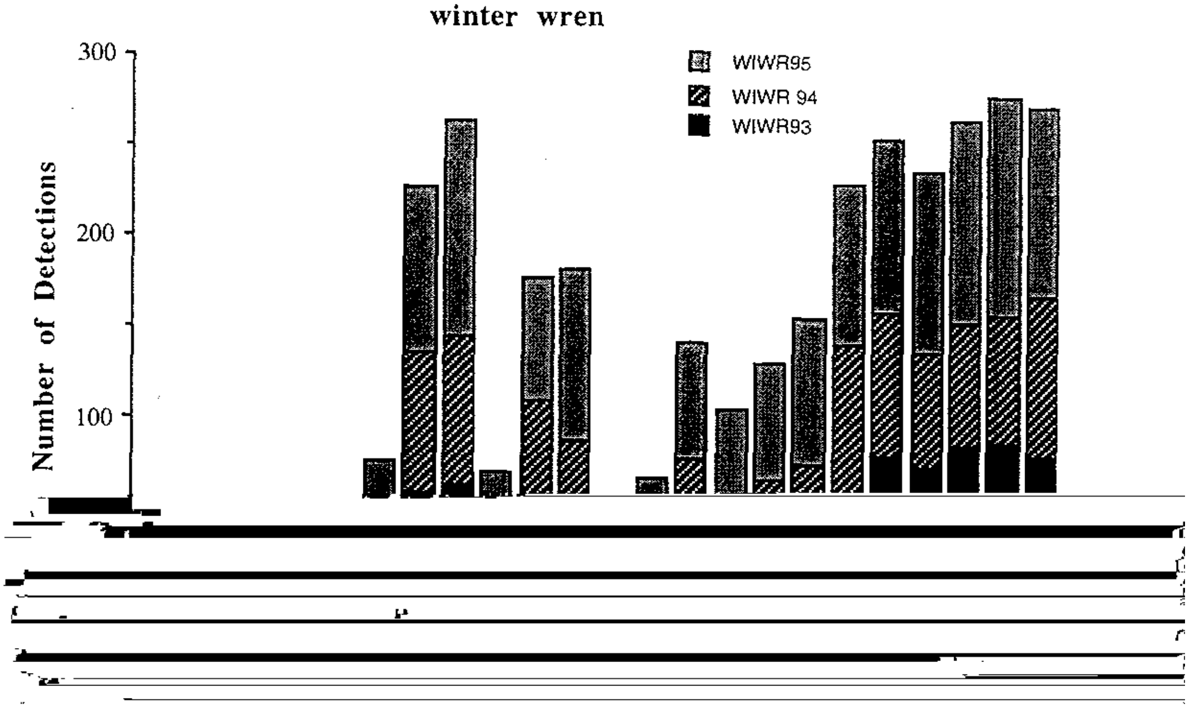


Figure 17. Number of detections of the winter wren among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Band-tailed pigeon

Band-tailed pigeons feed on a variety of seeds and fruits obtained from the tree canopy or shrub layer. This species is classified as a game species in the Pacific Northwest. Major population declines have occurred in band-tailed pigeon populations from northern California to Washington. This species only accounted for 0.3% of all bird detections in our study. There was substantial variation among years and forest age classes (Fig. 18). The band-tailed pigeon is difficult to detect because of its secretive habits and infrequent calling. More effort is needed to determine the status of this species in the managed forest landscape.

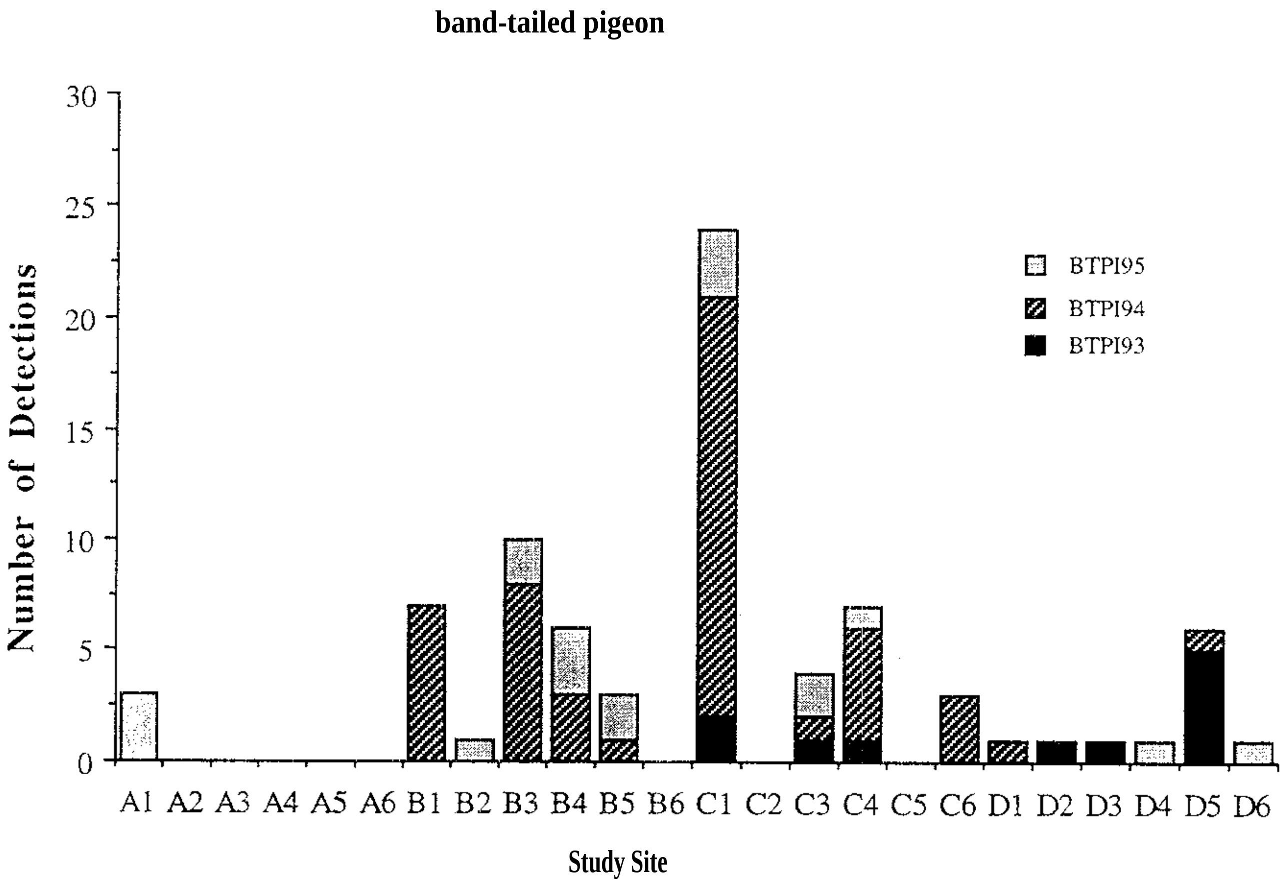


Figure 18. Number of detections of the band-tailed pigeon among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Brown-headed Cowbird

Only 17 brown-headed cowbirds were detected during this study and of these only 6 were detected within 50 m of count stations. Obviously, cowbirds did not find these managed forests suitable breeding areas. Consequently, the probable incidence of brood parasitism is likely to be extremely low at this point in time. This situation could change in the future since brown-headed cowbirds are relatively common in the Puget Sound lowlands, particularly in open valleys and at the edges of metropolitan areas. Rothstein (1994) has discussed the westward expansion of the cowbird, especially in California, Oregon, and Washington (see also Robinson and others 1995). Cowbird females are capable of Laying 30-40 eggs per season (',Scott and Ankney 1983), so a relatively small number of cowbirds could have an impact on their hosts if they invaded a small area.

Brown creeper

This species gleans insects and spiders from the surface and crevices of tree bark. Nesting also occurs in crevices or other irregularities on the surface of tree trunks. In this study, only 1.3% of all detections were of the brown creeper. It clearly showed a preference for harvest-age stands (Fig. 19) where it comprised 4.3% of all detections. In another study, Mariani and Manuwal (1990) have shown that it is more efficient for creepers to occupy older forests that have old trees with deep bark fissures because they would spend less energy and time finding prey there than in younger stands where prey density is lower and more widely scattered.

Management of brown creepers would benefit from the continued focus on providing a consistent supply of harvest-age stands in the managed forest landscape.

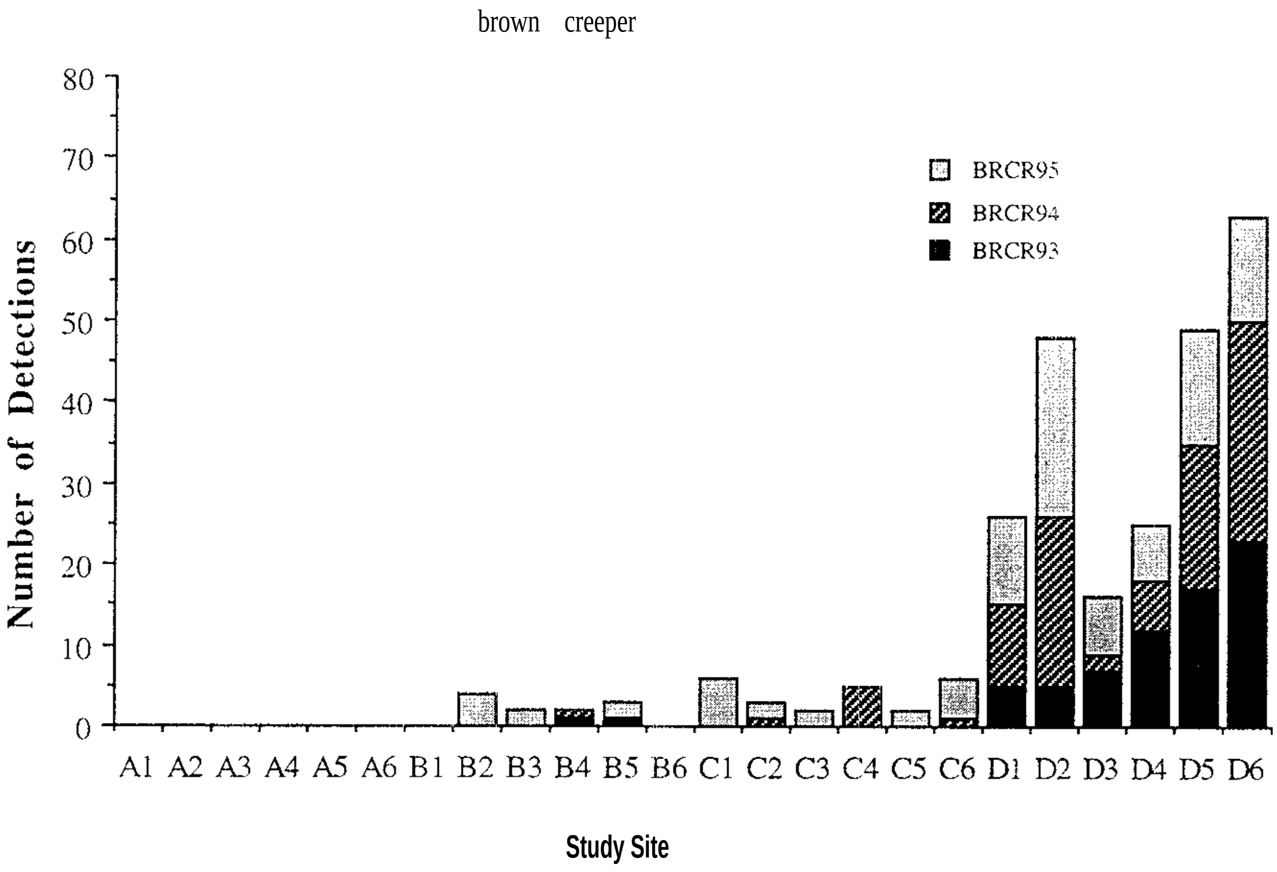


Figure 19. Number of detections of the brown creeper among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Red-breasted nuthatch

The red-breasted nuthatch is a cavity-nester that forages on bark insects and conifer seeds. It comprised only 0.7% of all bird detections and showed a habitat occupancy pattern very similar to the brown creeper (Fig. 20). In harvest-age stands, nuthatches comprised about 2% of the total detections. There was substantial among-year variation in abundance. Low sample size prevented statistical analysis of habitat variables and nuthatch abundance.

The abundance of the red-breasted nuthatch in managed forests was lower than expected compared with other published studies (e.g., Lundquist and Manuwal 1990; Carey and others 1991; Manuwal 1991). Forest managers need to provide suitable dead and dying trees to provide nest-sites, roost-sites, and feeding substrates More study is required to determine what factors are controlling the distribution and abundance of this species.

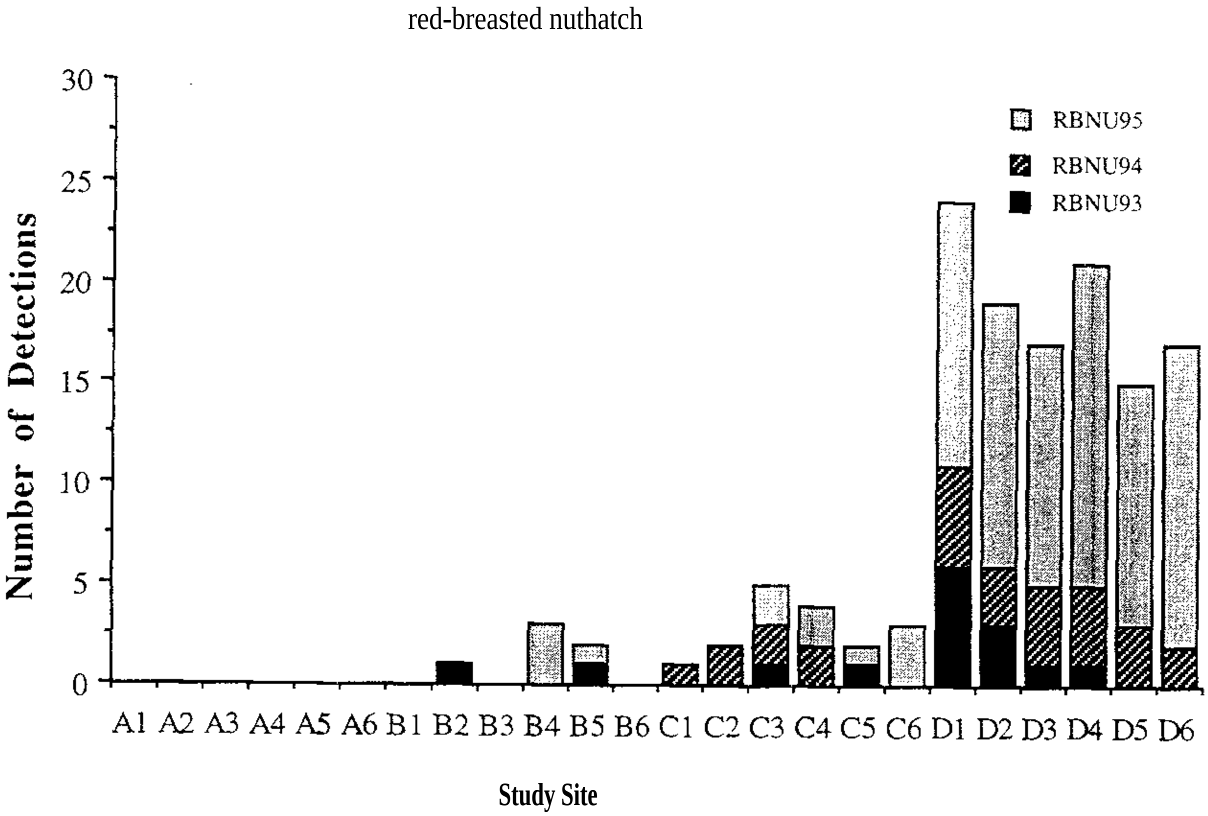


Figure 20. Number of detections of the red-breasted nuthatch among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Hairy woodpecker

The hairy woodpecker is a cavity-nester that feeds on bark insects and excavates nest and roost holes in trees. It is the most common woodpecker in the coniferous forests of the western Cascade Mountains (Manuwa11991). However, in this study, we found its abundance to be very low, comprising only 0.5% of all bird detections. It was most common in harvest-age stands (Fig. 21). Abundance differed significantly among years and forest age classes (Table 12). Low sample size prevented analysis of habitat variables.

Conservation efforts should focus on providing large-diameter dead and dying trees in the managed forest landscape.

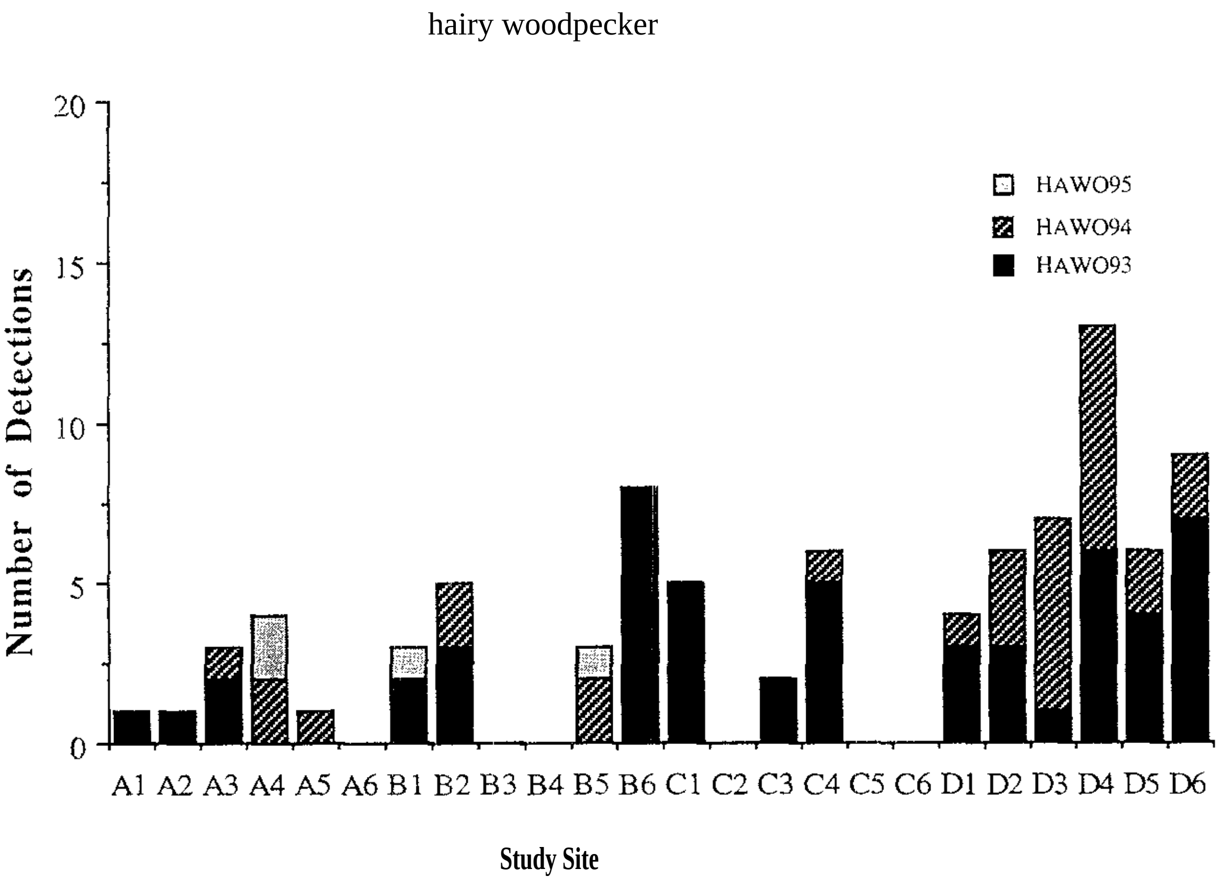


Figure 21. Number of detections of the hairy woodpecker among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Pileated woodpecker

A total of 27 pileated woodpeckers were detected in this study, but only 5 were within 50 m of point count stations (Fig. 22). The loud call and tapping of this species usually makes it easily detectable from distances well beyond 100 m. The detections were distributed in the following manner: clearcuts 3 detections, pre-canopy 8 detections, closed-canopy 0 detections, and harvest age 16 detections. Pileated woodpeckers are known to have large home ranges and can be quiet for long periods of time so they can go undetected. It is likely that our sampling does not accurately reflect either habitat affinities or relative abundance levels.

More research is needed to accurately assess the response of the pileated woodpecker to the managed forest landscape.

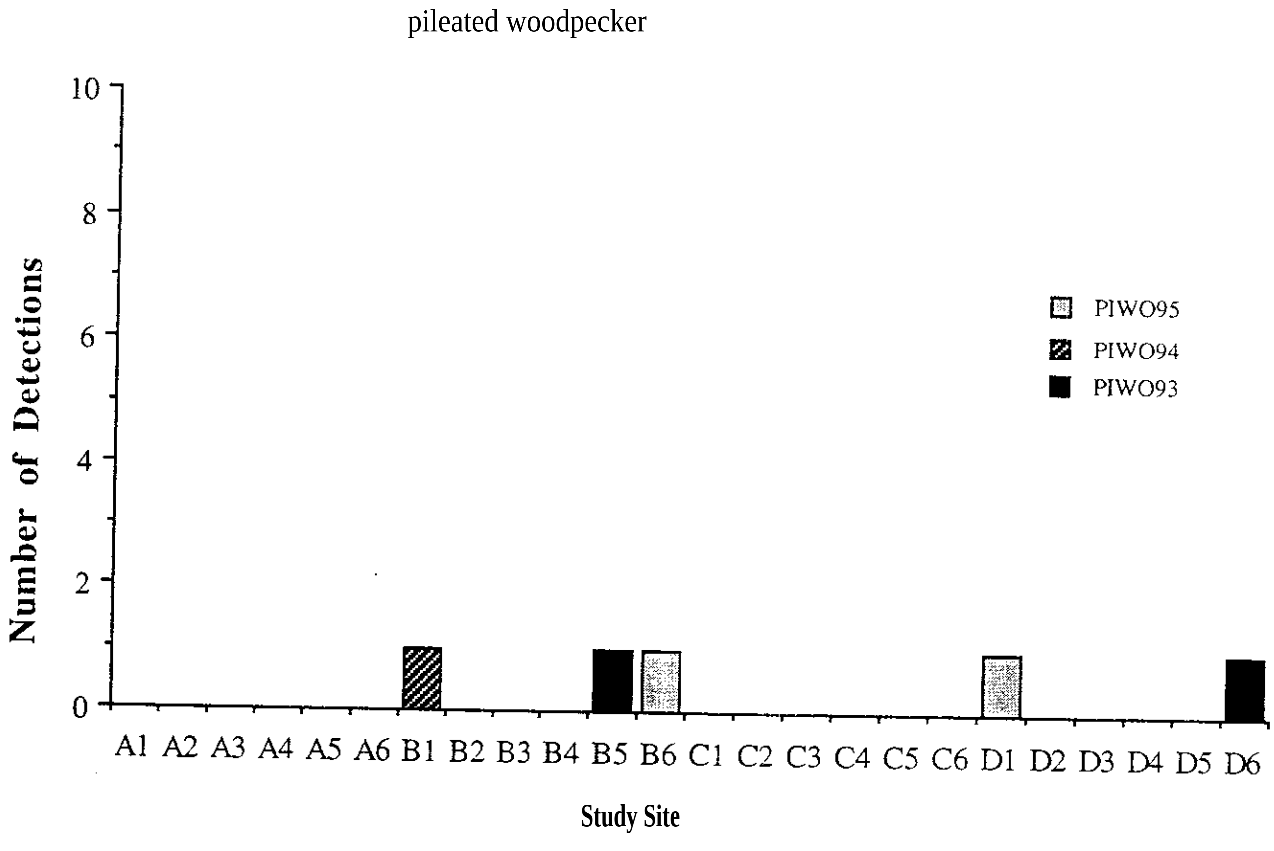


Figure 22. Number of detections of the pileated woodpecker among 4 forest structure classes during 1993~1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Red-breasted sapsucker

No red-breasted sapsuckers were detected in this study. This species is a cavity-nesting woodpecker that forages on the sap and insects from a variety of coniferous and deciduous trees. Its secretive habits made it difficult to detect. Nevertheless, even if we assume that the field observers failed to detect some of the birds, the abundance level must be extremely low. Even in natural forests of the western Cascades of Oregon and Washington, few sapsuckers are detected (Gilbert and Allwine 1991, Manuwa11991), but more were found in the Oregon Coast Range by Carey and others (1991).

Clearly, this species deserves special attention. More information is needed on its natural history, distribution, and abundance in managed forests.

Vaux's swift

This swallow-like species nests colonially in large hollow snags. It captures insects in the air space above forests and clearings. Only a single bird was detected in this study (site A in 1994). Since there are few large snags in the stands we studied, few swifts might be expected to occupy those forests.

Management of this species should focus on providing a constant supply of large-diameter snags across the managed forest landscape. Perhaps some experimental method could be developed involving the placing of large snags in pre-canopy managed forests that were extracted from other sites.

Willow flycatcher

This flycatcher feeds on flying insects which it captures in open areas such as clearcuts. Nests are usually placed in deciduous trees or shrubs. Willow flycatchers made up 2.4% of all detections. There was a clear affinity for clearcuts (Fig. 23). Two of the 6 pre-canopy stands (B1 and B4) also had willow flycatchers in them. Two individual flycatchers were detected in D4 and D6 but they could have been misidentified since the habitat was atypical for the species.

Clearcuts with substantial numbers of deciduous trees and shrubs are needed to maintain populations of this species. Use of herbicides to remove deciduous shrubs and trees could negatively impact this species.

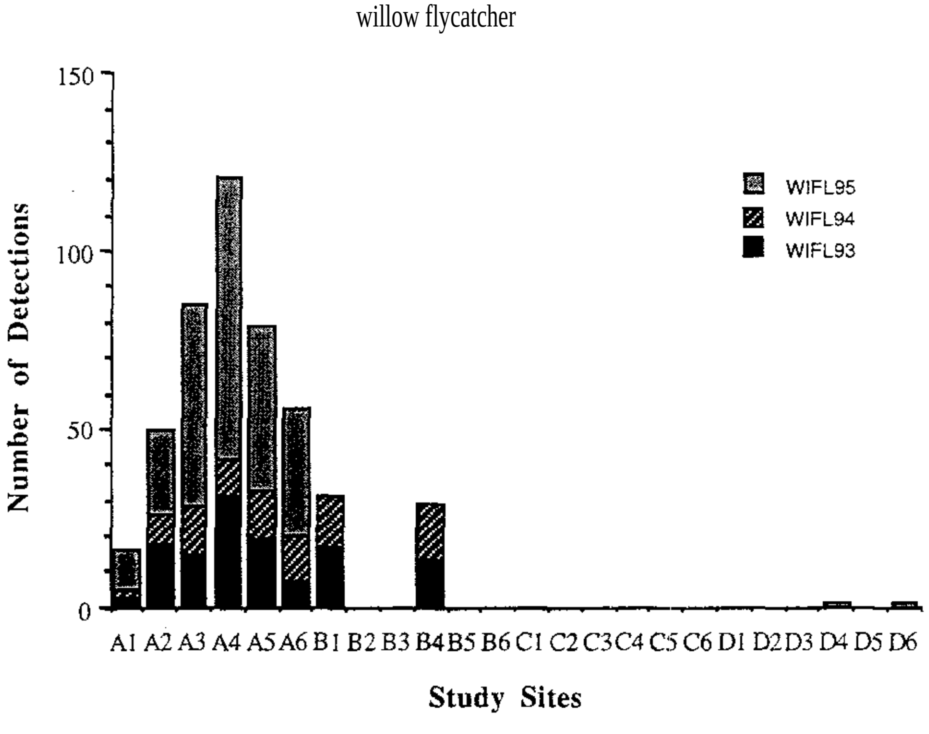


Figure 23. Number of detections of the willow flycatcher among 4 forest structure classes during 1993-1995. Stand types: A clearcut, B pre-canopy, C closed-canopy, D harvest age.

Raptors

Hawks and owls were rarely encountered during this 3-year study. Red-tailed hawks were occasionally seen over some sites but no nesting was documented on the study sites. The sharp-shinned hawk should be the most common hawk in these coniferous forests but only 1 was detected (beyond 50 m). Point counts may not be the best method to detect the presence of raptors but we expected to detect more than we did. Among the owls, only the great-horned and barred owls were detected. This too is surprising since the pygmy owl, and to a lesser degree the saw-whet owl, are relatively common in western Washington. One possible explanation is that observers did not arrive sufficiently early to hear the birds hooting.

LANDSCAPE-LEVEL CORRELATIONS

Landscape effects on birds were examined at the individual species and community levels. Linear stepwise regression coefficients were calculated for 28 bird species. Only birds with at least 30 detections were used in the analysis, Each year was treated separately since there were among-year variations in bird species richness and abundance. Nine FRAGSTAT indices were entered into the regression equations (Table 15). Details of the results of these regression analyses of the 28 species are in the Appendix Table A-2.

Significant relationships between individual species abundance existed for 6 of the 9 FRAGSTAT indices. Nine bird species had a positive and 8 species had a negative relationship with total clearcut area (CCAREA). Nine species were positively correlated with total area of mature forest (MAT_AREA) (Table 16). The varied thrush and winter wren also had negative responses to clearcuts so these 2 species may be attracted at the landscape level to more extensive stands of mature forests away from clearcuts. The Pacific-slope flycatcher, Wiison's warbler, hermit-Townsend's warbler, red-breasted nuthatch, brown creeper, hairy woodpecker, and evening grosbeak all had significant positive responses to the amount of mature forest in the 100-ha circle. The orange-crowned warbler was the only species associated with the amount of clearcut edge. Chestnut-backed chickadees had a negative association with edge density. The Swainson's thrush was negatively associated with habitat patches. Alternatively, the dark-eyed junco, white-crowned sparrow, and rufous-sided towhee were positively associated with interspersion and juxtaposition. This seems to suggest that these species are attracted to habitat patchiness.

At the community level, no significant relationships were found between bird species richness and area of clearcuts, area of mature forests (Figs. 24-25) and clearcut edge (1993, $R^2 = 0.031$, $p = 0.48$; 1994, $R^2 = 0.039$, $p = 0.43$; 1995, $R^2 = 0.054$, $p = 0.35$). Similarly, no significant relationships were found between the number of bird detections and area of clearcuts, area of mature forests (Figs. 26-27) and clearcut edge (1993, $R^2 = 0.020$, $p = 0.55$; 1994, $R^2 = 0.001$, $p = 0.94$; 1995, $R^2 = 0.002$, $p = 0.84$).

Table 15. Indices produced by FRAGSTATS used in landscape analysis of bird species abundance and community characteristics.

Index name (units)	Description[1]
CCAREA (ha)	Total area of clearcuts (3-8 yrs old)
CCED (m/ha)	Total amount of clearcut edge
MAT AREA	Total area of mature forest (50-80 yrs old)
PATCHES	Number of patches
ED (m/ha)	Edge density
MNN (m)	Mean nearest neighbor index
SHDI	Shannon's diversity index
IJI (percent)	Interspersion and juxtaposition index
CONTAG (percent)	Contagion index

See McGarigal and Marks (1995) for a complete description and definition of each index.

Table 16. Summary of responses of bird species to landscape metrics (see Table 15 for a description of metrics),

Variable	Bird Species	Response (+ or -)	Variable	Bird Species	Response
CCAREA	White-crowned sparrow	+	MAT_AREA	Pacific-slope flycatcher	
	McGillivray's warbler	+		Wilson's warbler	
	American goldfinch	+		Hermit/Townsend's warbler	
	Bewick's wren	+		Varied thrush	
	Cedar waxwing	+		Red-breasted nuthatch	
	Song sparrow	+		Brown creeper	
	Rufous-sided towhee	4-		Hairy woodpecker	
	Willow flycatcher	4-		Evening grosbeak	
	Common yellowthroat	4-		Winter wren	
	Winter wren			Swainson's thrush	
	Dark-eyed junco			American robin	
	Golden-crowned kinglet			Orange-crowned warbler	
	Chestnut-backed chickadee			Black-headed grosbeak	
	Wilson's warbler			Song sparrow	
	Hutton's vireo		IJI2	Dark-eyed junco	
	Varied thrush			White-crowned sparrow	
	Steller's jay			Rufous-sided towhee	
CCED	Orange-crowned warbler		ED	Chestnut-backed chickadee	
PATCHES	Swainsen's thrush				

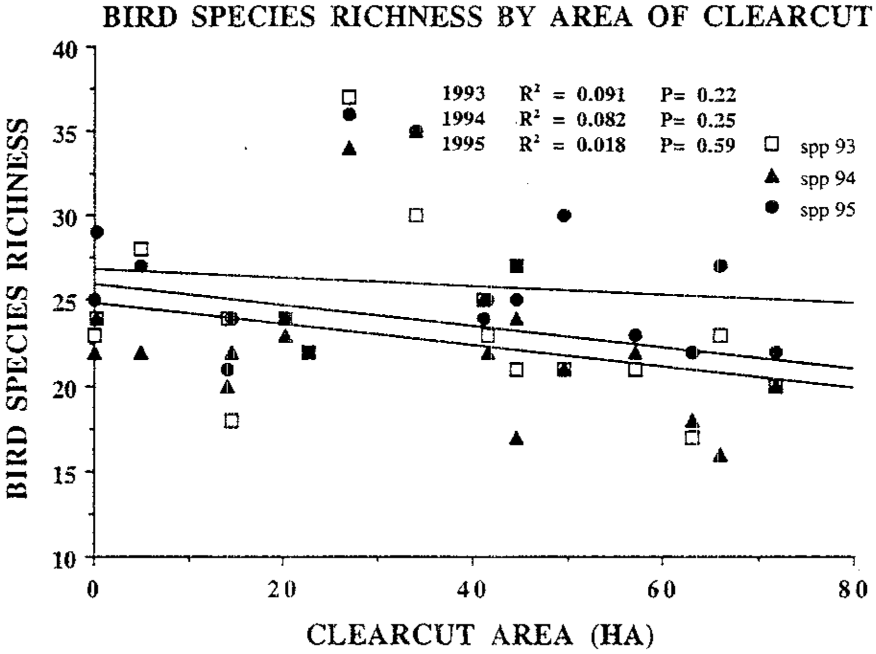


Figure 24. Number of bird species detected in study sites which varied in the amount of clearcut area within a IO0-ha circle surrounding the site.

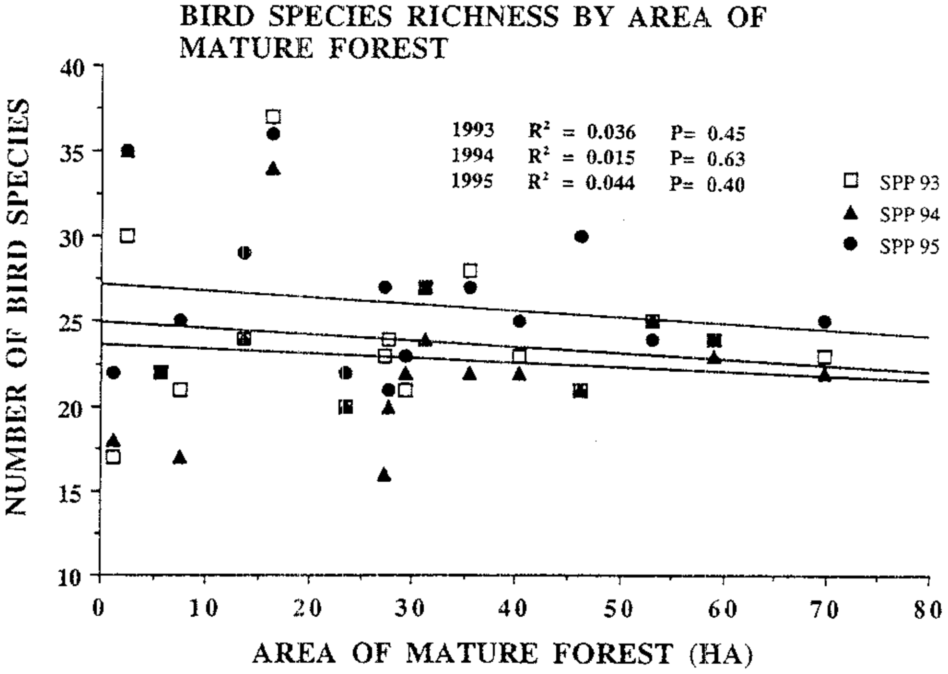


Figure 25. Number of bird species detected in study sites which varied in the amount of area of mature forest within a IO0-ha circle surrounding the site.

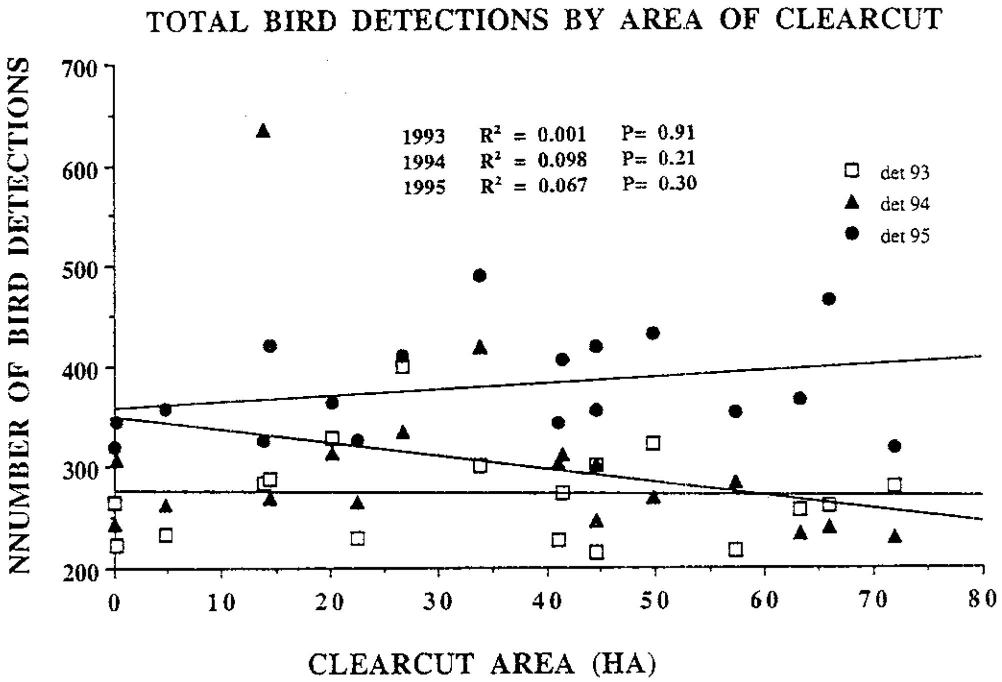


Figure 26. Number of birds detected in study sites which varied in the amount of area of clearcuts within a lO0-ha circle surrounding the site.

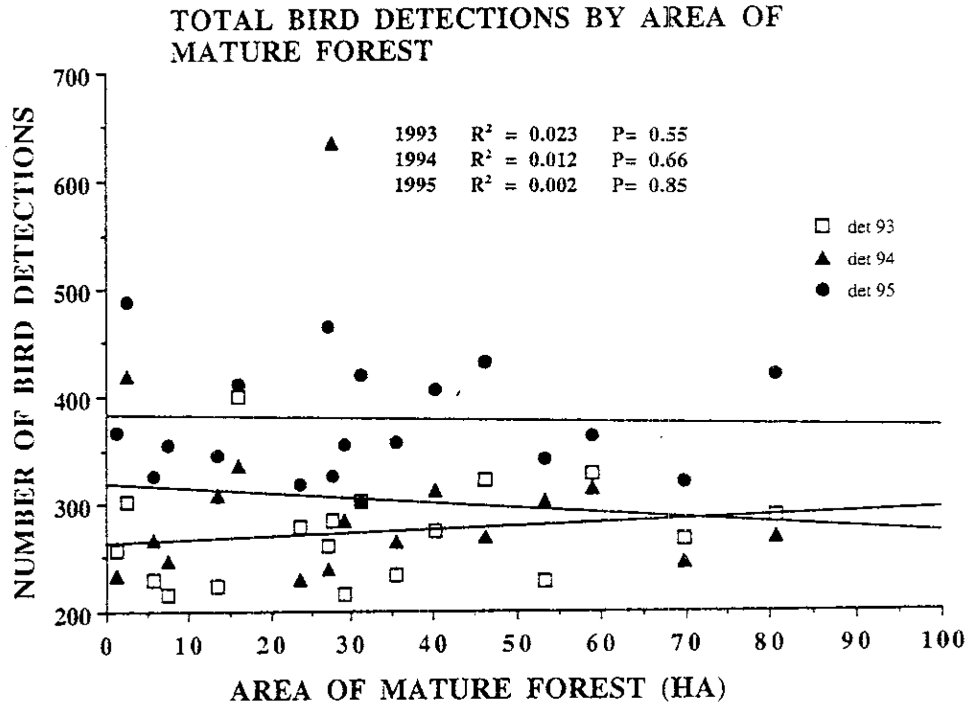


Figure 27. Number of birds detected in study sites which varied in the amount of area of mature forest within a lO0-ha circle surrounding the site.

Twenty-eight songbird species showed either significant negative or positive responses to landscape variables. The largest number of species (17) responded to the amount of clearcut area near the study sites. Virtually all species with a positive response are known to be associated with open, shrubby habitats, so even at the landscape level, these species tend to be most common in a landscape with a large amount of land in clearcuts. All 9 bird species typically forage or nest either on the ground or in shrubs and small trees. These species are known as pioneer species and typically are the first ones to colonize new clearcuts and fire sites. On the other hand, species having negative responses, such as the winter wren, golden-crowned kinglet and chestnut-backed chickadee, are most associated with canopied forests, so their responses are somewhat predictable.

Thirteen bird species responded significantly to the area of mature forest. Those with positive responses included species known to be associated with forests with a multi-layered canopy. These include the Pacific-slope flycatcher, Wilson's warbler, varied thrush, and winter wren. Furthermore, cavity-nesting species also showed a positive response to mature-forest area. This group included the hairy woodpecker and red-breasted nuthatch. Neither species was very common across this managed forest landscape, perhaps because patches of older mature forests are relatively few in number and are widely scattered. The evening grosbeak, a seed-eating finch, was also associated with mature-forest area. The relationships between this species and habitat characteristics at the individual forest stand and landscape levels are difficult to interpret. Although the species is adapted for eating conifer seeds, it is also known to opportunistically feed on defoliating insects such as spruce budworm (Manuwal, pers. obs.; Takekawa and others 1982). The hermit/Townsend's warbler complex normally is associated with young to mature coniferous forests, but is less common in very old stands and forests dominated by western hemlock (Manuwal 1991). Its positive response to area of mature forest may simply reflect that it prefers more extensive and easily accessible uniform stands of conifers.

Five species had a negative association with area of mature forest. These included the following species that are most common in edge habitat. The orange-crowned warbler showed a positive response with clearcut edge (Table 16) and is often found nesting on shrubby hillsides. The Swainson's thrush is associated with .open forests with a dense understory of deciduous trees and shrubs. Most of the mature forests in the areas around the study sites lacked this component. The American robin is uncommon in dense forests or nearly pure conifer stands and so would tend to avoid a landscape dominated by such forests. The black-headed grosbeak is strongly associated with deciduous trees and shrubs, particularly in riparian areas. Although some individual stands did have deciduous components, most did not and so this species would not be expected to be associated with a landscape dominated by dense stands of relatively large conifers. A similar argument could be made for the song sparrow which is clearly an edge species. Edges dominated by deciduous shrubs would be most attractive to this species. It would probably avoid areas dominated by mature coniferous forests. The chestnut backed chickadee was negatively associated with edge density, indicating that this bird may be an area-sensitive species.

The primary determinants of bird species richness and abundance appear to be at the stand level. The vast majority of birds associated with the managed forest landscape are small songbirds that have relatively small territories and home ranges. Less than 50% of the bird species showed any relationship with landscape variables Birds with large territories and home ranges such as the blue grouse, ruffed grouse, gray jay, common raven, pileated woodpecker, hawks, and owls were simply not sufficiently common to analyze. Landscape-level habitat attributes may provide an explanation for the distribution and abundance patterns of these species rather than species with less mobility.

MANAGEMENT IMPLICATIONS

None of the bird species detected in this study are federally classified as threatened or endangered species. However, there are 4 areas in which special management efforts should be considered: 1) increasing the amount of dead and dying trees; 2) retaining large dominant live conifers; 3) increasing the number of deciduous trees and shrubs; and 4) increasing bird species diversity.

Dead and dying trees

Compared with young natural forests (see Carey and others 1991, Gilbert and Allwine 1991, Manuwa11991) there are substantially fewer cavity-nesters, especially primary excavators, in intensively managed forests. Of particular concern are the low numbers of the red-breasted nuthatch, brown creeper, hairy woodpecker, pileated woodpecker, red-breasted sapsucker, and Vaux's swift. There were essentially no sapsuckers or swifts in the forested landscape we surveyed. Cavity-nesters require cavities for nesting and roosting, and suitable foraging sites which are usually dead or dying trees. Management efforts should be directed at providing these dead and dying trees across the landscape (see Raphael and White 1984, Zarnowitz and Manuwal 1985).

Feeding substrates must also be provided in order to maintain cavity-nester populations. With the exception of the hairy woodpecker, all cavity-nesters in Douglas-fir forests feed primarily on invertebrates found on live trees. The hairy woodpecker prefers dead trees for foraging (Lundquist and Manuwal 1990). Most species also show seasonal shifts in both foraging location and feeding behavior. Large diameter Douglas-fir are particularly important feeding substrates to woodpeckers, nuthatches and brown creepers (Lundquist and Manuwal 1990, Mariani and Manuwa11990). Managers could provide better feeding habitat by retaining some healthy and defective harvest-age Douglas-fir in harvested stands. The Vaux's swift may be of particular concern since its preferred nesting site is large hollow snags. The managed forests in this study lacked these structures.

large dominant conifers

The abundance of many bird species were positively correlated with large (50-100 cm d.b.h.) dominant Douglas-fir, true fir, and sub-dominant conifers 10-50 cm d.b.h and at least 3 m tall. Provision of these types of trees would enhance bird species diversity and potentially increase abundance levels of some bird species. One strategy that might be adopted is green-tree retention. Such retention would provide a legacy which would enhance structural diversity in the developing forest. If these legacies are retained indefinitely, they could provide nesting sites for the Vaux's swift once the trees died and became hollow.

Deciduous trees and shrubs

Several bird species require deciduous trees and shrubs for nesting and feeding. In clearcuts, these habitat features are important for the majority of species, especially the willow flycatcher, white-crowned sparrow, and American goldfinch. In the forest (stages B-D), the presence of deciduous vegetation increases structural complexity which supports higher numbers of the Wilson's warbler, black-throated gray warbler, and black-headed grosbeak. Herbaceous ground cover protects ground-nesting species such as the winter wren, dark-eyed junco, ruffed grouse, and blue grouse. Spraying of clearcuts with herbicides affects habitat selection by removing important habitat elements and may reduce breeding success. Pre-commercial and commercial thinning can enhance the abundance of some bird species (e.g., Artman 1990) but McComb and others (1993) and Dellasala and others (1996) recommend that uniform thinning be replaced by variable-spaced thinning to create additional canopy layers. Such thinning should be repeated about every 10 years since canopy closure would eventually reduce effectiveness of the previous thinning (Dellasala and others 1996).

Habitat and bird species diversity

Maximum community diversity could be accomplished by a combination of snag retention and production, green-tree retention, and variable-spaced thinning. Such a silvicultural strategy would approximate old-growth conditions which would probably increase abundance levels and species diversity over those now found in managed forests. Such habitat conditions should significantly increase cavity-nester abundance and possibly result in an increase in hawks and owls.

FUTURE RESEARCH NEEDS

Silvicultural strategies for increasing diversity

Preliminary investigations indicate that new silvicultural manipulations might increase biological diversity. However, new experimental studies should be conducted on the effectiveness of snag retention (number, decay class, and dispersion), green-tree retention, and uniform vs. variable-spaced thinning.

Winter carrying capacity

Manuwal and Huff (1987) found that in natural stands there was a substantial movement of permanent resident birds from young stands to old-growth stands from spring to winter. This implies that young forests have insufficient resources to support many birds and may act as "ecological sinks" in winter. Studies should be conducted comparing winter bird populations in managed forests with natural forests of comparable age.

Habitat quality

Although bird abundance levels are 1 indication of habitat quality, these data should be augmented with information on breeding success (Van Home 1983). Studies of nesting success of a few selected bird species representing different nesting and feeding guilds would help to evaluate bird response to different forest conditions.

Raptor abundance

Previous research in natural Douglas-fir forests (Manuwal, unpubl, data) indicated that there were more sharp-shinned hawks, northern goshawks, pygmy owls, and barred owls than in the managed forests discussed in this report. Hawks and owls appeared to be rare in the managed forests we surveyed. However, point counts are not designed to survey raptors. Special studies should be designed using appropriate methodology to more accurately assess raptor abundance in managed forests.

Stand size and predation

Several studies in other regions (for a review, see Faaborg and others 1995) have shown that forest fragmentation may affect breeding success. Studies should be conducted to evaluate the relationship betwen stand size and nest predation.

APPENDIX

Table A-1. Avian abundance in 4 different forest structure classes in western Washington during 1993-1995. includes detections within 50 m of point count station.

	1993	1994	1995	1993-1995
		Clearcut		
Total detections	1528	1535	2231	5294
Standard deviation	34	30	56	
Standard error	14	12	23	
Minimum count total	210	224	299	
Maximum count total	293	300	458	
Mean per stand	255	256	372	
		Pre-cenopy		
Total detections	1577	1801	2145	5523
Standard deviation	66	55	54	
Standard error	2’7	22	22	
Minimum count total	199	255	314	
Maximum count total	37’7	402	452	
Mean per stand	263	300	358	
		Closed-canopy		
Total detections	’1306	1205	1693	4204
Standard deviation	39	24	54	
Standard error	16	10	22	
Minimum count total	165	227	213	
Maximum count total	261	162	366	
Mean per stand	218	201	282	
		Harvest age		
Total detections	1634	1594	2186	5414
Standard deviation	38	23	45	
Standard error	16	9	18	
Minimum count total	213	229	305	
Maximum count total	312	287	417	
Mean per stand	272	266	364	
Grand total	6045	6135	8255	20,435

Table A-2. Summary of significant results from stepwise multiple regression of bird abundance against landscape metrics from 100-ha circles around the study sites.

Species	Source	Coefficient	F-ratio	R square	p
Winter wren	CCAREA	-2.637	8.757		0.010
	MAT_AREA	811699.550	6.211	0.594	0.025
Pacific-slope flycatcher	MAT_AREA	1,927	14.613	0.477	0.001
Dark-eyed junco	CCAREA	2.502	25.057		0,000
	IJI2	9387.686	5.995	0.630	0.027
Golden-crowned kinglet	CCAREA	-1.405	15.620	0.494	0.001
White-crowned sparrow	CCAREA	3.292	22.957		0.000
	IJI2	17011.299	2.442	0.605	0.139
Chestnut-backed chickadee	CCAREA	-1.718	15.224		0.001
	ED	561134.932	4.712	0.504	0.046
Wilson's warbler	CCAREA	-1,259	15.155		0.001
	MAT_AREA	59418,594	2.639	0.605	0.125
Swainson's thrush	MAT_AREA	-4052.495	2.430	0.355	0.140
	PATCHES	-489156.717	3.812		0.070
Hermit/Townsend's warbler	MAT-AREA	0.808	8.957	0.359	0.009
Hutton's vireo	CCAREA	-0.350	8.442	0.345	0,010
Varied thrush	CCAREA	-0.231	2.449	0.387	0,138
	MAT_AREA	5898.159	4,038		0.063
McGillivray's warbler	CCAREA	0,783	19.435	0.548	0.000
American robin	MAT_AREA	-0.317	4.329	0.213	0.054
Black-throated gray warbler	CCAREA	-0.331	9.549	0.374	0.007
American goldfinch	CCAREA	0.839	6.035	0.274	0.026
Orange-crowned warbler	CCED	525.000	3.247	0.382	0.092
	MAT_AREA	-0.002	8,717		0.010
Brown creeper	MAT_AREA	389.597	12.400	0.623	0.001
	MNN	209073.244	3.714		
Stellers jay	CCAREA	-0.226	10.227	0.390	0,006
Black-headed grosbeak	MAT-AREA	-0.137	4.796	0.231	0.04
Red-breasted nuthatch	MAT_AREA	0.290	20.325	0.560	0.000

Table A-2. Continued

Species	Source	Coefficient	F-ratio	R square	P
Bewick's wren	CCAREA	0.269	7.154	0.309	0.017
Cedar waxwing	CCAREA	0.159	2.683	0.144	0.121
Hairy woodpecker	MAT-AREA	0.129	14.970	0.483	0.001
Evening grosbeak	MAT_AREA	9.059	3.938	0.198	0.065
Song sparrow	CCAREA	1.067	6.820		0.020
	MAT_AREA	-744521.773	3.179	0.491	0.095
Rufous-sided towhee	CCAREA	1.361	22.816		0.000
	IJI2	5736.115	4.893	0606	0.043
Willow flycatcher	CCAREA	1.100	12.851	0.445	0.002
Common yellowthroat	CCAREA	0,873	7.924	0.331	0.012

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APPENDICES

Roost Site Characteristics of the Long-legged Myotis *(Myotis volans) ha the* Teanaway River Valley of Washington

by

Matthew W. Frazier

A thesis submitted in partial fulfillment
of the requirements for the degree of

Master of Science

University of Washington

i997

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ACKNOWLEDGMENTS

In recognition of his outstanding help in the preparation of [his manuscript, the author would like to thank his thesis advisor, Dr. Stephen D. West. Thanks also to the other committee members, Dr. Jim Agee and Dr. Dave Manuwal, for their assistance in preparing this thesis. Thanks to the Boise Cascade Corporation, Dave Volsen, Tim Quinn, Steve Dodsen, and Jeff Jones, for both the fundIng and the resources which helped to make this project a success. A most sincere thanks to Clint Wright for his help in deciphering the mysteries of GIS and to Josh Millspaugh for his assistance in the editing of the final paper. Finally, the author owes a debt of gratitude to all of the field assistants who worked with me on this project, without whose help the research would never have been completed.

DEDICATION

Each year, after the midwinter blizzards, there comes a night of thaw when the tinkle of dripping water is heard in the land. It brings strange stirrings, not only to creatures abed for the night, but to some who have fallen asleep for the winter. The hibernating skunk, curled up in his deep den, uncurls himself and ventures forth to prowl the wet world, dragging his belly in the snow. His tracks mark one of the earliest datable events in that cycle of beginnings and ceasings that we call a year.

The track is likely to display an indifference to mundane affairs uncommon at other seasons; it leads straight across country, as if its maker had hitched his wagon to a star and dropped the reins .....

Aldo Leopold
<u>A Sand County Almanac</u>

This thesis is dedicated to the memory of my grandfather, Joel Russell Frazier.

INTRODUCTION

Background

For much of the past century, managers of Pacific Northwest forests have adhered to the tenet that good timber management is good wildlife management. This view, however, has led to dramatically increased populations of some wildlife species and drastic declines in others (Sparks et al., 1994; Chubbs et al., 1993). Traditionally, the favored animals have been game species that benefit from high habitat diversity and the effects of high habitat interspersion, characteristics often associated with timber harvests. Recently, the attention of managers has turned to non-game species that were previously neglected in management decisions. For many of these species, patterns of habitat use and selectivity have not been adequately evaluated and their biological needs cannot yet be incorporated into the evaluation of management strategies. Bats (Chiroptera: Vespertilionidae), in particular, have often been overlooked in the development of past management plans. The first part of this study was designed to gather information on the basic habitat relationships and natural history characteristics of one native Washington bat, the long-legged myotis *(Myotis volans)*. Although it is one of the more common bats in Washington state, this species has only recently received significant scientific attention in this region.

The basic life history of the long-legged myotis is similar to that of several other local bats (e.g., M. *californicus*, and *M. lucifugus)* (Fenton and Barclay, 1980; Warner and Czaplewski, 1984; Simpson 1993). Like most bats, the long-legged myotis is nocturnal, utilizing a protective roost structure to sleep during the day and foraging at night. It is an insectivorous bat; most of its diet is composed of moths (Lepidoptera), but other invertebrate prey are taken as well (e.g., Diptera, Isoptera, Neuroptera, and Hymenoptera) (Whitaker et al., 1977, 1981; Nagorsen and Brigham, 1993). The bats copulate in the early fall, but the sperm is stored by the female until spring. Ovulation usually occurs between March and May, with parturition occurring from May to August. Age to maturity appears to vary with climatic conditions, but in most cases, both sexes are mature within one year. Banding studies show that the long-legged myotis can live for at least 21 years (Warner and Czaplewski, 1984).

The range of the long-legged myotis extends from the southern part of the Yukon territory in Canada to the central past of Mexico and from west central North America to the Pacific coast. There are four subspecies; ,*Myotis volans Iongicrus* is the subspecies that inhabits most of Washington (Warner and Czaplewski, 1984).

Traditionally, bats have been one of the least-studied vertebrate faunal groups in North America. Many of the early studies on bats suffer from lack of data because of the difficulties of studying bat natural histories. Recently, however, advances in micro-electronics have made possible the in-depth study of bat behavior by allowing the design of small, very light, radio-telemetry transmitters which can be attached to the bats. Transmitters are now widely used to study many aspects of bat biology, including movement patterns, roost site selection, and roost fidelity. Additionally, ultrasonic sound detector systems (e.g., the Anabat detector system) have allowed researchers to monitor species composition and habitat use over large, difficult-m-trap areas and in multiple areas simultaneously (Fenton and Bell, 1981; Anderson and Miller, 1977). Due in large part to these technological advances, bat research has blossomed in the last several years; many questions about the specific biology of individual species remain unanswered, however, as do questions regarding the geographic variability, associated with that basic biology.

One of the most basic questions regarding bat biology is what type of day roosts the bats require. Several studies have investigated the roost site requirements of the long-legged myotis in different geographic regions. Some of the roost structures that have been reported in the literature include the interiors of buildings (Dalquest and Ramage, 1946), within cracks in the ground (Quay, 1948), under flaps of exfoliating tree bark (Baker and Phillips, 1965; Ormsbee, 1995), and in cracks in cliff faces (Davis, 1978). Long-legged myotis have also been reported to use mines and caves as hibernacula (Schowalter, 1980; Warner and Czaplewski, 1984). The most recent studies of *Myotis volans* and other *Myotis* species in the Northwest have identified trees as dominant roost structures. In central Oregon, large snags, especially hollow cedar trees appeared to be chosen preferentially by long-legged myotis (Ormsbee, 1995). Studies of other *Myotis* species in Washington have shown similar results, as have studies for *Lasionycteris noctivagans, the* silver-haired bat (Campbell, 1993; Christy, i993). This study in the Teanaway River valley was designed to complement these past studies by identifying roost sites in an unstudied area and analyzing how bats distribute themselves in the patchwork of habitat types generated by managed forests.

The second part of the Teanaway bat study involved the compilation of a bat species composition list and a set of reference echolocation calls for the local species. Libraries of echolocation calls are commonly used for species identification when analyzing dam from ultrasonic detector systems, such as the Anabat system (Erickson and West, 1995; Grindal, 1995; Hayes and Adam, 1995). All of the native Washington bats use echolocation to navigate and to identify, and capture prey. This echolocation system is mostly ultrasonic, with frequencies between 20 and 50 kHz being the primary call composition components. Each bat species, however, uses a slightly different pattern of frequency modulation during the course of the call. These frequency patterns can be used to identify many native species (Thomas and West, [99I). The Wildlife Science Program at the University of Washington has collected an extensive library for the calls of western Washington’s bats. These reference calls from western Washington are currently being used in the analysis of bat echolocation data gathered on the east side of the Cascades. Thus, differences in the structure of calls used by bats on the east and the west sides of the Cascades could lead to biases in the analysis of the east-side studies. Previous studies of bat echolocation calls have identified significant intraspecific and geographic variability in call structure in several bat species (Brigham et al., 1989; Thomas et al., I987). To verify that there is no geographic variation occurring in the Teanaway which could bias the analyses of the Anabat data, the echolocation calls from the Teanaway can be compared to the west-side library calls.

Thus, this study had three objectives: to use live trapping to compile a species composition list for the Teanaway River Valley, to collect echolocation calls from trapped bats and compare those calls to calls collected on the west side of the Cascades, and to gather and analyze information regarding the habitat use patterns and roost site characteristics of the long-legged myotis,

Study Area

The study was designed in cooperation with the Boise Cascade Timber Corporation, which also provided the funding for most of the research. The research was done on approximately 21 ,400 ha of Boise Cascade land in the Teanaway River valley, near Cle Elum, Washington (Figure 1). Located on the east side of Washington's Cascade crest, this mountainous area contains several distinct vegetation types, including grand fir *(Abies grandis)* forests (Franklin and Dyrness, 1988), ponderosa pine *(Pinus ponderosa)* stands, aspen *(Populus tremuloides)* stands, wetland areas, and wet and dry meadows.

Most of the area is between 600 and 750 m in elevation. Many of the timber stands have been harvested, allowing comparisons between recently harvested and mature forests. Shelterwood cutting is the primary silvicultural technique; there are stands with several age and size classes and at several different residual tree densities. Understory vegetation is typical of drier, east-side forests with low, sparse shrubs in the uplands and dense thickets of vine maple *(Acer circinatum)* in the drainage bottoms and wetland areas. Coarse woody debris and snag densities differ between the timber stands depending on harvest regime.

The climate of the study area is typical of the forests of the east side of Washington's Cascade Crest. Average daily temperatures range from -3. i C° in January to 18.9 C° in July. Average annual precipitation is 57.2 cm with 32% being snowfall between the months of November and March (World Weather Disc, 1994). The ground is generally snow-covered from November to April. The balance of precipitation falls in spring and autumn, with little precipitation in the summer months.

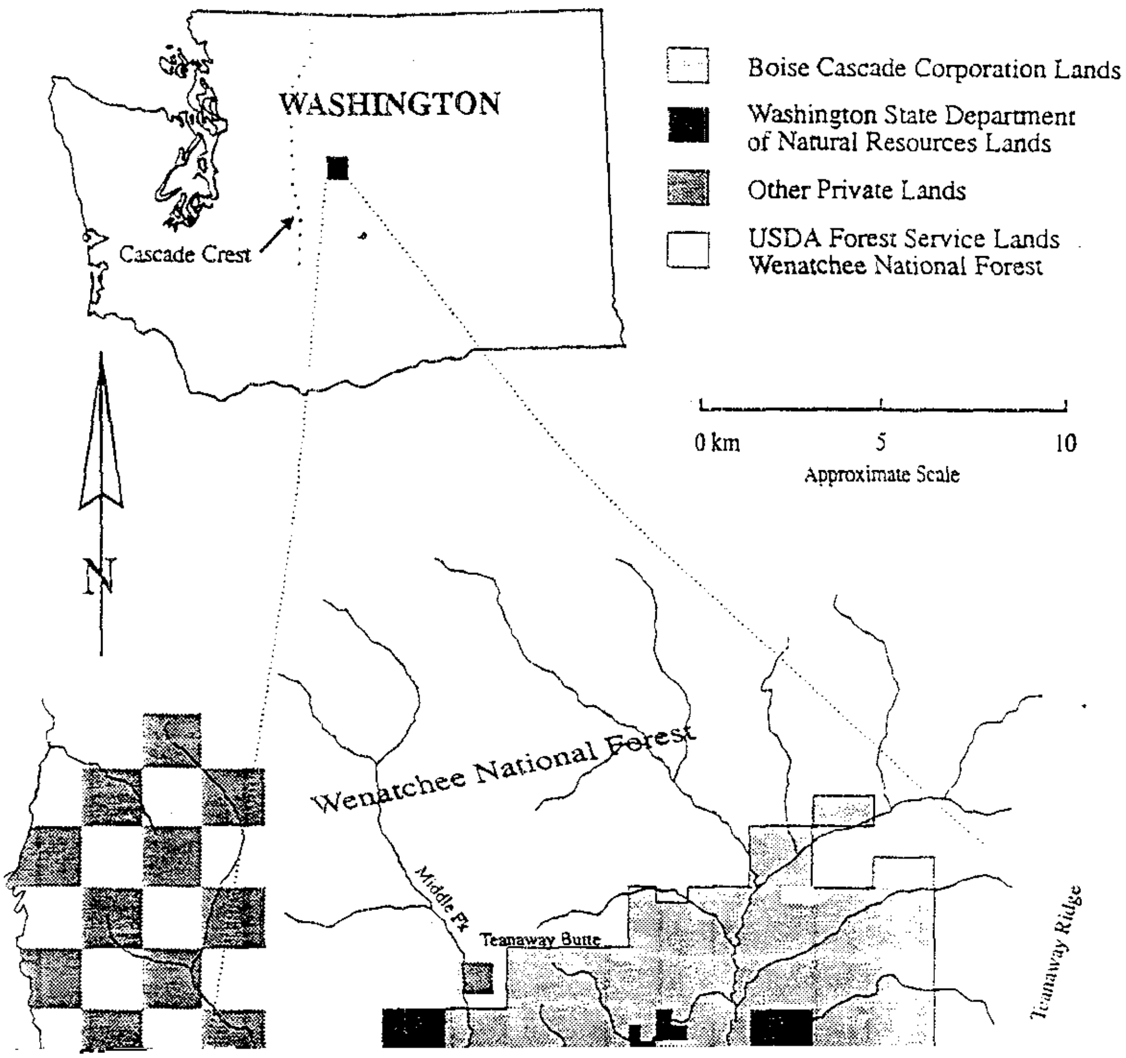


Figure 1. Study area location and land ownership boundaries. Study area includes USDA Forest Service lands for 1.6 km around the perimeter of Boise Cascade Corporation lands.

METHODOLOGY

General Trapping

Trapping was carried out from 11 July to 6 August, 1995. Bats were trapped in several different locations in the Teanaway River drainage using mist nets and harp traps. Mist nets were placed under bridges and were positioned so that the nets blocked free passage through most of the area under the bridge (Barbour and Davis, i969; Kunz, 1988). Any openings not covered by the mist nets were blocked with tarps. In most cases, nets were set up 1/2 to 1 hr before sunset. Nets were monitored continuously throughout the night by a two-person crew. Trapped bats were removed immediately for species identification, measurement (sex, weight, length, forearm length, hind toot, ear length, and wingspan) and then released. Time of capture and the occurrence of pregnancy and lactation were also noted for each bat.

Harp traps (Turtle, 1974; Kunz, 1988) were used primarily at the end of short, wide culverts and occasionally under bridges. Again, any area not covered by the trap was blocked with a tarp. Because the bats do not become entangled in these traps, there was no need for constant monitoring, Therefore, the harp traps were generally in place 1/2 m 1 hr before sunset and were checked for captures in the morning. Bats captured in the harp traps were measured immediately but not released until darkness the following evening. During the interim period between capture and release, the bats were kept in canvas bags.

The data from the capture events were analyzed using recession analysis to identify correlations between capture success and weather, temperature, and day of trapping season. For these analyses, weather was divided into 3 categories: clear, cloudy, and raining. Temperature was recorded at the beginning of the evening (usually near 9 p.m.) and was divided into categories based on 5.6 C° intervals. The temperature intervals used in the analysis were 10 - 15.5 C°, 15.6 - 21 C°, 21.1 - 26.5 C°, and 26.6 - 32.1 C°. Finally, the number of captures per night were analyzed by date to see if the number of captures per night was increasing, decreasing, or remaining constant as the season progressed. Only captures in the mist nets were used for these analyses. Captures in the Turtle traps were disregarded because of their extremely low number.(;.

Reference Call Collection

Reference calls were recorded for all bats at their time of release. The calls were recorded using an Anabat II bat detector (Titley Electronics, Australia) connected to an audio cassette tape recorder. In order to obtain the best possible reference call, one crew member released the bat from a location that forced the bat to fly toward the second crew member, who was operating the detector and recorder. Thus, the recorder got a good sample of calls from the bat as the bat flew to, past, and away from the recorder. When possible, the bat was also forced to fly toward some type of habitat structure, such as a patch of trees. This structure required the bats to use echolocation calls to avoid collisions, instead of only using distress calls as they flew away from a tormentor into open habitat.

After the call was recorded, it was analyzed using a computer and Anabat II software. This software creates a sonogram of the bat call in which frequency is displayed on the vertical axis and time is expressed on the horizontal axis. The resulting displays from these bats were then visually compared to reference calls recorded in previous studies on the west side of the Cascade Mountains. Key indicators used in evaluating the similarities between east-side and west-side reference calls included maximum frequency, minimum frequency, call duration, and the shape of frequency modulations within the call.

Roost Site Location and Characterization

Roost Site Location

From the bats caught in the mist nets and harp traps, I7 long-legged myotis were selected for use in the roost site characterization portion of the study and were affixed with radio-telemetry transmitters (Holohil Systems Model BD2, Holohil Systems Ltd., Ontario, Canada), each of which had a unique frequency between 150.000 and 151.000 MHz. The transmitters weighed approximately 0.65 g each. In order to be selected for this portion of the study, the bat had to weigh at least 8 g. This minimum weight was decided upon based on other studies (Hickey and Fenton, 1990; Campbell, 1993) which have shown that transmitters composing up to 7.5 % of body weight have little effect on the movement ability of bars.

The transmitters were attached to the bats' backs, between the shoulder blades, with the transmitter's antenna (approximately 13 cm in length) extending posteriorly. To obtain the best possible bond between the bat and the transmitter (Christy, i993) the fur on the area between the shoulder blades was trimmed with scissors The transmitter was glued to the bat's back using SKIN-BOND adhesive (United Medical, Largo, Florida). The transmitters were held in place for several minutes while the glue dried before the bats were released.

Every day for at least three weeks after a bat was released, standard radio-telemetry techniques (Mech, 1983) were used to locate its daytime roost locations. Bats were located by driving the roads throughout the study area until the signal for a bat was picked up on a radio-frequency scanner (Telonics Model TR-2 Receiver with TR-1 Scanner, Telonics, Mesa, Arizona) in combination with an H-antenna (Two-element H-antenna, Telonics, Mesa, Arizona). When a sisal was located, the crew followed it in the car until maximum signal strength was received. At that point, the car was parked and the signal was followed on foot until the bat's specific location was identified. The roost site and the route to it from the road were then flagged so that data on characteristics of the roost site and the surrounding vegetation could be gathered at a later time.

Roost Site Characterization

Global positioning system (GPS) data recorders were used to pinpoint the exact spatial coordinates of the roost. Measurements from the GPS field unit and a GPS unit at a known location were reconciled using differential correction so that random error could be minimized. These roost site locations were then used to create a point layer for a geographic information system (GIS) database using ARCINFO software (Environmental Systems Research Institute, Redlands, CA). This layer completed the spatial characterization for the roost sites.

Vegetative characteristics were then measured at each roost site and the immediate vicinity. First, the roost was classified by type (e.g., live tree, snag, rock outcropping, ground, man-made structure, or cave). For all roost types, aspect was measured using a compass and slope was measured using a clinometer. For live trees and snags, tree species, height, and breast-height diameter (DBH) were recorded. Trees were classified as "dominant" if they appeared to be a pan of the forest canopy. Finally, for snags, a brief description was written to characterize the condition of the tree (e.g., extent of exfoliating bark, broken tops, cracks).

Several measurements were also taken to characterize the vegetation in the area immediately surrounding the roost. First, canopy cover was measured using a moosehorn (Garrison, 1949; Mueller-Dombois and Ellenberg, 1974). Measurements were taken t0 m from the roost site along each of the primary, compass headings. Next, a 0.0202 ha plot, centered on the roost, was used to evaluate the groundcover surrounding the roost site. Average height, percentage cover by shrubs, percentage cover by grass, and percentage cover by "other" (including rock, bare ground, pine needle litter, etc.) were estimated visually and recorded. Finally, using a 0.0405 ha plot centered on the roost site, all trees over 2 m in height were identified by species and measured for breast-height diameter, height, and, where applicable, decay class and number of stems.

Analysis of Habitat Use

Habitat use of the bats was analyzed using a GIS database developed primarily by the Boise Cascade Corporation. Over the last several years, Boise Cascade has done extensive vegetation work to evaluate vegetative characteristics of the Teanaway Study Area, develop a comprehensive GIS database of that information, and verify, the accuracy of the vegetative classifications. The basic layers of the GIS database include land ownership boundaries, roads, streams, elevation, and stand type. The most important layer for the analysis of the roost site locations was the stand type layer. Using this layer, the Teanaway study area was broken down into three broad habitat classes based on vegetative characteristics: wet grand fir, dry grand fir, and other (including riparian areas, aspen stands, lowland ponderosa pine, etc.)

The division of wet and dry grand fir habitat types was based on guidelines established by the Boise Cascade Corporation. Each type is a grouping of several vegetative series (Williams and Smith, 1991) within the grand fir forest type (Franklin and Dyrness, 1988). The vegetative series composing the wet grand fir type contain species commonly associated with the west side of the Cascades while dry grand fir sites contain species more commonly associated with the east side of the Cascades (Table I).

To evaluate habitat use versus availability, the stand type layer was used to quantify the amount of each habitat type available to the bats. This layer was then overlain with the GIS point layer that was developed from the GPS locations at the roosts. The habitat types that were used by the bats were identified using this overlay. A chi-square test was used to compare the distribution of these roosts among the different habitats to the overall habitat availability on the landscape. A multinomial likelihood model was constructed to identify the assumptions of the test and to develop the appropriate expected value estimators. The major assumptions of tiffs test include equal probability of detecting roosts in all habitat types, equal availability of all habitats to a bat during any given decision-making event, and independence between nights. To satisfy the third assumption, each roost was counted only once in the analysis, regardless of how many nights an individual bat used the roost.

In a landscape as large as the Teanaway River Valley, the bats have a virtually unlimited number of possible roost trees. Thus, the probability that any individual tree will be used is very small. Additionally, the values of this use function will be discrete: (e.g., 0, 1, 2, etc.). For these reasons, bat use of individual trees can be assumed to be distributed Poisson. To test this hypothesis, the number of uses of each tree was summarized and the resulting distribution was tested for goodness-of-fit to the Poisson distribution using a chi-square goodness-of-fit test.

On the single stand level, paired t-tests were used to evaluate the differences between the DBH of roost trees and the average DBH of other dominant trees within the 0.0405 ha vegetation sampling plot. The same method was used to compare the heights of roost trees with the heights of surrounding trees. Chi-square tests were used to compare roost tree size to the average size of other canopy trees in the overall roost stand and to evaluate canopy closure at the roost site versus canopy closure in the surrounding stand. A Kolmogorov-Smirnov test was used 1:o evaluate the uniformity of roost distribution across the possible elevation gradient (elevation of roost site above drainage bottom / possible elevation above drainage bottom).

On a landscape scale, a chi-square test was used to compare the aspects of roost stands with the overall availability of different aspects on the landscape. A t-test was used to compare the differences in mean DBH of roosts on south-facing slopes and roosts on north-facing slopes. T-tests were also used to compare the slopes of roost site stands to overall landscape slopes and then to compare roost and landscape slopes on a habitat by habitat basis. The same

Table I. Components of wet and dry g-rand fir habitat types. Vegetative community types composing the dry grand fir and wet grand fir habitat classifications. The listed species are the indicative shrubs or grasses occurring with *Abies grandis* which are used to define a particular vegetative series.

Dry grand fir habitat type	Wet grand fir habitat type
Arctostaphylos nevadensis	*Arnica cordifolia*
Calamagrostis rubescens	*Acer circinatum*
Calamagrostis rubescens / *Lupinus* sp.	*Acer circinatum* / *Chimaphila umbellata*
Holodiscus discolor / *Chimaphila umbellata*	*Acer circinarum* / *Clintonia uniflora*
Symphoricarpos oreophilus	*Achlys triphylla*
	Symphoricarpos albus / *Chimaphila umbellata*
	Spirea betulifolia var. lucida
	Berberis nervosa
	Berberis nervosa / *Calamagrostis rubescens*

method was used to compare the mean slopes of wet grand fir and dry grand fir sites.

Snag density in roost sands was compared to average snag density on the landscape as a whole using a chi-square test. For this analysis, each stand across the landscape was assigned one of three categories based on snag density: poor (no snags or very little within the stand), fair (may have 1-2 snags per 4.047 ha), or good (average >_ 2 snags per 0.405 ha). The frequencies associated with each of these categories was used to calculate the expected values for the chi-square. A dead tree was only counted as a snag if it had a diameter of at least 20.54 cm and a height of at least 3.048 m. The criteria for inclusion in the snag count and the categories for classification of snag densities were developed by the Boise Cascade Corporation. The rationalization behind the criteria for snag determination was that snags of this size or greater can be utilized by most wildlife species which require snags as an integral part of their habitat; smaller snags are only useful for some species.

Finally, t-rests were used to identify differences in crown closure between roost stands and overall landscape averages. These rests for canopy closure were performed both for the roost stands in comparison to the overall landscape and for the roost stands in comparison to the landscape averages from their respective habitat types.

RESULTS

General Trapping

Altogether, 124 bats were captured during 65 trapnights (Appendix A). Thirty of these trap nights were with mist nets and 35 were with harp traps. Of the 124 bats caught, 16 escaped from the nets or during handling before a positive species identification could be made. Two juvenile bats were classified as unidentifiable beyond genus level. Both of these bats were *Myotis* sp. Thus, a total of 106 bats were positively identified (Table 2).

Regression analysis revealed that bats were caught in significantly larger numbers on wanner nights ($0.005 < p < 0.01$). The tests for correlations between captures and weather and between captures and day of the season yielded no significant results ($p > 0.05$).

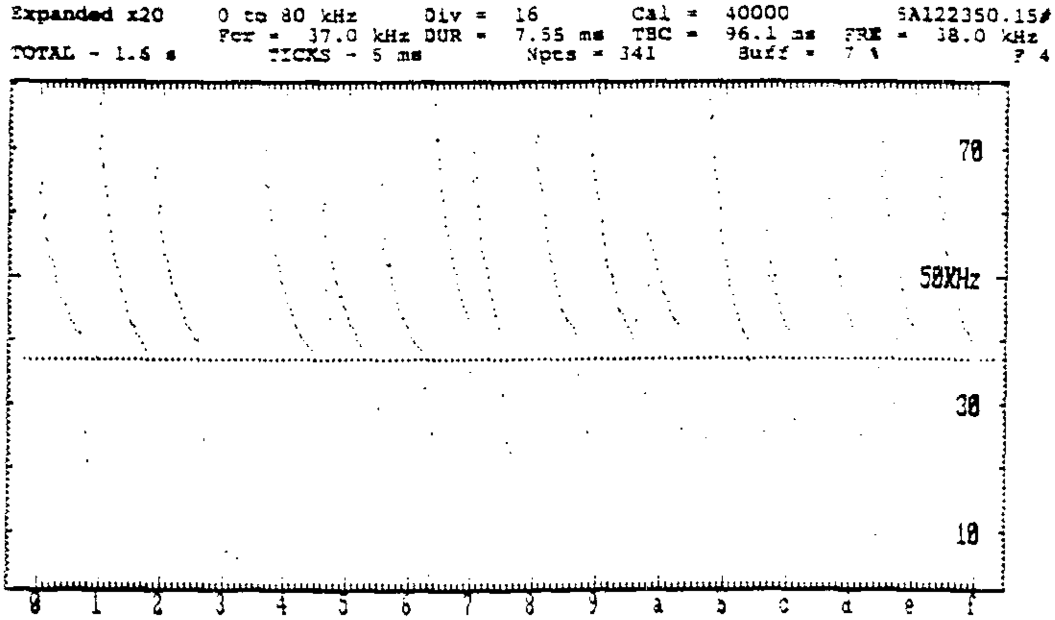
Reference Call Collection

Out of the 106 bats that were positively identified during trapping, 72 produced calls that were recorded on tape and transformed into sonograms using the Anabat software (examples in Figure 2). These sonograms varied widely in quality. The echolocation calls of the genus *Myotis* from the Teanaway study area (including California myotis, western small-footed myotis, Yuma myotis, little brown myotis, long-legged myotis, and western long-eared myotis) are easily identified by their short duration, steep frequency sweep (the calls modulate from a high frequency to a lower one during the course of each

Table 2. Capture summary. Total captures and relative abundance of positively identified bars. Teanaway River Valley. 1995.

Species Name (Scientific Name)	Number of Captures	Relative Abund. (%)
Long-legged myotis *(Myotis volans)*	38	35.9
Little brown myotis *(Myotis lucifugus)*	24	22.6
Yuma myotis *(Myotis yumanensis)*	16	15.t
Western long-eared myotis *(Myotis evotis)*	12	11.3
California myotis *(Myotis californicus)*	7	6.6
Western smallfooted myotis *(Myotis ciliolabrum)*	5	4.7
Big brown bat *(Eptesicus fuscus)*		1.9
Hoary. bat *(Lasiurus cinereus)*	2	1.9
Total number of positively identified bats	106	
Unidentifiable juvenile bats (Genus *Myotis)*	’3	
Bats that escaped before identification	16	
Total bats captured	i24	

Long-legged rayon. *Myotis votans:*



Western long-eared myotis. *Myotis evotis:*

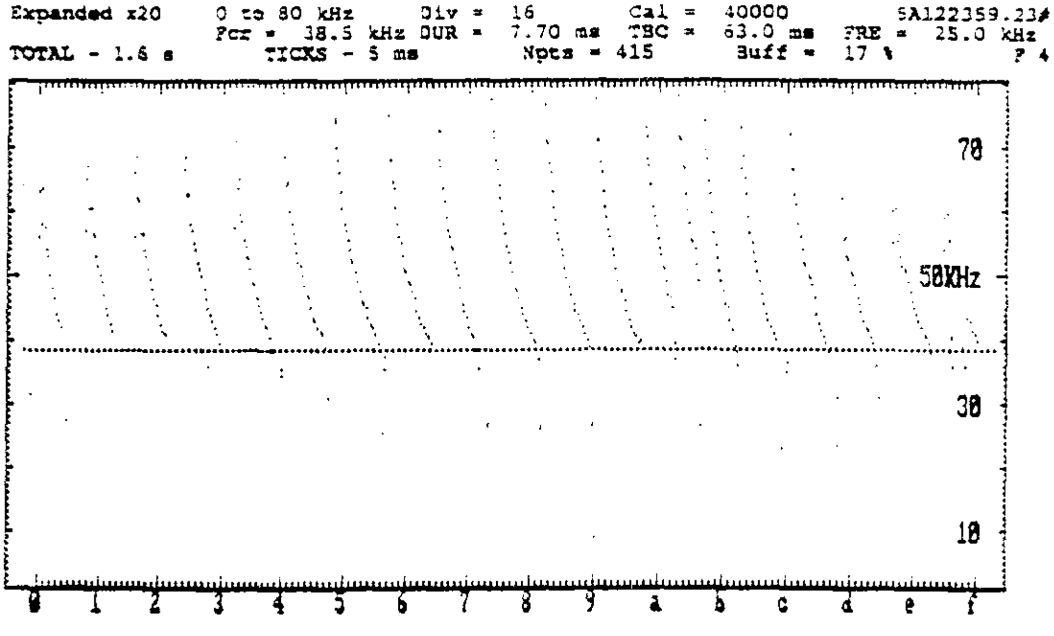
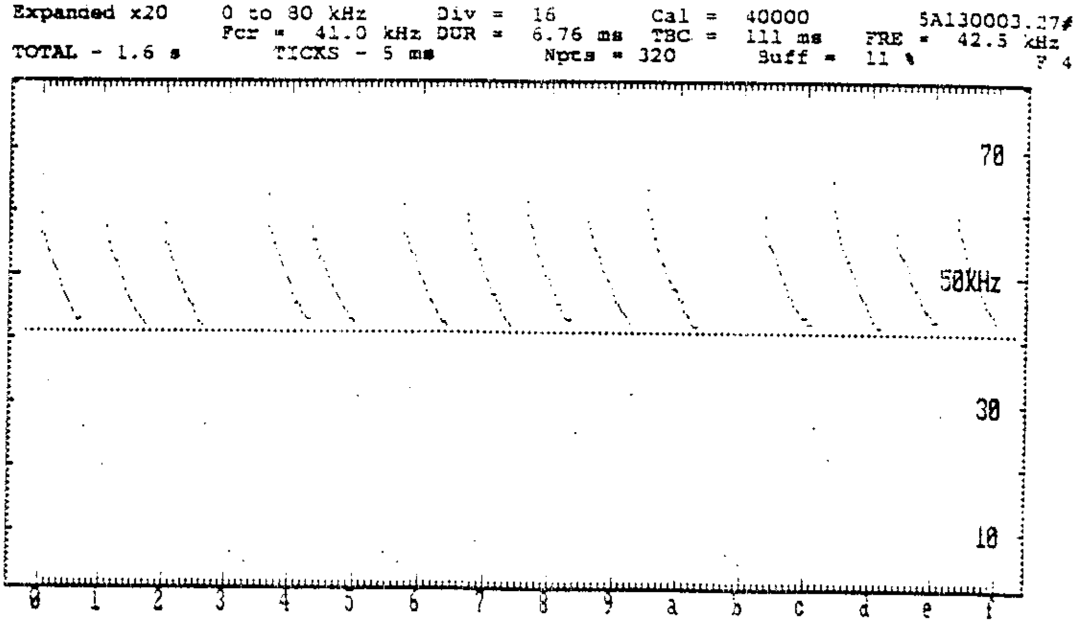
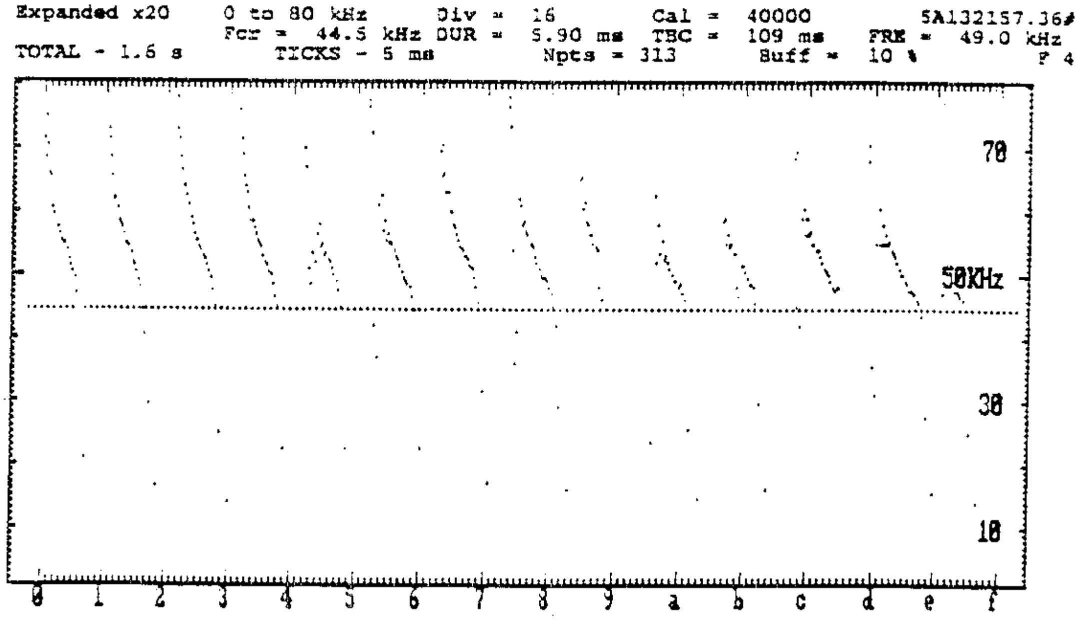


Figure 2. Sonograms. Examples of characteristic sonograms from each species of bat captured during the study.

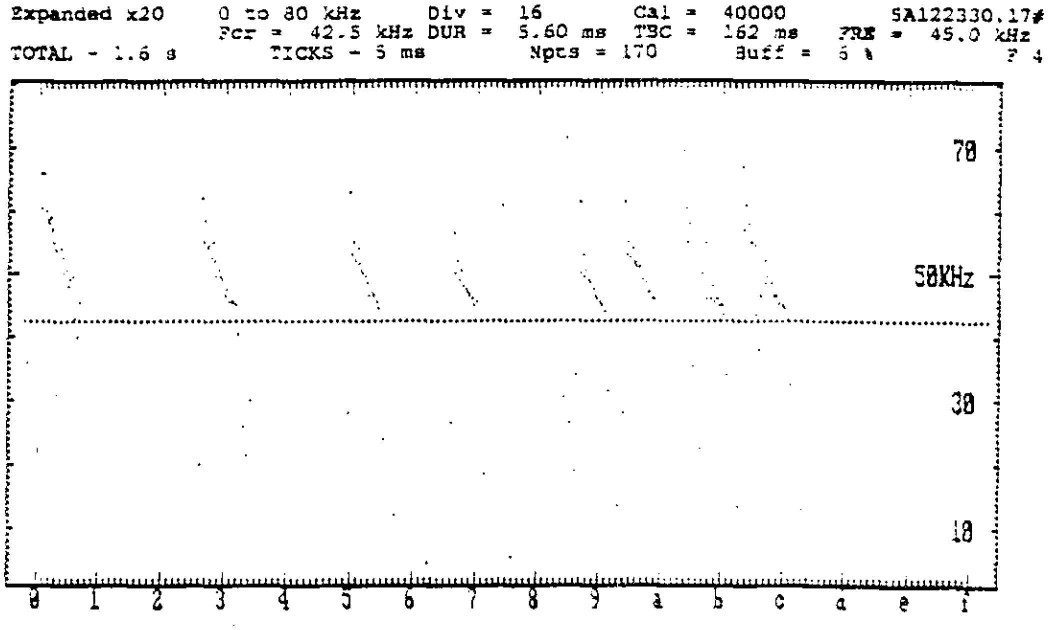
Little brown myotis. *Myotis lucifugus:*



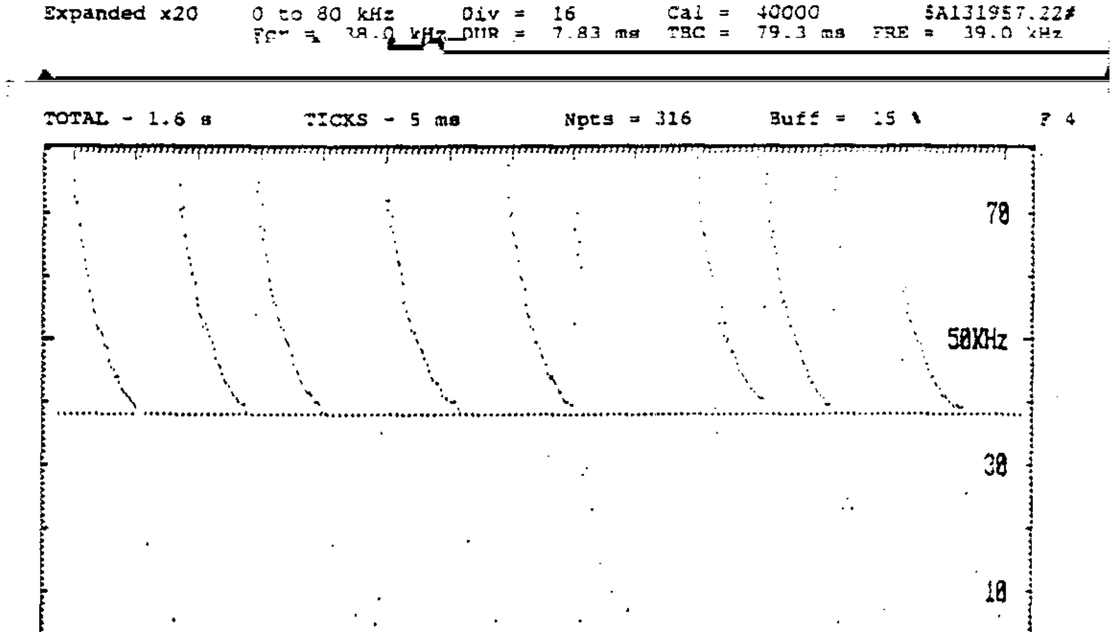
Western small-footed myotis, *Myotis ciliolabrum:*



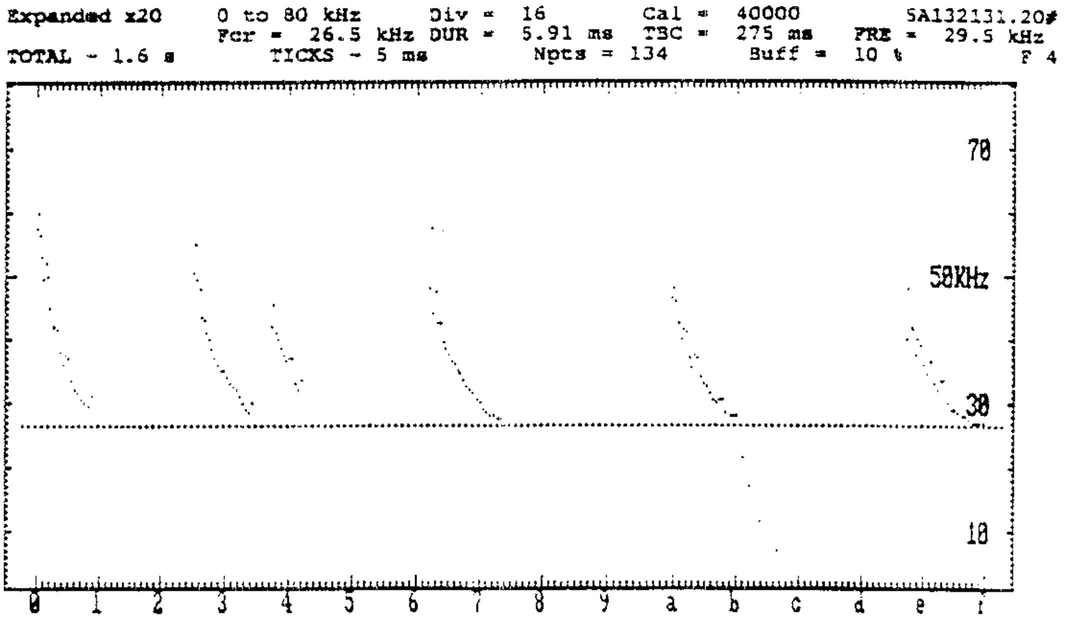
California myotis. *Myotis californicus:*



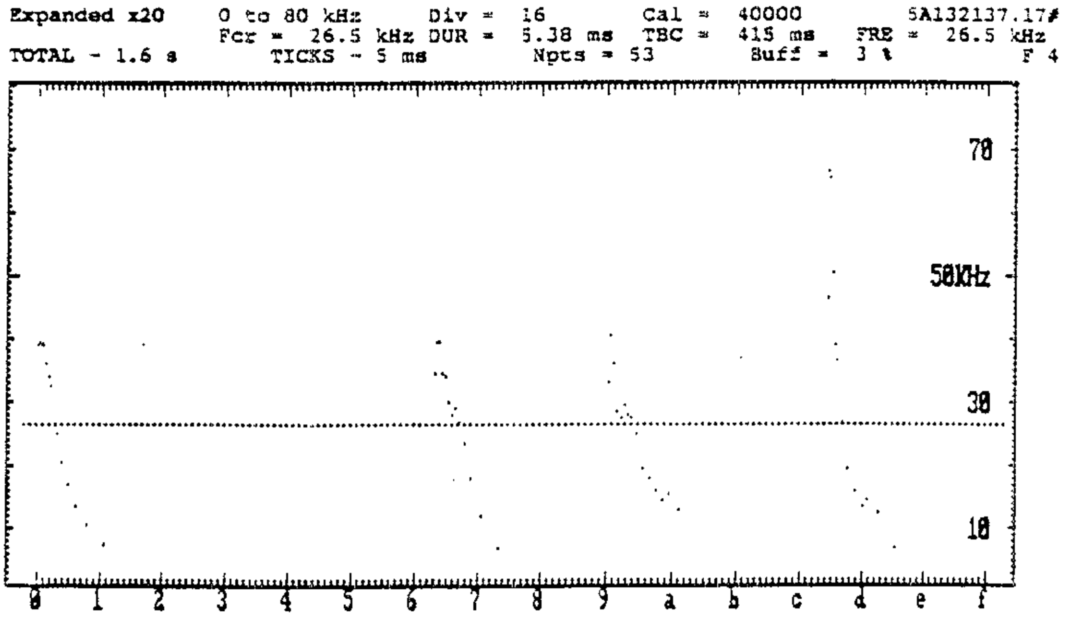
Yuma myotis, M*yotis yumanensis:*



Big brown bat. E*ptesicus fuscus:*



Hoary bat, *Lasiurus cinereus:*



call), and relatively high minimum frequency (usually 38 to 50 kHz). For this collection of *Myotis* species, it is impossible to consistently identify individual species based on the information recorded with file Anabat system. None of the bats, including the Yuma myotis which has often been identified in past studies based on the higher minimum frequency of its calls, has any call characteristics that are distinctly and reliably different from the others.

While the trapping efforts in this study met with limited success regarding the capture of larger bat species (hoary bats, silver-haired bats, and big brown bats), reference calls were recorded for two big brown bars and two hoary, bats. Each of these species can be positively identified based on its call characteristics. The calls of the big brown bat are similar in appearance to the calls of the *Myotis* group with regard to their short duration and their large frequency sweep. However, the minimum frequency of the big brown bat call is significantly and consistently lower than the minimum frequency of the *Myotis* calls (25-30 kHz for the big brown bats compared to 38-50 kHz for the Myotis).

The hoary bat can also be consistently identified. Again, one discernible difference between the calls of hoary bats and the other bats found in the Teanaway is the low minimum frequency of the calls, which is often as low as 10 to 15 kHz. The second characteristic is that the call appears less intense, especially in its lower frequencies. This lack of intensity, in the lower frequencies results in a sparseness of data points on the Anabar sonogram as the call enters the final sweep in its frequency modulation. This sparseness cart be distinguished from the other bat species in the Teanaway which tend to become more intense at the end of the call. Thus, the eight species that were caught in the Teanaway can be broken down into three groups for identification purposes: hoary bat, big brown bat, and *Myotis* group.

In evaluating the structure and characteristics of the calls recorded during this study, a major concern would be the differentiation of *Myotis yumanensis* from the other *Myotis* species which are normally classified as a group because they are indistinguishable. *Myotis yumanensis* is usually separated from this group based on the higher minimum frequency observed in its calls; however, the data from the Teanaway suggest that the calls of *Myotis ciliolabrum* span file gap between the minimums from most of the Myotis group and those of *Myotis yumanensis. Thus*, until there is additional evidence to suggest that these calls can be separated with a high degree of reliability, it would be prudent to group these species together into one *Myotis* group which includes *Myotis yumanensis*, at least on the Teanaway Ecosystem Project and other projects in the immediate vicinity.

Habitat Use by the Long-Legged Myotis

Of the 17 bats that were released with transmitters, 12 were female and five were male. The average weight of the females was 9.25 g (range: 8g to

11g) and none were pregnant or lactating. The average weight of the males was 9.4 g (range: 9g to 10g).

A total of 28 roost sites were identified (Appendix B); some of these roost sites were used repeatedly, for a total of 63 roost nights. The number of times that a roost was used varied from I to 7, with a mean of 2.2 uses ($s = 1.8$). The chi-square test rejected the null hypothesis that the use of roost trees is random ($p < 0.001$) (Table 3). Long-legged myotis are returning to the same roosts with greater frequency than expected.

Out of the 28 total roosts, 12 were m dry gand fir stands (46.4%), I5 were in wet grand fir stands (39.2 %), and one was in other habitat types (7.1%) (Figure 3). The test rejected the null hypothesis of habitat use being proportional to availability ($p<0.001$). In fact, the bats were using wet grand fir habitats significantly more than other habitat types (also $p < 0.001$), given the proportional availability of all types (Table 4). Of the 28 roosts, 25 were in snags and three were in trees that were fully live or partially dead.

The DBH of each roost tree was compared to the average DBH of the surrounding dominant trees using a paired t-test (Table 5). The trees selected as roosts by the bats were significantly larger ’than the surrounding trees ($p < 0.00I$). However, when a chi-square test was used to compare the roost trees to the average size of the overstory trees in the stands as a whole (Table 6), there was no significant difference in diameter ($0.25 <p<0.5$). The

Table 3. Roost fidelity. Number of nights on which an individual roost was used by the same bat. Mean number of uses = 2.2; s = 1.8. Results of the chi-square test: $p < 0.001$.

Number of rimes an individual roost was used	Frequency of occurrence
1	15
2	3
3	6
4	1
5	0
6	1
7	2

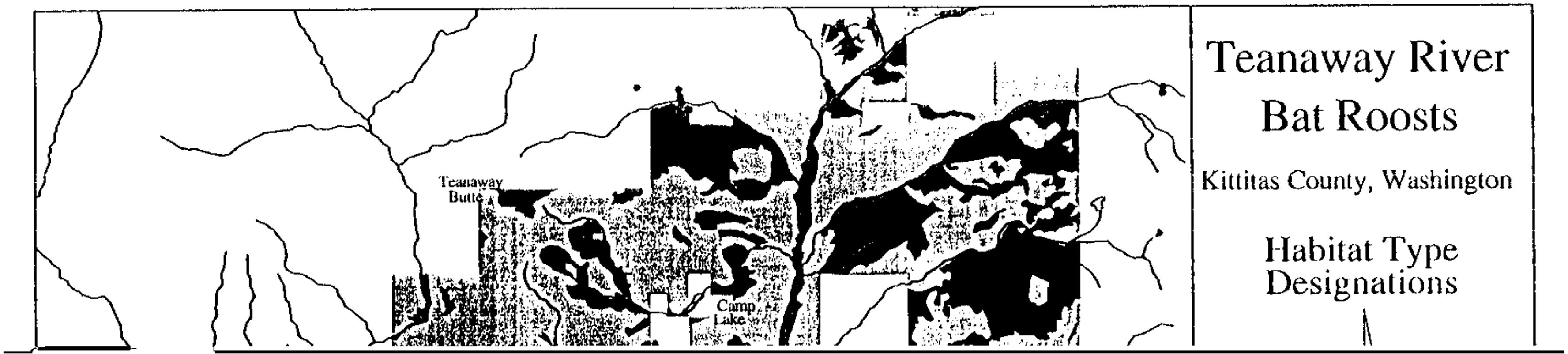


Figure 3. Habitat type map and roost site identification for Boise Cascade lands in the Teanaway River drainage.

Table 4. Availability of habitats. Comparison of habitat availability,, expected use, and actual use of each habitat type. Key to habitat types: DGF = dry, grand fir, WGF = wet grand fir, Other = other habitat types (hemlock, dry Douglas-fir, riparian, etc.) Chi-square test for use versus availability: $p < 0.001$.

Habitat type	Availability (ha)	Expected use frequency	Actual use frequency
DGF	11805	15.44	t2
WGF	4615	6.04	15
Other	4985	6.52	1

Table 5. Roost tree diameters. Comparison of roost tree diameters to the average diameter of surrounding canopy trees. Paired t-test results: $p < 0.001$.

Breast-height diameter of roost trees (cm)	Average breast-height diameter of surrounding trees (cm)
114.7	65
72.8	53
46.6	22
34.2	24
36.7	I3
43.7	32
73.2	39
28.3	18
45.1	36
28.6	33
66.3	52
43.3	35
41.9	46
54.7	I1
53.5	13
52.7	23
73.0	20
22.8	17
25.8	19
43.0	33
39.2	62
66.6	19
62.1	34
67.0	7
30.2	28
38.2	27
29.5	33

Table 6. Roost tree and stand diameters. Comparison of roost tree diameters to average size of overstory trees throughout the stand. Key to tree size classes: Class 1 = 0 to 7.62 cm DBH, Class 2 = 7.63 to 20.07 cm DBH, Class 3 = 20.08 to 40.39 cm DBH, Class 4 = DBH _> 40.40 cm. Results of chi-square test: 0.25 < p <0.5.

Roost tree size (cm)	Roost tree size class	Average stand size class
73	4	3
52.7	4	3
73.2	4	4
28.3	3	4
41.9	4	4
114.7	4	4
28.6	3	3
67	4	3
66.6	4	3
43.7	4	3
78.4	4	3
66.3	4	4
38.2	3	3
45.1	4	3
39.2	3	3
62.1	4	3
29.5	3	4
22.8	3	4
43.3	4	3
34.2	3	4
36.7	3	3
30.2	3	4

average roost tree had a diameter of 50.3 cm (s=20.5, min=22.8, max = 114.7).

The height of the roost tree was also compared to the average height of the surrounding dominant trees (Table 7). Again, using a paired t-rest, the roost trees were taller than the surrounding canopy trees ($0.001 <p<0.002$). The average height of roost trees was 27.6 m (s=10.3, rain=9.4, max=48.5).

Next, the canopy closure at the roost site was compared to the canopy closure of the surrounding stand (Table 8). There was no significant difference in the canopy cover ($0.2 < p < 0.5$). The mean canopy cover in the roost stands was 38%, (s=29, ram=t, max=86). Similarly, a chi-square rest was used to evaluate the frequency with which the roost tree was of the same species as the dominant trees in the stand (Table 9). Again, the results proved not to be significant ($0.75 < p < 0.9$). Of the 28 total roosts, 16 were in grand fir, seven in ponderosa pine, four in Douglas-fir, and one in a cottonwood.

Finally, the roost was characterized by distance to water and elevation above drainage bottom. The mean distance to water was 330 m (n=28, s=373) with a minimum distance of 0 m and a maximum distance of I248 m. The average elevation above the drainage bottom was 47.8 m (n=28, s=44.2) with a minimum elevation of 1.5 m and a maximum elevation of 158 m. The elevation of each roost above the drainage bottom was also compared to the potential elevation from the drainage bottom. This ratio of elevation to potential elevation was evaluated using a Kolmogorov-Smirnov rest to evaluate

Table 7. Roost tree heights. Comparison of the height of roost trees to the average height of surrounding canopy trees. Results of paired t-test: **0.001** < p < 0.002.

Roost tree height (m)	Average height of surrounding canopy trees (m)
18.3	i7.7
26.5	26.8
40.2	27.4
36.0	I5.2
33.2	22.9
36.9	14.6
26.2	23.5
38.4	31.1
21.9	21.0
16.8	16.4
9.4	18.3
12.2	29.6
9/7	18.3
36.7	24.7
48..5	7.6
29.6	14.6
44.5	4.3
28.6	34.4
16.,4	10.0
15.7	13.7
27.7	18.9
2’7	24.4
37.5	I5.2
28.6	22.8
29.6	4.9
32.6	28.9
21.9	20.7

Table 8. Canopy closure. Comparison of canopy closure at the roost site to canopy closure in the surrounding stand. Results of paired t-test: $0.2 < p < 0.5$.

Canopy closure at roost site (%)	Canopy closure in surrounding stand (%)
82.50	15
32.50	90
1.25	55
7.50	*55*
80.00	70
46.25	75
10.00	20
25.00	45
17.50	35
7.00	30
37.50	60
68.75	90
53.75	90
6.25	20
67.50	20
86.25	70
35.00	70
7.50	0
76.25	55
70.00	50
48.75	50
5.00	5

Table 9. Tree species. Comparison of roost tree species with the dominant tree species in the surrounding stand. Key to species codes: D = Douglas-fir *(Pseudotsuga menziesii)*, P = ponderosa pine *(Pinus ponderosa)*, G = grand fir *(Abies grandis)*, B = cottonwood *(Populus* sp.) Results of chi-square test: $0.75 < p < 0.9$.

Roost tree species	Dominant stand species
D	D
P	D
P	P
P	G
G	P
B	B
P	B
G	P
P	D
G	G
G	D
P	P
G	D
P	P
G	D
G	D
G	P
G	B
P	P
G	D
G	G
G	G

the uniformity of the distribution across the elevation gradient. The test indicated that the distribution cannot be differentiated from uniform ($0.05 < p < 0.1$).

In addition to the habitat use versus availability test and the comparisons between roost characteristics and those of the stand, several tests were carried out to compare the stands in which the roost sites occurred to the overall habitat conditions across the landscape. First, the aspects of the roost stands were compared to the overall aspects on the landscape (Table 10). There were significant differences between the stands used by the bats and the overall availability of land with each particular aspect ($p < 0.001$). In particular, bats tended to roost on the northern slopes. To elicit differences which may have caused this selection, the DBH of roost trees with southern aspects was compared to the DBH of roost trees with northern aspects using a t-test to compare the means (Table 11). There was no significant difference between the DBH measurements on the north and south aspects ($0.2 < p < 0.5$).

The slopes of the roost site stands were also compared to slopes across the study area landscape (Table 12). A t-test showed that, overall, the stands in which bats chose to roost were not as steep as the average stands across the landscape ($0.01 < p < 0.02$). Roosts that occurred in wet grand fir and dry grand fir stands were also, respectively, compared to the average landscape slope values for each of these habitat types using the t-test. The wet grand fir stands with roosts showed no significant difference in slope from the average

Table 10. Aspect. Comparison of the aspects of roost stands and the overall aspects on the landscape. Key to aspect codes: I = NE (22.6° to 67.5°), 2 = E (67.6° to 112.5°), 3 = SE (112.6° to 157.5°), 4 = S (157.6° to 202.5°), 5 = SW (202.6° to 247.5°), 6 = W (247.6° to 292.5°), 7 = NW (292.6° to 337.5°), 8 = N (337.6° to 22.5°), 9 = level. Results of chi-square test: $p < 0.001$.

Aspect	Actual frequency	Expected value	Roost stand frequencies
1	66	1.7612	0
2	49	1.3076	0
3	I52	4.0544	0
4	259	6.9076	4
5	I50	3.9984	3
6	62	1.6520	1
7	98	2.6124	2
8	131	3.4944	12
9	83	2.2120	6

Table 11. Diameters by aspect. Comparison of roost tree diameters on north and south aspects. Result of t-test: $0.2 < p < 0.5$.

Roost trees on northern aspects (270° to 89°)	Roost trees on southern aspects (90° to 269°)
114.7	72.8
34.2	46.6
36.2	73.2
43.7	45.1
28.3	28.6
66.3	53.5
43.3	22.8
41.9	43.0
54.7	67.0
52.7	74.8
73.0	29.5
25.8	
39.2	
66.6	
62. i	
30.2	
38.2	
Mean = 19.8	Mean = 19.9
S.E. = 2.11	S.E. = 2.27

TabLe 12. Landscape slopes. Compare, son of slopes of roost stands and average slopes across the landscape. For all habitat types: mean slope = 31.6, s.d. = 18.02, rain = 0, max = 80. For all dry grand fir habitats: mean slope = 32.4, s.d. = 16.50, rain = 0, max = 80. For all wet grand fir habitats: mean slope = 28.7, s.d. = 19.98, mm = 0, max = 70. Result of t-test: 0.01 < p < 0.02.

Slopes (%) in dry grand fir roost stands	Slopes (%) in wet grand fir roost sands
2O	50
0	50
10	0
0	0
I0	40
10	40
10	20
	20
	30
	40
	0
	60
	40
	I0
Sample mean =: 8.6 S.E. = 6.90	Sample mean = 28.6 S.E. = 5.43

wet grand fir stand on the landscape ($p > 0.5$). The dry grand fir stands, however, were significantly flatter than the average dry, grand fir stand ($.01 < p < .02$). Furthermore, when the mean slopes of wet grand fir roost stands and dry grand fir roost stands were compared using a t-test, they were significantly different ($p < 0.001$). Snag densities in roost stands did not differ from the snag densities on the rest of the landscape ($0.5 < p < 0.75$).

Finally, the crown closure of roost stands was compared to the crown closure of stands of similar habitat type using a t-test (Table 13). In these comparisons, neither the wet grand fir nor the dry grand fir roost stands were significantly different in canopy closure from the average stand of the respective habitat type (several tests performed, mostly $p > 0.5$).

Table 13. Crown closure of similar habitats. Comparison of crown closure in roost stands and crown closure across the landscape in areas of similar habitat type. For all habitat types: mean crown closure = 43.4, s.d. = 28.94, min = 0, max = 100. For all dry grand fir habitats: mean crown closure = 46.5, s.d. = 26.81, min = 0, max = 95. For all wet grand fir habitats: mean crown closure = 50.9, s.d. = 30.87, min = 0, max =: 100. Several tests, mostly $p>0.5$; none significant at $p < 0.05$.

Crown closure (%) in dry grand fir roost stands	Crown closure (%) in wet grand fir roost stands
7O	9O
75	9O
45	60
35	0
20	70
5	55
3O	50
	50
	20
	70
	20
	9O
	55
	55
Sample mean =: 40.0	Sample mean = 55.3
S.E. = 9.64 ~M	S.E. = 7.29

DISCUSSION’

General Trapping

When evaluating the results from the live trapping, it is important to remember that all of the methods used to capture bats are biased (Tidemann and Woodside, i978; Kunz and Brock, 1975; Cranbrook and Barrett, 1965; Dalquest, 1954). In the case of mist nets and harp traps, the positioning of the net usually results in the capture of smaller, lower-flying bat species. In the Teanaway study area, these low-flying bats are represented mostly by the different species of myotis. Larger, higher-flying bats, such as the big brown bat and the hoary bat, will tend to be under-represented by the sampling methods used in this study because they generally fly in areas where it is difficult to place the nets. Thus, in viewing the results from the live trapping, the species composition list is probably more important than the biased evaluations of relative abundance.

The data should, however, give a fairly unbiased evaluation of the relative abundance of the different *Myotis* species, which are more similar morphologically and ecologically than the larger bat species. Information about the relative abundance of the *Myotis* bats is particularly important because of the inability to distinguish the calls of these species in the Teanaway using ultrasonic detector systems. Thus, the relative abundance estimates for the *Myotis* species can be applied to other studies in the Teanaway to gain an estimate of the species breakdown of the indistinguishable bats classified as "*Myotis* group.’ However, due to the small sample size of this study and the effects that other sources of variation (such as elevation, habitat type, availability of roost structures) could have on the outcome of related studies, it is important that these results be carefully evaluated for their applicability before they are used in other studies.

Reference Calls

The analysis of bat calls using the echolocation detector systems is one of the most dominant techniques m current bat research. The advent of this technology has allowed bat researchers to sample both more efficiently and more thoroughly while at the sane time lowering the cost of sampling. One of the problems with this new technology is that the extent of inter- and intra-specific variation in call structure is still unquantified for most species. As shown by this study, there can be differences in call structure between geographic locations which limit or alter the interpretation of data gathered at a particular site. Thus, as previous authors have emphasized (Brigham, Cebek, and Hickey, 1989; Thomas, Bell, and Fenton, 1987), it is critical that reference calls be gathered from the same geographic area that is going to be sampled with the ultrasonic detectors. Furthermore, because there is also significant variation in call structure between individual bats, it is advisable that a series of several calls from each species be used as reference calls so that the full spectrum of call variability can be incorporated into the analysis.

Habitat Needs of the Long-legged Myotis

In the Teanaway River Valley, the long-legged myotis roosts predominantly in trees; there appears to be a significant preference for snags. In particular, the bats select trees with large amounts of exfoliating bark, presumably for shelter and thermo-regulation. The roost trees tend to be significantly larger in diameter and taller in height than the surrounding trees. While it is unclear exactly why the bats would prefer these larger snags, one possibility is that they are simply easier to identify from the air than other suitable trees which are smaller in diameter or which do not exceed the surrounding canopy in height. Additionally, trees of larger diameter are more likely to have appropriate pieces of exfoliating bark to provide shelter for the bats. These factors appear to be the dominant criteria for roost site selection and can, to a large degree, be used to explain the results of the other tests and analyses.

The bats exhibited a strong preference *for* wet grand fir stands. This fact is hardly surprising considering the characteristics of these stands. The wet grand fir stands tend to be more dense with vegetation and have more structural diversity,, including multiple age classes among the trees. To a large degree, this structural diversity may be the result of selective harvesting and fire suppression over the last century; this management history provides another reason that wetter sites may be preferred over drier sites. Many of these stands were logged in the early 1900s. Thus, the ability of the wetter stands to produce larger trees more rapidly may result in a higher density of trees with the structural characteristics necessary for bat roosts. As these larger trees mature and die, they persist in the forest structure as large snags, towering above the surrounding younger canopy. Fire suppression may also preserve these snags in numbers greater than would have been present historically because the removal of tire from the landscape may allow older snags to remain standing for long periods of time.

If the long-legged myotis uses wet grand fir habitats because of their structural characteristics, then the significant results of the test for aspect would also be expected. Wet grand fir stands rend to be found on more northern slopes where there is more moisture and generally cooler conditions. Thus, in locating these stands, the bats will use northern slopes in greater proportion than would be expected based on their availability.

Statistical tests showed canopy closure to be an insignificant factor in roost site selection. This result follows logically from the conclusion that the hats key on large snag structures which extend above the surrounding canopy. If the bats are selecting the roosts based on supra-canopy characteristics, then there would be little reason for them to consider the density of the canopy itself. However, other studies which evaluated canopy cover have shown that the area immediately around bat roosts tends to have a lower canopy density than the surrounding stand (e.g., Campbell, I993).

In evaluating these contradictory conclusions, the most logical explanation is that the canopy density in the Teanaway is lower than the canopy density in these other study areas; none of the other studies was carried out in an area with the same plant associations as those found m the Teanaway. While it is outside of the scope of this study to compare the vegetative characteristics of the Teanaway to the characteristics of other :study areas, extensive past and current logging in the Teanaway have had a dramatic effect on the structure of most of the local vegetative communities. Thus, it is possible that, due to harvesting or other environmental factors, the canopy density in the Teanaway is, on average, low enough that it is not a factor in roost selection; yet in other areas, the canopy cover may be significantly dense to require the bats to search for openings when identifying possible roost sire locations. Furthermore, the species of bat studied by Campbell (1993) was significantly larger than M. *volans*. Thus, the larger bars may have needed a less dense canopy to maneuver when approaching and departing the roost, while smaller bats (e.g., the long-legged myotis) may not have the same area requirements.

Additionally, the results showing the significance of slope in roost selection can be explained using the bats' preference for larger trees and [he difference in habitat structure between the wet and dry grand fir sites. Given similar soil characteristics, gentle slopes rend to drain water more slowly than steeper slopes. Thus, stands with gentle slopes will tend to retain more moisture for longer periods of time, resulting in the development of more moist stands. The vegetation resulting from this additional moisture is the characteristic used to make the distinction between wet and dry grand fir stands. Thus, sites with more gentle slopes would be more likely to develop wet grand fir stands than would similar sites on steeper slopes. This additional moisture also allows larger trees to be produced more quickly and in greater densities. Applying these concepts to the Teanaway landscape, it makes sense that the long-legged myotis would be more likely to select a roost in a stand with a more moderate slope. In these flatter sites, the bat would be more likely to find the wet grand fir stands which tend to produce the structural characteristics, large trees in particular, which the bats select for roosting

One of the more baffling characteristics of the roost site selection observed in this study is the height above the drainage bottom where the bats roost. Economy of energy would suggest that if bats use river corridors for travel purposes, as they appear to, then it would be more energy-efficient, for travel, to select a roost site which is (close to that travel corridor than to select a roost location which is farther away. The data failed to confirm this hypothesis. One possible explanation for this result is that there are other energetic factors that have a greater effect on the long-legged myotis than the energetic costs of travel. For example, since riparian areas are generally cooler than slightly elevated areas, the energetic costs of thermo-regulation might fail to compensate for the energy saved by avoiding travel if the bat roosts low in the drainage. Another possible explanation of the results from this test is that the statistical test was simply not sensitive enough due to insufficient sample size. With $0.05 < p < O. i$, the results of the test were a borderline case for rejection; a more extensive dataset or a study which addressed the bats' relative energetic costs might help to better identify the importance of roost position within the drainage.

It is also surprising that bats did not appear to select stands with higher-than-average snag densities. Since the bats appear to strongly prefer to roost in snags, the results of this test may be a reflection of the resolution of the categories (poor, fair, and good) that were used in the analysis. These gross classifications were the categories used by Boise Cascade to classify the stands in the GIS database; thus, these groupings provided the only information available on landscape-level snag availability. Presumably, with a larger sample size and with a more detailed database of snag availability, some difference in use might be detected. Another possible explanation for the result of this test is that gross snag availability is not art adequate index of roost availability. The results of this study show that diameter and height are both important factors in determining the suitability of a roost site. Thus, if the snags counted in the vegetation analysis are not of adequate size (in DBH and / or height) the snag density measures may be inappropriate for estimating roost availability. This problem would most likely occur in stands that have a relatively even age and size composition due to past logging or stand-replacing fires. A more useful measure of snags available for bat roosts might be to sample snags with exfoliating bark that extend above the canopy in height and have a larger DBH than the stand average.

Finally, it was determined that bats were not selecting roost sites out of the landscape at random, but rather, were returning repeatedly to individual roosts. This roost fidelity is not uncommon among bats and has been previously reported for long-legged myotis (Ormsbee, 1995). This fidelity makes ecological sense in many respects. Bats returning to a previously used roost may continue to experience adequate protection from predators and from environmental conditions. Additionally, if the position of the previously used roost is known and it is in a good location, the bat may benefit energetically by avoiding the search for a new roost site, especially if roosts are scarce. If roost sites are not scarce, however, these factors become less important; the most significant reason for returning to the same roost would be the threat of not finding another one. Because none of the bats in the study were lactating or pregnant, there is little reason to assume that they had biological ties to any particular roost. While this study did not directly address roost scarcity or try to identify the factors that are currently most limiting for the long-legged myotis population, the repeated use of the same roosts, on up to 7 nights in some cases, implies that roosts sites are either a limiting or a sensitive factor for the bats.

The data from the this study imply that *M. volans* identifies roost trees primarily based on three key characteristics: diameter, height, and condition. These findings are similar to the conclusions of similar studies (Ormsbee, 1995;

Campbell, 1993). Of equal importance is the conclusion that these characteristics may not be evaluated in absolute terms, but in relation to the surrounding habitat. Height, in particular, appears to be selected based upon the relative height of the potential roost to the surrounding canopy rather than the absolute height of the tree. Because they are volant, bats have a very different perception of the world than most mammals. It is likely that in selecting a roost, at least at the initial level, interest in a particular area is based upon large scale and supra-canopy characteristics. Understory composition probably has little to do with roost selection, except with regard to how it influences the structure of the upper levels of the canopy. This perspective can probably be applied to many areas of bat research to both aid in understanding bats' selection processes and to focus research efforts on key habitat variables.

MANAGEMENT IMPLICATIONS

Reference Calls

Only one conclusion was drawn from the comparison of reference calls from the Teanaway and from the west side of the Cascades: it is not possible m identify *Myotis yumanensis* calls from the calls of other *Myotis* species based on the minimum call frequency. Thus, on the Teanaway Ecosystem Project, conducted jointly by Boise Cascade and the University of Washington Wildlife Science Group, it would be prudent to group these bars into one category. Other studies on the east side of the Cascades should consider a similar protocol unless it can be ascertained that the calls of these groups can be positively identified in that particular locale.

Habitat Needs of the Long-legged Myotis

The roost site fidelity exhibited by *M. volans* in the Teanaway River Valley, in combination with the preference of *M. volans* for larger snags, leads to important management implications. The results of this study show that habitat modification will probably have direct and important ramifications for bats because of their reliance on roost sites with specific characteristics. In the Teanaway River Valley, *M. volans* uses primarily large snags which protrude significantly from the surrounding canopy. Thus, if land managers do not address the need for a continual supply of these large trees, it is likely that the roosting habitat of the long-legged myotis will be reduced over the next several decades. Faced with a roost site decline of this type, the future of the M. *volans* population in the Teanaway may depend largely on the bats' ability, to use alternate roost structures, such as rock crevices and buildings. While there is documentation that the bats have used these structures in other locales, this study located no *M. volans that* were using roost structures other than trees.

Current management practices of shelterwood cutting can lend themselves to the development of acceptable roost sires under certain circumstances. To maintain the long-legged myotis population in the Teanaway, significant efforts will have to be made to allow patches of trees to grow to larger sizes. These patches of trees will, as they age and die, become the dominant supra-canopy structures that the bats appear to select as roost structures. The patches should be frequent and well distributed across all habitats, especially in the wet grand fir sites which have the potential to grow larger trees faster than the drier sites. Periodic thinning, and possibly even fertilization, may be appropriate within these patches to allow for accelerated growth of these potential roost trees.

At this time, there is little research which :suggests appropriate patch sizes or distribution requirements for bat roosts. To find the best balance of patch size and distribution, several key factors must be considered, including daily movement capabilities of the bats, the bats' willingness to use the same roost repeatedly, seasonal variation in roost location and roosting needs, and home range characteristics.

For example, a study could be designed to evaluate daily movement patterns by locating both day roosts and also by tracking the bats' nocturnal foraging movements. By tracking the movements of several bats over the course of several nights, a researcher could obtain a good estimate of the approximate area used by the bats and also obtain important information about how the bats move on the landscape (e.g., do these bats use rivers as travel corridors?). This information could then be used to identify the proper distribution of roost patches on a managed landscape. Similar studies could answer questions regarding roost fidelity and the change of roosting needs over the course of a season (e.g., are there elevational changes in roosting location that correspond to seasonal temperature changes?). Ideally, these factors will be the focus of future experiments which will help to coalesce the thoughts of current researchers into concrete numbers that can be used for management.

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APPENDIX A

Appendix A: Capture data. This appendix includes a list of capture data from all of the animals captured during this study in the Teanaway River Valley in 1995. The following abbreviations are used in the table: ID = capture sequence number for an individual animal; Species = four-letter genus and species code for species identification; Date = date of capture; Time = time of capture (for bats caught in a Turtle trap, the time of capture is unknown); Sex = sex of the trapped animal, male or female; WT = weight in gains; TL = total length of the bat from the tip of the nose to tip of tail (ram); FA = forearm length (ram); HF = hind-foot length (ram); Ear = ear length from base of notch to tip (mm); WS = wingspan (ram); Notes = additional capture information, including pregnancy, lactation, injuries, and escapes (both before and after identification); MYSP = *Myotis* species (species unidentifiable within that genus); MYYU = *Myotis yumanensis,* Yuma myotis; MYVO = *Myotis volans*, long-legged myotis; MYCA = *Myotis californicus*, California myotis; MYLU = *Myotis lucifugus*, little brown myotis; MYEV = *Myotis evotis*, western long-eared myotis; MYCI = *Myotis ciliolabrum*, western small-footed myotis; EPFU = *Eptesicus fuscus*, big brown bat; LACI = *Lasiurus cinereus*, hoary bat.

ID	Species	Date	Time	Sex	WT	TL	FA	HF	Ear	WS	Notes
1	MYSP	7/11/95	21:55								escaped
2	MYLU	7/11/95	22:20		8		32				escaped
3	MYCA	7/12/95	21:48	M	6	69	25	4	11	220	
4	MYCA	7/13/95	21:34	M	7	75	36	10	10	210	
5	MYCI	7/13/95	21:43	M	6	90	35	6	13	225	
6	MYSP	7/13/95	22:11								escaped
7	MYCA	7/19/95	21:40	M	5	75	35	6	10	220	
8	MYLU	7/19/95	20:00	M	8	81	39	8	12	235	
9	MYLU	7/19/95	20:00	M	7	85	37	7	12	230	
10	MYLU	7/19/95	20:00	F	11	81	40	7	7	235	
11	MYSP	7/19/95	20:00								escaped
12	MYEV	7/19/95	22:43	M	9	100	42	10	12	255	
13	MYLU	7/19/95	23:08	M	8	95	44	12	13	250	
14	MYSP	7/19/95	23:23								escaped
15	MYLU	7/19/95	23:23	M	8	85	38	8	12	220	
16	MYVO	7/19/95	23:23	F	9	76	38	8	11	245	
17	MYLU	7/19/95	23:40	M	7	60	40	7	13	225	
18	MYSP	7/19/95	0:04								escaped
19	MYSP	7/20/95	21:40								escaped
20	MYLU	7/20/95	22:08	M	7	88	34	6	12	210	
21	MYEV	7/22/95	21:30	F	6	92	42	12	18	260	
22	MYSP	7/22/95	21:57								

23	MYLU	7/22/95	23:00	M	8	76	36	8	8	230	
24	MYLU	7/22J95	23:30	M	6	87	35	7	9	255	
25	MYEV	7122795	0:00	F	8	87	39	9	9	240	lactating
26	MYEV	7/25/95	20:55	M	8	78	36	7	19	235	
27	MYYU	7/25/95	n/a	F	5	81	3!5	9	14	225	
28	MYYU	7/26/95	21:39	F	5	91	33	7	9	227	
29	MYEV	7/27/95	21:55	M	7	84	40	8	17	221	
30	MYYU	7/29/95	21:33	M	5	85	3!5	7	11	245	
31	MYSP	7/29195	21:33								escaped
32	MYSP	7/29/95	22:52								escaped
33	MYLU	7/29/95	23:27	F	8	92	39	7	9	235	
34	MYSP	7/29/95	1:07								escaped
35	MYLU	7/30/95	22:19	F	6	91	41	7	11	251	
36	EPFU	7/30/95	2:10	M	21	130	53	9	12	310	
37	MYLU	7/30/95	2:10	M	7	91	38	9	9	243	
38	MYLU	7/30/95	2:10	F	11	92	38	8	9	246	
39	MYVO	7/30/95	2:10	F	11	99	39	8	9	250	
40	MYVO	7/30/95	2:45	F	11	97	39	7	11	250	
41	MYLU	7/30/95	2:45	F	9	91	40	8	9	248	
42	MYSP	7/30/95	2:50								escaped
43	MYSP	7/30195	2:50								escaped
44	MYSP	7/30/95	2:54								escaped
45	MYSP	7/30/95	3:02								escaped
46	MYVO	7/30/95	3:05	M	9	83	41	7	9	237	
47	MYVO	7/30/95	3:08	F	12	94	40	6	11	259	
48	MYVO	7/30/95	3:30	F	12	100	41	8	11	270	
49	MYVO	7/30/95	4:26	F	13	102	43	7	11	248	
50	MYLU	7/30/95	4:26	F	10	93	40	7	12	241	
51	MYVO	7/30195	4:26	F	12	98	39	7	9	250	
52	MYVO	7/31195	22:20	F	7	88	38	8	11	248	
53	LACI	7/31/95	22:25	M	11	98	45	9	12	260	
54	MYLU	7/31/95	22:25'	F	8	90	41	7	1	249	
55	MYYU	7/31/95	23:06	F	7	84	34	7	10	238	
56	MYYU	7/31/95	23:06	M	6	80	35	8	11	237	
57	LACI	7/31195	23:25	M	13	92	43	7	12	270	
58	EPFU	7/31/95	2:30	M	16	112	46	10	13	300	
59	MYLU	8/6/95	21:32	M	7	93	38	7	13	223	
60	MYLU	8/6/95	22:58	F	8	86	39	7	11	239	
61	MYVO	816/95	22:58	F	9	86	39	6	12	256	
62	MYVO	8/6/95	0:26	F	10	94	39	6	11	243	
63	MYVO	8/6/95	1:20	F	9	91	39	.5	12	263	
64	MYVO	8/6/95	1:43	F	10	92	41	6	11	252	
65	MYSP	8/6/95	2:12								escaped
66	MYVO	8/6/95	2:32	M	9	90	35	5	10	243	
67	MYSP	8/7/95	21:31								escaped
68	MYVO	8/7/95	0:55	F	8	93	39	7	9	260	
69	MYVO	8/7/95	0:55	F	9	92	39	7	11	255	
70	MYCl	8/11/95	n/a	M	4	82	32	5	10	245	
71	MYVO	8/11195	22:30	F	9	92	38	7	9	250	
72	MYSP	8111/95	22:54								escaped

73	MYVO	8/11/95	0:10	F	9	95	35	7	10	264	
74	MYVO	8/11/95	0:44	F	11	88	39	8	9	263	
75	MYVO	8/11/95	1:04	M	9	91	38	8	9	272	
76	MYVO	8/11/95	1:17	M	10	89	39	8	10	245	
77	MYVO	8/11/95	1:58	F	10	93	38	9	9	262	
78	MYVO	8/11/95	2:15	F	11	102	40	6	10	248	
79	MYVO	8/11/95	2:31	M	9	97	41	8	10	268	
80	MYVO	8/11/95	2:36	M	10	87	40	8	9	260	
81	MYVO	8/11/95	2:37	M	9	95	39	6	10	242	
82	MYVO	8/11/95	3:01	F	10	96	39	6	8	258	
83	MYCI	8/12/95	n/a	M	4	82	32	4	11	222	
84	MYCI	8/15/95	n/a	F		81	33	3	10	213	
85	MYCA	8/16/95	21:02	F		75	33	4	12	204	
86	MYEV	8116195	23:40								escaped
87	MYCA	8/20195	20:45	F	5	81	34	6	9	229	
88	MYVO	8/20/95	2:45	F	11	85	39	8	12	260	
89	MYEV	8/21/95	2:53	M	8	92	42	7	17	254	
90	MYCI	8/23/95	21:03	M	6	83	31	5	11	221	
91	MYLU	8/23/95	23:00	F	8	74	35	7	11	230	
92	MYVO	8/27/95	20:25	F	8	89	40	6	11	258	
93	MYVO	8/27/95	n/a	F	7	86	40	7	11	252	
94	MYCA	8/27/95	n/a	M	5	77	32	4	10	230	
95	MYVO	8/29/95	n/a	M	6	80	40	6	10	228	
96	MYLU	9/1/95	10:00	M	5	75	36	6	10	225	
97	MYVO	9/1/95	10:00	F	6	82	40	9	12	240	
98	MYVO	9/1/95	10:00	F	9	91	40	8	13	275	lactating
99	MYEV	9/1/95	10:00	F	7	82	38	8	14	254	
100	MYCA	9/2/95	21:45	F							escaped
101	MYVO	9/2/95	n/a	M	8	90	38	9	15	258	
102	MYVO	9/2/95	n/a	M	6	78	37	7	10	224	
103	MYVO	9/2/95	n/a	F	8	100	38	7	14	254	
104	MYVO	9/2/95	n/a	F	6	80	39	10	10	241	
105	MYSP	9/2/95	20:45								escaped
106	MYEV	9/2/95	21:12	F	6	82	32	8	13	235	
107	MYEV	9t2/95	21:45	M	5	75	36	10	13	224	
108	MYLU	9/2/95	21:55	F	6	83	37	6	8	234	
109	MYYU	9/2/95	22_:15	F	6	69	35	9	11	224	
110	MYYU	9/2/95	1:05	M	7	86	34	7	12	230	
111	MYYU	9/2/95	1:45	F	7	80	34	6	12	240	
112	MYLU	9/3/95	23:15	M	5	72	37	6	9	231	
113	MYVO	9/3/95	23:15	M	6	84	39	6	12	251	
114	MYCA	9/3/95	n/a	F	4	71	34	4	11	215	
115	MYYU	9/3/95	20:25	F	6	79	35	8	10	232	
116	MYYU	9/3/95	20:25	F	5	72	32	8	11	236	
117	MYYU	9/3/95	20:25	M	6	78	34	10	11	230	
118	MYYU	9/3/95	20:25	M	6	70	30	9	10	221	
119	MYYU	9/3/95	20:25	F	8	69	34	8	8	234	
120	MYYU	9/3/95	20:25	F	6	74	34	8	12	226	
121	MYYU	9/3/95	20:25	F	4	75	32	8	12	228	
122	MYYU	9/3/95	20:25	M	5	70	30	10	11	230	

123	MYLU	9/3/95	20:25	M	6	70	4(}	9	11	232	
124	MYEV	9/3/95	20:25	M	5	70	35	8	14	226	broken humerus
125	MYEV	9/3/95	20:25	F	6	73	35	7	14	232	
126	MYEV	9/3/95	20:25	M	5	68	31	**8**	11	220	

APPENDIX B

Appendix B. Roost sit locations. Coordinates of roosts in degrees west longitude and degrees north lattitude. Minutes and seconds have been expressed as fractions of degrees.

Longitude	Lattitude
120.884240	47.347680
120.884670	47.348963
120.884183	47.344825
I20.882137	47.345494
I20.883824	47.346713
I20.895088	47.349286
120.817237	47.297953
120.838965	47.288330
120.876040	47.269968
I20.876036	47.269981
120.849121	47.324912
120.766II9	47.348445
120.83698I	47.328349
120.844502	47.327971
120.890608	47.306111
120.891437	47.290058
120.898477	47.289638
120.883206	47.277221
120.858299	47.286816
I20.856091	47.292086
I20.822099	47.292869
120.81684I	47.297029
I20.811844	47.294604
120.819390	47.3162’44
120.818063	47.315886
120.819277	47.311712
120.889934	47.280875
120.870388	47.263889

APPENDIX B

INTENSIVE STUDY: NORTHWESTERN SALAMANDERS

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INTRODUCTION

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 amphibian sampling, 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 2 approaches: trapping and individually marking migrating and dispersing populations at breeding ponds, and following selected large individuals using radio-telemetry. The information described below represents preliminary results from the first 2 years of an on-going Ph.D. research project. A full description and analysis of this research will be available when the dissertation is completed.

RESEARCH AT BREEDING PONDS

RATIONALE

The purpose of this research is to investigate the breeding migration in the spring and the juvenile dispersal in the fall of the local population of northwestern salamanders Data on the size and demography of the migrating and dispersing populations, the timing of migration and dispersal activities, and the directionality of movement and duration of stay of individual salamanders were collected at 2 breeding ponds.

METHODS

This study was conducted at breeding ponds at the University of Washington's Charles L. Pack Experimental Forest near Eatonville, WA. Pack Forest is a working e×perimental tree farm and is composed primarily of a mosaic of managed Douglas-fir *(Pseudotsuga menziesii)* dominated forest ranging from clearcuts to 70-yr-old harvest age stands. The 2 study ponds, Tower and Twin, are located on a north-facing slope at an elevation of 400 m. The ponds are >1 km apart and are considered to be used by 2 independent populations of salamanders. Tower pond varies from 3 to more than 4 m at its deepest point (depending on the season) and is approximately 0.33 ha in size. Twin pond varies from 2-3 m deep and is approximately 1200 m^2· Both ponds have diverse aquatic habitat and are surrounded by a narrow margin of senescent red alder *(Alnus rubra).* At both ponds, the uphill (southern) side of the pond is a slope of mature Douglas-fir forest, and the downhill (northern) side is an open area; clearcut at Tower and a grassy elk meadow at Twin. Both ponds have confirmed populations of neotenic *A. gracile* and neither have fish or bullfrogs *(Rana catesbiana).* Other pond-breeding amphibians observed at these ponds include long-toed salamanders *(Ambystoma macrodactylum),* roughskin newts *(Taricha granulosa),* western toads *(Bufo boreas),* Pacific tree frogs *(Hyla regilla),* and red-legged frogs *(Rana aurora).*

Each breeding pond was encircled with a continuous drift fence with pitfall traps located at 3-m long breaks along the fence. The drift fence was located between 1 and 3 m uphill from the pond high-water mark, depending on obstacles and edge slope. Assuming no breaks in the fence, this method should theoretically capture all animals entering and leaving the ponds. In reality, intermittent damage to the fence by elk *(Cervus elaphus),* coyotes *(Canis latrans),* local teenagers *(Homo sapiens destructus),* and windthrow probably allows a small, unknown number of animals to get by the fence without detection.

In the spring, in-bound migrating salamanders were caught in the drift fence pitfall. traps, marked with a PIT-tag (a permanent individual mark), and released into the pond. Out-bound salamanders were again caught in the drift fence traps, checked for their identification number, and released outside of the fence. In the fall, out-bound dispersing juveniles are given a PIT-tag as they leave the pond. At each capture, all individuals were sexed, weighed, measured, and checked for their ID number, and the trap number of their capture was noted. In the next season, returning animals that already had PIT-tags are clipped on the right-rear toe to tell the in-bound and out-bound animals apart (this mark was indistinguishable by the next year). These methods were designed to generate a demographic profile of salamanders entering and leaving the pond as well as data on the timing of entrance and exit movements, the duration of stay at the pond, and the upland habitat where salamanders migrated.

RESULTS

In the 1994 breeding season, 432 salamanders were marked entering Tower pond to breed (the fence at Twin wasn't completed). Of these captures, 78% were males. In 1995, 612 salamanders entered Tower pond and 237 entered Twin pond, of which 83% and 87% were males, respectively. Adult males weighed an average of 20.1 g (range 10.1-28.6 g) and measured an average of 81.1 mm snout-vent length (range 63.4-95.4 mm) and 196 mm total length (range 154-228 mm). Adult females weighed an average of 24.1 g (range 12.6-43.0 g) and measured an average of 89.6 mm snout-vent length (range 78.3~108.0 mm) and 196 mm total length (range 161-245 mm). in both years, a small number (<10 per pond) of subadult metamorphosed individuals also appeared at the breeding ponds.

Dispersing newly metamorphosed juveniles numbered over 1500 at Tower pond in 1994, and 1400 and 600 at Tower and Twin ponds respectively in 1995. Due to elk damage to several sections of the drift fence, and to salamander removal from the traps by raccoons *(Procyon lotor),* river otters *(Lutra canadensis),* coyotes, and people, total numbers of dispersers were certainly higher in both years. Dispersing juveniles weighed an average of 4.0 g (range 2.0-10.5 g) and measured an average of 47.5 mm snout-vent length (range 39.3-68.8 mm) and 95.8 mm total length (range 79.3-140.9 mm). Most of these juveniles still had gill hubs visible beside their paratoid glands; these nubs were observed to last up to 3 weeks after metamorphosis under captive conditions.

The beginning of the breeding season migration ,occurred with the first spring thaw (Feb. 28 in 1994 and Jan. 15 in 1995) and captures continued through April. The migration peaked during the last week of March and the first week of April in both years when 84% of the captures occurred. The average time spent inside the drift fence was 8 days for females and 20 days for males. Dispersal of metamorphosing juveniles began in the 2nd week of September, within a day or 2 of the first fall rains. Dispersal continued through the 1 st week of December and peaked in the middle 2 weeks of October when half of all captures occurred. This coincided with the onset of continuous rain, and animals would appear in traps in pulses following nights of heavy precipitation.

Both breeding and dispersing individuals showed a strong preference for entering and exiting the ponds on their forested sides. Figure 1 shows a comparison of the numbers of animals using the forested side traps and the animals using the open side traps. Of the 69 traps at Tower pond and the 49 traps at Twin pond, almost exactly half were adjacent to each type of habitat while at least 75% of the salamanders used traps on the forested side in both years and at both ponds.

DISCUSSION

Most of these results generally agree with other accounts of northwestern salamander natural history. The 2 most interesting results of this work are the extreme male-biased sex ratio apparent in the adult pepulation, and the preference for entering and exiting the ponds along the forested side by both adults and juveniles.

A male biased sex ratio in migrating adult salamanders has been reported for *Ambystoma jeffersonianum* (Douglas 1979), *A. maculatum* (Husting 1965, Sexton and others 1986), and *A. macrodactylum* (Beneski and others 1986), but none were higher than 2:1 males to females. The unusually high ratio of males observed could be due to several possible life history attributes. One possibility is that there are more males than females in the terrestrial population. Dissection of a subset of dispersing juveniles in a later year of this research showed close to a 50:50 sex ratio, suggesting that a higher. overall number of females in the terrestrial population would probably be due to a low female survival rate. However, there was not large difference in the weights and lengths of the 2 sexes as would be expected if a differential survival rate existed. Such a high male-biased sex ratio was also not apparent in the fall amphibian sampling data

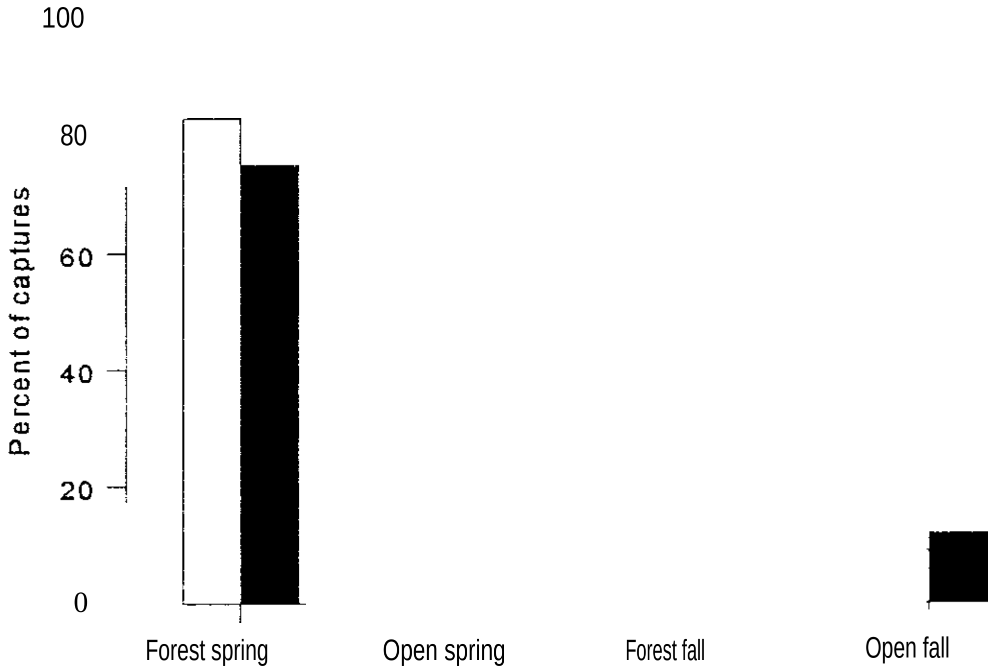

Figure 1. Percent of salamanders caught in traps adjacent to forested and open habitat at Tower and Twin ponds. Both ponds are surrounded by roughly half of each habitat type.

of the Landscape Study. A second possibility is that males may breed every year while females may breed only every other year because of the energetic constraints of producing egg masses. Differential breeding intervals between males and females has been documented for many amphibians (Duellman and Trueb 1986). Further, many of the males may be breeding with the neotenic female.,; living in the ponds. Courtship behavior has been documented between a metamorphosed male and a neotenic female in northwestern salamanders (Knudsen 1960).

The orientation towards the wooded section of the pond edge by emigrating juveniles and adults has also been observed in *A. maculatum* (Shoop 1965, Sexton and others 1986), *A. talpoideum* (Hardy and Raymond 1980), *Notophthalmus viridescens.* (Hurlbert 1969), and *Taricha granulosa* (Pimente11960). Considering the sensitivity of salamanders to extremes of temperature and their need for moist microhabitat, a tendency towards orientation towards the more microclimaticaliy buffered habitat is not surprising. This observed preference is most likely not simply an artifact of low survival in the open habitat since metamorphosing juveniles leaving the ponds for the first time had a higher percentage of individuals orienting towards the forest than the breeding adults. This leads to the question of how canopy removal affects the orientation out of a breeding pond of members of both the existing terrestrial population and newly metamorphosed animals.

RESEARCH USING RADIO-TELEMETRY

RATIONALE

The purpose of this research was to quantify movement patterns and habitat use of individual salamanders moving away from breeding ponds and in upland (non-breeding) habitat. Radio-telemetry methods allow *data* collection on the directionality, duration, and distance of each movement, the duration of stay at each location, and the associated surface structures and microhabitat of locations. These data produced a more accurate and detailed picture of movement activities and habitat use than trapping techniques.

METHODS

This study was conducted in the TFW Landscape study stands at Champion Pacific's Kapowsin Tree Farm and at the 2 breeding ponds at Pack Forest (see description above). Selected northwestern salamanders captured in the Landscape study fall amphibian sampling were used for' winter radio-telemetry. Salamanders caught in the breeding-pond drift fences were used for spring telemetry.

We conducted a pilot study investigating the feasibility of using radio-transmitters on northwestern salamanders in 1994. A surgical technique for transmitter implantation was successfully developed and tested on 10 salamanders. No weight loss, difference in movement distance and timing, or behavioral change was observed after surgery. Radio-transmitters were surgically implanted into the peritoneal cavity of the salamanders. The implantable transmitters (Holohil model BD-2G, Holohil Systems Ltd., Carp, Ontario) weigh 1.85 g, have a battery life of 4 months, and have a range of at least 60 m. The salamanders were anaesthetized with MS-222 during surgery and were released after 1-2 days recovery in the lab. At tile end of the 4-month battery life, transmitters were surgically removed and the salamanders were released.

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 8 during the spring (post-breeding season) months.

RESULTS

The movement activities of the salamanders showed several interesting and consistent patterns. After several days of initial post-release re-orientation, movement activities were generally characterized by a single large movement followed by an extended stay at a location point. Figures 2 and 3 show example maps of the movements of 5 of the radio-tracked salamanders in the upland and pond habitat, respectively. Movement directionality did not differ significantly from random except for those salamanders moving away from the breeding pond. The distances traveled between locations and the number of days spent at a location point are shown in Table 1. Locations were never revisited. Salamander movements within a resting location were continuous and ranged from a few centimeters to 0.5 m depending on the cover object size (see Fig. 1 for an example).

Salamanders were tracked to a location point usually associated with a cover object (e.g., coarse-woody debris, sword ferns, etc.) except in a few instances when the individual was found moving above ground. Almost half of the 55 cover objects used were sword ferns *(Polystichum munitum),* a ubiquitous forest understory species in our study area. Table 2 lists the type and number of other cover objects used by the salamanders. At these location points, the salamanders were found under or against the cover object at a depth of 1-8 cm in leaf litter, usually just above the litter-soil interface. Once the rains stopped in late spring, the salamanders became increasingly

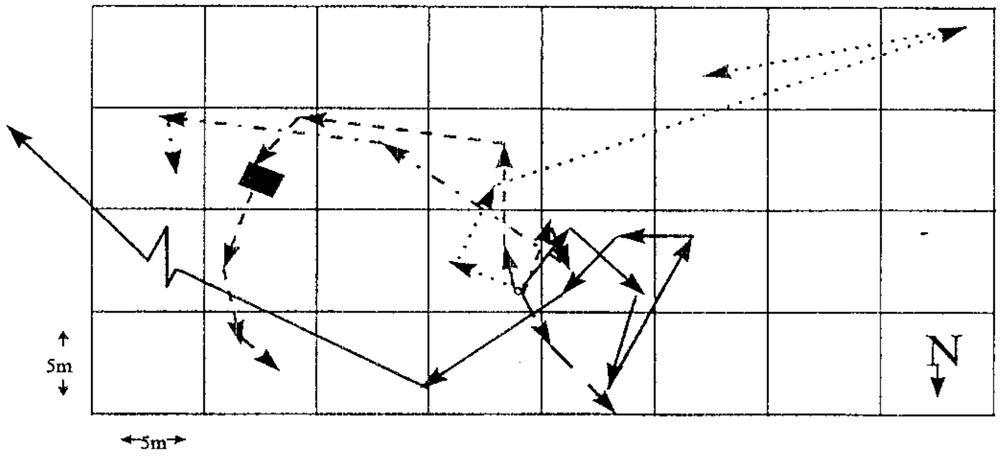

Figure 2. Map of movements over a 2 month period of 5 salamanders in upland (non-breeding) habitat. The grid lines represent 5 m squares. These salamanders were all released at the same point (lower middle of the map) and slowly moved away from each other. The upland habitat in this stand (D4 of the Landscape Study) is mature Douglas-fir forest. The rectangle in the upper left part of the map represents the area of micro-movements made by that salamander around a large sword fern.

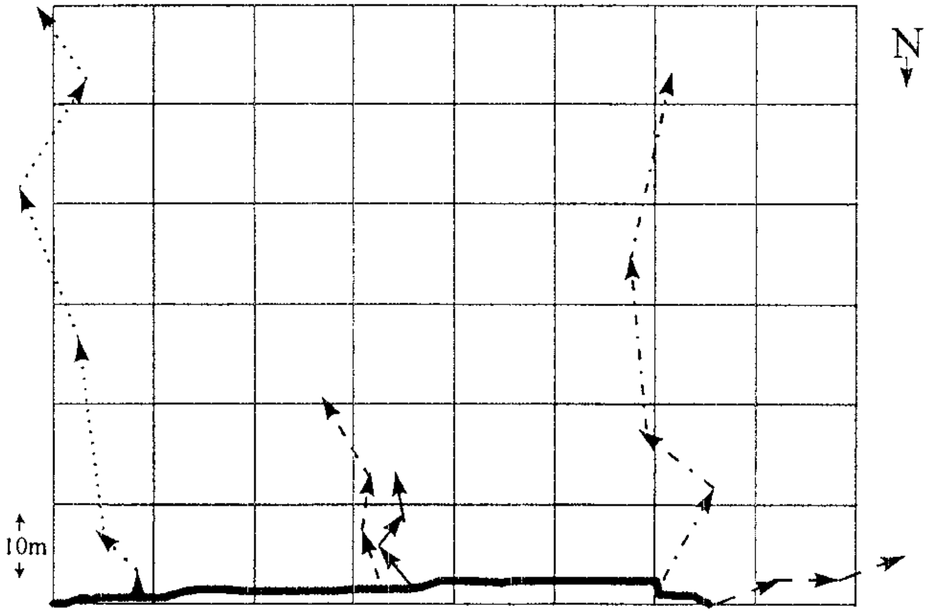

Figure 3. Map of the movements over a 2-month period of 5 salamanders migrating away from Tower pond. Grid lines represent 10-m squares. The salamanders were released at their capture locations along the drift fence. All 5 salamanders moved upslope into mature Douglas-fir forest.

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

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

difficult to locate as they moved into small mammal burrows >1 m deep, presumably to avoid desiccation.

Within the given time period, the movements of all radio-tagged salamanders were often temporally synchronous with each other and with a change in weather conditions (Fig. 4). Although the total number of moves during the study period varied between individuals, days when only 1 of the salamanders moved were rare. Synchronized movement usually occurred within 24 hours of the first rain after a short cold dry spell.

DISCUSSION

The results of the 1994 and 1995 radio-telemetry suggest several intriguing aspects of salamander movement patterns. Most notable is the apparent lack of movement restriction to a home range, and the distinctive synchrony of movements with climatic variables. Detailed research of northwestern salamander home ranges has not been done although there is a continuing assumption that they do use them. In contrast, the observations from this research suggest that a northwestern salamander's home range is either the entire area covered by the animal in a season or year or life-time, or it is the area used within a single cover object and is therefore constantly shifting as the salamander moves from 1 cover object to the next. If the defining purpose of the home range concept (to maximize resource acquisition efficiency through familiarity of a given area) is applied to northwestern salamander movements, then there appears to be no home range.

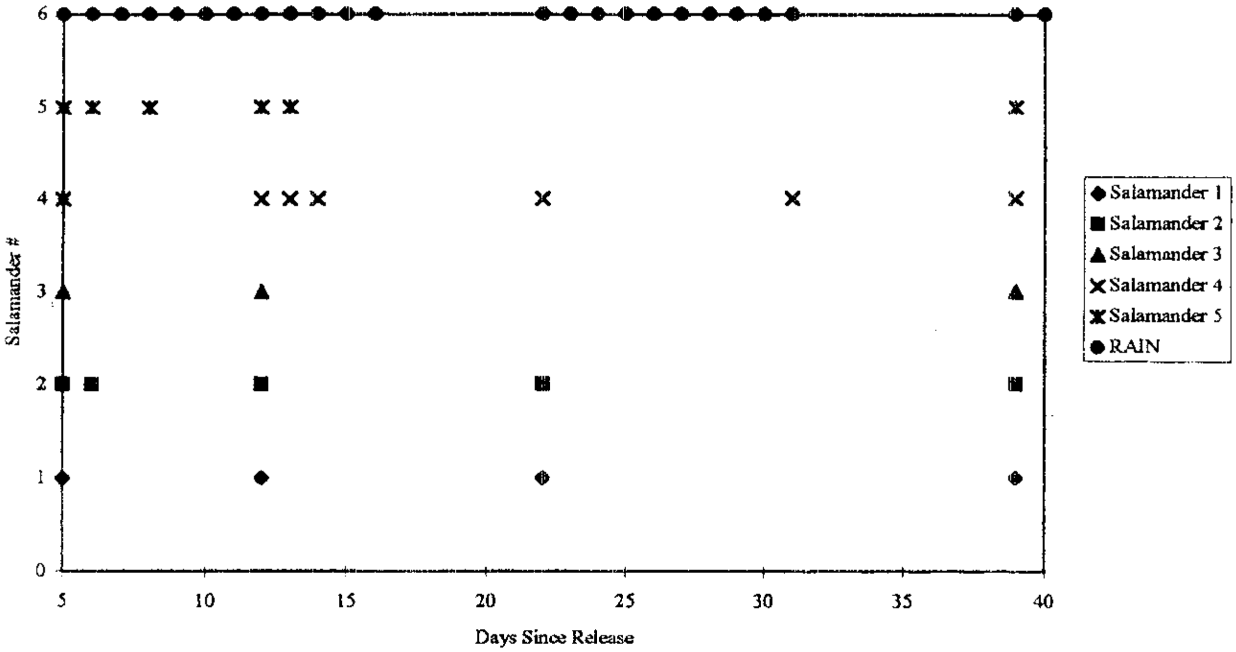

Figure 4. Days of rain and days on which individual salamanders (# l-5) moved during a forty day period. This is an example of the synchrony observed in movement initiation by the salamanders with each other and with precipitation. The top line of dots represents days when precipitation occurred.

The synchrony of radio-telemetry movements with precipitation, along with the correspondence to warm, wet weather of migration and dispersal onset at the breeding ponds, suggests 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, but no research has directly addressed this relationship. This correlation intuitively makes sense, given the vulnerability of amphibians to desiccation and to extremes of temperature.

Previous to this research, radio-telemetry of salamanders had only been done on hellbenders *(Cryptobranchus alleganiensis),* a large fully aquatic river dweller (Stouffer and others 1983). A goal of these 2 years of research was to test our methods and to obtain a baseline dataset of salamander movements so that a more detailed study of movement patterns and habitat use could be started. We were successful in accomplishing this and a 2rid radio-telemetry study using a larger sample size of salamanders and incorporating more refined microclimate and microhabitat data collection is now underway in the former Landscape study harvest-age stands.

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Habitat utilization and home range size of the bobcat
in managed forests of western Washington

by

Levon Phillip Yengoyan

A thesis submitted in partial fulfillment of the requirements
for the degree of

Master of Science

University of Washington

1995

Approved by Stephen D. West
(Chair of Supervisory Committee)

David Manuwal

Program authorized to offer degree College of Forest Resources

Date 6 March 1995

Signature

University of Washington

Abstract

Habitat utilization and home range size of the bobcat in managed forests of western Washington

by Levon Phillip Yengoyan

Chair of the Supervisory Committee: Associate Professor Stephen D. West
College of Forest Resources

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 75 I independent locations for six male and four female bobcats indicated a mean annual home range size of 14.4 km2 for nudes and 8.4 km2 for females. Home range size and movement indexes differed between sexes ($P < 0.05$) but not between seasons (winter vs. summer and breeding vs. non-breeding). A density estimate of 0.22 cats / km2 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 I978 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. Habitat analysis based on availability within the study area showed young stands (12-25 years old) to be the most and harvest-age stands (50-70 years old) to be the least preferred. 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. Preferred habitat appeared to be related to abundant understory vegetative cover and prey availability.

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ACKNOWLEDGMENTS

I thank the members of my committee, Keith Aubry, Dave ManuwaL and especially my chairperson Steve West, for all of their advice and assistance. Special thanks to Dave Brittell at the Washington Department offish and Wildlife for all of his expertise, advise, and encouragement. His help was invaluable in the execution of this study.

I am particularly indebted to those who assisted me in the field work. Roger Reeves and Darrell King taught me more about bobcats than I could ever have learned in a library. Dawn Johnson and Lamont Glass spent many days and nights taking telemetry locations. Suzie, Duke, and Rufus whose unending enthusiasm made k all possible.

Thanks to all my friends and fellow graduate students for their support and vital contributions to the various stages of this project. I am especially indebted to Michael Smith for his many long hours of GIS consulting under such difficult conditions.

Funding for this study was provided in part by the State of Washington through the Timber, Fish, Wildlife Agreement for the research project, *Wildlife use of managed forests- a landscape perspective. The* contracts FY92-009 and FY94-001 to Stephen D. West and Keith B. Aubry were administered by the Washington Department of Natural Resources. Funding was also provided by Champion International Corporation (Agreement 1>,-593 to Stephen D. West). I particularly thank Brian Gilbert for all of his help and commitment to this project and Kerry. Persing for the donation of her Wildlife Stewardship Award of the Forest Products Industry to this project. Additional financial support was arranged by Dave Brittell and provided by the Washington Department of Fish and Wildlife through the Washington Cooperative Fish and Wildlife Research Unit at the University of Washington (Agreement F93-IM-224). The trait is supported by the National Biological Service; the University of Washington; the Washington State Departments of Ecology, Fish and Wildlife, and Natural Resources; and the Wildlife Management Institute.

INTRODUCTION

Cats are one of the most highly evolved of all mammalian predators. Everything from their behavior to their specialized molars and retractable claws, is geared toward the pursuit and capture of prey. Due to this specialization, cats occupy a special niche at the top of the ecological pyramid with the more general predators and their prey at lower trophic levels. This specialization and the fact that felids occur in such low densities, make them extremely susceptible to excessive exploitation, habitat alteration, and decreases in prey abundance. This sensitivity suggests that felids may be good indicators of environmental condition in terms of quality and quantity of their prey and habitat (Koehler 1987).

Before the 1970’s bobcats *(Felis rufus)* were classified primarily as predators or nuisance animals and there was little interest in their status or management in the United States. This changed in the early 1970% when bobcat fur prices and trapping efforts increased due to a ban on the importation of most exotic "spotted cat" furs imposed by the Convention on International Trade in Endangered Species of Wild Flora and Fauna of 1973. Because of this, bobcats received increased attention from private, state, and federal organizations. Many studies were implememted to study the bobcats’ present status, trends in their populations, and their ranges to determine if numbers of bobcats were sufficient to allow far exploitation.

Early studies of bobcats focused on their distribution (Pollack 1950, Young 1958), general life history (Erickson 1955, Young 1958), food habitats (Pollack 1951, Gashwiler et al. 1960, Sweeney 1978), and depredation on game animals (Marston 1942, Matson 1948, Young 1958). More recent studies include population dynamics (Crowe 1974, Fritts and Sealander 1978, Knick et al. 1985), social organization (Bailey 1972), home range and movements (Marshall and Jenkins 1966, Bailey 1972, Brittell et al. 1979) and habitat selection (McCord 1974, Miller and Speake 1978, Knowles 1981, May 1981, Smith 1984, Rolley and Ward }985).

Few studies have been published from the western slates and information from Washington is sparse. Sweeney (1978) collected a total 0f204 bobcat carcasses from hunters and trappers from 1975 to 1977. He used the specimens to investigate diet, reproduction, and population structure of bobcats in western Washington. These data were also used in a comparison study of food habits of bobcats in eastern and western Washington (Knick et al. 1984). Other studies used carcasses to estimate population characteristics in eastern and western Washington (Knick et al. 1985). Brittell et al. (1979) radio-tagged 25 bobcats to study home range size, movement, density, and habitat use.

While a number of studies have looked at habitat selection of bobcats (McCord 1974, Miller and Speake 1978, Knowles 1981, May 198 }, Smith 1984, Rolley and Ward 1985), these studies have all occurred in relatively unmanaged ecosystems. Miller and Speake

(1978) reported that instrumented bobcats intensively used areas that had been recently togged, and that logging practices provided food and cover for bobcat prey species. In Oklahoma, Rolley and Ward (t985) found bobcats often used young-aged forests that supported higher numbers of bobcat prey species. The question of how habitat use is affected by extreme ecosystem alteration, such as intensively managing forests for timber production, has not been thoroughly addressed.

In Washington State, this question is especially relevant. The managed forests of Washing-ton encompass approximately 70,060 km^2 of which about 63% are on state and private lands (Card et al. 1985). Bobcat management on these lands is important for two reasons. First, bobcats are hunted and trapped for sport and furs with no bag limit. More detailed information on bobcat use of managed forests is needed to insure that harvest is kept at a sustainable level. Second, the major prey species of the bobcat in western Washington are mountain beaver *(Aplodontia tufa)* and snowshoe hare *(Lepus americanus)* (Sweeney 1978). Both of these animals feed on young trees and can have a major economic impact on managed forests (Bittner and Rongstad 1982, Feldhamer and Rochelle 1982). Mountain beaver in particular are economically important because they damage tree seedlings and saplings (Borrecco and Anderson 1980). In the Pacific Northwest, timber production is reduced by mountain beavers on approximately 1400 km2 of forested land, causing damage estimated at millions of dollars a year (Evans 1987, Hacker and Coblentz 1993). This has made extermination of mountain beaver necessary for tree farm management in some areas. A further understanding of bobcat ecology would assist us in maintaining adequate bobcat population levels to help reduce these losses.

In 1987, the Timber, Fish, Wildlife Agreement (TFW) introduced a framework for management practices on state and private lands. 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’s 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, before we can manage lands in this manner, it is necessary, to be able to analyze and predict the response of wildlife to various stand and landscape conditions (West and Aubry 199 I). Insights into the response of wildlife to forest management may help to elucidate the behavior of the system as a whole. Because the bobcat is an important predator in western Washington, studies of its behavior can contribute to an overall understanding of wildlife-habitat relationships in managed forests.

To investigate the impact of land use practices on wildlife, a TFW project entitled *Wildlife use of managed forests- a landscape perspective* was developed (West and Aubry 1991). The objectives of this project were to describe species composition and abundance levels of wildlife communities occurring in forests managed primarily for timber harvest. It examined wildlife habitat relationships at two spatial scales: the landscape and the stand level. Since stands are the building blocks of landscapes? stud,ring the effects of timber harvest on wildlife at the stand scale is necessary, to understand and model landscape-level processes. By studying bobcat habitat use in terms of seral stage, a larger comprehensive database of stand- and landscape-level habitat relationship s in managed forests can be developed.

As an adjunct to the TFW project, this study, conducted on a timber farm in western Washington, was designed to obtain information on bobcat use of managed forests. The primary objectives of this study were to:

1. determine bobcat habitat use, specifically in terms of the various seral stages found in a landscape managed primarily for timber production;
2. determine bobcat home range size and estimate density;
3. describe bobcat movement patterns and spacing; and
4. compare results to a similar study done in 1978 to determine changes in bobcat ecology between the two studies.

NATURAL HISTORY

Taxonomic Classification

The bobcat belongs to the Order Carnivora and Family Felidae. Since the beginning of this century, taxonomists have identified as many as 14 subspecies of bobcats based on color variations (Seton 1929, Hall and Kelson 1959). However, these are no longer believed to be distinguishable taxa with real biological or managerial significance (McCord and Cordoza 1982). Today, three subspecies of bobcat are recognized (Koehler 1987). In the state of Washington, two distinct subspecies occur. *Fells rufus fasciatus* is found in western Washington. *Felis rufus pallescens is* found in eastern Washington and across the remaining United States.

Physical Description

The bobcat is about twice the size of the average domestic cat *(Felis catus). The* rail tends to be shorter and the hind legs longer than the domestic cat. Overall, the bobcat is much more muscular and compact, characteristics that better enable them to spring at and catch their prey (Kelson 1946). The facial plane of the bobcat is very abrupt with a deeper jaw allowing for a wider opening of the mouth. Bobcats are digitigrade with sharp retractile claws. They have four toes on the hind feet while the front feet have a fifth toe that is raised (McCord and Cordoza 1982).

The pelage of the bobcat is generally a yellowish or reddish brown with black or dark brown streaks and spots. The tail has similar coloration with the addition of several dark bands that become more distinct at the tip. Their fur is dense, short, ,and very soft. Coloration of the bobcat varies widely although no true color phases occur (Ulmer 1941). Two molts take place each year with the winter coat tending to be longer and grayer then the summer coat. Bobcats in the northwest are said to have more colorful fur with more distinct spots then their counterparts in other areas of North America (McCord and Cordoza 1982).

Bobcats tend to be dimorphic in size with males usually larger than females. The weights of male bobcats range from 7.5 to 25.8 kg while females weigh from 3.8 to 15 kg (Young 1958). in general males weigh approximately 33% more; than females (McCord and Cordoza 1982). This dimorphism is also found consistently in standard measures of bobcat size. McCord and Cordoza (1982) averaged standard measurements from several different studies and found that males had an average total length of 869 ram, a tail length of 148 mm, a hind foot length of 170 ram, and an ear length of 66 mm. In contrast, females had measurements of 786, 137, 155, and 66 ram, respectively.

Distribution

Young (1958) described the historic distribution of the bobcat to include southern Canada, the entire United States and southward into Mexico to just below the 18th parallel. The current distribution of the bobcat is almost the same but it is absent in several midwestern areas. Its disappearance from those areas is attributed to intense agricultural practices and the removal of forests (McCord and Cordoza 1982). Historically and currently, the bobcat is distributed throughout the state of Washington (Dalquest 1948, Ingles 1965).

Home Range and Territoriality

Bobcats are solitary felids that establish well-defined home ranges or territories within which they forage and breed. According to Barley (1972) the primary, function of bobcat territoriality is spacing of individuals to insure an adequate supply of resources. Also, by performing one's activities, such as hunting, in the same area, bobcats develop a familiarity with their territory that allows them to utilize that area's food resources more efficiently (Tinbergen 1957). In most areas, territories of resident bobcats exclude other bobcats of the same sex, but will overlap with cats of the opposite sex. This inter-sexual overlap of territories may promote a more efficient breeding system (Bailey 1972). By having a home range that overlaps several females, a male bobcat could improve his chances of breeding with those females.

The exclusivity of bobcat territories is rigidly maintained by a combination of visual and olfactory signs that advertise a bobcat's presence without any physical confrontations (Bailey 1972). Bobcats mark their territories by depositing scats or urine, making scrapes on the ground, or marking with scents from anal glands (Bailey 1972). Territoriality. helps maintain the solitary, nature of bobcats, provides an even distribution of resources, and along with prey densities and habitat conditions, regulates *bobcat* population densities.

Home range size is reported to range from 0.6 km^2 to over 201 km^2 and varies with prey availability, habitat conditions, and bobcat density. (McCord and Cordoza 1982). In general, females have smaller home ranges than males (Koehler 1987). In westem Washington, male home ranges vary from 6.5 km^2 to 15.5 km^2 while female home ranges vary, from 3.9 km2 to 8.4 km^2 (Brittell et al. 1979).

Diet

The bobcat, like most predators, will eat prey that falls within certain size limits. Across its range, the bobcat most frequently preys upon animals that weigh from 700 g to 5.5 kg (Rosenzweig 1966). This includes rabbits (leporids) and large rodents. Next, the bobcat ,wil1 feed on larger prey (ungulates), followed by smaller prey weighing from 150 to 700 g (rats, squirrels, etc.) and then upon very. small prey (mice, shrews, moles) (McCord and Cordoza 1982). Also like most predators, the bobcat is opportunistic and will feed on almost anything that is available including carrion, insects, fish, birds, reptiles, and amphibians.

Leporids appear to be the primary food component of the bobcat throughout most of ks range (Miller and Speake 1978, Berg 1979). In the state of Washington, the snowshoe hare is not the primary food source, but is still an important one for bobcats. Sweeney (1978), in a study of bobcat food habits in western Washington, found that snowshoe hare made up 33.9% of their diet. The main prey species was the mountain beaver which comprised 48.6% of their diet. Deer *(Odocoileus hemionus)* and elk (Cervus *elaphus)* also were present as food items (5.6%). While the bobcats' ability to kill deer has been well documented (Marston 1942, Erickson 1955, Fritts 1973, McCord 1974), its appearance in the diet of western Washington bobcats is mostly attributed to scavenging after the hunting season (Sweeney 1978, Brittell, J.D., Washington Department offish and Wildlife, pers. comm)

Reproduction

Bobcats generally breed from February to April although they are capable of breeding throughout most of the year (Crowe 1975). In western Washington. the main breeding season is mid-February to mid-March with the majority of births occurring from late April through late May (Sweeney 1978). Females reach sexual maturity during their first year or shortly after their first birthday while males are able to breed after 2 years (Crowe 1975, Sweeney 1978). However, Bailey (1972) found that only resident bobcats with established territories reproduce and raise litters. Litter size ranges from one to five kittens with three being the average (Erickson 1955, Bailey 1972, Crowe 1975, Sweeney 1978).

Habitat

Bobcats are able to inhabit a wide variety of habitat types from swamplands to deserts and from high mountain ranges to dense coniferous forests (Koehler 1987). Their range is only restricted in the northern latitudes, where the snow is very deep, and in some areas of the midwestern states, where agriculture is so extensive that it has eliminated swamps, forests, and rock outcroppings.

Typical bobcat habitat varies across its range and can include swamps., forests, bogs, rocky ledges, or even a agricultural areas with an abundance of early successional stages (McCord and Cordoza 1982). Rugged areas with caves, rock outcroppings, and ledges provide natural denning sites, cover for hunting, protection from humans, and excellent overall habitat (Bailey 1974, McCord 1974). Other key factors for bobcat habitat include prey abundance, protection from severe weather, rest areas, and densely vegetated areas (Rollings 1945).

STUDY AREA

This study took place on Champion International's Kapowsin Tree Farm located in Pierce County., Washington (Figure 1). The tree farm encompassed approximately 500 km2 (Gilbert, B., Champion International Corporation, pers. comm) and fell within the physiographic province of the southwestern Cascade range. It was characterized by wet winters and dry summers with an annual precipitation that ranged from 800 to over 3000 mm (Franklin ,and Dyrness 1973). Elevation on the tree farm ranged from 200 to just over I500 m. The surrounding area was mainly rural land with Mr. Rainier National Park and Gifford Pinchot National Forest to the east.

The Kapowsin tree farm provided an ideal study location for several reasons. The forest stands were dominated by Douglas-fir *(Pseudotsuga mensiesii)* and western hemlock *(Tsuga heterophylla)* second growth, ranging in a?e from recent clearcut to stands over 60 years old, and were representative of the managed forest lands of western Wash/nEon. The area supported a population of bobcats and had controlled access to monitor hunting and limit poaching. The tree farm was also logistically advantageous with easy. access on numerous logging roads to all areas, making catching and monitoring of bobcats easier. Finally, this area was the site of another bobcat study done in 1978 (Brittell et al. 1979). This allowed for some comparison of results.

Within the Kapowsin tree farm, cats were caught in two separate areas in an attempt to study the range of variability found there. The north Kapowsin study area was currently

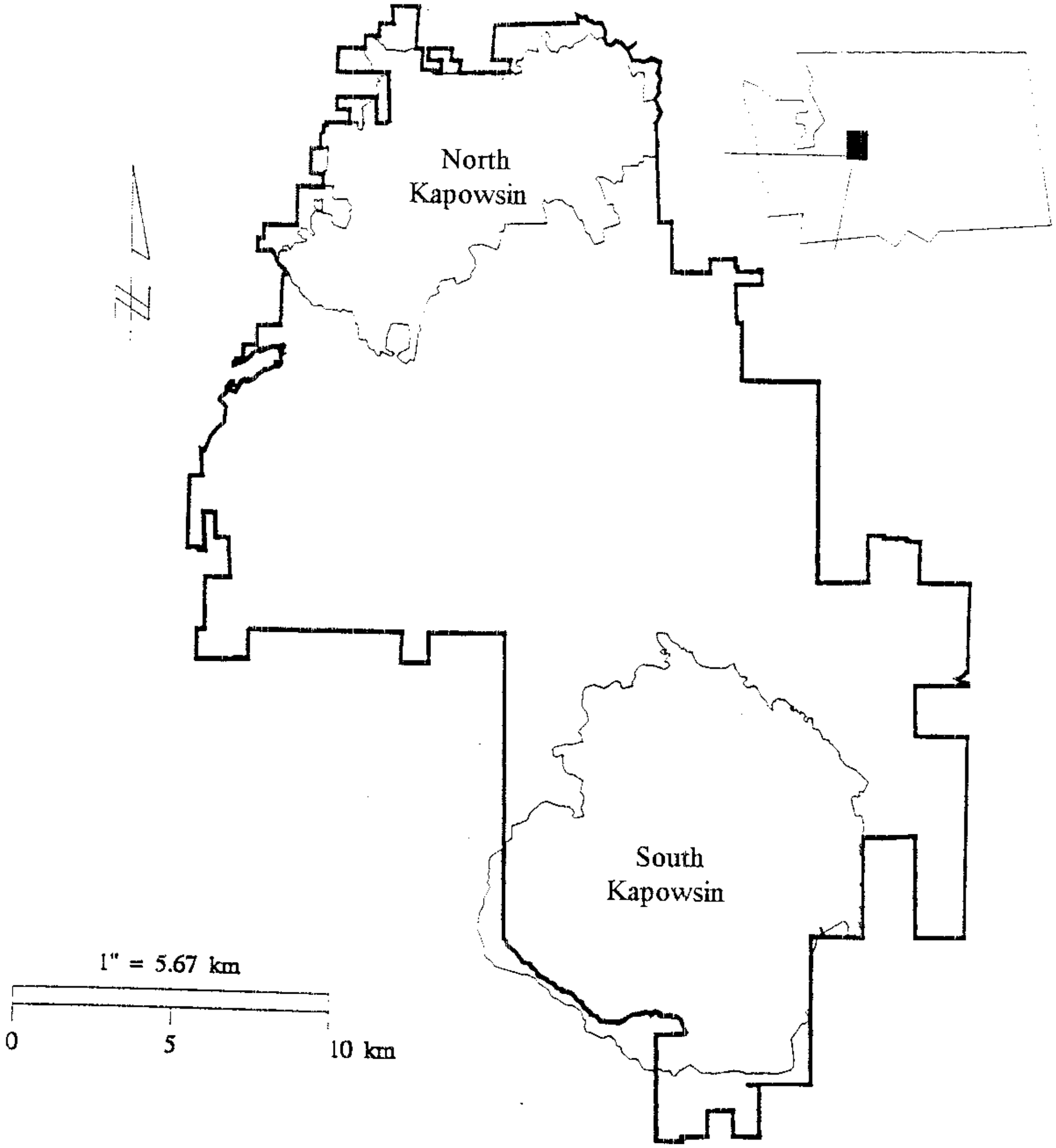

Figure 1. North and south Kapowsin study areas on the Kapowsin Tree Farm,

Pierce Co., WA, 1994.

undergoing its third harvest and had many small clearcuts and young stands interspersed with more mature forests. Activity. in this area was heavy due to on-going logging operations and abundant road access. Virtually all of the annual precipitation in north Kapowsin fell as rain, allowing bobcat hunters easy access during the winter hunting season. The topography in this area was gradual and there were few steep slopes or rocky clips.

The south Kapowsin study area was quite different. Stands in this area were much larger and recent logging was minimal. The higher elevation of south Kapowsin resulted in slower growing trees and more snowfall during the winter months. Activity here was lower due to a lack of active logging, an extensive road closure program, and deep snow that limited hunter access in the winter. The topography was more dramatic with steeper slopes, higher peaks, and many rock outcroppings.

METHODS AND MATERIALS

Capture and Handling

Bobcats were captured with the use of hound dogs from May I993 through August 1993 and April 1994 through June 1994. The dogs were driven along roads in various parts of the two study areas until they struck a cat scent. They were then released to follow the scent, eventually chasing the cat up a tree. Treed cats were immobilized with Ketamine Hydrochloride (1 mg / lb) via a dart fired from a Palmer dart rifle (Palmer Chemical & Equipment Co., Douglasville, GA). Cats were then weighed, measured, and radio-collared. Measurements recorded included color, total length, girth, right foreleg length, neck diameter, right rear shank diameter, and right rear pad dimensions. Capture location, time, drug dosages, sex, approximate age, and overall condition were also recorded. A numbered, blue Washington Department of Wildlife (WDW) tag was placed in the right ear of male bobcats and in the left ear of females. Each cat was fitted with a radio collar (Telonics, Mesa, AZ) that weighed approximately 180 g and had a battery life of 18 months to 2 years. Collars were equipped with mortality signals and 15 to 20 cm external antennas. Each collar was tuned to a specific frequency in the 151 MHz range. After processing, each cat was released and observed until it had recovered enough to leave.

Radio-Telemetry Methods

Collared cats were relocated from time of capture until the end of the study in September 1994, except for those that moved or died. Cats were monitored dally during the summer months and two or three tunes a week during the fall, winter, and spring. Locations were taken throughout the day and night in order to obtain information on all parts of the cats' circadian activity.

Relocation of collared cats was done using a two~element hand-held directional antenna and a Telonics TR4 receiver. Since cats are elusive and often hide in dense cover, locations were determined by triangulation from known points throughout the study area. Ninety-seven fixed stations were established in north Kapowsin and 150 in south Kapowsin. These fixed stations consisted mostly of road intersections. A Geographic Information System (GIS) road layer of the Kapowsin tree farm was obtained from Champion International. It was projected to the Universal Transverse Mercator (UTM) projection system and used to find UTM coordinates for each of the 247 tracking stations.

Locations of bobcats were determined by triangulation of bearings from two or more of these telemetry stations. The general position of the bobcat was first found using an omni-directional antenna. A directional antenna was then used to obtain telemetry bearings by determining the direction of the strongest signal and sighting along the antenna with a compass (Silva Ranger Type 15 Compass, Silva Co., Stockholm, Sweden). This was repeated at several different stations to get the best possible estimate of location. Approximately 3-4 minutes were needed to drive from one station to the next and take another beating. Only groups of bearings taken within 10 minutes of each other were used for one triangulation. The length of time between beatings is not believed to have resulted in large location errors. Telemetry bearings were recorded on forms filled out for each tracking session. Cat I.D. number, telemetry station, time, bearing, and activity status were recorded for each signal direction. Weather conditions were also recorded for the day in which the tracking session took place.

Bobcat locations were estimated from two or three beatings using Locate II (Pacer, Truro, Nova Scotia, Canada). This program used the UTM coordinates of the fixed telemetry stations, the beatings, and an estimate of bearing error to determine the actual location of the cat. Telemetry beating error was calculated by taking several beatings on radio-collars placed at unknown points. The true beating was then determined for each collar and the standard deviation of the beating error was calculated. A UTM coordinate for the cats' location as well as the area of the associated error polygon was obtained using the Max/reran Likelihood Estimation (MLE) procedure. These UTM coordinates were then input into Arc/Info (ESRI, Inc., Redlands, CA) to develop a GIS layer of cat locations and their associated I.D. numbers, dates, and times.

Only independent locations were used to determine home range size and habitat utilization. Independence of locations was important because auto-correlated data points used in home range models will tend to underestimate the true home range size. The magnitude of this error is related to the degree of dependence between the successive locations (Swihart and Slade 1985). White and Garrott (1990) reported that, as a general role of thumb, two locations can be considered independent if sufficient time has elapsed for the animal to move from one end of its home range to the other. In this case, two locations were said to be independent if they were at least 12 hours apart and if one period of high activity, dawn or dusk, occurred within that 12 hour period. This rule was further substantiated by Litvaitis et al. (1987) who calculated that bobcat locations more than 12 hours apart were independent based on the relationship of time and distance moved between consecutive locations.

Cover Types

Because the objective of this study was to determine bobcat use of managed forest, the study took place in an area managed primarily for timber production. This type of forest management turns the landscape into a mosaic of forest stands at different stages of maturity, rather than a variety, of vegetation types. Habitat type for this study referred to six stages of forest succession each with distinct structural components. Ages mentioned to describe the cover types are approximations and were not used as a basis for defining a stand. Dominant overstory species consisted of Douglas-fir and western hemlock with some red alder *(Alnus rubra)* and big leaf maple *(Acer macrophyllum)* in the more mesic sites. Understory vegetation consisted predominantly of Oregon grape *(Berberis nervosa)*, bracken fern *(Pteridium aquilinum)*, sword fern *(Polystichum munitum)*, fireweed *(Epilobium angustifolium)*, and Canada thistle *(Cirsium arvense)*.

The "Newcut" cover type consisted of stands that had been cut since July 1991. Trees in these stands were either absent or newly planted and! less than 0.3 m tall. Annual vegetation provided some cover in these stands in the summer, and slash leg over from logging was present year round. This cover type was only present in north Kapowsin.

"Clearcut" stands were approximately 2 to 5 years old. These stands had a well established herb stratum and trees that were less than 1 m tall. These young trees were not yet having a major impact on the herbaceous vegetation but, along with the herb stratum, did provide low cover.

The "Reprod" cover type had trees that were 1 to 4 m tall These stands were 4 to 12 years old and were dominated by trees. These trees had not yet begun to close and form a canopy. This allowed sunlight to reach the ground and a dense herb and shrub layer to form. The combination of trees and herbaceous vegetation provided extensive cover in these stands.

Trees in the "Young" stands were 13 to 25 years old and 4 to 10 m tall. A tree canopy had started to form in this stage, causing the lower branches on the conifers to die. There were many gaps in the canopy that allowed sunlight to reach the ground. The growth of herbs and shrubs in these gaps provided patches of abundant cover.

"Mature" stands were 25 to 50 years old with trees over 10 m tall. These stands were densely stocked and a wide variety of tree diameters were present. The tree canopy had completely formed allowing very little light to reach the ground. Therefore, there was virtually no herbaceous material on the ground and little cover.

The "Harvest" cover type had mature trees 50 to 70 years old which were almost ready to be harvested. These trees had uniform stem diameters and were widely spaced, usually due to commercial thinning. The closed canopy of the previous stage had opened up, allowing moderate amounts of light to reach the ground. This resulted in a re-establishment of the herb and shrub layer which provided low-level cover.

Vertical vegetative cover was quantified for each habitat type. A transect consisting of 10 sampling points, each 50 m apart, was walked in four randomly selected stands in each habitat type. At each point, two measurements of vertical vegetative cover were taken using a coverboard as described by Nudds (1977). A coverboard 2 m high, 1 dm wide, and marked at 0.5 m intervals was held by an assistant 15 m from the sampling point on either side of the transect. The percentage of the board obscured by vegetation in each 0.5 m layer was recorded using a density score that corresponded to a mean value within a range of deciles (i.e. 1 corresponds to the range of 0 to 10 percent, 2 corresponds to the range of I0 to 20 percent, etc.).

Habitat Map Development

Habitat maps were created for both study areas within the Kapowsin tree farm. Each study area was defined as the area that had been hunted with dogs. To develop a landcover map to analyze habitat use, a satellite image from Landsat V's Thematic Mapper (TM) was obtained from the Washington Department of Wildlife through the Washington Gap Analysis Project and the USDA Forest Service Pacific Northwest Research Lab. This image was created from the energy reflectance from earth in seven different wavelengths and was taken on 7 July, 1991. The image was subset to the study area and classified using ERDAS Imagine (ERDA& Inc., Atlanta, GA). An unsupervised classification was performed using bands 3, 4, 5 and 6 with a convergence value of 0.95. This procedure reduced the total number of spectral classes to 75.

The unsupervised classification scene was then displayed in Arc/Info along with road and stand boundary layers. Based on aerial photographs, Champion stand maps, and extensive ground truthing, boundaries were drawn around contiguous areas of each habitat type by manual on-screen digitizing in Arcedit. These polygons were then assigned names corresponding to their habitat type.

Data Analysis

Home range size was calculated using three different methods. These were minimum convex polygon (Hayne 1949), harmonic mean (Dixon and Chapman 1980), and adaptive kernel (Worton, 1989). Minimum convex polygon (MCP) home ranges were calculated using all independent locations for each cat. Harmonic mean (HM) estimates of home range were calculated at a 95% contour. The Adaptive Kernel (ADK) estimator of home range was used in most of the analyses in this study. It was calculated at a 100% contour to define all the areas the cats had used. a 95% contour to define the cats home range or areas where the cat traversed "in ks normal activities of food gathering, mating, and caring for young" (Burr 1943), and a 50% contour to define core areas or areas of greater use.

Home range size for each method at each contour, as well as linear distance between successive locations, were calculated using Program CALHOME (U.S. Fish and Wildlife Service). Along with the home range estimates and movement distances, this program also provided the coordinates of perimeter data points for each home range estimation. These coordinates were imported into Arc/Info, and GIS layers of cat home ranges were created.

Comparisons were made for a number of different home ranges using an F-test of equal variances, and a t-test for differences in mean home: range size. Differences in home range size were tested by sex, season, breeding season study area, and study. Seasons were designated as winter (November - April) and summer (May - October). Breeding season was designated as February through July and non-breeding season as August through January. Study area comparisons tested for differences in north Kapowsin and south Kapowsin. All of these comparisons were tested using 95% ADK and 50% ADK estimates of home range. Finally, 95% HM home ranges from this study were compared with those found by Brittell (1979) who studied bobcats in the same area. The three methods of home range were also compared. Correlation analysis was performed to see which methods were more highly correlated with sample size.

The degree of intra-sexual home range overlap was calculated for adjacent male and female areas. Inter-sexual home range overlap was calculated for males overlapping females, and females overlapping males. This was done with the 95% HM, 100% ADK, 95% ADK, and 50% ADK home range estimates. Arc/Info was used to intersect adjacent home ranges, calculate the area of overlap, and compute the area of each cover type within the overlapping area. Percentage overlap was compared with that found by Brirtell (unpublished data) using a t-.test.

As done by Brittell (unpublished data), density was calculated using two methods based on home range size and mean home range overlap estimations. For this analysis, home ranges were assumed to be circular, equal-sized, and packed together in a hexagonal pattern. Maximum theoretical density was calculated; 1) estimating densities for males and females separately and assuming total overlap of populations, and 2) considering males and females together with separate but partially overlapping home ranges. Population estimates were obtained by extrapolating density figures for each study area. Density and population estimates were done using the 95% ADK home ranges estimate and the 95% HM method.

Mean distance between consecutive locations of 14 days or less was computed as an index of bobcat movement. These data were compared by sex, season, breeding season, and study area using a t-test.

The areas where bobcats established their home ranges represented a prior selection of habitat. Once home ranges were established, bobcats may have selected for different areas within them. Habitat selection may occur in at each of these two levels, therefore, habitat utilization must be examined in two stages. First, since the bobcats lived in a certain part of an arbitrarily defined study area, home range and core area selection within the study area was examined. Friedman's test (Friedman 1937, Conover 1980) was used to test if the ranks of differences between use and availability were the same for all habitats. Use was defined as the proportion of a particular habitat type in a cat's 95% and 50% ADK home range. Availability was defined as the proportion of a particular habitat type within the study area. These differences were ranked and tested, treating cats as blocks and habitat types as treatments. If the test result was significant, a multiple comparison test (alpha = 0.05) on the difference between selection and availability (Conover 1980) was used to determine differences in the relative selection of each habitat type. This type of analysis was also performed comparing habitats within core areas to available habitats with/n the home ranges.

The second stage of the analysis was performed to investigate bobcat habitat utilization within their home range. Habitat use versus availability was determined by comparing the observed frequency of locations in each habitat type,, to an expected frequency of use based on the proportions of each habitat type within a cat's home range. Arc/Info was used to determine the total area of each habitat type within a cat's home range and the number of locations within each habitat type. This analysis was performed using the ADK home range at each of the three contour levels.

Once the proportion of each habitat type available to the bobcats was determined, expected frequencies of telemetry fixes were calculated, by assuming that all the habitat types were chosen randomly. The Chi-square statistic was employed to determine if each habitat type was used in proportion to its availablity. Rejection of the null hypothesis at $p < 0.05$ indicated that cover types were not used in proportion to their availability.. If this occurred, then the Bonferroni Z-statistic used by Neu at al. (1974) and clarified by Byers et al. (i984) was used to determine if some cover types were being selected for (preferred) or selected against (avoided). Habitat use was also determined by season and by time of day. Time of day was broken down into four six-hour periods; AM crepuscular (0400 - 1000), day (1000-1600), PM crepuscular (I600-2000), and night (2000-0400).

It is important to mention that the terms "prefer" and "avoid" will be used to designate selection for and against even though they imply that bobcats are making a conscious evaluation of each habitat type. In reality, there is no way of knowing if this is actually the case. Therefore, if one habitat is said to be preferred, this means that more time is spent in that habitat type than would be expected by chance alone. Conversely, avoidance means that less time is spent in that particular cover type than would be expected by chance alone.

RESULTS

Capture

A total of 11 bobcats, seven males and four females;, were captured during the course of tins study. Seven bobcats were captured during the first capture season between 13 May 1993 and 31 August 1993. Four bobcats were captured during the second capture season between 8 April 1994 and 3 July 1994. Also captured were five mountain lions which were released without processing.

In north Kapowsin, four bobcats were captured in 22 days of hunting with hounds. Number 47 was an adult male captured on 29 July 1993. Number 07 was captured on 15 August 1993 and was sighted with kittens that summer; she was the only female caught in this area. Number 00 was a male caught during the second season on 19 April i994. All three of these cats were radio-tracked from time of capture to the end of the study and were all alive when last relocated. The final cat caught in north Kapowsin was No. 11, a juvenile male caught on 29 August 1993. Number 11 was radio-tracked for a month before disappearing. He was relocated once by plane several miles from his normal range, and killed by a hunter on 29 January 1994.

In south Kapowsin, seven bobcats were captured in. 27 days of hunting. Number 12 was a male captured on 20 May 1993, who was tracked until mid-January 1994 when he disappeared; his fate is unknown. Number 31 was a female captured on 2 June t993 and was believed to have had kittens that year. She was tracked throughout the summer before her mortality signal activated on 21 September 1993. Her carcass was found, mostly eaten, and her cause of death is unknown. Number 05 was a female caught on I3 June I993, and No. 43, a male, was also caught during the first season on 24 June 1993. Both of these cats were alive at the end of the study. During the second capture season, two males were caught, No. 45 and No. 41, on 24 April 1994 and 3 June 1994, respectively. One lactating female, No. 14, was also caught during the second season on I0 June 1994. All three of these cats were alive when last relocated on 6 September 1994. Identification number, date of capture, physical data, and number of independent locations for the l 1 captured bobcats are presented in Table 1.

Radio-Telemetry

A total of 790 radio locations were recorded for the l i bobcats. Of these, 751 were determined to be independent. Overall standard deviation of the bearing error angle was 1.63. The mean size of the error polygons for the 751 independent locations was 0.0038 km^2. This area was approximately 2 by 2 pixels on the GIS layers. Cat No. 11 was excluded from all further calculations because he was only followed for a short time and an insufficient number of locations were collected for him.

Habitat Map and Vertical Vegetative Cover

North Kapowsin (Figure 2) encompassed 64.72 km^2 and had all six cover types present. South Kapowsin (Figure 3) encompassed 112.71 km^2 and had only five of the six cover types present (Table 2). Mean cover values and standard deviations were calculated for

Table 1. Capture data and number of relocations for 11 bobcats captured on the Kapowsin Tree Farm, Pierce Co., WA, 1994.

Total length measurement in mm. Weight in kg. Cats last relocated on 6 Sep 1994 were alive at the end of the study.

I.D.#	Ear Tag Number	Sex	Study Area (North/South)	Date Captured	Wt.	Total Length	Number of Relocations	Date Last Located
00	258-Right	M	North Kapowsin	19 Apt 1994	10.5	1023	47	6 Sep 1994
05	253-Left	F	South Kapowsin	13]tin 1993	7.0	897	139	6 Sep 1994
07	256-Left	F	North Kapowsin	15 Aug 1993	6.8	943	109	6 Sep 1994
11	257-Right	M	North Kapowsin	29 Aug 1993	8.6	968	8	18 Nov 1993’
12	251-Right	M	South Kapowsin	20 May 1993	11.4	923	64	14 Jan 1994’*
14	262-Left	F	South Kapowsin	3 Jul 1994	8.0	88t	23	6 Sep 1994
31	252-Left	F	South Kapowsin	2 Jun 1993	7.8	910	42	21 Sep 1993’**
41	260-Right	M	South Kapowsin	3 Jun 1994	9.8	986	25	O Sep 1994
43	254-Right	M	South Kapuwsin	24 Jun 1993	Il.I	10911	130	6 Sep 1994
45	259-Right	M	South Kapowsin	24 Apt 1994	11.6	935	49	6 Sep 1994
47	255-Right	M	North Kapowsin	29Ju11993	11.1	1038	115	6Sep 1994

* Shot by hunter on 29 Jan 1994. ** Disappeared and fate remains unknown. *** Cause of death is unknown.

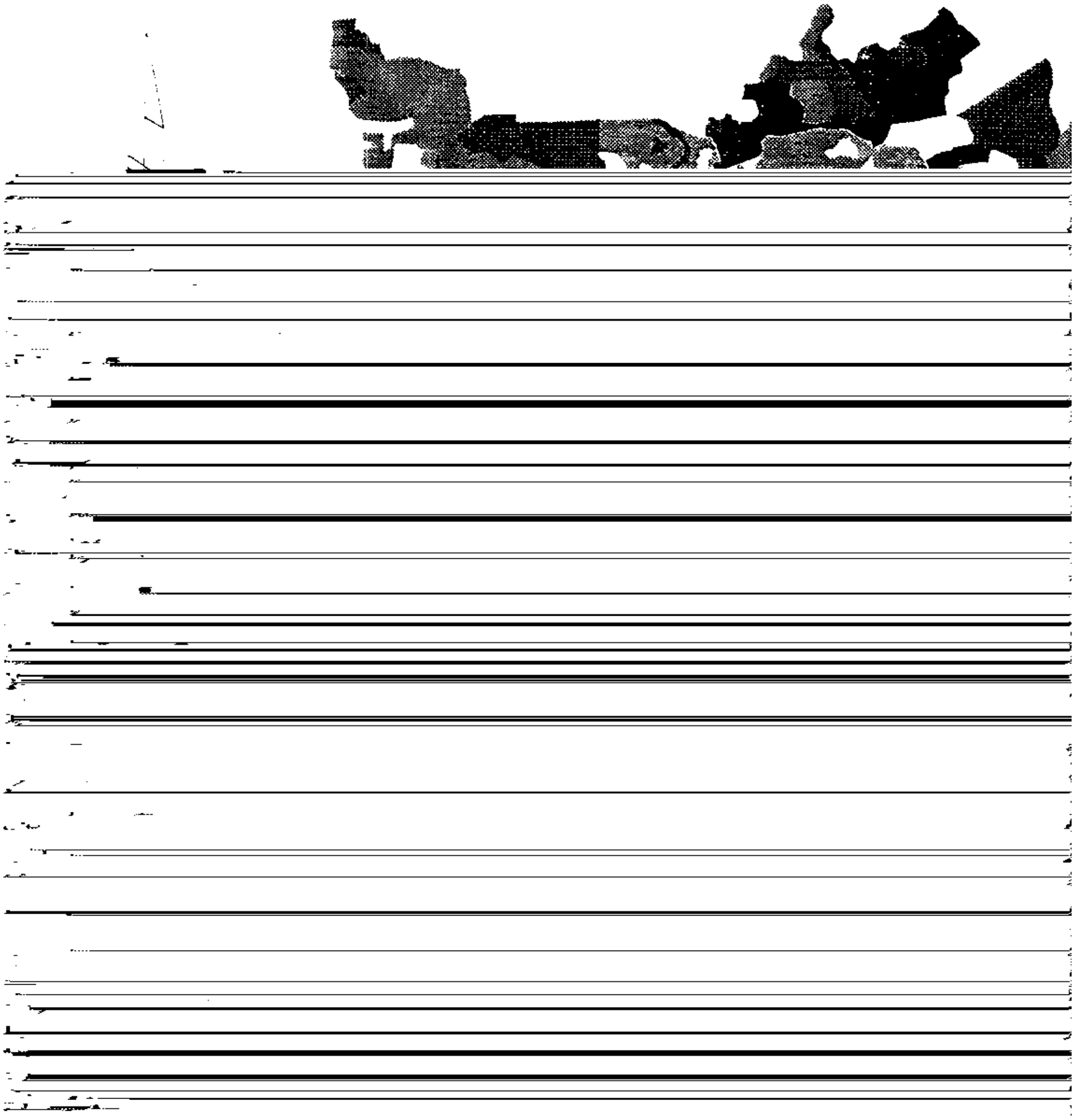

Figure 2. Map of cover types in north Kapowsin study area, Kapowsin Tree Farm Pierce Co., WA, 1994.

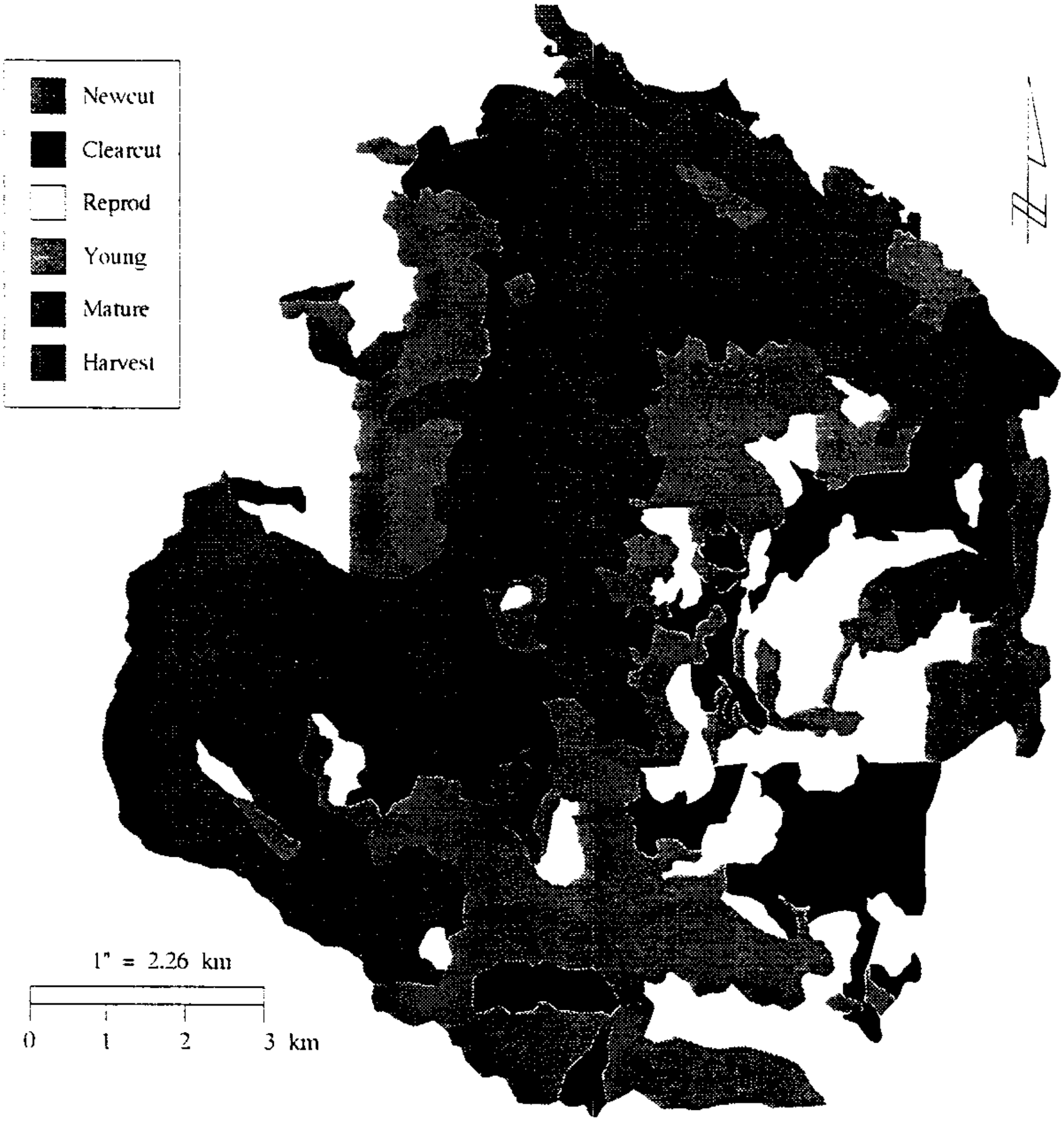

Figure 3. Map of cover types in south Kapowsin study area, Kapowsin Tree Farm, Pierce Co., WA, 1994.

Table 2. Total area of six different cover types in two study areas on Kapowsin Tree Farm, Pierce Co., WA, 1994.

Study Area	Cover Type	Area (km2)	Percent of Total Area
North Kapowsin	Newcut	3.17	4.91
	Clearcut	9.08	14.03
	Reprod	6.57	10.14
	Young	21.89	33.82
	Mature	2.61	4.04
	Harvest	21.40	33.06
	Total	64.72	100.00
South Kapowsin	Clearcut	13.56	12.03
	Reprod	15.74	13.97
	Young	32.79	29.09
	Mature	26.32	23.35
	Harvest	24.30	21.56
	Total	112.71	I00.00

each layer within each cover type (Table 3). Analysis of variance showed that all cover types exhibited differences in the amount of vegetation at different heights above ground level ($P < 0.001$) (Table 4). The smiler F-values in the Reprod, Young, and Mature cover types corresponded to a more uniform distribution of vegetation at all heists. Reprod and Young cover types had the greatest overall mean cover values and were the densest. Newcut. Clearcut, and Harvest cover types were moderately dense with most of the cover occurring in the lowest layer. The Mature cover type was the least dense with little cover at any of the heist layers. The vegetation structure of all six cover tyes in each layer can best be shown as a foliage profile (Figure 4). A layer by layer comparison of all six cover types was also performed and all layers showed significant differences among the habitats ($P < 0.001$).

Home Range

Home range was calculated for 10 bobcats: four females and six males. Home range estimates varied in size (Table 5) and shape (Figure 5) depending on the method used. The MCP and 95% ADK estimates were not different ($P = 0.939$). The 95% HM method produced smaller size estimates that were different from the MCP ($P = 0.036$) and the 95% ADK ($P=- 0.022$) methods. Correlation analysis showed the 95% ADK method to be the least correlated ($r = 0. 158$) with the number of locations used in the estimation. The MCP estimation was more highly correlated ($r = 0.481$) and the 95% HM estimation was the most highly correlated ($r = 0.74$) with the number of locations. All further home range estimations are based on the 95% ADK unless otherwise noted. Home range calculations

Table 3. Mean cover values for each habitat type broken down by layer above the ground on Kapowsin Tree Farm, Pierce Co,, WA, 1994. Values are mean density, value within range of deciles = standard deviation with number of cover measurements in parenthesis.

Cover Type	Overall Mean	Layer (m),	Mean Density,
Newcut	3.778	0.0 - 0.5	9,475 = 0.914 (80)
		0.5- 1.0	4.225- 2.556 (80)
		1.0- 1.5	1.075 - 1.741 (80)
		1.5 - 2.0	0.335 = 0.913 (80)
Clearcut	2.834	0.0- 0.5	6.925 ± 2.293 (80)
		0.5- 1.0	3.213 = 2.067 (80)
		1.0- 1.5	0.913 = 1.046 (80)
		1.5 -2.0	0.288 = 0.556 (80)
Reprod	8,1.41	0.0 - 0.5	9.888 = 0.390 (80)
		0.5- 1.0	9,388 = 1.206 (80)
		1.0- 1.5	7.375 ± 2.071 (80)
		1.5 - 2.0	5.913 ± 2.720 (80)
Young	7.016	0.0 - 0.5	8.588 ± 1.733 (80)
		0.5- 1.0	6.638 ± 2,094 (80)
		1.0- 1.5	6.225 ± 2.387 (80)
		1.5 - 2.0	6,613 ± 2.264 (80)
Mature.	1.147	0.0- 0.5	2,238 ± 1.593 (80)
		0.5- 1.0	1.000 = 0.968 (80)
		t.0- 1.5	0.763 = 0.767 (80)
		1.5 - 2.0	0.582 = 0.688 (80)
Harvest	4.125	0.0 - 0.5	8.975 ± 1.147 (80)
		0.5- 1.0	4.123 ± 2.062 (80)
		1.0- 1.5	1.850 ± 1.592 (80)
		1.5 - 2.0	1.563 ± 1.200 (80)

Table 4. Variation in vegetation density within six habitat types on Kapowsin Tree Farm

Pierce Co., WA, 1994.

Cover Type	Layer (m)	Mean Density	F-value	Significance Level
Newcut	0.0- 0.5	9.475	491.91	P < 0.001
	0.5- 1.0	4.225		
	1.0- 1.5	1.075		
	1.5 - 2.0	0.338		
Clearcut	0.0 - 0.5	6.925	263.97	P < 0.001
	0.5- 1.0	3.213		
	1.0- 1.5	0.913		
	1.5 - 2.0	0.288		
Reprod	0.0 - 0.5	9.888	81.51	P < 0.001
	0.5- t.0	9.388		
	1.0- 1.5	7.375		
	1.5 - 2.0	5.913		
Young	0.0 - 0.5	8.588	49.92	P < 0.001
	0.5 - 1.0	6.638		
	1.0- 1.5	6.225		
	1.5 - 2.0	6.613		
Mature	0.0 - 0.5	2.238	39.31	P < 0.001
	0.5 - 1.0	1.000		
	1.0- 1.5	0.763		
	1.5 - 2.0	0.582		
Harvest	0.0 - 0.5	8.975	394.21	P < 0.001
	0.5- 1.0	4.123		
	1.0- 1.5	1.850		
	1.5 - 2.0	1.563		

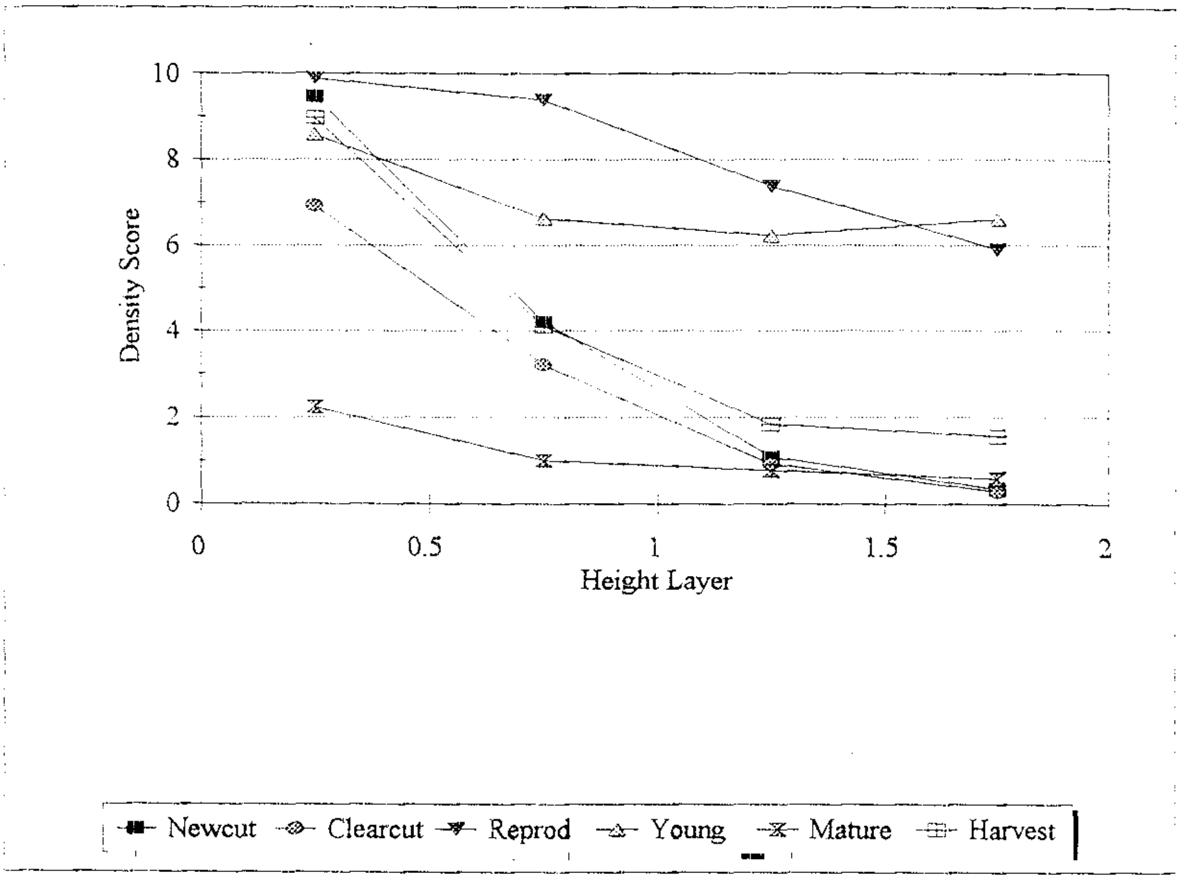

Figure 4. Vegetation profile for six cover types on the Kapowsin Tree Farm, Pierce Co., WA, 1994.

Table 5. 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 M/n/mum Convex Polygon (MCP), Harmonic Mean (HM), and Adaptive Kernel Estimator (ADK) at various contour levels. Area measurement in km2. Movement distance ill km Grid cell size in m.

I.D. #	100% MCP	95% HM	100% ADK	95% ADK	50% ADK	Mean Distance	Grid Cell Size
Males							
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	
Females							
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	

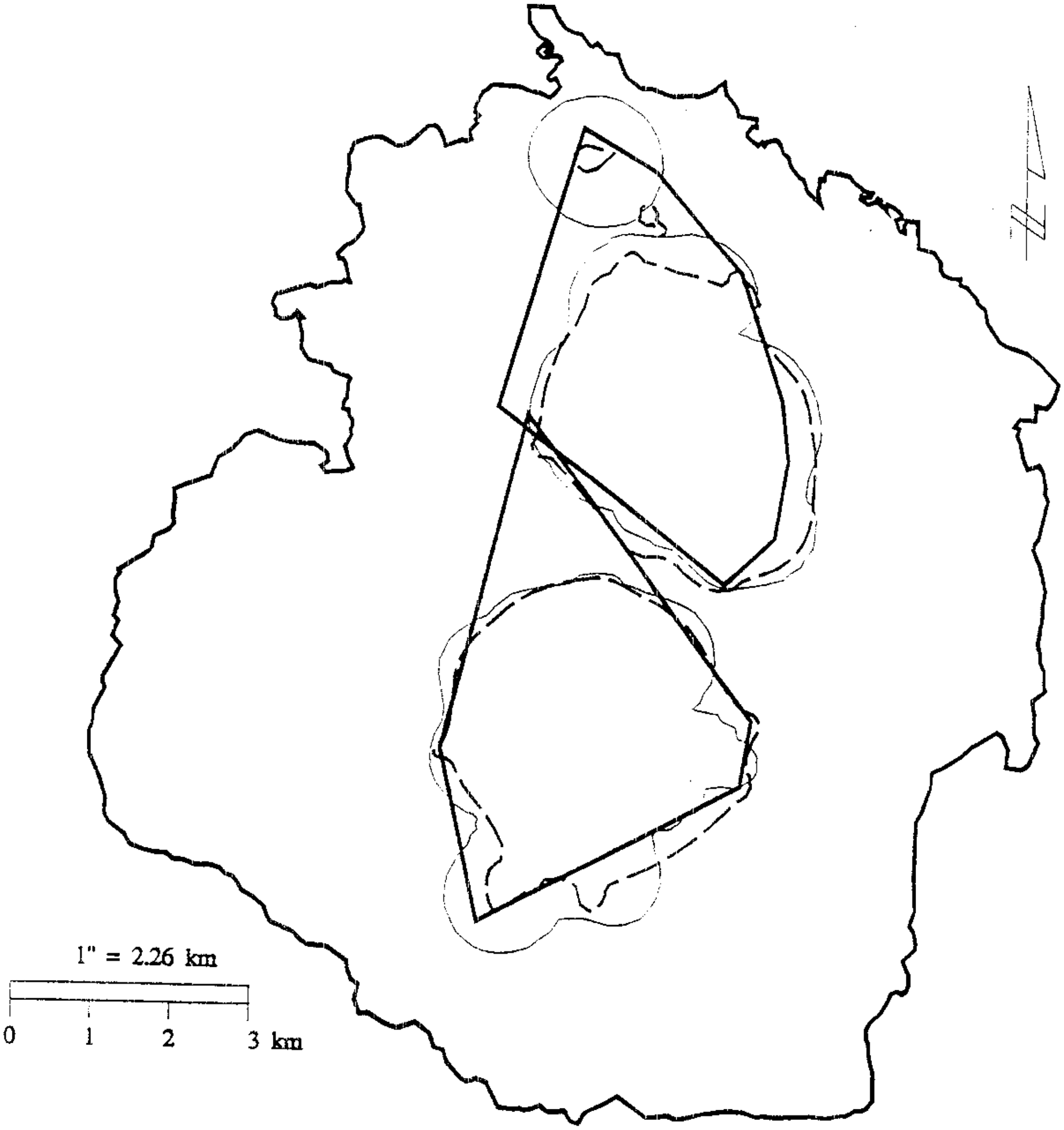

Figure 5. Home ranges for two bobcats (#05 and #43) in south Kapowsin study area using three methods of home range estimation.

(MCP =, 95% ADK - ,95% HM =...........)

using the ADK method at a 100%, 95%, and 50% contour indicate various levels of home range use (Figure 6).

Mean annual home range size for males was 14.37 km2 with a range of 10.89 to 18.68 kin:. Mean annual home range size for females was 8.44 km^2 with a range of 4.36 to 13.56 km^{2}· Mean annual core area size (50% ADK) for males was 2.72 km^2 with a range of 1.77 to 3.42 km^{2}· For females, the mean annual core area size was 1.33 km2 with a range of 0.66 to 2A5 km^{2}· Home range size differed between males and females (P = 0.028) as did core area size (P = 0.011). The mean annual home range size of males and females combined was I 1.41 km^{2}, and the core area size was 2.03 km2. Home ranges and core areas in north Kapowsin (Figures 7 and 8) were not different (P = 0.493 and P = 0.944 respectively) than those in south Kapowsin (Figures 9 and 10).

While mean home range and core area size did change between seasons (both winter vs. summer, and breeding vs. non-breeding), none of these differences were significant (P > 0.05). Mean male home range size was 210/o larger in the summer (May - October) than winter (November - April). Mean core area size, on the other hand, was 40% larger in winter than in summer. Mean female home range and core area size were larger in the winter than in the summer by 36% and 90°/0 respectively. Mean home range and core area sizes were larger during the non-breeding season (February - July) than during the breeding season (August - January) for males and females. Home range size

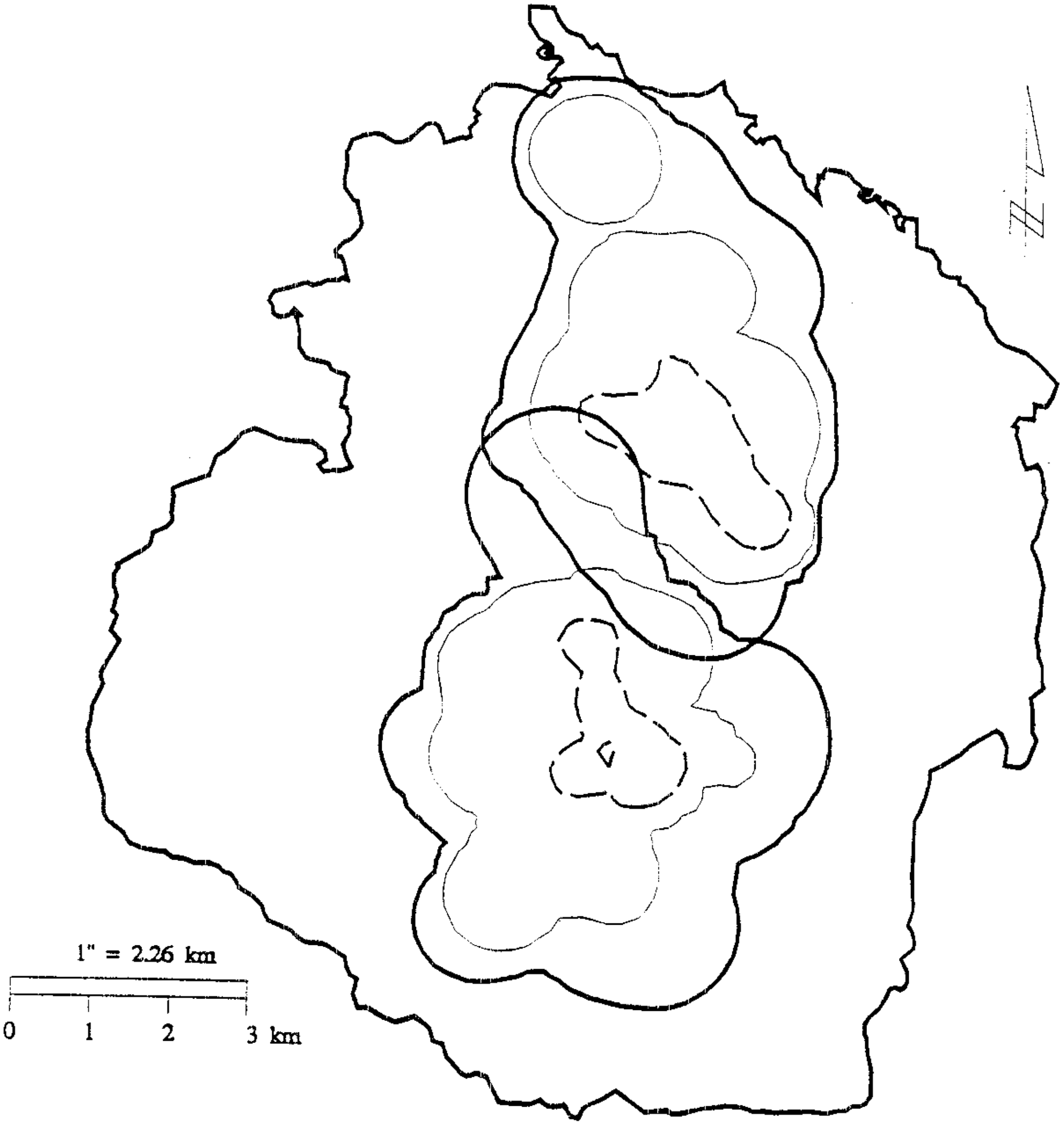

Figure 6. Home ranges for two bobcats (#05 and g43) in south Kapowsin study area using the Adaptive Kernel method at three contour levels of use.

(100% ADK ,95%ADK= ,50% ADK ....)

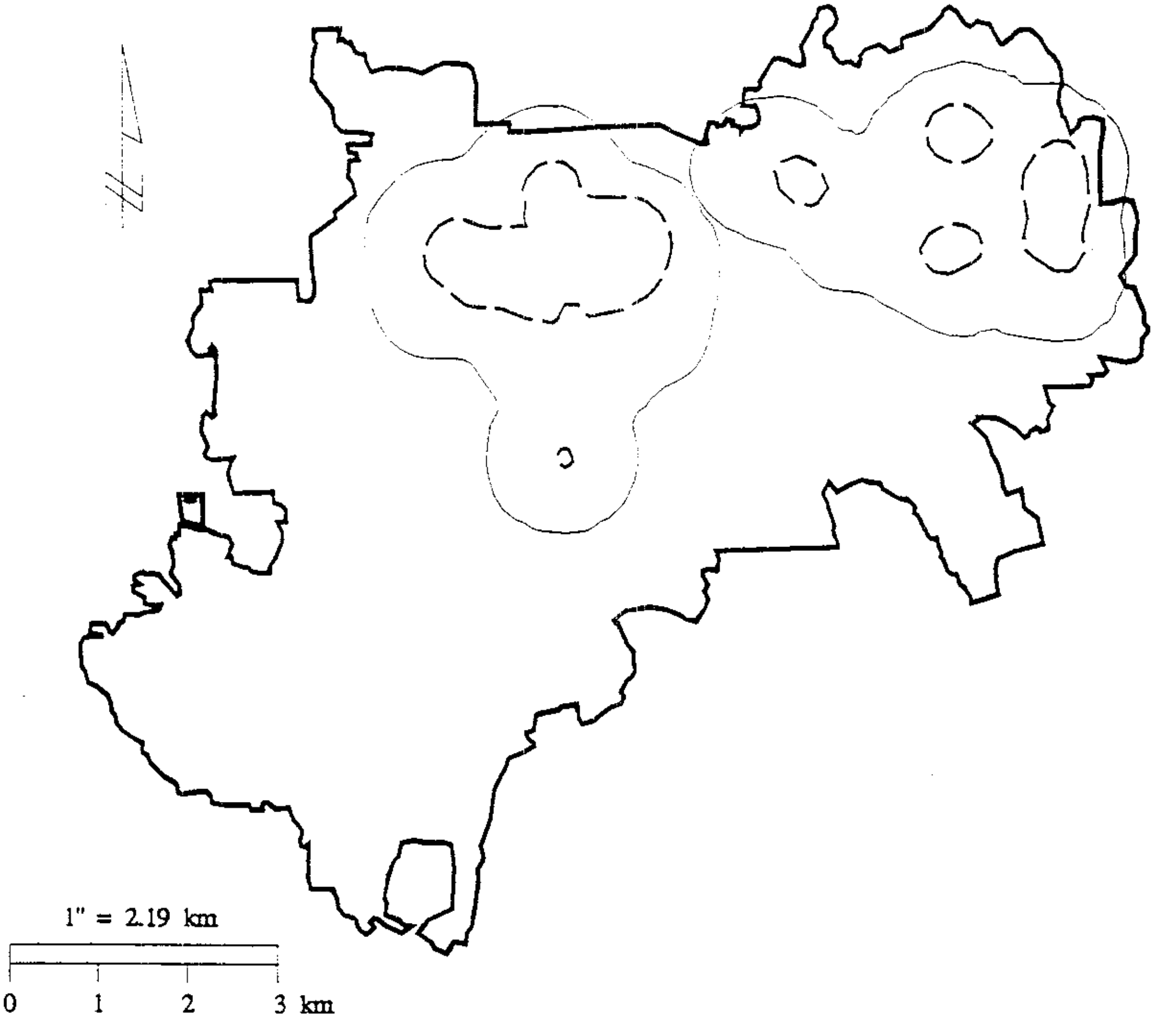

Figure 7. Home ranges and core areas for two male bobcats (#00 and #47) in north Kapowsin study area, Kapowsin Tree Farm, Pierce Co., WA, 1994.

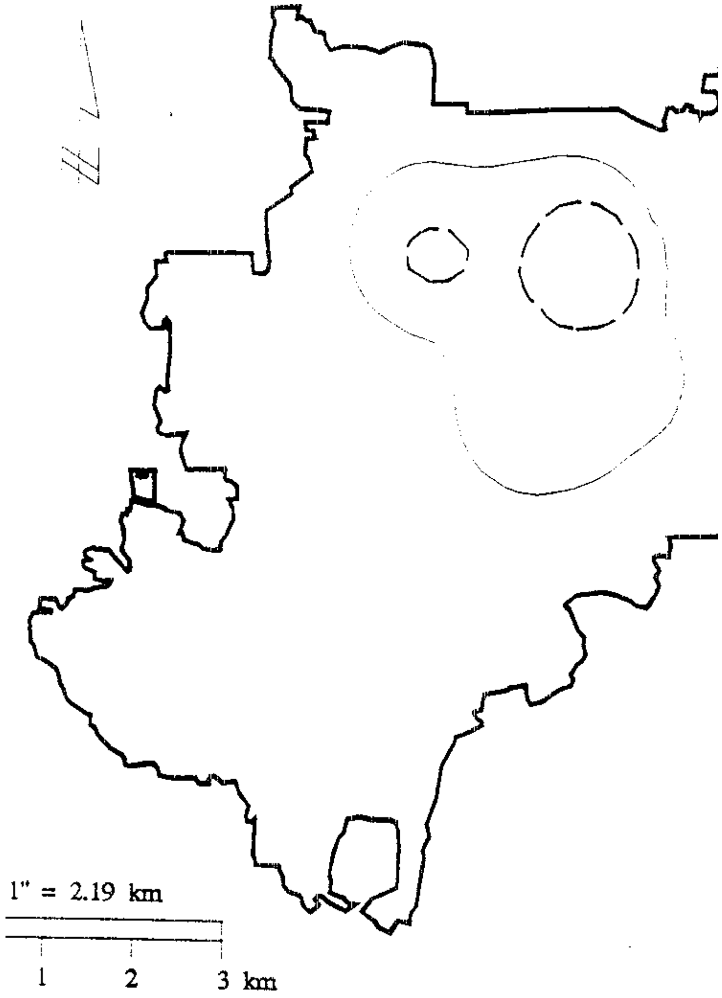

Figure 8. Home range and core area for one female bobcat (#07) in north Kapowsin study area, Kapowsin Tree Farm, Pierce Co., WA, 1994.

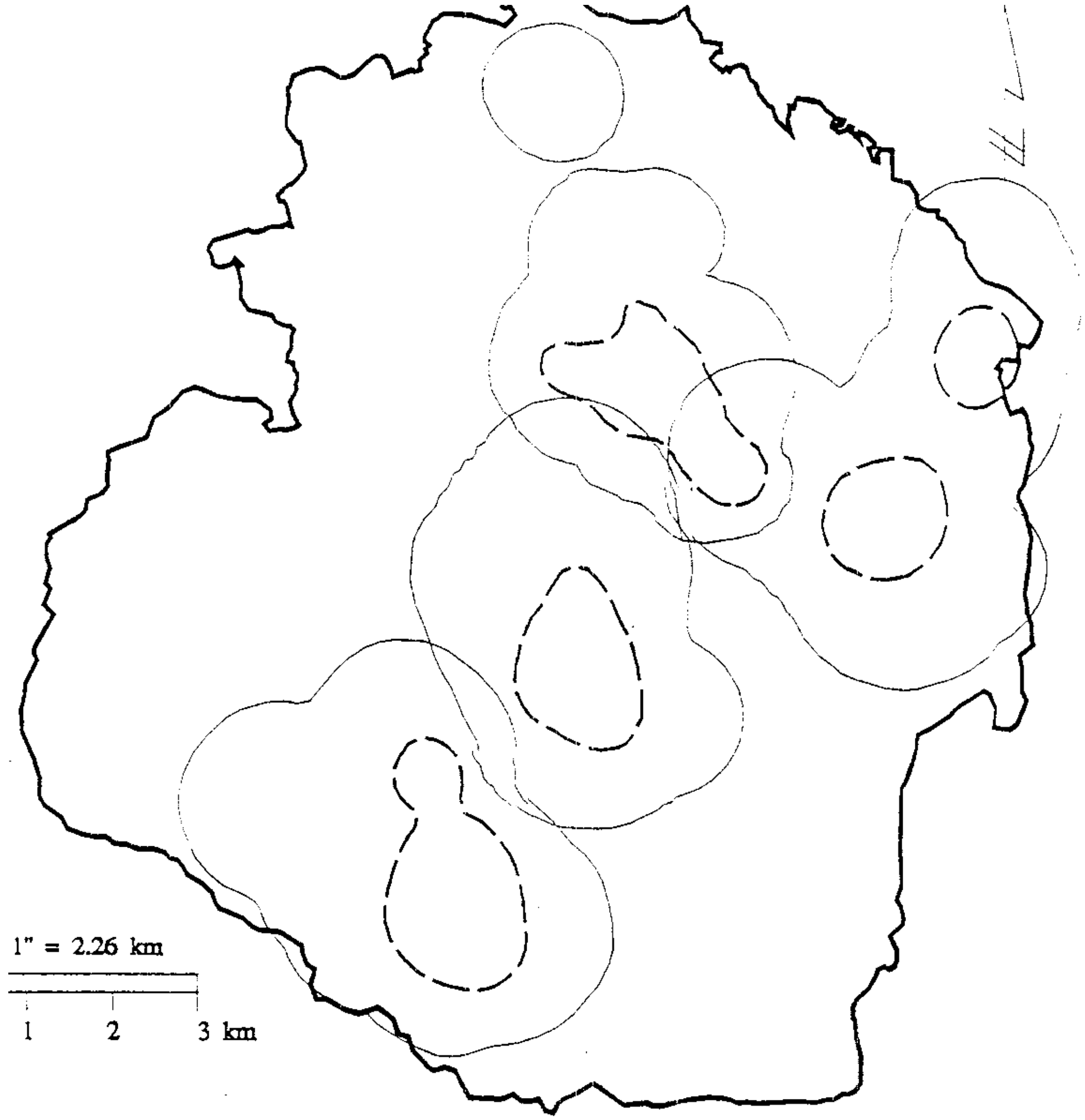

Figure 9. Home ranges and core areas for four male bobcats (#12, #41, #43, and ,445) in south Kapowsin study area, Kapowsin Tree Farm, Pierce Co., WA, I994.

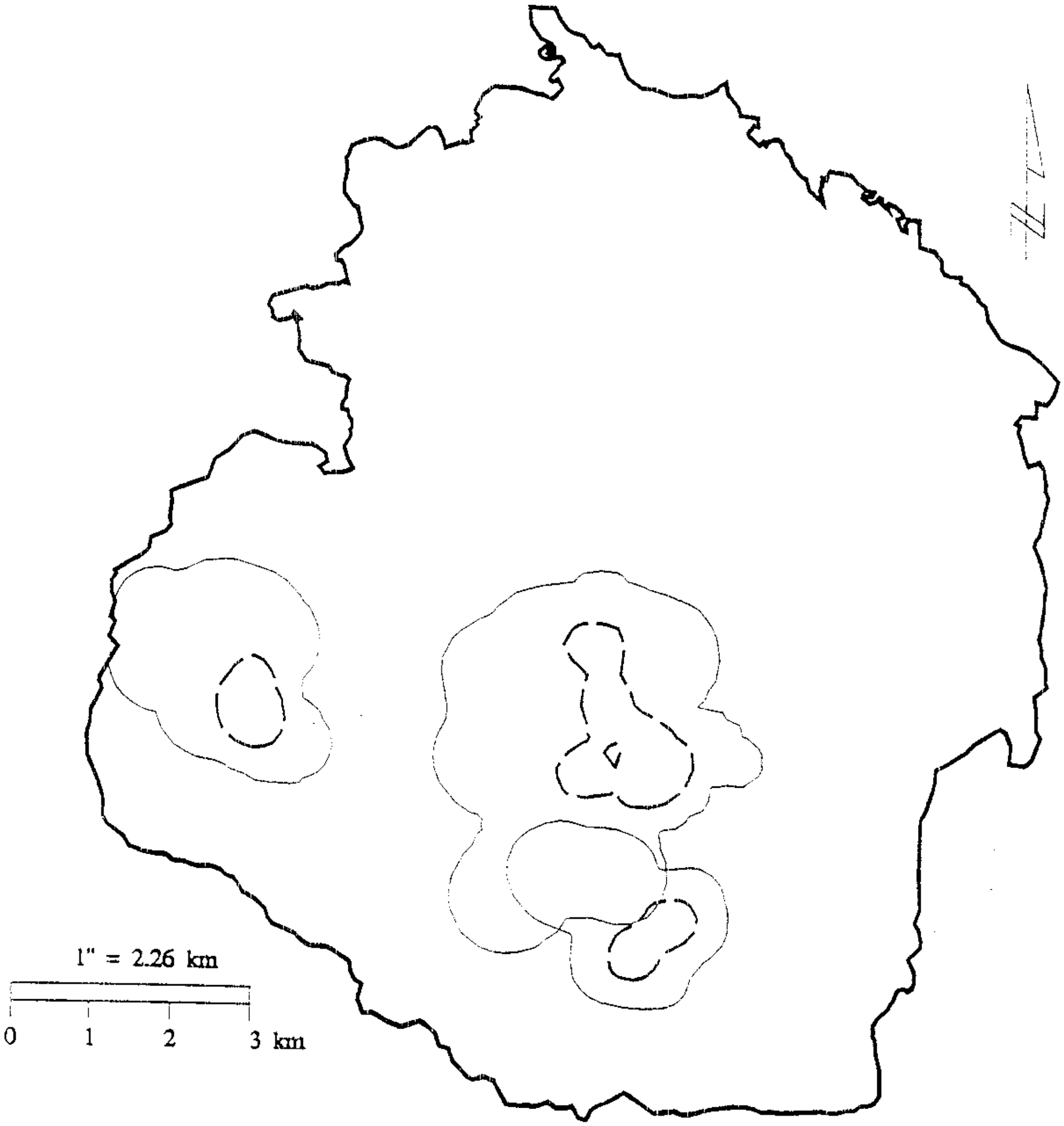

Figure 10. Home ranges and core areas for three female bobcats (#05, #14, and #31) in south Kapowsin study area, Kapowsin Tree Farm. Pierce Co., WA, 1994.

during the non-breeding season was 12% larger for males and 59% larger for females. Core area size was 32% larger for males and 40% larger for females.

Home range was also calculated using the 95% HM method. Using this method, mean annual home range size was 8.57 km^2 for males and 5.97 km^2 for females. This was also the method used by Brittell (unpublished data), who studied bobcats in the same area in 1978. There was no significant difference in mean annual home range size between the two studies for males (P - 0.616), females (P = 0.52), or both sexes combined (P = 0.378).

Overlap of home ranges occurred between males, females, and males and females (Table 6). Based on the 100% ADK home range, males showed a larger percentage of intra-sexual overlap than when using the 95% ADK estimation. Overlap of male core areas did not occur. Only two females had adjacent ranges. Their ranges overlapped based on the 100% ADK and the 95% ADK, but their core areas did not. Intersexual overlap was larger than intra-sexual overlap. Based on the 100% ADK. male home ranges overlapped those of females 1.56% more than females overlapped those of males. Based on the 95% ADK, males overlapped female home ranges 8.72% more than females overlapped those of males. Core areas overlapped in only two associations, with male core areas still overlapping those of females more than females overlapped those of males (17.47%).

Table 6. Mean percent overlap of adjacent bobcat home ranges on Kapowsin Tree Farm_ Pierce Co., WA, 1994.

Association Type	Home Range Type	Number of Associations	Mean % Overlap
Intra-Sexual			
Males	100% ADK	10	15.85
	95% ADK	10	6.83
	50% ADK	10	0.00
	95% HM	10	0.83
Females	100% ADK	2	48.88
	95% ADK	2	30.46
	5O% ADK	2	0.00
	95% ElM	2	0.44
Inter-Sexual			
Males overlapping females	100% ADK	8	35.15
	95% ADK	8	31.60
	50% ADK	2	67.12
	95% HM	8	20.87
Females overlapping males	i00% ADK	8	33.59
	95% ADK	8	22.88
	50% ADK	2	49.65
	95% HM	8	23.25

Percent habitat type in the overlapped areas were similar for both intra- and inter-sexual associations using the t00% ADK home range and the 95% ADK home range (Table 7).

Based on the 95% HM method, male home ranges overlapped those of females 2.38% less than females overlapped those of males. Adjacent male and adjacent female home ranges overlapped, but in much smiler percentages than using either of the ADK estimators (Table 6). Differences in the amount of inter-sexual overlap between this study and that done by Brittell (unpublished data) were not significant for males overlapping females ($P = 0.684$) or females overlapping males ($P = 0.617$). lntra-sexual overlap, however, was significantly different for adjacent male ($P < 0.001$) and adjacent female ($P = 0.002$) home ranges.

Density

Using 95% ADK home range estimates, bobcat density for the two study areas was 0.0981 male bobcats per km^2, and 0.3353 female bobcats per km^2. This gives a population estimate of 28 (6 males and 22 females) for north Kapowsin (64.72 km^2) and 49 (I1 males and 38 females) for south Kapowsin (112.72 km2). When males and females were considered together, density was 0.219 cats per kart2. Corresponding population estimates were I4 for north Kapowsin and 25 for south Kapowsin.

Using 95% HM home range estimates and considering sexes separately, population estimates were smaller. North Kapowsin had an estimated population of 19 cats made up

Table 7. Percent area of cover types within inter- and intra-sexual overlap of bobcat home ranges on the Kapowsin Tree Farm, Pierce Co., WA, 1994.

Home Range Type	Cover Type Newcut	Clearcut	Keprod	Young	Mature	Harvest
Intra-Sexual Overlap_						
100% ADK	1.55	13.06	11.82	45.63	16.03	11.91
95% ADK	0.00	I3.49	t7.67	48.51	18.36	1.97
Inter-Sexual Overlap_						
100% ADK	1.56	7.55	11.02	42.59	22.07	15.21
95% ADK	2.87	6.69	15.19	46.13	17.17	11.95

of eight males (0.122 male / km2) and 11 females (1.024 females / km2). In south Kapowsin, using the same density estimates, there were 33 cats total (14 males and 19 females). Population estimates were larger when considering the sexes together. A density of 0.349 cats per km2 gave population estimates of 23 cats in north Kapowsin, and 39 cats in south Kapowsin.

Movement

Mean distance between consecutive locations of 14 days or less was significantly different for males and females (P = 0.017). Males had a mean distance of 1.58 km and a standard deviation of 0.16 km between locations. Females had a mean distance of t. 18 km and a standard deviation of 0.31 km between locations, The distribution of distances between locations showed both males and females to be <2 km from their previous location over 70% of the time (Table 8). Only male cats were located >5 km from their previous location (n = 2).

Seasonal differences in distance between locations were not significant for males (P = 0.097) or females (P = 0.332). Mean distance for males was 1.51 km in the summer and 1.92 km in the winter. Mean distance for females was 1.2 km in the summer and 1.56 km in the winter. Similarly, differences in distance between locations during the breeding and non-breeding season were not significant for males (P = 0.802) or females (P = 0.307). Mean distance for males was 1.57 km during the breeding season and 1.6 km during the non-breeding season. Mean distance for females was 1.32 km during the breeding season

Table 8. Distribution of distances (km) between consecutive radio-locations of 14 days or less and average distance travelled by l0 bobcats on the Kapowsin Tree Farm, Pierce Co., WA 1994.

	Number of Locations								
I.D.#	0- I (km)	1-2 (km)	2-3 (km)	3-4 (km)	4-5 (km)	5-6 (km)	6-7 (km)	Total	Average Distance (km)
Males									
00	16	22	5	I	2	0	0	46	1.41
12	20	21	16	6	0	0	0	63	1.68
41	8	8	5	3	0	0	I	24	1.83
43	38	54	25;	9	4	1	0	129	1.62
45	14	25	6	2	1	0	0	48	1.43
47	33	51	27	3	0	0	0	114	1.51
Total	129	180	82	24	7	1	1	424	1.58
Females									
05	53	42	32	10	1	0	0	138	1.48
07	36	52	15	3	2	0	0	I08	1.42
14	13	7	I	1	0	0	0	22	0.89
31	24	16	I	0	0	0	0	4I	0.93
Total	[26	117	49	14	3	0	0	309	1.18

and 1.7 km during the non-breeding season. Mean distance did not differ significantly between north and south Kapowsin (P = 0.800).

Habitat use

Analysis of habitat utilization in the first stage was significant (P = 0.012) that the differences in use versus availability were not the same for all habitat types when comparing the 95% ADK home range to the entire study area. The ordering of habitat types and significant differences determined by the multiple comparisons procedure from least to most preferred (left to fight) were:

Harvest Clearcut Mature Newcut Reprod Young

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. Comparisons of use versus availability were not significant when comparing core areas to the entire study area (P = 0.147), or core areas to the home range (P -- 0.843).

In the second stage of the habitat utilization analysis availability of cover types within a cat's home range was compared with the number of relocations in each habitat (Figure 11). Chi-square tests of habitat use versus availability within the 100% ADK, 95% ADK, and 50% ADK home ranges were significant in several cases (Table 9). Using the 95% ADK, three cats showed significant differences in use versus availability of cover types.

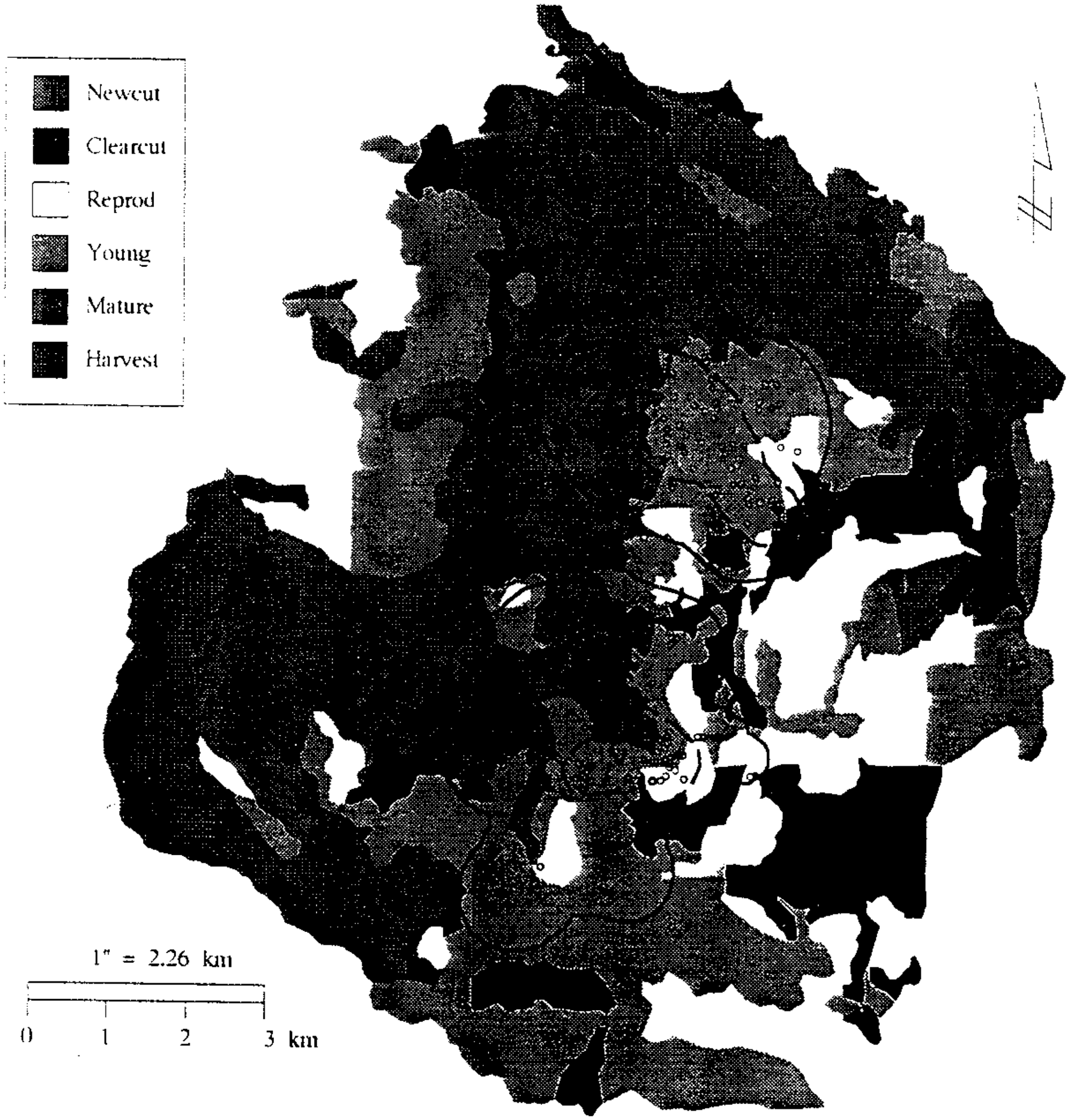

Figure 11. Home ranges, core areas, and locations for two cats (#05 and #43) on map of cover types in south Kapowsin study area, Kapowsin Tree Farm, Pierce Co., WA, 1994.

Table 9. Chi-square values and significance for bobcat habitat use within three levels of the Adaptive Kernel (ADK) home range on the Kapowsin Tree Farm, Pierce Co., WA, 1994.

Ho: Bobcats use each cover type in proportion to its abundance within their home range.

	100% ADK		95% ADK		50% ADK	
I.D. #	X^2	Significance	X^2	Significance	X^2	Significance
00	3.229	P = 0.520	0.931	P = 0.818	1.616	P = 0.656
05	19.223	P < 0.001’	14.042	P = 0.007*	1.175	P- 0.882
07	22.339	P < 0.001’	7.306	P -- 0.199	4. 155	P = 0.385
12	9.877	P = 0.043*	7.741	P = 0.102	0.592	P = 0.744
14	6.347	P = 0.012’	5.724	P = 0.017’	**	
31	5.953	P = 0.051’	1.466	P = 0.480	**	
41	***		8.852	P = 0.065	4.778	P=0.189
43	69.214	P<0.001*	47.232	P<0.001*	3.410	P-0.333
45	2.856	P = 0.582	4.515	P = 0.341	0.955	P = 0.812
47	10.843	P = 0.055	5.012	P = 0.414	7.298	P = 0.121

* Significant.

** Not analyzed due to only one cover type within core area.

*** Not valid due to insufficient sample size.

These three cat& as well as three others, showed significant differences when the analysis was performed using the 100% ADK home range. Finally, within each cat's core area, there was no significant difference in use of cover types versus their availability.

Further analysis of these diferences using the Bonferroni confidence intervals showed patterns of preference and avoidance that varied between cats (Table 10). The patterns were generally consistent for the three cats who exhibited differences at the 95% and 100% ADK contour levels. The patterns for all six cats exhibiting differences were also similar to those found in the first stage of the analysis.

Habitat use was also analyzed by season and by time of day based on the 95% ADK home range. Four cats showed seasonal differences in habitat use, all occurring during the summer. The patterns of use, however, were generally the same as those during the whole year. In three cases (all males), the Harvest cover type was avoided in the summer, while there was no differential use when analyzed over the entire year. In the final case, a female bobcat preferred the Harvest cover type during the summer while showing no preference or avoidance during the rest of the year. Two cats showed significant differences in habitat use based on time of day. Both cats avoided Clearcuts during the day. One of these cats also avoided Clearcuts and preferred Young stands during the PM crepuscular time period.

Table 10. 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.

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

DISCUSSION

Home Range

Home range has been defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). This definition, however, proves to be inadequate and often leads to subjective determinations of what is considered "normal". To develop objective, repeatable methods of home range calculations, much emphasis has been placed on developing a numerical process to estimate an animal’s home range (White and Garrott 1990).

Three different methods were used in this study. The Minimum Convex Polygon (MCP) is the oldest home range estimator and has several disadvantages. These include its inability to describe home ranges with concave shapes and its strong correlation between number of locations and home range size (White and Garrott 1990). This was the method most commonly used in previous bobcat ,studies and its use here was solely for the purpose of comparisons. The Harmonic Mean (HM) method has several advantages over the MCP. This non~parametric method estimates the home range as a utilization distribution, allows for the definition of centers of activity, and makes no assumptions of shape. However, Worton (1987) cautioned that HM estimates of utilization distributions were dependent on the map scale used and that results may be misleading and should be interpreted with care. In this study, the 95% HM was the most highly correlated with number of locations. It was included for comparisons, specifically with Brittell (unpublished data) who did a bobcat study in the same area in 1978. The Adaptive Kernel

Estimator (ADK) turned out to be the best model based on its low correlation between home range size and number of locations. It was believed to be the most appropriate estimator for this study, and was used for most of the analyses. The ADK method is similar but more complex than the HM, and provides; a truly probabilistic utilization distribution that is well suited to an analysis of range use (Harris et al. 1990). When discussing home range it is important to consider the type of estimation procedure used, and to remember that all types have shortcomings that may prevent an accurate portrayal of what is actually occurring in nature.

Home ranges for bobcats in this study fell within the range reported by other researchers, but were relatively small. Across its range, bobcat home ranges have varied widely in size 15ore 0.6 to 201.0 km^2 (McCord and Cordoza 1982). Bobcat home range size can vary, considerably due to sex, age, population density, prey density, estimation technique, season, geographic area, and whether or not individuals are hunted (Knowles 1981, McCord and Cordoza 1982). Even with these considerations, the variability in bobcat home range size across it’s geographic range appears; to have some trends. Bobcats appear to have very small home ranges in the southeast, and larger ranges in the north and west (Table 1 I). The relatively small home ranges found in this study may indicate that the Kapowsin tree farm provides good habitat and abundant prey for bobcats. As mentioned earlier, it is important to note which home range estimation technique was used

Table 11. Home range estimates and movements of bobcats for several regions of the United States, Home ranges were calculated using some type of minimum area method and are in km^2. Movement numbers in km.

	Home Range		Movements		
Region	M	F	M	F	Reference
Southeast					
South Carolina	3.9	2.5	4.8	2.6	Marshall and Jenkins i966
South Carolina	20.8	10.4	8.7	6.2	Buie et al. 1979
Louisiana	4.9	1.0	4.8	2,6	Hall and Newsom 1978
Northeast					
Minnesota	62.0	38.0	4.3	2.6	Berg 1979
West					
California	73.0	43.0			Zezulak 1981
California	28.0	17.5			Zezulak and Schwab 1980
Northwest					
Idaho	42. i	19.3	1.8	1,2	Bailey 1972, 1974
Montana	83.3	17.8	4.9	1.1	Knowles 1981
Montana	63.0	88.2	3.9	4.0	Smith 1984
Washington	13.0	10.1	1.6	1.2	This Study

in the analysis. Results from this study confirm that home range size can vary dramatically using the same data but different enumeration processes. Even with this variability home ranges appear to be consistently small, but results should be interpreted with some caution.

In Washington, bobcat home range size appears to be smaller hi the western coastal areas, and larger in the more arid, open regions east of the Cascade mountains (Brittell 1979). Brittell (1979) found mean annual home range size for males to be 9.39 km^2 and 8. I 1 km^2 for females. These results were not significantly different from those found in this study when using the same home range estimation technique. While the pattern of habitats in this area have changed between the two studies, a mosaic of seral stages still remains. Much of the forests were harvested and replanted and there still exists a wide variety of successional stages common to the patchwork landscapes found in the managed forests of western Washington. Bobcat home range size is often thought to vary with food abundance and distribution (Buie et al 1979, Kitchings and Story, 1979, and Zezulak 1981). Since the patchwork of forests in western Washington provided early regeneration stages as well as mature forest stages, populations of bobcat prey species have probably remained relatively stable over the last decade and a half and may have resulted in the similar home range sizes found in the two studies.

Other factors may have influenced the results found in this study. Two of the females monitored in this study (No. t4 and No. 31) were only followed for a short period of time and were believed to have had kittens. Female home ranges have been known to decrease in size during certain times of the year, and this is believed to be related to caring for kittens and increased den site activities (Zezulak 1981, Witmer and deCalesta 1986). By only monitoring these cats when they were caring for young, the mean female home range size may have been artificially low. The other two females were also thought to have had kittens. Since they were tracked throughout the entire study their home range estimates were probably more accurate. Ideally, a larger sample of female cats monitored for a longer period of time would be used to obtain a more accurate estimate of female home range size.

The possibility of female home range sizes being artificially low could be one reason that male and female home range size was found to be different. Other researchers have also found female home range size to be smaller than male’s. Bailey (1974) found male home ranges to be 4 to 12 tunes larger than female’s in Idaho and that females appear to stay in an area for several days, using their ranges more intensively. Litvaitis et al. (1986) found male home range in Maine to be 2 tunes as large as females in one study area, but equal in another. These findings were similar to Fuller et al. (1985) who studied bobcats in Minnesota. This difference in home range size has been attributed to the fact that females alone raise the young and therefore their movements are restricted (Bailey 1974). Females must spend most of their tune protecting and providing food for her young in localized areas around den sites. Males, on the other hand, have no family raising responsibilities and are therefore able to range further. Male home range sizes may also be larger as they attempt to mate with many females. Lirvaitis et a111986) hypothesized that home range size was correlated with body weight and that sexual dimorphism in body size of bobcats accounted for differences in home range sizes.

When comparing home range sizes between different seasons, some differences were present but none of these were significant. Mean home range size of males decreased in the winter, while home range size of females increased in the winter. Some studies have found seasonal variation in bobcat home range size (May 1981, Smith 1984). The increase of home range size in the winter is most likely due to the increased energy demands brought on by winter, coupled with the decreased availability of prey (McNab 1963). The lack of significant seasonal variation in this study was most likely due to two factors. First, seasonal weather fluctuations in the study area may not have been extreme enough to cause any variations. North Kapowsin received little if any snow during the winter months. Although south Kapowsin may have had more extreme winter conditions than north Kapowsin, differences were not dramatic. Buie (1979) had similar results when studying bobcats in South Carolina and also attributed the lack of significant findings to mild winter weather. Second, the breakdown of seasons in this study were quite broad. This was done to insure an adequate number of locations to obtain an accurate estimation of home range size. The categories, however, may not have been specific enough to detect seasonal changes in home range size.

These broad seasonal definitions, may also have had an impact in the analysis of home range variation between the breeding and non-breeding season. Again, differences in home range size were present (home range size increased during the non-breeding season for males and females), but were not significant. Home range size of females would be expected to be smaller during the breeding season while caring for young. Male home range size, on the other hand, might be expected to increase during part of the breeding season as each male attempted to mate with as many females as possible. A tighter definition of each season may show significant differences, but at the cost of having a less reliable home range estimate.

While bobcats may establish home range territories, these areas are not always mutually exclusive (Etkin 1964). Bobcat home ranges overlap both intra- and inter-sexually with other bobcats. As expected, overlap was greatest when using the 100% ADK and smaller when using the 95% ADK. This makes sense because the 95% ADK was used to define areas where the bobcat normally ranged, while the 100% ADK encompassed all locations which might include exploratory movements by the cats. Since bobcats actively define their territories, overlap at the edge where bobcats travel to leave scents and marks would be expected. No intra-sexual overlap of core areas was found as expected. Inter-sexual overlap of core areas was relatively large. However, this estimate was based on the association of only two cats and may not be truly representative.

Inter-sexual overlap was greater than intra-sexual overlap, a phenomena that was also found by Bailey (1972) and Miller and Speake (195'8). Inter-sexual overlap is important because it allows for males and females to mate with each other. Additionally, Altmann and Altmann (1970) felt that overlap of home ranges (both intra- and inter-sexual) usually resulted from a restricted spatial distribution of an essential resource. In both intra- and inter-sexual overlap areas, the Young cover type was always the most abundant. This proved to be a type that was preferred by many of the bobcats. Although it does not appear to be a restricted resource, it may have inch a good prey base that it was shared by several individuals.

Overlap between females was greater than between males. While other studies have found this as well (i.e. Zezulak (1981) found three to four females in California overlapping up to 36%) it is not usually the case. Bailey (1972) found female-female overlap to be the least of all association types and noted that bobcats appear to be more intolerant of individuals of the same sex. McCord and Cordoza (1982) also found that home ranges of bobcats may overlap, but that females rarely trespass on ranges of other females. The large degree of overlap in this study was based solely on the association of two females. Because these two females were often found very close to each other and one appeared to be younger, it was thought that one may have been the daughter of the other. If indeed they had been related, this might explain why their ranges overlapped to such a large extent.

Brittell (unpublished data) reported that male home ranges overlapped those of females 25.5% and females overlapped males 30.2%. This inter-sexual overlap was not significantly different from that found in this study when using the same home range method. Intra-sexual overlap was significantly larger in Brittell's study than in tiffs one. Britell reported intra-sexual home range overlap to be 12.3% for males and 18.9% for females. Brittell (unpublished data) thought the small degree of overlap for bobcats in western Washington was due to plentiful food and cover combined with mild winter temperatures. It appears that this may still be the case. The decrease in intra-sexuat overlap may indicate that habitat and prey conditions have improved between the two studies, inter-sexual overlap may depend more upon male - female relationships, and has not decreased in response to habitat and prey conditions.

Density

The territorial nature of bobcat social systems combined with the availability of prey and habitat conditions, work together to regulate bobcat densities (Brittell unpublished data). Similar to home range size, bobcat densities vary throughout their geographic range from 0.01 to 2.7 bobcats per I km^2 (McCord and Cordoza 1982). Since it is unlikely that the entire study area was completely packed, the more conservative estimate of density (0.219 cats / km^2) is believed to be the most appropriate one. This density falls within the range of estimates given by McCord and Cordoza (1982). Using the same density estimation and home range methods, density for this study (0.349 cats / km2) was the same as that found by Brittell (0.3 cats / kin^2) (unpublished data).

The density, estimate from this study appeared reasonable. Bailey (1972) reported a density of 0.05 cats / km: in Idaho. Miller and Speake (1978) found bobcat density in South Carolina to be 0.77-1.16 cats /km^2. It also appeared feasible that 5 km2 could provide a bobcat with a years supply of food. If a bobcat consumed approximately 100 mountain beaver and 60 snowshoe hare in a year (Sweeney 1978) then this area would be sufficient based on a density of 700 mountain beaver/km^2 (Feldhamer and Rochelle 1982) and lower snowshoe hare densities. Snowshoe hare densities have been reported to range from I3 hares / km2 to over 1100 hares / km2 depending on the stage of their ten year cycle (Bittner and Rongstad 1982). In western Washington, hares do not cycle to such high abundance levels and their densities are probably at the lower end of this range. This may be the reason bobcats have switched to mountain beaver as their primary food source in this area.

Movement

Much of the discussion of home range size can also be applied to the analysis of movement. Average distance between locations was significantly greater for males than for females. The results from this study were similar to Bailey (1972) who reported distances between daily radio fixes of males to be 1.8 km and females 1.2 km (Table 13). Marshall and Jenkins (I966) found average daily movements of males (4.8 km) to be greater than females (2.6 kin). Berg (1979) detected male movements to be 61% greater than females. Similar to home range size, female movements are thought to be smaller because they are restricted by kittens (Bailey 1972). Males would be expected to move more to maintain their larger territories (Brittell unpublished data). It is also important to note that the results from this study are based on distance between successive relocations up to 14 days apart. These numbers, therefore, should be viewed as an index of movement rather than a quantification of actual distance travelled.

Seasonal differences in movement, while expected to be significantly different, were not. Average distance did increase in the winter for both males and females, perhaps in response to lower prey availability. The milder climates in western Washington may have played a role in the lack of significant findings. The opposite was reported in Idaho where Bailey (1.972) found movements to be more restricted in the winter. This may be because deep snows can hamper bobcat movements, but would not be a factor in western Washington. Changes during the breeding season may also have been expected as males travel more to visit more females, and females travel less to care for their young, Again, the definitions of season may have been too broad to detect significant differences,

Habitat Use

The two stages of habitat utilization analysis used in this study had similar remits. The order of habitat type preferences determined in the first stage were generally consistent when bobcat use of habitats within their home ranges was analyzed. The second stage analysis of habitat utilization did have variable results between cats, but some patterns were present.

The first stage of the analysis investigated how bobcats select areas in which to establish their home ranges. Friedman's test provided an order of preference of the habitat types based on the proportion of habitats within a cat's home range and the proportion of habitats available within the study area. The question of availability was a critical one. Obviously, an arbitrary study boundary drawn by a researcher will not accurately describe what a bobcat sees as available, but nevertheless, a boundary, had to be delineated. For this study, the study area was defined as the region that had been hunted with dogs. While it was known that not all cats in this area were caught, there was at least some idea of the extent of the bobcat population. The second analysis defined available habitat as the area w/thin the animals home range and was performed, at three different home range contour levels. This analysis also had its shortcomings because k was based on an estimation of home range that may not have been completely accurate.

The first stage of analysis indicated that bobcats prefer Young habitat types the most and Harvest habitat types the least when choosing where to establish their home ranges. The fact that bobcats establish home ranges containing less preferred habitat types may indicate that a healthy population exists. Competition for preferred habitats and other social pressures may force bobcats to use less preferred habitat types. This may be especially true for juvenile or weaker bobcats.

Young stands were the preferred habitat and had the largest percentage of any cover type in the core areas for 8 of 10 cats. However, these percentages were not different from those in the rest of the home range or in the entire study area. The lack of significance when analyzing habitats within core areas indicates that bobcats are selecting their core areas based on something other than availability of habitat. These may include rocky areas for rest sites, denning areas for females, or some other factor of habitat quality.

Analyzing habitat use at three different home range contour levels in the second stage showed some similar trends as well. Based on the core area (50% ADK) there was no difference in use for any of the cats. At the 95% ADK contour level we start to see some divergence between use and availability and at the [00% ADK we see even more. It appears that cats must establish their ranges based not only on habitat but on social factors as well. Core areas are intra-.sexually exclusive and used extensively throughout. The larger home range contour levels encompass more unused marginal habitat, but may be necessary for survival and social (male / female) interactions. As these outer home range areas are used in the analysis, patterns of habitat preference and avoidance begin to appear.

The differential use of habitats found in this study were most likely the result of the various amounts of cover within each habitat type. Cover is a very important component of good bobcat habitat (Brittell umpublished data). McCord (1974) concluded that prey abundance and environmental conditions alone were not sufficient in determining why bobcats select dense cover types, and that it was necessary to look at behavioral factors as well. Bobcats, like most felids, stalk their prey. This secretive hunting method makes cover an essential part of bobcat survival. Thick cover can also be used for security in places where natural ledges and rock outcroppings are not available (McCord and Cordoza 1982).

The need for cover has been well documented in several studies. Brittell (unpublished data) found bobcats in western Washington to avoid open grass-forb communities, and attributed this to the lack of security cover. Koehler (1987) reported similar results in Idaho where bobcats avoided grasslands and fields where cover was sparse. Bobcats have been reported to use agricultural areas if prey and cover were present (McCord and Cordoza 1982). They have been eliminated from areas in the midwest where agriculture was so intensive it destroyed cover and prey habitat. As shown by these and other studies, prey abundance was also a critical factor for good bobcat habitat. Litvaitis et al. (1986) reported that bobcats in Maine preferred habitats where snowshoe hare were plentiful. Knowles (1981) had similar results in Montana. She reported that bobcats preferred dense understories where potential prey (lagomorphs and rodents) were most abundant. In western Washington, mountain beaver and snowshoe hare distribution and abundance in the various seral stages undoubtedly played a key role in bobcat habitat use. Mountain beavers inhabited densely vegetated areas and were commonly found in the initial seral stages of forest succession after clearcutting (Feldhamer and Rochelle 1982). Snowshoe hare occupied a variety of habitats, but preferred dense, second-growth-type forests (Bitmer and Rongstad 1982). Snowshoe hare also benefit from the landscape mosaic of seral stages found in the managed forests of western Washington. Wolff(1980) reported that patchy environments which provide refuge in winter and open feeding in summer benefit hares by allowing them to shift their use seasonally.

In this study, cover and prey availability appeared to be requirements for good bobcat habitat, and definite trends were apparent for some cover types. These trends were consistent across both stages of habitat use analyses. Bobcats selected home ranges encompassing both the preferred and the avoided habitat types that were available within the study area. This suggests that more than habitat was driving bobcat spacing and use patterns. Since bobcats are territorial the position of other cats in the area may have just as important a role in the selection of home ranges as the type of habitat.

The Newcut cover type was not preferred or avoided by any cats in any analysis. This habitat had little cover, and was not very abundant in the study areas. It made up only 5% of North Kapowsin and was not present at all in South Kapowsin. It was present in two cats home ranges in small proportions (6% and 7%), and was used by these cats. It might have been expected that bobcats would avoid this cover type, however, abundant prey may have induced cats to go into these areas. Hacker and Coblentz (1993) reported that many I year-old clearcuts in Oregon supported mountain beaver population levels higher than those of surrounding stands and that they appeared to select for small (<25 cm diam) woody cover. Keith and Surrendi (1971) reported that hares abandoned newly burned areas, but returned within 15 months when vegetation had re-sprouted.

Clearcuts and Harvest stands had a similar vegetative structure to Newcuts and were highly abundant, but were avoided in most cases. Both of these types had quite a bit of vegetation at the lowest level (0.0 - 0.5 m), moderate cover at the 0.5 - 1.0 m level, and were very sparse in cover above that. It appeared that the overstory canopy present in Harvest stands was not as important to bobcats as the understory vegetation. It also appeared understory vegetative cover > 1 m was important for bobcats. This may seem counter-intuitive since bobcats are relatively small and should be able to hide in cover closer to the ground. Bobcats may use vegetation > 1 m as security cover from potential aerial predators. The association w/th understory vegetation > 1 m may also be explained by examining habitat use of bobcat prey species. Pietz and Tester (1983) studied habitat selection of snowshoe hare in Minnesota. They found a strong correlation between hare use and percent cover of shrubs over 1 m tall and no correlation between use and percent cover in the 0.5 - 1.0 m layer. They attributed this to snow fall that buried the lower layers during the winter making them unavailable for browsing.

Another reason clearcuts may have been avoided was that they suffer seasonal extremes of climate more than most other types. They were quite hot and dry in the summer due to the lack of trees to block the sun. Mountain beaver are restricted to moist environments because their primitive kidneys are unable to efficiently concentrate urine. Why this is not a factor in Newcuts is unknown, but could possibly be due to a greater availability of succulent vegetation or the presence of small creeks that were observed in the Newcut stands (Schmidt-Nielsen and Pfeiffer 1970, Nungesser and Pfeiffer 1965). Both of these could have provided sufficient moisture for mountain beavers. Similarly, in the winter the lack of trees in Clearcuts allowed for deep snow accumulation and no thermal cover. This would not have been a problem for Newcuts which were present only in North Kapowsin which received very little snow. Bobcats were known to avoid snow depths greater than I5 cm (Marston 1942, McCord 1974) and this may have been the reason Clearcuts were avoided to such an extent.

Young stands were the most preferred habitat type of bobcats. These stands had abundant vegetative cover at all levels, but were also quite patchy, making travel easier. It would appear that Reprod stands would also be preferred by bobcats because of their extensive cover. These stands were preferred in some cases and avoided in others. Cats may have viewed Reprod stands as marginal habitat because they may in fact have had too much cover. These stands were so dense at almost every level that they may have been difficult to travel in and difficult to visually locate prey in. The patchiness of Young stands may also have been beneficial for mountain beaver. Neal and Borrecco (1981) concluded that openings in sapling stands were an important component of mountain beaver habitat.

The Mature stands were the most bare, and were avoided in some cases and preferred in others. One female had almost her entire range made up of Mature trees. She appeared to be a younger cat and may have resorted to this cover type out of necessity because k was the only area available. No other cats preferred this cover type. This may be an example of how the adaptability of bobcats allows them to exist in marginal habitat until the opportunity arises to move to a better area.

While some researchers have found bobcat habitat use to vary seasonally (Knowles 1981, Smith 1984), this was not generally the case in this study. Only four instances of differential use were detected, three of which followed the annual trends. Similar to home range size, the most likely reason for this was the lack of extreme winter conditions on most of the study area.

Habitat use by time of day also yielded few significant results. Two cats avoided clearcuts during the day. This would be expected because cats would want cover during the daylight hours. Brittell (unpublished data) found that bobcats used second-growth forests (20 - 70 years old) more and regrowth (10 - 20 years old) and shrub-seedling cover types less during the crepuscular hours. Rolley and Warde (1985) also found diel differences in bobcat habitat use and attributed them to the crepuscular activity of bobcats, the crepuscular activity of some bobcat prey species, and differences in prey abundance between the habitat types.

Other studies have shown bobcats to use logged areas. Miller and Speake (1978) found that farming and logging provided food and cover for bobcat prey species. Miller and Speake (1978) found that areas with logging and farming provided food and cover for bobcats. In Oklahoma, Rolley and Ward (1985) found that bobcats used young-aged clearcuts that supported high numbers of rabbits and rodents, while mature forests with lower prey densities were used very little. Hall and Newsom (1978) reported that mid-successional stages on cutover areas were the centers of bobcat activity in the hardwood bottomlands of Louisiana.

It appeared that logging, like fire, returned forests to early successional stages that provided good cover and abundant prey for bobcats. The managed forests of western Washington provided a continuous cycle of harvest and regrowth. While not all of the stages of forest succession were preferred by bobcats, the intensity of forest management in this area provided many early successional stages mixed in with clearcuts and mature forests. While other studies have documented preferred use of early successional stages, this study timber defined which, seral stages were preferred and avoided. Bobcats appeared to be adaptable enough to survive in the marginal habitats created by timber harvest, while taking advantage of the preferred habitats with high prey abundance. They may therefore benefit from tire patchwork mosaic of seral stages and the continuous cycle of growth and harvest found hi managed forests of western Washington.

MANAGEMENT IMPLICATIONS

Neither good quality habitat nor available prey appear to be lacking in these two study areas on the Kapowsin tree farm. The small home range sizes computed for this area may mean that overall habitat conditions are good for bobcats. Density and population estimates seem to indicate that a relatively healthy population of bobcats exists here. However, care must be taken when trying to apply these results to the rest of the tree farm or to other areas in western Washington. Home range sizes are only numerical estimates and should be used with caution as an indicator of overall conditions or in an estimation of density and abundance. Habitat quality is an important part of a healthy bobcat population. While results from this study may apply to other areas with similar habitat types, numbers may be significantly different where the availability of habitat types varies from that found in this study.

The implementation of certain management practices can promote healthy bobcat populations that can sustain the pressures of harvest. Healthy populations would also put increased pressure on bobcat prey species that may reduce losses to the timber industry. Bobcat populations depend on quality habitats for cover and prey. The Young cover type was the most preferred of all cover types. Other early and mid-successional stages were also used. Habitats interspersion would likely benefit bobcats by ensuring the presence of preferred habitats throughout the harvest-regrowth cycle. Thinning of stands to open canopies and promote the growth of understory vegetation may also promote bobcat populations. The Harvest age stand was the least preferred in this study. However, these results should not be applied to older forests elsewhere. Harvest stands in this managed forest are relatively young. Other, more mature, stands with less canopy closure and a more developed understory may benefit bobcats. A study of bobcat use of old forests and other forest types would be necessary to fully understand bobcat habitat use in western Washington.

Although logging provides favorable habitats for bobcats, increased road access wig make them more susceptible to harvest. Bobcats have few natural enemies except for humans. Survival rates of 81% have been reported for unexploited populations (Koehler 1987). Fuller et al. (1985) reported survival rates of 56% for harvested populations and 19% where there was significant poaching. Roads are used by bobcats as travel routes in the winter (McCord 1974) which may increase their vulnerability to hunters.

Habitat management to promote bobcats would also promote bobcat prey species. Because high populations of bobcat prey would not benefit forest managers, increasing bobcat survival rates may be a better approach. An expanded road closure program may decrease hunter take and increase bobcat survival rates promoting a healthy population. Road closure programs should be established in areas with low bobcat densities. Continued monitoring of bobcat populations to detect changes in productivity or density can be used to determine when and where road closure programs should be established. Because the Kapowsin Tree Farm has controlled access, all bobcats taken during the hunting season can be checked to obtain information on sex ratios, age ratios, reproductive status, and location of capture. Because bobcats have a polygamous mating system, populations can withstand a greater harvest of males than females. Similarly, age ratios with a high number of young cats being harvested may indicate that productivity is high. A lack of pregnant females may indicate high densities that could lead to more transient, non-reproductive individuals. Finally, by relating these data to different parts of the tree farm road closures could be initiated as needed. It should be mentioned that the interpretation of these types of data are debatable and should be used with caution. These data are best used as part of a long-term monitoring project that could provide information on population trends.

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