Differences in the Ability of Vegetation Models to Predict Small Mammal Abundance in Different Aged Douglas-Fir Forests[1]

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Abstract.—Three trapping techniques for small mammals were used in 47 study stands in northern California and southern Oregon and resulted in different capture frequencies by the different techniques. In addition, the abundances of mammals derived from the different techniques produced vegetation association models which were often quite different. Only the California red-backed vole *(Clethrionomys californicus)* showed any association with stand age, and no species had any marked associations with the moisture regime of the stands or the geographical region.

Habitat association patterns have been presented for many small mammal species (e.g. Rosenzweig 1973, M'Closkey 1975, Dueser and Shugart 1978, MacGracken, et al. 1985). In most instances, models representing habitat use have been derived for a single species using a single trapping technique. Most community based studies have also used a single trapping technique. Individual species, however, have different sensitivities to capture, making it difficult to compare capture rates across species (Seber 1981).

To better understand the habitat associations across a sequence of forest ages in the Pacific Northwest, we studied the population status in selected forest stands in northern California and southern Oregon during summer and fall of 1984 and 1985. This study was part of a U.S. Forest Service research project extending from northern California through Oregon and north into Washington (e.g. Ruggiero and Carey 1984, Manuwal and Huff 1987). The impacts of the harvesting of old-growth forests on vertebrate populations in this area are uncertain (Hagar 1960, Raphael and Barrett 1984, Raphael et al. in press).

We trapped mammals over a gradient of different-aged forest stands using three techniques. Our primary objectives were: (1) to determine if the relative abundance of each species differed between the stands; (2) to determine which habitat variables were associated with the relative abundances of each species; and (3) to study the efficiency of different trapping techniques. In this paper we discuss differences in habitat models derived from different techniques for the five most abundant species of small mammals.

Methods and Materials

Study Area

We selected 47 study stands in three regions of northwestern California and southwestern Oregon. These stands represented a successional gradient typical of the Douglas-fir communities of the region. Stands ranged in elevation from 414 m to 1,556 m and were generally dominated by Douglas-fir in association with tanoak *(Lithocarpus densiflora)* and madrone *(Arbutus menziesii)*. Three low elevation stands had a redwood *(Sequoia sempervirens)* component; four high elevation stands in the Cave Junction region were dominated by white fir *(Abies concolor)*.

Fifteen stands were located at each of three regions (in the vicinities of Branscomb and Willow Creek, California, and Cave Junction, Oregon), with an additional 2 stands at Butte Creek, near Dinsmore, California. These stands were divided into three age classes based on core samples of 2 to 10 of the dominant Douglas-firs in each young and mature stand (up to approximately 180 years of age) (B. Bingham, USFS Pacific Southwest Station, pers. commun.). In old-growth stands, tree cores could not always be taken because of large tree size and rotten tree cores, thus some stand ages were based on rings counted on stumps in adjacent clearcuts, along roads, or on core samples provided by local Forest Service offices. Each forest stand was assigned to one of three age classes: young forest < 100 years; mature forest 100-180 years; and old-growth forest, > 180 years. Those that were classified as old-growth forest were further classified as to moisture regime: dry, mesic, or wet, based on species composition and percent cover of the herb and shrub layers of the stand (B. Bingham, pers. commun.). All young and mature stands represented the modal, or mesic moisture class.

An index to the yearly solar radiation was derived by the method of Frank and Lee (1966), which is based on slope, aspect, and latitude. Values are largest on south-facing, moderate

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slopes, and lowest on north-facing, steep slopes.

Mammal Trapping

A single trapping grid for snap/livetrapping was established in each stand in 12 rows, with 12 trap stations per row. Trap stations were placed at 15-meter intervals resulting in a grid 165 m x 165 m. Each stand was relatively homogeneous, and grids located in each stand were, in most cases, separated from different habitat types by at least 100-m of the same habitat.

In 1984, two snaptraps ("Museum Special") were placed in 1984 at each trap station within 1.5 meters of the grid coordinate on all 47 stands. Six stands were trapped simultaneously (two in each region) for five days (four nights) until all stands were sampled (July 3 to August 31). In 1985, a single Sherman livetrap (7.6 x 8.9 x 22.0 cm) was used at the same stations on 43 of the stands; six stands again were trapped during each five-day session from July 9 to August 30. We did not livetrap four stands (two in Branscomb area and two in Cave Junction area). In both years, each trap was placed alongside downed logs, brushy vegetation, or rodent runways. Baited with peanut butter and oat groats in 1984, and oat groats and sunflower seeds (3:1 ratio) in 1985, the traps were left in place for four nights. We feel that the four nights of trapping did not significantly alter populations between years. In the analyses below, we standardized captures to the number per 1000 trap-nights.

We used pitfall traps to sample small mammal populations on all 47 stands during both 1984 and 1985. A pitfall grid consisted of six rows of six pitfall traps per row at 15 m spacing in each stand. Grids were located usually more than 100 m from snap and pitfall grids. Traps were two No. 10 cans taped together and sunk until the top was flush with the ground. A funnel collar to prevent animals from escaping was made from a margarine container with the bottom cut out. We propped a cedar shake 3-4 cm above the opening to the pitfall trap to act as a cover.

Traps were examined at 5-day intervals for 50 days in October and November 1984, and for 30 days in October 1985. In the analyses that follows, we used the number of mammals captured unstandardized for effort.

The complication that not all capture methods were used in both years of the study, resulted in an unknown year-effect that may influence capture frequency. Despite this problem, we feel that the data are instructive as to the variety of models produced, and the implications for investigators.

Table 1.—Vegetation variables measured for each cluster of trapping stations in a study of small mammal abundance in Douglas-fir forests of southern Oregon and northern California, 1984-85.

Ground cover	Vegetation variables	
Rock	Herb	Dogwood
Soil	Grass	California hazel
Small Litter	Fern	Pines
Moss	Douglas-fir	White and black oaks
Lichen	Tanoak	Salal
First litter layer	Pacific madrone	Manzanita
Second litter layer	Live oaks	*Rosa* spp.
Solar index	Oregon grape	*Rubus* spp.
Decay class[a] 1 and 2 logs	Redwood	California laurel
Decay class 3, 4, 5 logs	Poison oak	Huckleberry
	True fir	Big-leaf maples
	Alders	False cedars

[a]Thomas (1979:80).

Vegetation Sampling

Vegetation for each snap/livetrap grid was measured on 16 plots overlaying the 144 trap stations. Nine vegetation plots were uniformly distributed among the 36 pitfall stations. Vegetation and structure were measured in 5.6 m and 15 m radii circular plots. On each plot, we recorded: percent cover of ground cover variables (i.e. rocks, woody debris); percent cover of vegetation at five height strata; and counts of trees and snags in varying size classes.

We averaged the percent cover values for 25 vegetation stations (16 in the snap/livetrap grids plus nine stations in the pitfall grids), to obtain mean values of percent cover for 11 ground cover variables and 24 species of plants (or groups of species) in each of the 47 stands (table 1). We combined some taxa into genera prior to calculating means: the true firs (*Abies* spp.), alders (*Alnus* spp.), huckleberries (*Vaccinium* spp.), live oaks (*Quercus* spp.), manzanita (*Artemesia* spp.), various roses (*Rosa* spp.), and *Rubus* spp. The vegetation data were vertically stratified into five levels: ground (0-0.5 m), shrub level (>0.5-2.0 m), mid-canopy (>2.0 m-midlevel), canopy (those trees at the average height of the stand), and supercanopy (those trees substantially above the canopy). Mean values for cover by stand were combined into two strata: "understory" included ground and shrub layers, while "canopy" incorporated mid-canopy, canopy, and supercanopy.

The small and medium trees (<50 cm dbh) were counted on a 5.6 m circular plot, while large trees (≥50 cm dbh) were counted on a 15 m circular plot. The counts of 18 species of trees were averaged over the stations for each grid and were used in an all-subsets regression.

Analyses

We used one-way analysis of variance (ANOVA) to evaluate differences in mammal abundances relative to three stand age classes, three moisture classes of the old-growth stands in each of the three regions (Branscomb and Butte Creek area, Willow Creek area, and Cave Junction area).

These analyses were done on the three separate sets of data, without reference to the each other. Interaction among the factors was ignored in these analyses. When significant differences were found among capture frequencies of individual species by classes of: age, moisture, or study area, a multiple comparison test was used to determine which of the groups were significantly different. A Tukey test (Zar 1984:186) was performed if variances were found to be equal, while a Games and Howell modification was used in the case of unequal variances (Keselman and Rogan 1978).

Pearson product moment correlation coefficients were calculated between capture frequencies for each combination of trapping techniques and between capture frequencies and vegetation means over all stands. Variables from ground cover, herb and shrub cover, and canopy trees were included in all-possible-subsets regression analyses for each small mammal species when a significant correlation existed with capture frequency from any capture technique. Five-variable models were selected for each species when greater than 100 individuals were captured by a particular technique. Vegetation variables were excluded when found on less than 25% of the stands.

Results and Discussion

Twenty-three species of small mammals were captured during the study, though several were represented by only a few individuals (table 2). The three techniques differed in their effectiveness in captur-

Table 2.—Number of captures by species and trapping technique, from a study of small mammals in northern California and southern Oregon, 1984 and 1985.

Species	Pitfalls	Snaptraps	Livetraps	Total
Trowbridge's Shrew (*Sorex trowbridgii*)	892	357	101	1350
Pacific Shrew (*Sorex pacificus*)	33	70	11	114
Vagrant Shrew (*Sorex vagrans*)	1	1	0	2
Pacific Water Shrew (*Sorex bendirii*)	1	0	0	1
Shrew-Mole (*Neurotrichus gibbsii*)	40	27	5	72
Coast Mole (*Scapanus orarius*)	1	0	0	1
Chipmunks (*Tamias* spp.)	2	33	282	317
Golden-mantled Ground Squirrel (*Spermophilus lateralis*)	0	0	1	1
Northern Flying Squirrel (*Glaucomys sabrinus*)	6	1	8	15
Botta's Pocket Gopher (*Thomomys bottae*)	5	2	0	7
Deer Mouse (*Peromyscus maniculatus*)	115	524	404	1043
Pinyon Mouse (*Peromyscus truei*)	16	205	213	434
Dusky-footed Woodrat (*Neotoma fuscipes*)	2	4	28	34
Bushy-tailed Woodrat (*Neotoma cinerea*)	0	0	5	5
California Red-backed Vole (*Clethrionomys californicus*)	572	161	101	834
Red Tree Vole (*Arborimus longicaudus*)	1	0	0	1
California Vole (*Microtus californicus*)	14	14	5	33
Long-tailed Vole (*Microtus longicaudus*)	2	0	0	2
Creeping Vole (*Microtus oregoni*)	6	5	10	21
Black Rat (*Rattus rattus*)	1	0	0	1
Pacific Jumping Mouse (*Zapus trinotatus*)	3	11	0	14
Short-tailed weasel (*Mustela erminea*)	0	0	6	6
Number of Trapnights[a]	135,360	55,284	23,367	214,011

[a]*Totals were adjusted for traps damaged by bears, etc.*

ing different species of mammals. Five species had sufficient captures (≥ 100 individuals or more, by one or more of the trapping techniques) to undergo intensive analyses. These were the California red-backed vole, deer mouse, pinyon mouse, Trowbridge's shrew, and the combined chipmunk species.

Associations with Area, Age, and Moisture Class

Most mammals were found in all three areas, with the exception of three species with only 1-2 captured. The California red-backed vole had significantly fewer captures in the more southerly Branscomb region than in the central and northern regions (table 3). The vole's abundance was significantly correlated with true firs ($r = 0.46$, $P < 0.05$), which were found on 11 stands in the north and no stands in the south. The two mice *(Peromyscus)* species exhibited the opposite trend with captures significantly greater in the south than in the north. The pinyon mouse was correlated with solar index which is generally greater in the southern area. The shrews and chipmunks were found equally in all areas.

The red-backed vole was the only species to have a significant association with age of the forest stand ($P < 0.01$). This confirms the study of Raphael and Barrett (1984) and Raphael (this volume) in the Willow Creek area. Our capture frequency was fairly low in stands aged at less than 150 years, while greater densities were evident in many older stands (fig. 1). No such relationship was found for the deer mouse, although Raphael and Barrett (1984) earlier showed a significant association with age in the Willow Creek area.

We tested the abundance of small mammals in the three moisture classes of old-growth forests: dry, mesic, an wet. Among the five mammal species with large sample sizes, there were no differences in capture frequency according to the various moisture classes.

Therefore, we found that within our study areas in the Douglas-fir type, there were few significant or strong associations between five small mammals and age of the forest stand. The stands chosen to represent the different age and moisture classes in this study were all naturally occurring. The young stands originated from fire or other catastrophic events, rather than by timber harvest, and therefore often were heterogeneous in character with structural and floristic components similar to old-growth stands. Scattered old trees and abundant dead and down material were sometimes present in young stands, characteristics which are absent from stands that originated from clearcuts; results in even-aged stands may be very different.

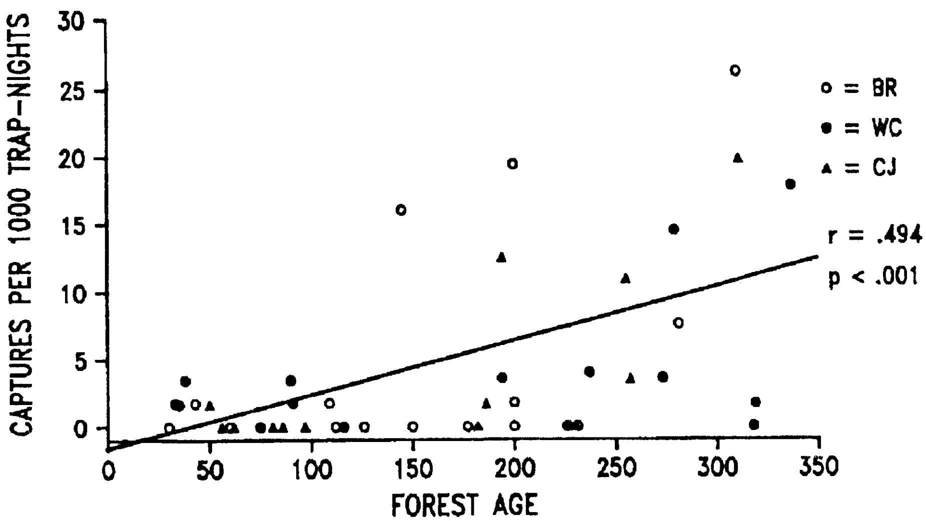

Figure 1.—Captures of California red-backed voles per 1000 trapnights in a study of small mammal abundance relative to stand age, 1984-1985. BR = Branscomb stands, WC = Willow Creek stands, CJ = Cave Junction stands.

Table 3.—Significance of differences in capture frequency by area for five species of small mammals. The areas are CJ = Cave Junction, WC = Willow Creek, and BR = Branscomb and Butte Creek. Methods with no significant differences in capture frequencies at the various areas are indicated by NS; dashed lines indicate inadequate sample size.

Species	Snaptrap	Livetrap	Pitfalls
California red-backed vole	NS	NS	BR<WC+CJ
Deer mouse	CJ<WC+BR	CJ<WC+BR	NS
Pinyon mouse	CJ<BR	CJ<BR	—
Trowbridge's shrew	NS	NS	NS
Chipmunks	—	NS	—

Effectiveness of Capture

Captures of small mammals varied greatly by trapping technique (table 1). The two mice were most effectively captured by baited snap and livetraps. Very few individuals were collected in unbaited pitfalls. Microtine voles, shrews, and moles were trapped most efficiently by the pitfall traps and somewhat by snaptraps. Sciurids and woodrats were captured almost exclusively by livetraps.

We correlated the captures of each species by the different techniques. We found significant correlation between capture frequencies only in those techniques effective at sampling large numbers of a particular species (table 4). Demonstrating the closest agreement between techniques were the pinyon mouse (r = 0.88 between snap and livetraps) and the vole (r = 0.73 between the two years of pitfall traps). The Trowbridge's shrew, on the other hand, showed no relationship between captures by pitfalls and snaptraps (r = 0.14), or pitfalls and livetraps (r = 0.09). Biological interpretation of such varied results may be very difficult, as discussed in the following.

Vegetation Models

Depending on which method was used to predict the dependent variable, we obtained very different vegetation models, potentially resulting in very different biological interpretations. Models from snap and livetrapping show that areas with high captures of pinyon mice were characterized by high densities of pacific madrone and tanoak, high solar index, and bare soils (r^2 = 0.64 and 0.65) (table 5). Four of the five habitat variables were identical in both models suggesting that within our study area, the pinyon mouse used dryer, southern exposures with exposed soils and large amounts of hardwoods.

Models developed for the Trowbridge's shrew from snaptrap and pitfall methods were quite different (table 6). Only one variable was included in both models, and the association with dogwood trees switched from negative to positive. Both models included some indication of greater use of older stands, i.e., the model using snaptrap data included well decayed logs and the livetrap model incorporated the decomposed litter layer, representing a well developed layer of organic soil. The inconsistency in these vegetation models was predicted by the lack of correlation between capture frequencies by the two techniques. It appears that in our Douglas-fir habitat type, the shrew may be broadly distributed, independent of finer vegetation composition.

Models for the red-backed vole developed from capture frequencies associated with different trapping techniques (table 7) were more similar than those for the shrew, but less similar than those for the pinyon mouse. In models developed from snap and livetrap captures, three of the five variables were selected by both models. Models from pitfall and snaptrap data shared two of the five variables selected. Models from pitfall and livetrap capture data also shared two of the five variables selected, but one of these variables switched from a positive to a negative association. Only the response to an abundant herbaceous layer was consistent in models from all three trapping techniques. Interpretation of the snaptrap model suggests that

Table 4.—Correlation between years and methods of the capture frequency of four small mammal species in snaptraps (Snap), livetraps (Live), or pitfall traps (Pits). (Chipmunks were only caught in significant numbers in livetraps and could not be compared).

	Between years		Within years	
	Snap84/live85	Pits:84/85	84:pits/snap	85:pits/live
California red-backed vole	0.540**	0.727**	0.459**	0.162
Deer mouse	0.392**	0.015	-0.092	0.320*
Pinyon mouse	0.884**	0.124	0.250	0.320*
Trowbridge's shrew	0.102	0.332*	0.141	0.088

* = $P < 0.05$.
** = $P < 0.01$.

Table 5.—Habitat association models for the pinyon mouse determined from capture frequencies by two different trapping techniques used. NS indicates the variable was not selected, + or - indicates a positive or negative association with capture frequency.

Selected predictor variables	Snaptrap	Livetrap
Exposed rock	NS	+
Bare soil	+	+
Solar index	+	+
Poison oak	-	NS
Tanoak	+	+
Pacific madrone	+	+
R^2	0.64	0.65

Correlation between capture frequencies of the two techniques = 0.88.

Table 6.—Habitat association models for the Trowbridge's shrew determined from capture frequencies by two different trapping techniques used. Symbols as in table 5.

Selected predictor variables	Snaptrap	Livetrap
Highly decayed logs	+	NS
Fern	+	NS
Dogwood shrub	+	NS
Dogwood tree	-	+
Deciduous oaks	+	NS
True firs	NS	+
Tanoak	NS	-
California hazel	NS	+
Deep litter layer	NS	+
R^2	0.59	0.55

Correlation between capture frequencies by two techniques = 0.14.

the vole is associated with a fairly moist habitat (abundant herbs and presence of huckleberry). The pitfall model also suggests an association with a moist habitat (more herbs and lichens and less solar index). The livetrap model includes some indication of moist habitats (herbs, *Rosa* spp., and huckleberry) but also a suggestion of a dryer habitat (solar index).

The deer mouse, despite its abundance, had large differences between variables selected in habitat models (table 8). Its relative abundance did not appear to be associated with the same habitat variables in the same way for the three different trapping techniques. Only two of the 12 variables selected in these models were included in more than one model with the same sign (avoidance of *Rosa* spp. and preference for areas with California laurel). Model disparity may, of course, simply indicate that one or more of the techniques estimated the dependent variable with considerable bias, thus producing an erroneous model.

The chipmunks were captured primarily by livetrapping. The resulting 5-variable model suggests that chipmunks were more common in the true fir stands at high elevation that had an understory of live oaks and huckleberries (table 9).

While we are sure that there would be some seasonal differences in the habitat association patterns from autumn captures in pitfalls and summer captures in snap and livetraps, we suggest that this seasonal effect would be much less than the differences that we noted, because of the relatively low vagility of the small mammals involved.

All capture methods are assumed to sample individuals of a given species at some unknown proportion of their true abundance. These proportions, within a species, likely differ by capture method. If the capture efficiency of all methods were consistent across sampled areas, then the rank correlation of abundance between methods should be close to 1.0. However, for most species that we studied, correlations of capture frequencies between methods were low and the ranking of stands based

Table 7.—Habitat association models for the California red-backed vole determined from capture frequencies by three different trapping techniques. Symbols as in table 5.

Selected predictor variables	Snaptrap	Livetrap	Pitfall
Herbs	+	+	+
Rose	-	+	NS
Huckleberry	+	+	NS
False cedar	+	NS	NS
Douglas-fir	+	NS	+
solar index	NS	+	-
Live oaks	NS	-	NS
Lichen	NS	NS	+
Grass	NS	NS	+
R^2	0.58	0.55	0.63

Correlation between capture frequencies: snaptrap and livetrap = 0.54 (P < 0.01); snaptrap and pitfall = 0.50 (P < 0.01); pitfall and livetrap = 0.16 (NS).

Table 8.—Habitat association models for the deer mouse determined from capture frequencies by three different trapping techniques. Symbols as in table 5.

Selected predictor variables	Snaptrap	Livetrap	Pitfall
Lichen	-	NS	NS
True firs	-	NS	NS
Douglas-fir	-	NS	+
California laurel	+	+	NS
Pacific madrone	-	NS	NS
Manzanita	NS	-	NS
Rose	NS	-	-
Dogwood	NS	+	NS
Deciduous oaks	NS	+	NS
Lower litter layer	NS	NS	+
Herbs	NS	NS	+
False cedars	NS	NS	-
R^2	0.33	0.38	0.63

Correlation between capture frequencies: snaptrap and livetrap = 0.39 (P < 0.01); snaptrap and pitfall = -0.09 (NS); pitfall and livetrap = 0.32 (P < 0.05).

Table 9.—Habitat association models for the chipmunks determined from capture frequencies by livetrapping. Symbols as in table 5.

Selected predictor variables	Livetrap
True fir	+
Douglas-fir	-
Lichen	+
Vaccinium	+
Live Oaks	+
R^2	0.59

on capture frequencies varied considerably depending on technique used. This suggests that the assumption of a constant proportion of captures, within a given method, across sampled areas was violated.

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Literature Cited

Dueser, R.D. and H.H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89-98.

Frank, E. C. and R. Lee. 1966. Potential solar beam irradiation on slopes. U.S. Dept. Agric. For. Serv. Res. Pap. RM-18.

Hagar, D.C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. Ecology 41:116-125.

Keselman, H.J. and J.C. Rogan. 1978. A comparison of the Modified-Tukey and Scheffe methods of multiple comparisons for pairwise contrasts. Journal of the American Statistical Association 73:47-52.

MacGracken, J.G., D.W. Uresk, and R.M. Hansen. 1985. Habitat used by shrews in southeastern Montana. Northwest Science 59:24-27.

M'Closkey, R.T. 1975. Habitat Dimensions of white-footed mice, *Peromyscus leucopus*. American Midland Naturalist 93:158-167.

Manuwal, D.A. and M.H. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest sere. Journal of Wildlife Management 51:586-595.

Raphael, M.G. and R.H. Barrett. 1984. Diversity and abundance of wildlife in late succession Douglas-fir forests. p. 352-360. *In* New Forests for a Changing World. Proceedings 1983 Convention of the Society of American Foresters. 650 pp.

Raphael, M.G., K.V. Rosenberg, and B.G. Marcot. In press. Large-scale changes in bird populations of Douglas-fir forests, Northwestern California. Bird Conservation 3.

Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54:111-117.

Ruggiero, L. F. and A. B. Carey. 1984. A programmatic approach to the study of old-growth forest-wildlife relationships. p. 340-345. *In* Proceedings of the 1983 convention of the Society of American Foresters: New forests for a changing world. Society of American Foresters, Bethesda, MD.

Seber, G.A.F. 1981. The estimation of animal abundance and related parameters. Second Edition. Oxford University Press, New York.

Thomas, J. W. (Ed.). 1979. Wildlife habitats in managed forests. USDA Forest Service Agriculture Handbook No. 553.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J. 718 pp.