

# Impacts of Forest Harvesting on the Long-toed Salamander (*Ambystoma macrodactylum*) at Opax Mountain

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## INTRODUCTION

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Natural biodiversity in forests has become the focus of increased attention in recent years and maintaining this biodiversity is now an important management goal. Amphibians are an important, though somewhat invisible, component of forest biodiversity, differing considerably from other vertebrates in their physiology, behaviour and role in food webs. Their small size and ability to convert energy very efficiently makes them an important link in the food chain between their vertebrate predators and the biomass of smaller invertebrates that would otherwise be inaccessible to the higher trophic levels (Pough 1983). Some aspects of amphibian biology (e.g., highly permeable skin, ectothermy) restrict their ability to deal with fluctuating conditions, which makes them sensitive to habitat alteration. Loss of habitat has been identified as a factor contributing to recent declines in amphibian populations around the world (Blaustein et al. 1994).

Reductions in species richness, diversity, and the overall abundance of amphibians have been associated with logging in several forest ecosystems. These include forests in the Pacific Northwest (Raphael 1988; Welsh and Lind 1988) and eastern United States (Enge and Marion 1986; Pough et al. 1987; Petranka et al. 1994), and in coastal British Columbia (Dupuis et al. 1995). The loss of moist and cool microhabitats has been suggested as a possible cause for observed reductions. Forest harvesting can affect amphibians by altering aquatic habitats as well. Corn and Bury (1989) found that the species richness, density, and biomass of aquatic amphibians was higher in streams in uncut forests. This may be the result of increased sedimentation rates in streams in cut forests. These results might be difficult to extrapolate to ecosystems in the Interior of British Columbia because of differences in climate and in the amphibian species present.

Although some North American amphibians are entirely terrestrial or entirely aquatic, most depend on both terrestrial and aquatic habitats to complete their life cycle. Long-toed salamanders breed and lay eggs in temporary or permanent ponds in spring, and move into the terrestrial environment for the remainder of the year. Aquatic habitats must be suitable for the development of eggs and larvae (e.g., sufficient food and cover, suitable temperatures). When this development is complete, larvae undergo metamorphosis into the terrestrial form. Terrestrial habitats must provide cover, food and winter refugia for juvenile and adult salamanders (Orchard 1988). Downed wood may play an important role in protecting amphibians from desiccation and extremes of temperature, as well as providing an abundance

of small invertebrates for food. Connectivity between terrestrial and aquatic habitats is also important, as individuals must be able to move between habitats to survive and reproduce. Removal of the forest canopy adjacent to breeding ponds and in terrestrial habitats used by amphibians has the potential to alter the suitability of these habitats for use by amphibians.

Our understanding of the effects of forest management on amphibians in British Columbia is limited, especially for the dry interior of the province. This information is required to examine how effective the current Forest Practices Code Biodiversity Guidelines are likely to be for maintaining amphibians in forest ecosystems. The objectives of this study are to investigate the effects of reduced canopy cover on long-toed salamanders, in both aquatic and terrestrial habitats. The relative importance of downed wood to long-toed salamanders in forested and clearcut areas is evaluated as well.

## METHODS

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**Study Site** The Opax Mountain research area is located in the Interior Douglas-fir zone northwest of Kamloops. The area consists of two sites, Mud Lake and Opax Mountain, to which six partial-cutting treatments have been applied (see Klenner and Vyse, these proceedings, p. 128). More than 100 wetlands are found across the site, including marshes and open-water ponds, with sizes ranging from 16 m<sup>2</sup> to 1.8 ha. A small lake is located in the centre of the Mud Lake site as well. Many of these ponds are ephemeral, drying up before the end of the summer in most years. The application of the partial-cutting treatments across the study area has resulted in ponds with a range of canopy cover conditions.

Although the focus of this study is on the long-toed salamander, spotted frogs, Pacific treefrogs, and western toads also use the research area.

**Aquatic Habitat** To investigate the effects on long-toed salamanders of logging adjacent to breeding ponds, I measured the relative abundance of breeding salamanders and emerging juvenile salamanders at ponds with canopy cover conditions ranging from complete canopy removal to no canopy removal (including natural variation in canopy cover). Surveys of breeding long-toed salamanders were conducted between mid-April and the end of May 1996, using pop-bottle funnel traps (Adams et. al. 1997) around the perimeter of 28 ponds (14 at each site). There were two trapping sessions at each site. I recorded the snout-to-vent length, total length, weight, and sex of each salamander captured.

The relative abundance of juvenile salamanders emerging from breeding ponds was measured with arrays of drift fences and pitfall traps at regular intervals around the perimeter of 21 ponds (n=12 at Mud Lake, n=9 at Opax Mountain). When possible, the same ponds were used as those for the spring breeding surveys, but this was not possible in some cases because of early drying of ponds. Sampling was continuous between early August and mid-October, for 70 and 59 consecutive days of sampling at Mud Lake and Opax Mountain, respectively. For each salamander captured, I recorded snout-to-vent length, total length, weight, and stage of development. In addition to relative abundance, this yielded information on the timing of emergence and the size and condition of emerging juveniles.

An index of adjacent canopy cover for each pond was calculated from 24 vertical canopy readings measured with a “moosehorn” device. Readings were taken at eight locations around the pond, with three distances for each location (pond edge, and 5 and 10 m out from pond edge). Ponds were assigned to three pond permanence classes (permanent, semi-permanent, and temporary), based on the dates they dried in 1995 and 1996. Permanent ponds retained water beyond mid-September in both years, temporary ponds dried before the end of July in both years, and semi-permanent ponds dried after July and before mid-September in at least 1 year. As none of the ponds sampled for emerging juvenile salamanders was temporary, there are only two pond permanence classes in the juvenile analyses.

I used stepwise multiple regression to determine which independent variables explained variation in the capture rates of both breeding and juvenile long-toed salamanders between ponds, and variation in the median emergence dates of juvenile salamanders. Canopy cover index, pond permanence, pond size, and site were the variables included in both the breeding salamander and juvenile salamander regression analyses. Trapping session was an additional variable in the breeding salamander analysis.

#### Terrestrial Habitat and the Role of Downed Wood

To investigate the effects of harvesting and the importance of downed wood to long-toed salamanders, I measured the relative abundance of salamanders in plots experimentally manipulated to study the relationships between small mammals and downed wood. Combinations of harvesting treatment (1.6-ha patch cut, uncut forest) and downed wood treatment (high volume, low volume) were sampled at each site, with grids of 25 pitfall traps. To include a range of seasons and weather conditions, the relative abundance of long-toed salamanders between treatments was assessed in five trapping sessions between early June and mid-October. Sessions were four to eight nights in duration, consistent within sessions. For each individual captured, I measured snout-to-vent length, total length, weight, and sex. I used sketches of the yellow dorsal pattern of the salamanders to identify recaptured individuals.

A repeated measures ANOVA was used to examine the effects of the harvesting and downed wood treatments on capture rates of long-toed salamanders across trapping sessions.

## RESULTS

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#### Aquatic Habitat

**Capture Rates of Breeding Salamanders:** A total of 1053 long-toed salamanders were captured in the spring breeding surveys, 688 at Mud Lake and 365 at Opax Mountain. Overall capture rates for ponds were not significantly different between the two sites (t-test,  $df = 26$ ,  $t = 0.49$ ,  $p = 0.63$ ), with mean values of 51 and 38 salamanders per 100 trap-nights for Mud Lake and Opax Mountain, respectively (Figure 1).

Canopy cover index, pond permanence, and trapping session explained approximately two-thirds of the observed variation in capture rates of breeding long-toed salamanders between ponds ( $R^2 = 0.684$ ,  $n = 28$ ,  $p < 0.001$ ). Breeding salamander capture rates showed a positive relationship with canopy cover index. Rates were highest for permanent ponds and lowest for

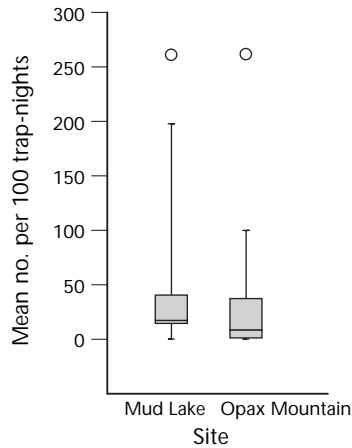


FIGURE 1 *Capture rates of breeding long-toed salamanders at breeding ponds by site. Lines within box plots show median values.*

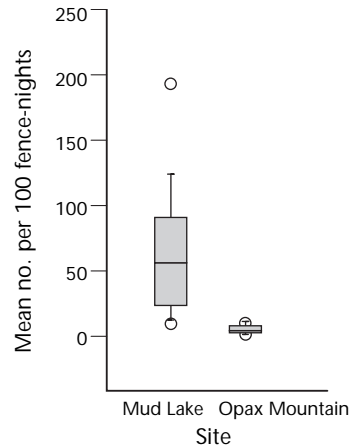


FIGURE 2 *Capture rates of emerging juvenile long-toed salamanders by site. Lines within box plots show median values.*

temporary ponds, and rates were higher in the early than in the late trapping session.

**Capture Rates of Juvenile Salamanders:** A total of 2758 juvenile salamanders emerging from breeding ponds were captured, 2603 at Mud Lake and 155 at Opax Mountain. Capture rates for ponds at the Mud Lake site were significantly higher than at Opax Mountain (t-test,  $df = 11$ ,  $t = 3.78$ ,  $p = 0.003$ ), with very little overlap in values (Figure 2).

Observed trends differed between sites as well. At Opax Mountain, canopy cover index was the only significant variable and it showed a negative relationship with juvenile capture rate ( $R^2 = 0.522$ ,  $n = 9$ ,  $p = 0.02$ ). Both canopy cover index and pond permanence were significant variables at the Mud Lake site ( $R^2 = 0.788$ ,  $n = 12$ ,  $p < 0.001$ ), but in this case the relationship between canopy cover index and capture rate was positive. Higher capture rates of emerging juvenile salamanders at Mud Lake were associated with the more permanent ponds.

**Median Emergence Dates of Juvenile Salamanders:** Median emergence date showed a positive relationship with canopy cover index at Opax Mountain ( $R^2 = 0.651$ ,  $n = 9$ ,  $p = 0.009$ ); juvenile salamanders emerged earlier from ponds with a low canopy cover index. A smaller portion of the variation in median emergence dates at Mud Lake was explained by the independent variables. Emergence was slightly earlier from permanent ponds than from semi-permanent ponds ( $R^2 = 0.329$ ,  $n = 12$ ,  $p = 0.03$ ). There was less variation in median emergence dates at Mud Lake than at Opax Mountain, the range at Mud Lake being August 27 to September 23 versus August 22 to October 3 at Opax Mountain.

Terrestrial Habitat and the Role of Downed Wood

Harvesting and downed wood treatments showed no significant effect on the capture rate of long-toed salamanders in the terrestrial habitat ( $F_{\text{HARV}(1,1)} = 0.522$ ,  $p = 0.6$ ;  $F_{\text{DW}(1,1)} = 23.75$ ,  $p = 0.17$ ). Differences between sites were significant ( $F_{\text{SITE}(1,1)} = 223.25$ ,  $p = 0.047$ ), with 90% of the individ-

uals captured over the year at the Mud Lake site. The very low sample size at Opax Mountain makes meaningful statistical analysis difficult.

Long-toed salamanders were active above ground throughout the field season, but capture rates were highest overall in the October trapping sessions. At both sites, capture rates of long-toed salamanders were low in the patch cuts during the summer trapping sessions and increased in the October trapping sessions (Figure 3). Capture rates in uncut treatment units showed less variation between sessions, although rates at Opax were low across all sessions (Figure 3).

A breakdown of captures into adult and juvenile long-toed salamanders shows that a large portion of the increase in capture rates from the summer to fall sessions results from increased captures of juvenile salamanders. During summer trapping sessions (June and August), adult salamanders outnumbered juveniles in both forest and patch-cut treatment units at Mud Lake (Figure 4a). While adult and juvenile capture rates were similar in forested units in the fall (October) trapping sessions, juvenile rates were roughly twice that of adults in the patch-cut units (Figure 4a). A similar trend is observed in the patch cuts at Opax Mountain in fall, though capture rates in summer session were quite low (Figure 4b).

## DISCUSSION

### Aquatic Habitat

The positive relationship between canopy cover index and capture rate of breeding long-toed salamanders may reflect a preference of breeding salamanders for ponds with higher canopy cover, but many amphibians show strong site-fidelity and would return to their natal pond to breed rather than selecting breeding sites with specific attributes. Another explanation is that lower capture rates at low canopy cover ponds result from the reduced suitability of the surrounding terrestrial habitat, as ponds with a low canopy cover index were often in areas of low canopy cover overall. Raymond and Hardy (1991) found the number of mole salamanders returning to a breeding

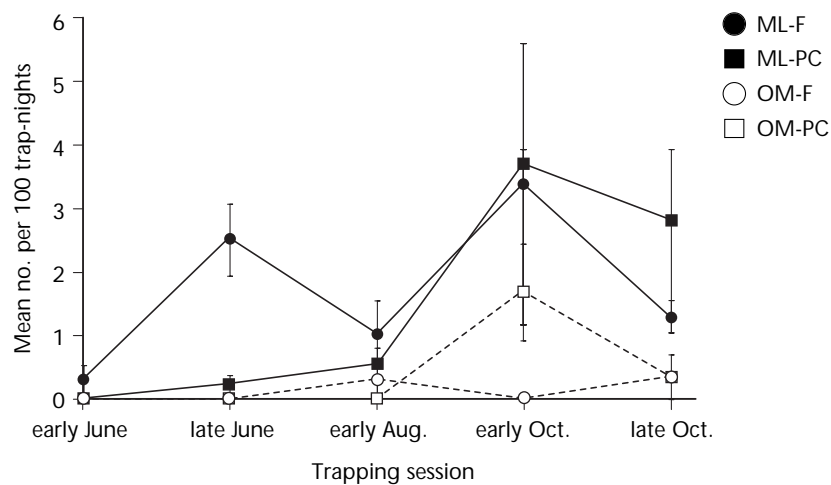


FIGURE 3 Capture rates of long-toed salamanders in pitfall grids by site and harvesting treatment across trapping sessions,  $\pm$  1 standard error. ML- Mud Lake; OM- Opax Mountain; F- uncut forest; PC- patch cut.

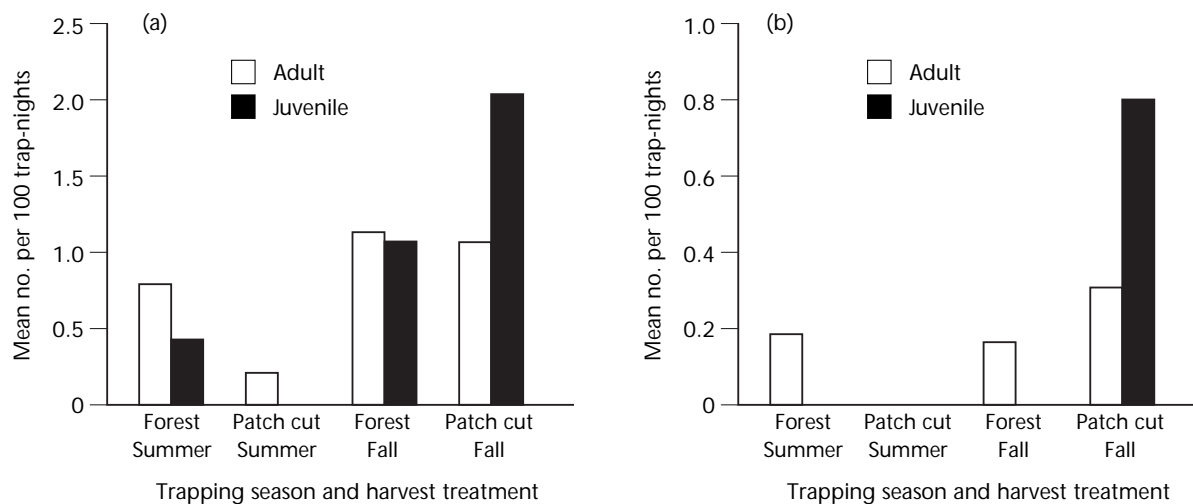


FIGURE 4 Long-toed salamander capture rates in summer and fall trapping sessions by harvesting treatment and age class (adult, juvenile) at (a) Mud Lake and (b) Opax Mountain. Values for summer sessions are means of early June, late June and August trapping sessions. Values for fall sessions are means of the early and late October trapping sessions.

pond was affected by logging in an adjacent area. A third possibility is that the number of breeding salamanders follows from the number of juveniles emerging in previous years. The year 1996 was the third breeding season following logging in the winter of 1993, so that two post-logging cohorts may be contributing to the 1996 breeding population.

The positive relationship between canopy cover index and capture rate of emerging juvenile long-toed salamanders at Mud Lake supports the idea that the relationship observed for the breeding population follows from patterns of abundance of juveniles. However, the relationship between canopy cover index and juvenile capture rates was negative at Opax Mountain. This difference may relate to differences in elevation between sites. Opax Mountain is at a higher elevation and has a shorter growing season than Mud Lake, which may restrict the number of larvae that are able to metamorphose, as amphibian larvae must reach a minimum size and stage of development before they can undergo metamorphosis (Wilbur 1980). Warmer water temperatures resulting from increased light penetration might lead to higher larval growth rates in the more open ponds, which would allow more larvae in low canopy cover ponds to reach the minimum size required for metamorphosis to occur.

The large difference in capture rates of juvenile salamanders between sites suggests that development of larvae may indeed be constrained at Opax Mountain, since the number of breeding salamanders was not significantly different between sites. This may result in fewer emerging salamanders overall, or in some cases the smaller larvae may be able to overwinter in the ponds (if they retain water over the winter). Overwintering of larvae has been observed in long-toed salamanders, more commonly at higher elevations (Howard and Wallace 1985). If larvae were overwintering and emerging earlier on in the next season, they would not have been captured in the drift fence arrays, which were not open until August.

The earlier emergence of juvenile salamanders from low canopy cover ponds at Opax Mountain can also be explained by increased larval growth rates in more open ponds. There was less variation in median emergence

dates at Mud Lake, suggesting that most larvae were able to develop in the time available.

Pond permanence influenced capture rates of breeding long-toed salamanders and of juvenile salamanders at Mud Lake, but not juveniles at Opax Mountain. Later drying of ponds has been associated with increased production of juveniles in other Ambystomatid salamanders (Shoop 1974; Semlitsch 1987).

Although no significant effects of harvesting or downed wood treatment were detected using ANOVA, trends in the mean capture rates of long-toed salamanders between uncut forest and patch cuts suggest that long-toed salamanders respond differently to uncut forest and patch cuts. During the summer months, conditions in the patch cuts appear to be less suitable for the aboveground activity of long-toed salamanders. It may be that individuals are not resident there, or they may be inactive and remain underground in a state of aestivation while aboveground conditions are unsuitable. The increase in capture rates in patch cuts in the fall may be the result of milder temperatures at that time, permitting more aboveground activity, or more likely the dispersal of individuals to their winter refugia. The higher capture rates of juvenile salamanders in the patch cuts than in the forest in the fall might result from increased activity from warmer temperatures.

The lack of difference in long-toed salamander capture rates between downed wood treatments may indicate that they do not use downed wood, or it may be the result of limitations in the application of treatments. Removal of downed wood from the "low" treatment units was meant to remove or destroy all downed wood structure that could be used by small mammals. Because downed wood removal in the forest was done by hand, large well-decayed logs could often not be completely removed. In these cases, the structure of any remaining wood was destroyed, sometimes leaving behind large amounts of very decayed woody debris, which could provide important habitat for salamanders. Long-toed salamanders were found on several occasions under logs and in well-decayed woody debris. Analysis of capture rates versus proximity to downed wood at individual pitfall traps may be a more suitable analysis.

#### SUMMARY

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Logging adjacent to breeding ponds does appear to influence the abundance of long-toed salamanders, although the degree to which this may affect populations in the long run is not apparent from this study. The Riparian Management Guidelines of the Forest Practices Code do not require a riparian management zone around wetlands smaller than 1.0 or 0.25 hectares (depending on the subzone). All ponds sampled in this study were smaller than this, as are many of the wetlands used by amphibians. This may have implications for amphibians in the Interior Douglas-fir zone, especially for those species with more restrictive habitat requirements than the long-toed salamander (which is a habitat generalist).

Results regarding use of uncut forest versus 1.6-ha patch cuts by long-toed salamanders were somewhat inconclusive, but observed trends suggest that removal of the forest canopy does have implications for long-toed salamanders. Although patch cuts were used by salamanders in October, they likely

represent less suitable habitat than uncut forest during the summer season, when conditions are warm and dry.

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#### REFERENCES

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- Adams, M.J., K.O. Richter, and W.P. Leonard. 1997. Surveying and monitoring amphibians using aquatic funnel traps. *In* Sampling amphibians in lentic habitats. D.H. Olsen, W.P. Leonard, and R.B. Bury (editors). Society for Northwestern Vertebrate Biology, Olympia, Wash. pp. 47–54.
- Blaustein, A.R., P.D. Hoffman, D.G. Hokit, J.M. Kiesecker, S.C. Walls, and J.B. Hays 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? *Ecology*. 91:1791–5.
- Corn, P.S. and R.B. Bury 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39–57.
- Dupuis, L.A., J.N.M. Smith, and F. Bunnell 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology* 9(3):645–53.
- Enge, K.M. and W.E. Marion 1986. Effects of clearcutting and site preparation on herpetofauna of a north Florida flatwoods. *Forest Ecology and Management* 14:177–92.
- Howard, J.H. and R.L. Wallace 1985. Life history characteristics of populations of the long-toed salamander (*Ambystoma macrodactylum*) from different altitudes. *American Midland Naturalist* 113(2):361–73.
- Orchard, S.A. 1988. Wildlife Habitat Handbooks for the Southern Interior Ecoprovince, vol. 4: Species notes for amphibians. B.C. Ministry of Environment, Victoria, B.C. WHR-35.
- Petranka, J.W., M.P. Brannon, M.E. Hopey, and C.K. Smith 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* 67:135–47.
- Pough, F.H. 1983. Amphibians and reptiles as low-energy systems, *In* Behavioural energetics: The cost of survival in vertebrates. W.P. Aspey and S.I. Lustick (editors). Ohio State University Press, Columbus, Ohio. pp. 141–88.

- Pough, F.H., E.M. Smith, D.H. Rhodes, and A. Collazo 1987. The abundance of salamanders in forest stands with different histories of disturbance. *Forest Ecology and Management* 20:1–9.
- Raphael, M.G. 1988. Long-term trends in abundance of amphibians, reptiles and mammals in Douglas-fir forests of Northwestern California, *In* Management of amphibians, reptiles and small mammals in North America. R.C. Szaro, K.E. Severson, and D.R. Patton (editors). Proceedings of the Symposium, Flagstaff, Ariz., July 1988. United States Department of Agriculture Forest Service, General Technical Report RM-166. pp. 23–31.
- Raymond, L.R. and L.M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. *Journal of Herpetology* 25(4):509–12.
- Semlitsch, R.D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. *Copeia* 1987(1):61–9.
- Shoop, C.R. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55:440–4.
- Welsh, H.H. and A.J. Lind 1988. Old growth forests and the distribution of terrestrial herpetofauna, *In* Management of amphibians, reptiles and small mammals in North America. R.C. Szaro, K.E. Severson, and D.R. Patton (editors). Proceedings of the Symposium, Flagstaff, Ariz., July 1988. United States Department of Agriculture Forest Service, General Technical Report RM-166. pp. 439–55.
- Wilbur, H.M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67–93.

# Effects of Experimental Harvesting Treatments on the Demography of Mice and Voles at Opax Mountain

WALT KLENNER

## INTRODUCTION

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Mice and voles are small granivores and herbivores, which I am monitoring as indicators of change in grass, forb, and shrub cover and habitat structure. Because of their importance to avian and terrestrial carnivores (Banfield 1974; Ehrlich et al. 1988), changes in the diversity or abundance of mice and voles will likely have consequences for terrestrial food webs. Mice and voles can also have a large influence on forest regeneration and plant communities, by reducing the efficiency and increasing the costs of seeding and planting operations, and by mediating changes in plant species composition (Sullivan 1979a; Hulme 1996). Small mammals also perform important roles in the ecological processes of forested ecosystems. Some species, such as the red-backed vole (*Clethrionomys gapperi*) and deer mouse (*Peromyscus maniculatus*), distribute mycorrhizal fungi, which are essential to conifer seedling survival (Amaranthus and Perry 1989). When feeding on fungi, ingested spores can pass through the digestive tract without damage or loss of viability (Trappe and Maser 1976) and then establish contact with roots once the feces are expelled.

The documented effects of forest management practices on mice and voles are highly variable. Several studies have shown an increase in deer mouse populations and a decline in red-backed vole populations in response to clearcutting (Gashwiler 1970; Scrivner and Smith 1984) and partial cutting (Medin 1986). Others noted little response by either species to harvesting or vegetation management (Sullivan 1979b; Medin and Booth 1989; Runciman and Sullivan 1996), or only an increase in deer mouse populations alone (Sullivan and Krebs 1981; Walters 1989). In the Pacific Northwest, Corn and Bury (1991) found little to indicate that species distribution or abundance was consistently related to forest age or specific habitat structure, with the exception of known habitat specialists such as the shrew mole (*Neurotrichus gibbsii*) or red tree vole (*Phenacomys longicaudus*). However, Carey and Johnson (1995) found greater numbers of mice and voles in old forests, and clear relationships to shrubs, herbs, and downed wood. In addition to the direct effects of habitat structure, the response to habitat edges (Walters 1989) or use of forested leaf strips by mice and voles (Yahner 1982; Diffendorfer et al. 1995) have received little attention.

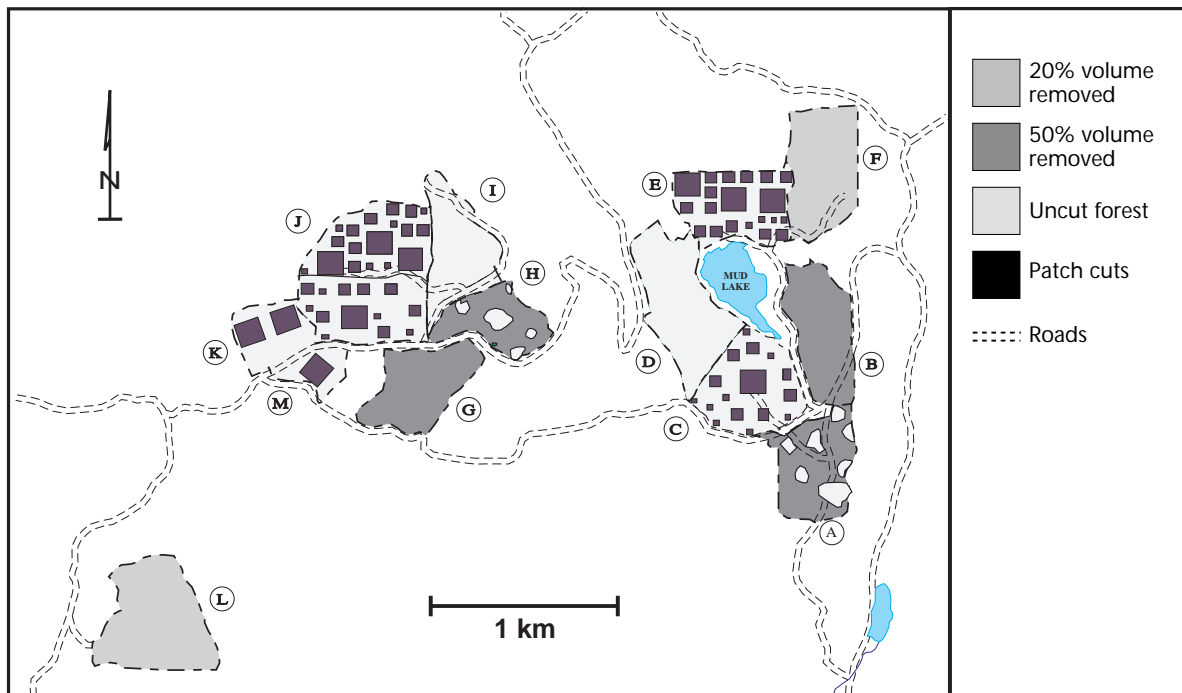
A shift in species composition or an increase in the abundance of some species of small mammals may not be a desirable change. Deer mice and chipmunks (*Tamias amoenus*) have been identified as important nest predators of songbirds (Wilcove 1985; Rudnicky and Hunter 1993). Habitat

changes favouring species such as chipmunks, deer mice, or voles, which damage seedlings, may compromise the overall objective of maintaining biodiversity, and increase the costs of reforestation. The current study provides information on the habitat requirements of mice and voles in dry Douglas-fir forests, and measures their responses to changing habitat structures and patterns in relation to harvesting treatments at the Opax Mountain silvicultural systems site.

## STUDY AREA AND METHODS

The Opax Mountain Silvicultural Systems Project consists of two replicates of each of the following treatments in a randomized block design (Figure 1):

- 20% merchantable volume removal using individual-tree selection (units F, L in Figure 1);
- 50% merchantable volume removal using individual-tree selection (units B, G);
- 35% merchantable volume removal, consisting of 75% of the treatment unit area harvested as 50% merchantable volume removal using individ-



**FIGURE 1** Harvesting treatments at the Opax Mountain research site: 20% volume removal using individual-tree selection (units F, L); 35% volume removal: consisting of 75% of the treatment unit area harvested as 50% volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H); 50% volume removal using individual-tree selection (units B, G); patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K); patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); uncut controls (units D, I).

ual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H);

- patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K);
- patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); and
- uncut controls (units D, I).

Each replicate block is 20–25 ha and was harvested in winter 1993–1994. For a more complete description of the Opax Mountain site, see Klenner and Vyse (these proceedings).

Mark-recapture  
Livetrapping

Some of the variability in response to habitat changes may relate to the use of retrospective study areas, where previous site history is unknown, or the use of different sampling methodologies. Galindo-Leal (1990) noted several differences between livetrapping and snap (kill) trapping. Snap trapping does not provide information on long-term population demography, and this may limit the utility of these data. For example, density information alone may not be adequate to assess habitat quality (van Horne 1983), or to differentiate between source and sink habitats (Pulliam 1988). In addition, short-term livetrapping or snap trapping does not allow for a detailed analysis of survival, which is likely the most important demographic parameter (Lebreton et al. 1992).

To monitor mouse and vole populations in relation to the treatments, 1-ha trapping grids were established on each of the treatment units. One trapping grid (100 × 100 m, including a buffer around the outermost traps) was established on a representative site within each replicate block. On the 20% removal patch-cut treatment (units C and K), the trapping grid was designed to represent the habitat types following harvest: approximately 80% of the trapping grid was in forested habitat, while 20% was in the patch cut. On the 50% patch-cut treatment, one sampling grid was placed within the largest harvest opening (1.6 ha), and another straddled a 0.4-ha opening and leave strips between the harvest openings. Twelve trapping grids are currently used to sample mouse and vole responses to the harvesting treatments, and an additional six trapping grids were established to monitor mouse and vole responses to the edges and leave strips created by patch-cut harvesting.

Each trapping grid consisted of a 7 × 7 array of stations, with one Longworth-style livetrapping at each station. Traps were baited with oats, sunflower seeds, and a slice of apple, and the nest chamber of each trap was filled with coarse brown cotton for insulation. During each trapping session, the traps were set for two overnight periods (approximately 1 hour before sunset until 3 hours after sunrise). Captured animals were tagged with individually numbered ear-tags, and were identified to species, with their weight, sex, and reproductive condition recorded before the animals were released at the point of capture. Between trapping periods, traps were locked open to allow animals to enter and maintain familiarity with the traps. When capture success exceeded 80% for the 49 traps on a sampling grid on both nights of a trapping session, an additional 25 traps were added at alternating stations to prevent trap saturation by captured animals. Trap numbers were increased as necessary to keep capture success below 80%. Each grid was trapped once every 3 weeks during May–October from 1994 to 1996.

Population Density  
and Survival

Livetrapping data were checked for errors and analyzed with the Jolly-Seber model for mark-recapture data (programs from Dr. C.J. Krebs, University of British Columbia, Department of Zoology). These programs were used to calculate estimates of density, trappability, survival, growth, reproductive condition, average body weight, and home range size.

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## RESULTS

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In this report, I present the results of an ongoing study on the demographic responses of mice and voles to the experimental silvicultural treatments at Opax Mountain. For brevity and clarity, the analyses and discussion focus on two key aspects of demography—population density and survival. Trappability, body weight, and reproduction were assessed (preliminary analyses only), but no significant differences were found between the experimental treatments. An analysis of species richness and diversity, the effect of habitat structure on mouse and vole abundance, and an analysis of the use or avoidance of edges and forested leave strips will be presented in subsequent reports.

Mark-recapture  
Livetrapping

From May 1994 to October 1996, 22 mark-recapture trapping sessions were conducted at the Opax Mountain site, representing 25 225 trap-nights (Table 1). The most common small mammal captured was the red-backed vole, followed by deer mice, yellow-pine chipmunks (*Tamias amoenus*), meadow voles (*Microtus pennsylvanicus*), heather voles (*Phenacomys intermedium*), and long-tailed voles (*Microtus longicaudus*).

Population Density  
and Survival

Across the first 3 years of this study, populations of red-backed voles decreased at the Opax Mountain site regardless of treatment (Figure 2), with a decline to approximately 30% of the 1994 density by 1996. In 1994, red-backed vole populations were approximately the same across all treatments, but by 1996, red-backed voles were seldom caught in the large patch-cut openings, but remained at a density of approximately 20 animals per hectare on the control grids. Red-backed vole populations on the other treatments were similar to those on the control grid. Populations on the Opax Mountain control replicate were higher than at the Mud Lake replicate, but

TABLE 1 *Total number of individual small mammals captured at the Opax Mountain research site over 22 trapping sessions from 1994 to 1996 (25 225 trap-nights)*

Species	Individuals captured
Red-backed voles	2806
Deer mice	848
Chipmunks	222
Meadow voles	213
Heather voles	15
Long-tailed voles	7
Total number of individuals	4111

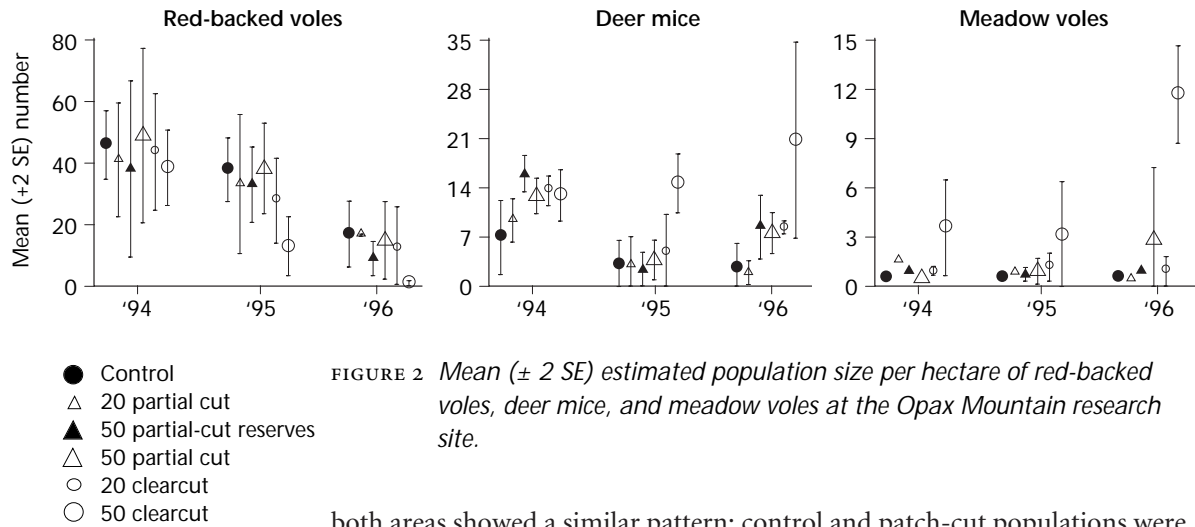


FIGURE 2 Mean ( $\pm 2$  SE) estimated population size per hectare of red-backed voles, deer mice, and meadow voles at the Opax Mountain research site.

both areas showed a similar pattern: control and patch-cut populations were the same in 1994 (the first year after harvest), then began to diverge in 1995, with populations on the control areas consistently higher than on the large patch-cut openings (Figure 3).

Both deer mice and meadow voles showed the opposite pattern, increasing in abundance in the large openings relative to controls after harvest (Figure 2). Deer mice did not respond until 1995, but meadow voles were already more abundant in 1994, and this difference increased in 1996. The

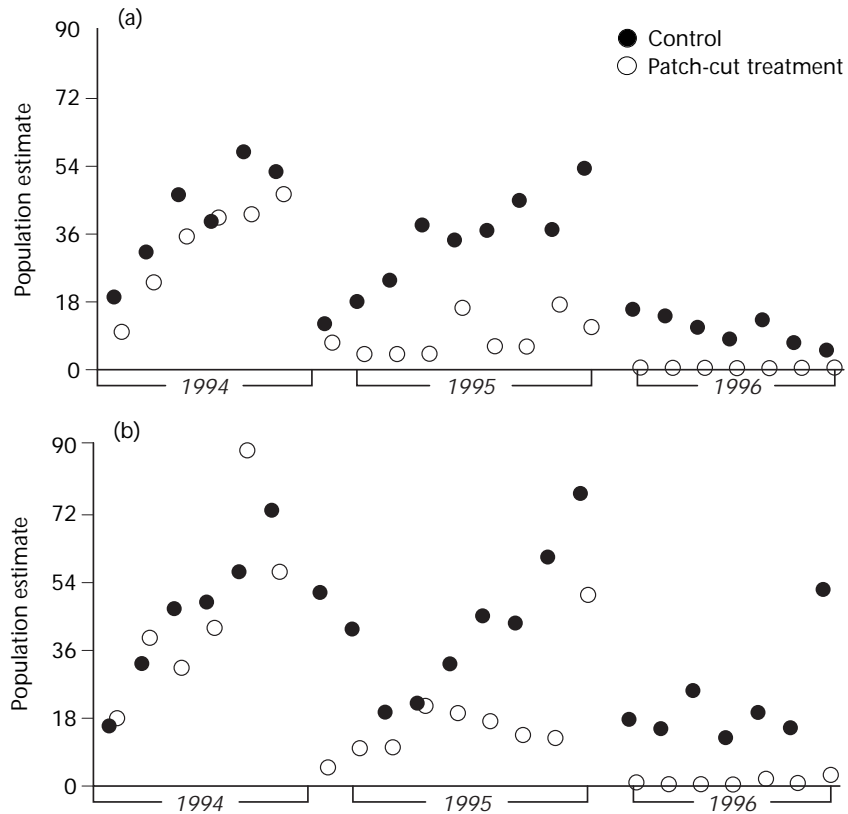


FIGURE 3 Population estimates for red-backed voles per hectare on control and 1.6-ha patch-cut treatments at the (a) Mud Lake and (b) Opax Mountain research sites.

population density of deer mice and meadow voles on the other treatments was similar to the control. The different response by red-backed voles compared to deer mice and meadow voles likely reflects the change in the abundance of the habitat structures used by these species following harvesting. In response to diminished canopy cover and an increase in the abundance of grass and forbs (see Miede et al., these proceedings, p. 211), red-backed vole populations diminished, but the other two species increased. Red-backed voles spend considerable time feeding on the fruiting bodies of fungi (Maser and Trappe 1984) and arboreal lichens that have fallen to the ground, while deer mice are largely granivores (i.e., feed on the seeds of grasses and forbs) and meadow voles are herbivores, feeding primarily on grasses.

Although both heather voles and long-tailed voles were caught at the Opax Mountain site, too few were captured to provide meaningful analyses (15 and seven captures, respectively)

The survival of red-backed voles across all treatments was similar in 1994 and 1995, but in 1996 survival in the 50% patch-cut area was less than on the control site (Figure 4). High variability occurred between the two replicates, especially on the other five treatments. The survival rates of deer mice were similar between treatments, but meadow voles did not survive as well on the control grids compared to the 50% patch-cut areas. The survival rate for meadow voles on the other treatments was intermediate between the control and patch-cut treatment. Note, however, that these survival rates reflect the probability of recapture, which is a function of survival and the lack of emigration.

#### SUMMARY

The response of mice and voles to the experimental harvesting treatments at the Opax Mountain site illustrates that no one treatment is either good or detrimental to all species. The removal of canopy cover in the patch cuts, along with associated habitat changes resulted in a decrease in both the density and survival of red-backed voles in these habitats. A strong habitat perturbation is required to effect such a change in species composition. On the other harvest treatments, no clear differences were evident in the abundance of red-backed voles, deer mice, or meadow voles. Although red-

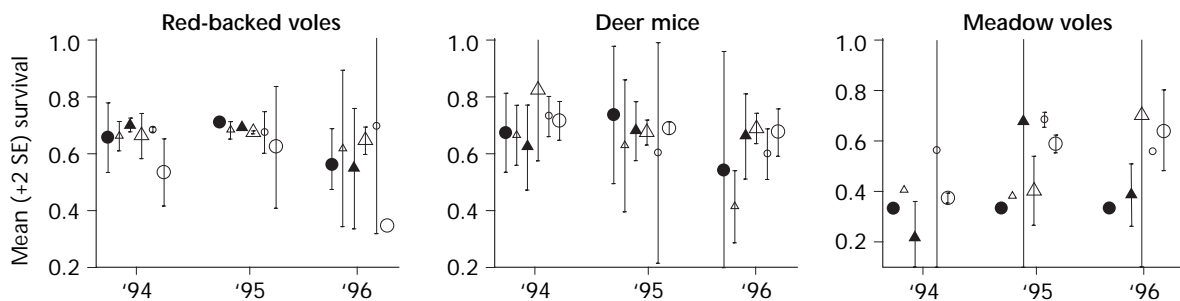


FIGURE 4 Mean ( $\pm$  2 SE) 4-week probability of survival for red-backed voles, deer mice, and meadow voles at the Opax Mountain research site.

backed voles largely disappeared from the large patch-cut openings, they were replaced by meadow voles and deer mice. This shift in species composition will likely offset any reduction in small mammal numbers on the treatments, but may have wider-reaching implications. For example, meadow voles are known to damage conifer seedlings, and deer mice are important nest predators (Wilcove 1985; Rudnicky and Hunter 1993). Where damage to regenerating conifers is a concern, large openings (1.6 ha) may not be appropriate and individual-tree selection partial cutting or small patch-cut openings may be advisable. A similar issue to consider is the threefold increase in deer mouse abundance on the 50% patch-cut areas. Hence, to avoid enhancing the habitat for this species, low-impact individual-tree selection partial cutting may be necessary.

The duration of the changes in the small mammal community, although not addressed in the present study, must also be considered when assessing the effects of harvesting. Following disturbance, successional changes are initiated, which lead to the re-establishment of a mature forest on the site. Although the abundance of some species may decline as an acute response to the disturbance, the duration of this effect should be considered when assessing the utility of a particular treatment, as well as the effects on other resource issues, such as insect pests or recreation. It is unlikely that all values can be maintained with one management prescription; therefore, landscape planning will be necessary to ensure that a diversity of treatments is applied in space and time.

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#### REFERENCES

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- Amaranthus, M.P. and D.A. Perry. 1989. Interaction effects of vegetation type and Pacific madrone soil inocula on survival, growth, and mycorrhiza formation of Douglas-fir. *Canadian Journal of Forest Research* 19:550–6.
- Banfield, A.W.F. 1974. *The mammals of Canada*. National Museum of Canada, Ottawa, Ont.
- Carey, A.B. and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5(2):336–52.

- Corn, P.S. and R.B. Bury. 1991. Small mammal communities in the Oregon Coast range. *In* Wildlife and vegetation of unmanaged Douglas-fir forests. L.F. Ruggiero, K. B. Aubry, A.B. Carey, and M.H. Huff (editors). U.S. Department of Agriculture, Forest Service, Portland, Oreg. General Technical Report PNW-GTR-285. pp. 241–53.
- Diffendorfer, J.E., M.S. Gaines, and R.D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76(3):287–9.
- Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster, Inc., Toronto, Ont.
- Galindo-Leal, C. 1990. Live-trapping vs. snap-trapping of deer mice: a comparison of methods. *Acta Theriologica*. 735: 357–63.
- Gashwiler, J.S. 1970. Plant and mammal changes on a clear-cut in west-central Oregon. *Ecology* 51(6):1018–26.
- Hulme, P.E. 1996. Herbivory, plant regeneration and species coexistence. *Journal of Ecology* 84:609–15.
- Lebreton, J.-D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Maser, C. and J.M. Trappe (editors). 1984. The seen and unseen world of the fallen tree. U.S. Department of Agriculture, Forest Service, Portland, Oreg. General Technical Report PNW-164.
- Medin, D.E. 1986. Small mammal responses to diameter-cut logging in an Idaho Douglas-fir forest. U.S. Department of Agriculture, Forest Service, Ogden, Utah. Research Note INT-362.
- Medin, D.E. and G.D. Booth. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. U.S. Department of Agriculture, Forest Service, Ogden, Utah. Research Paper INT-408.
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *American Naturalist* 132:652–61.
- Rudnicki, T.C. and M.L. Hunter, Jr. 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. *Ecological Applications* 3:357–66.
- Runciman, J.B. and T.P. Sullivan. 1996. Influence of alternative conifer release treatments on habitat structure and small mammal populations in south central British Columbia. *Canadian Journal of Forest Research* 26:2023–34.
- Scrivner, J.H. and H.D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce-fir forest in Idaho. *Northwest Science* 58(3):171–6.
- Sullivan, T.P. 1979a. The use of alternative foods to reduce conifer seed predation by the deer mouse (*Peromyscus maniculatus*). *Journal of Applied Ecology* 16:475–95.

- \_\_\_\_\_. 1979b. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. *Canadian Journal of Zoology* 57:1636–48.
- Sullivan, T.P. and C.J. Krebs. 1981. An irruption of deer mice after logging of coastal coniferous forest. *Canadian Journal of Zoology* 11:586–92.
- Trappe, J.M. and C. Maser. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. *Mycologia* 68:433–6.
- van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901
- Walters, B.B. 1989. Small mammals in a subalpine old-growth forest and clearcuts. *Northwest Science* 65:27–31.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–4.
- Yahner, R.H. 1982. Microhabitat use by small mammals in farmstead shelterbelts. *Journal of Mammalogy* 63:440–5.

# Effects of Experimental Harvesting Treatments on the Demography and Behaviour of Scurids at Opax Mountain

WALT KLENNER

## INTRODUCTION

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The three scurids commonly found in forested habitats of the Kamloops Region (red squirrel [*Tamiasciurus hudsonicus*], northern flying squirrel [*Glaucomyx sabrinus*], and yellow-pine chipmunk [*Tamias amoenus*]) represent species with a range of life history requirements (Gurnell 1987). Flying squirrels appear to require mature forests with large snags, arboreal lichens, patches of shrubs, and sporocarps (Maser et al. 1986; Rosenberg and Anthony 1992; Carey 1995; McDonald 1995). Red squirrels depend largely on the conifer seeds and fungi produced in mature coniferous forests (Smith 1968; Rusch and Reeder 1978; Gurnell 1983, 1987), while chipmunks prefer early seral habitats dominated by shrubs, forbs, and grasses (Medin 1986; Walters 1989). Scurids play an important role in terrestrial food webs. They are prey for several terrestrial and avian predators (Carey 1995), and flying squirrels are an important mechanism in the dispersal of mycorrhizal fungi (Maser et al. 1986; Maser and Maser 1988).

The harvesting treatments at the Opax Mountain silvicultural systems site removed varying proportions of the mature forest canopy (see Klenner and Vyse, these proceedings). Given the natural history of the three scurids and the different harvesting prescriptions at the Opax Mountain site, red squirrels, flying squirrels, and chipmunks should exhibit different responses to the various treatments employed. Few studies have examined scurid populations in relation to alternative harvesting systems that are designed to manipulate specific habitat structures and patterns. Squirrels are usually less abundant in managed forests than in old forests (Patton et al. 1985; Buchanan et al. 1990; Carey et al. 1992). However, the presence of remnant green trees and snags, shrubs, and hypogeous fungi appear to maintain flying squirrel populations (Carey 1995; McDonald 1995), and young stands of lodgepole pine can support substantial populations of red squirrels (Sullivan and Moses 1986). Although an increase in the abundance of scurids would indicate an increase in the amount of prey available to small carnivores, an increase in the abundance of chipmunks or red squirrels may not always be desirable. Chipmunks and red squirrels are known nest predators of ground-nesting songbirds (Wilcove 1985; Rudnicki and Hunter 1993), and red squirrels can cause extensive damage to young conifer plantations (Sullivan et al. 1990).

This study provides information on the habitat requirements of scurids, and measures their responses to the changing habitat patterns in relation to harvesting treatments at the Opax Mountain silvicultural systems site. The study will provide information on the long-term demographic response of

sciurids to changes in several habitat structures, including grass and forbs, shrubs, canopy cover, downed wood, snags, and mature hardwoods and conifers. Also being evaluated are the role of landscape features, such as habitat edges between mature forest and harvested openings, the loss of suitable habitat (mature conifers) within territories, and the use of forested leave strips between patch-cut openings.

## STUDY AREA AND METHODS

The Opax Mountain Silvicultural Systems project consists of two replicates of each of the following treatments in a randomized block design (Figure 1):

- 20% merchantable volume removal using individual-tree selection (units F, L in Figure 1);
- 50% merchantable volume removal using individual-tree selection (units B, G);
- 35% merchantable volume removal, consisting of 75% of the treatment unit area harvested as 50% merchantable volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H);

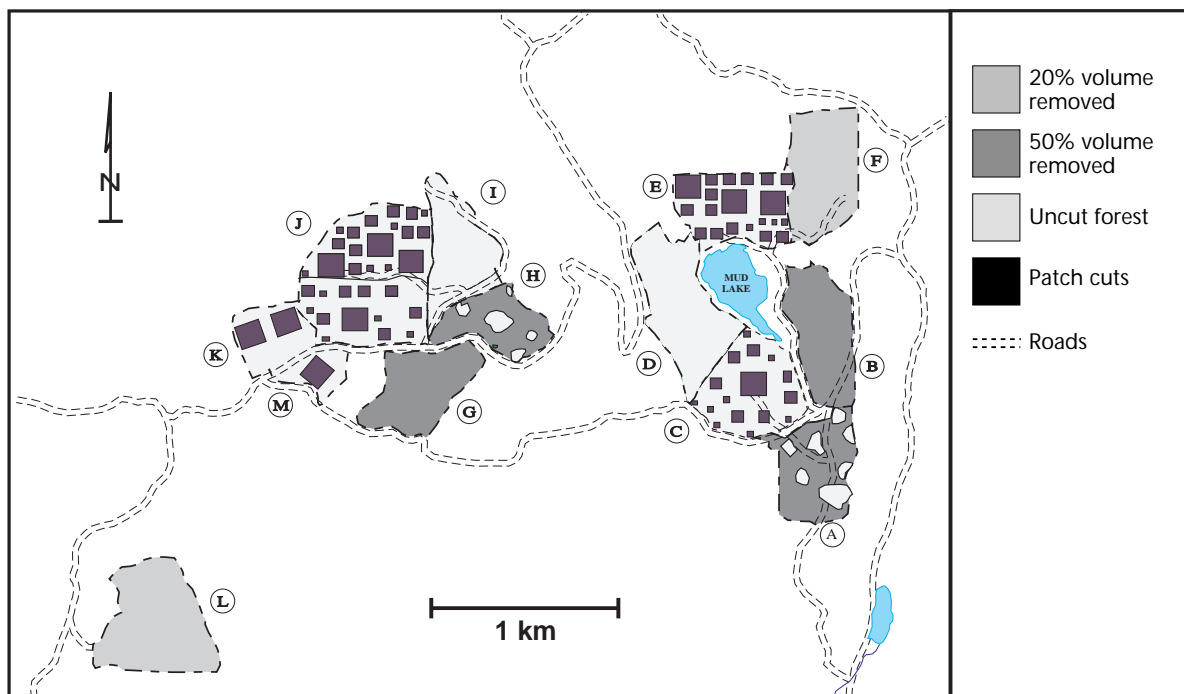


FIGURE 1 Harvesting treatments at the Opax Mountain research site: 20% volume removal using individual-tree selection (units F, L); 35% volume removal; consisting of 75% of the treatment unit area harvested as 50% volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H); 50% volume removal using individual-tree selection (units B, G); patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K); patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); uncut controls (units D, I).

- patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K);
- patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); and
- uncut controls (units D, I).

Each replicate block is 20–25 ha and was harvested in winter 1993–1994. For a more complete description of the Opax Mountain site, see Klenner and Vyse (these proceedings).

Mark-recapture  
Livetrapping

The experimental design of the Opax Mountain trials is a randomized complete block with six treatments and two replicates of each treatment. To monitor sciurid populations, 9-ha trapping grids (300 × 300 m) were established on representative sites within each treatment unit to encompass the conditions created by the experimental harvesting. For example, on the 20% patch-cut removal area, approximately 80% of the trapping grid is in forested habitat, while 20% is in the patch cut. Twelve trapping grids were used to sample population responses to the harvesting treatments. These grids were surveyed into a 30-m grid to facilitate a uniform trap spacing and to record precisely the movements of radiotelemetry-tagged squirrels.

Each trapping grid consisted of a 10 × 10 array of stations, with one Tomahawk live-trap (model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) at alternate stations along each row of the grid, for a total of 50 traps per grid. Traps were baited with a small amount of sunflower seed (approximately 10 g) and a slice of apple. Each trap was fitted with an insulated nest chamber (a 1-L plastic jar with a small entrance hole in one end and filled with coarse brown cotton). Traps were covered with a 50 × 50 cm piece of heavy roofing paper to protect captured animals from wind and rain.

During each trapping session, traps were set for two overnight periods (approximately 1 hour before sunset to 4 hours after sunrise the following morning) on consecutive nights. Overnight trapping is necessary to capture flying squirrels, which are nocturnal, and the early morning trapping captures red squirrels and chipmunks. Captured animals were individually ear-tagged, identified to species, and their weight, sex, and reproductive condition recorded before being released at the point of capture. Each grid has been trapped once every 4 weeks during the snow-free period (April to October) from 1994 to 1996.

Population Density  
and Survival

Livetrapping data were checked for errors and analyzed with the Jolly-Seber model for mark-recapture data (programs from Dr. C.J. Krebs, University of British Columbia, Department of Zoology). These programs calculate estimates of density, trappability, survival, growth, reproductive condition, average body weight, and home range size.

Behaviour and Spatial  
Use of Habitat  
in Relation to Gaps  
and Edges

In 1996, the evaluation of habitat use in relation to gaps and edges focused on tracing the movements of red squirrels in unharvested habitat and in relation to the patch-cut openings at Mud Lake (treatment units D [control] and C [patch cut]). Radio transmitters (Holohil Systems, Carp, Ontario; model PD-2c, approx. 2.6 g) were attached to 12 red squirrels to trace their movements. The relatively low number of recapture events on individual animals from livetrapping alone make home range and movement estimates from trapping data tenuous.

Five hectares in the control area and 10 ha in the patch-cut area were surveyed and marked into a 10-m grid. This allowed me to determine the locations of animals and to assess their use or avoidance of areas within their home range. In September and October, animals were fitted with radio-transmitters for periods of 1–3 weeks, and their movements traced from dawn to 1100 hr and from 1700 hr until dark. With radio-transmitters I was able to find squirrels regardless of their behaviour and location in the study area, thereby providing an unbiased assessment of behaviour and movements in relation to habitat features. Animals were chosen at random from a list and followed for a 30-minute focal period. I recorded spatial use and the amount of time spent at a location during the 30-minute sample, as well as all behaviours observed. At 30-second intervals (marked by a timer), I recorded instantaneous samples of behaviour.

While following transmitter-equipped red squirrels, I collected the following information:

- the location of the animal;
- species, dbh, and decay class of the tree in which the animal was located;
- behaviour (e.g., foraging on the ground, alert, resting, territorial defense); and
- time spent at the sampled location.

Forty different behaviours were identified and classified into five main categories:

1. foraging on the ground,
2. foraging in trees,
3. territorial defense,
4. resting, and
5. general movement.

These behaviour categories were used to characterize activities in the different habitat conditions within the home range in order to differentiate between the animal's home range and territory (the exclusive core area of the home range that is actively defended), and to assess time budgets in relation to habitat features within an animal's home range. These data were entered into a database, error checked, and transferred to an ARCVIEW 3.0 GIS database. I used these data to determine the minimum convex polygon estimate of home range size and the use of habitat within openings (> 5 m from the edge), near edges (5 m into the opening and 5 m into the forest), and in the forest (5–15 m into the forest).

## RESULTS

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In this report, I present the results of an ongoing study on the foraging behaviour of red squirrels and demographic responses of sciurids to the experimental silvicultural treatments at Opax Mountain. In the analyses, I include demographic data for the 1994–1996 period. For brevity and clarity, the analyses and discussion focus on two key aspects of demography—density and survival. An analysis of trappability, reproduction, body weight

changes, the effect of habitat structure on sciurid abundance, the effect of different levels of harvesting on territory size, and activity budgets in relation to habitat features within the territory will be presented in a subsequent report.

Mark-recapture  
Livetrapping

From April 1994 to October 1996, I conducted 19 mark-recapture trapping sessions at the Opax Mountain site. During this period, I captured red squirrels a total of 2621 times, yellow-pine chipmunks 645 times, and northern flying squirrels 645 times during 25 200 trap-nights of sampling effort.

Population Density  
and Survival

Population density and survival estimates were calculated for the three species of sciurids captured at the Opax Mountain site using Jolly-Seber mark-recapture population estimates (Figure 2). The three species of sciurids responded to the silvicultural treatments in a manner consistent with current

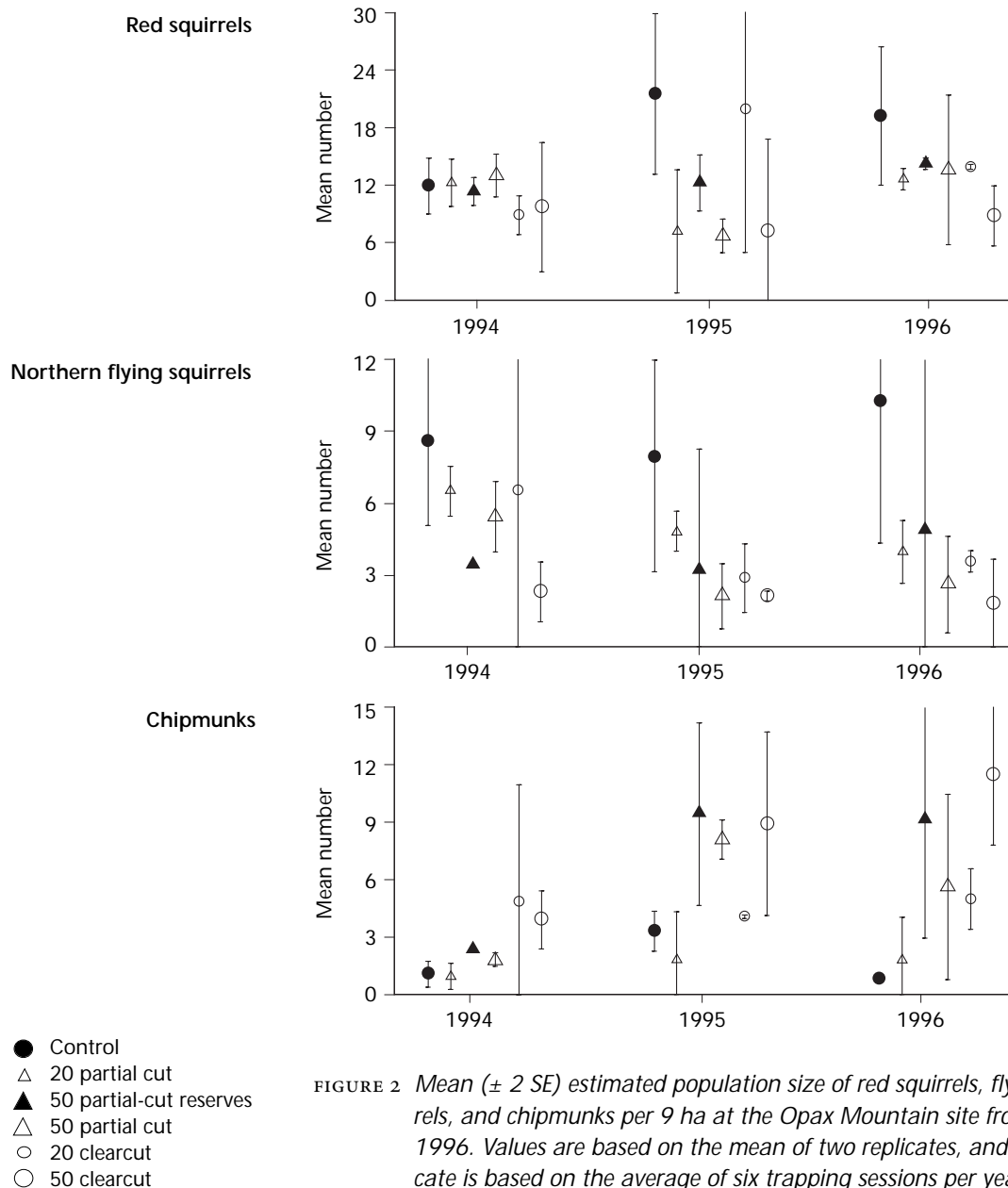


FIGURE 2 Mean ( $\pm 2$  SE) estimated population size of red squirrels, flying squirrels, and chipmunks per 9 ha at the Opax Mountain site from 1994 to 1996. Values are based on the mean of two replicates, and each replicate is based on the average of six trapping sessions per year.

information on their natural history. Red squirrels show a moderate decline in density with increasing amount of timber harvested from the site, with the greatest differences between the control (highest density) and the 50% patch-cut (lowest density). This pattern began to develop in 1995, the second year after harvesting, and was most evident in 1996. The development of this pattern may reflect the food caching ability of red squirrels and hence the presence of residual food on the treatment areas after harvest (Smith 1968), or the site tenacity of some animals. Northern flying squirrels showed a stronger pattern of decline following the experimental treatments, with a decrease to approximately 30% of the control-block densities on the 50% patch-cut areas. This decline was evident when sampling was initiated in 1994 (approximately 4 months after harvest), and was consistent in all 3 years. In contrast, chipmunk densities increased with increasing level of timber removal. This pattern began in 1994 and was most evident in 1996.

To examine more closely the changes in red squirrel, northern flying squirrel, and chipmunk population densities over time in relation to an experimental treatment, population estimates for each trapping session in the control and 50% patch-cut treatments are illustrated in Figures 3–5. The mean of two replicates is indicated, and illustrates both the consistent differences over time between the two treatments, and the variability between replicates in some of the individual 2-day sampling sessions.

To examine the relationship between changes in sciurid population density and the amount of timber removed from the treatment areas, population density estimates were scaled to compensate for the amount of timber removed (Figure 6). For example, population estimates on the 20% timber volume removal areas were multiplied by 1.25, and those on the 50% removal areas by 2.0. These “adjusted” estimates allowed me to examine whether the changes in population density in response to the treatments were greater than what would be expected as a consequence of the removal of timber only. Red squirrel population density decreased in proportion to the amount of timber removed, while the density of northern flying squirrels decreased and that of chipmunks increased at a rate greater than expected from the amount of timber removed.

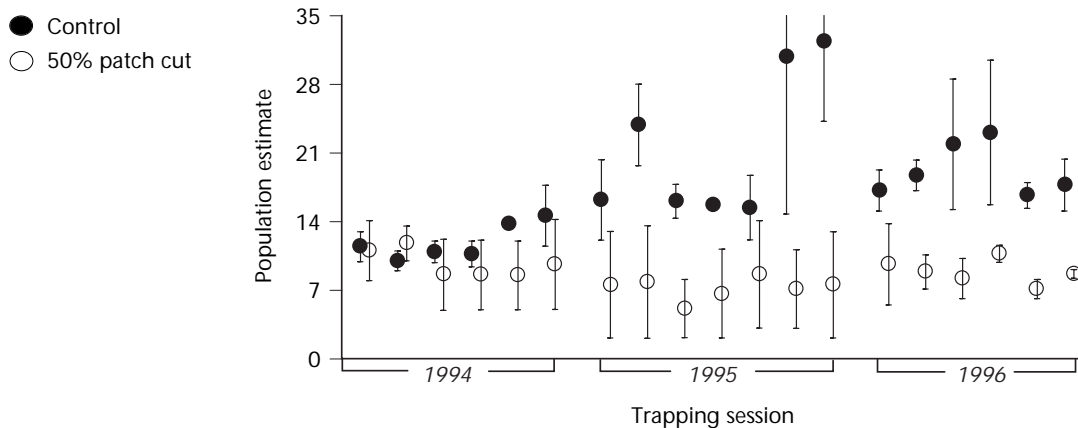


FIGURE 3 Mean ( $\pm 1$  SE) estimates of red squirrel population density per 9 ha for control and 50% patch-cut treatments at the Opax Mountain site. Values are based on the mean of two replicates.



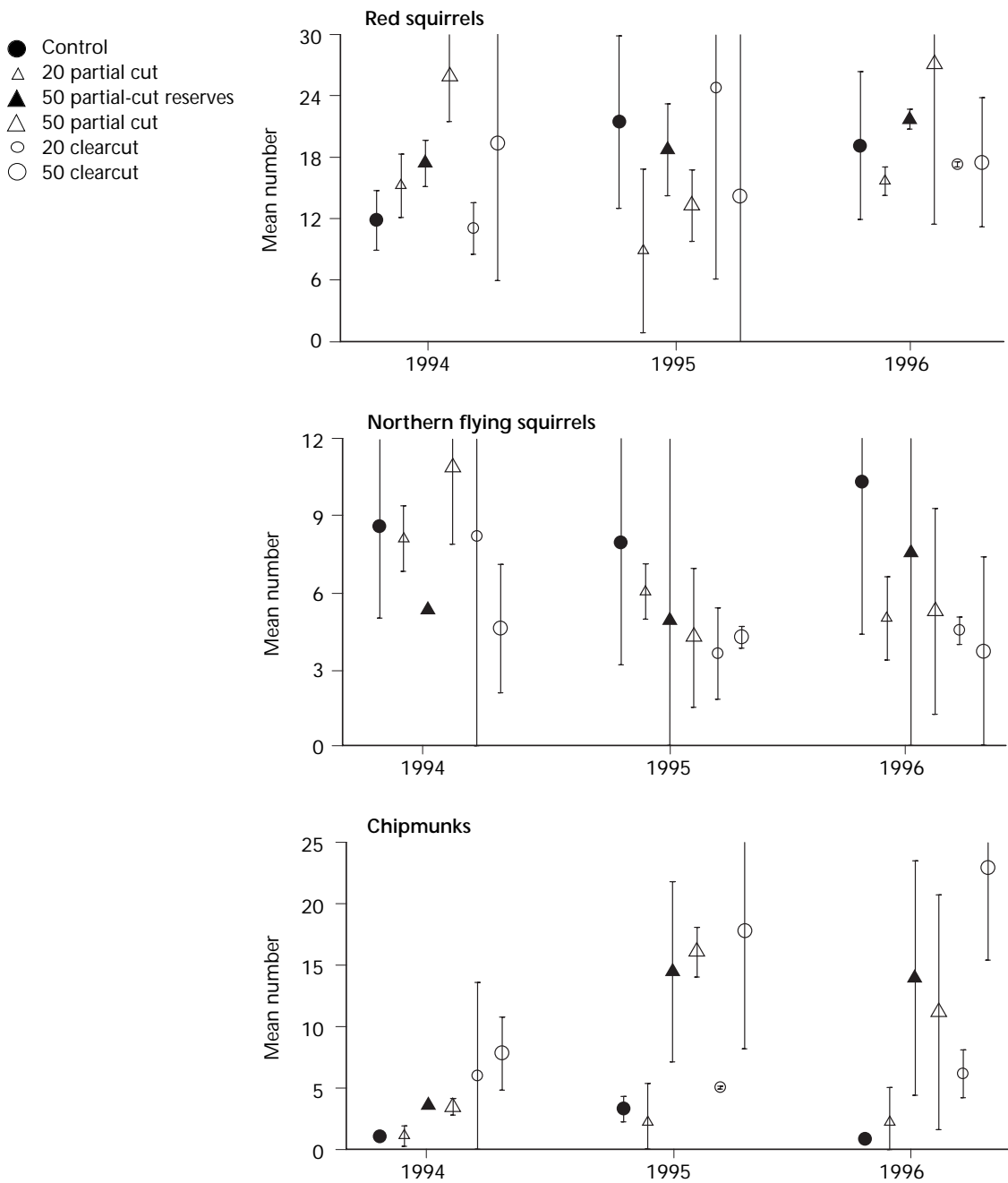


FIGURE 6 Mean ( $\pm 2$  SE) population estimates per 9 ha for red squirrels, flying squirrels, and chipmunks by treatment. Population estimates are adjusted to compensate for the amount of timber removed from each of the treatment areas (e.g., for control = population estimate  $\times 1$ ; for 20% removal = population estimate  $\times 1.25$ ).

I also assessed the survival of red squirrels, northern flying squirrels, and chipmunks in relation to the experimental treatments (Figure 7). Unlike population density, survival estimates for red squirrels and northern flying squirrels show no pattern according to harvesting treatment, which indicates that the survival of the animals remaining in the study area was not affected by habitat conditions in the different treatments. Monthly survival estimates for red squirrels averaged approximately 90% from 1994 to 1996. Survival es-

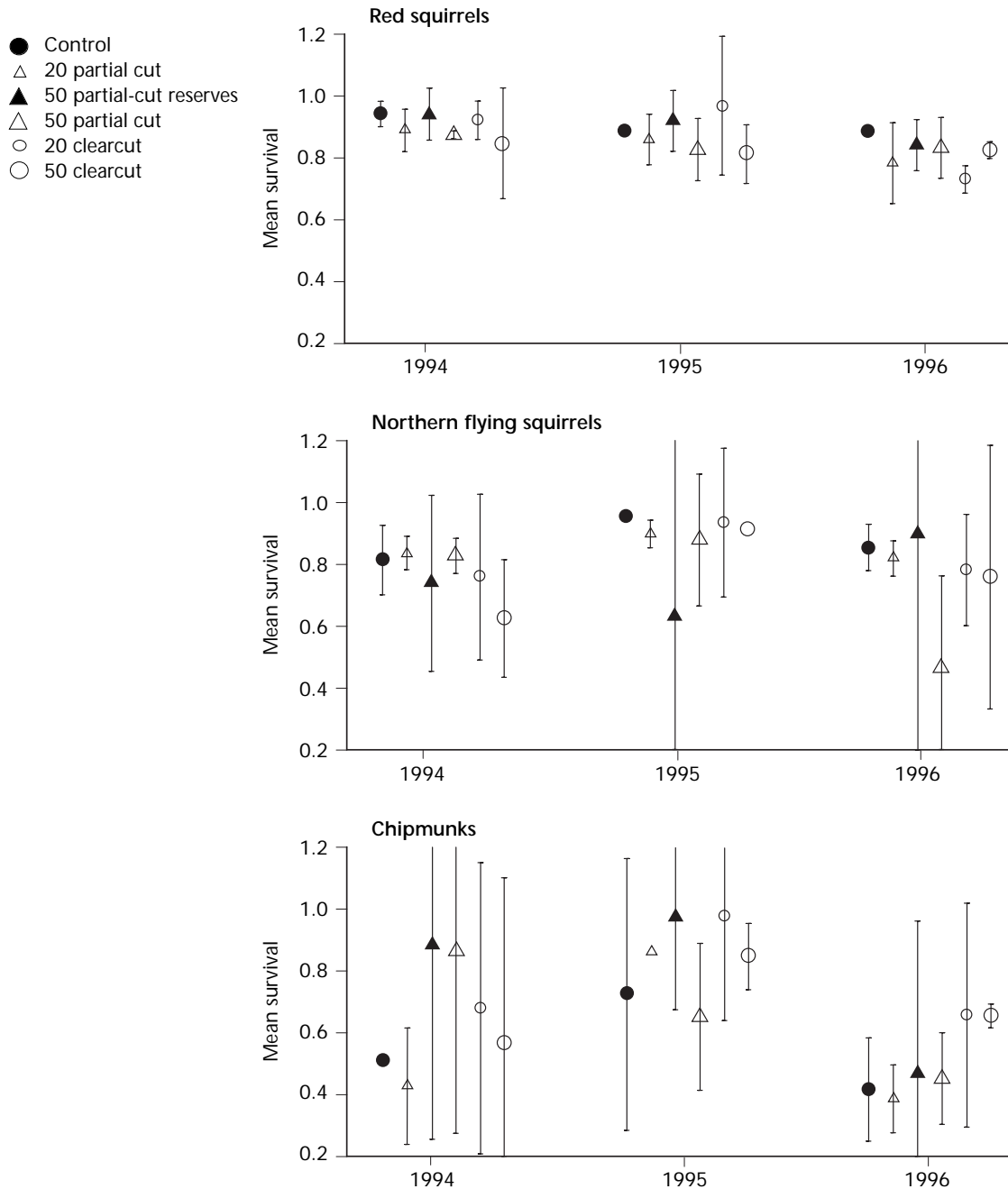


FIGURE 7 Mean ( $\pm$  2 SE) 4-week probability of survival for red squirrels, flying squirrels, and chipmunks by treatment at the Opax Mountain site from 1994 to 1996. Values are based on the mean of two replicates, and each replicate is based on the average of six trapping sessions per year.

timates for northern flying squirrels were slightly lower, averaging about 85%. Chipmunks in the harvested areas may possibly survive better than on the controls. This pattern was not evident in 1994 and 1995, but a higher survival was evident on the 50% patch-cut areas compared to the control in 1996.

During September and October 1996, 12 red squirrels were fitted with radio-transmitters on the 20% patch-cut and control blocks near Mud Lake (blocks C and D). I traced the movements of these animals in the openings, edges, and forested habitats created by the patch cuts, and recorded their behaviour every 30 seconds. Approximately 3600 observations were recorded on 11 of the 12 animals; the other animal lost its radio-transmitter after only 2 days of monitoring.

The home ranges of red squirrels averaged 1.35 ha ( $n = 11$ ,  $SE = 0.31$ ; 5% of outermost locations deleted), and territories averaged 0.59 ha ( $n = 11$ ,  $SE = 0.055$ ). Red squirrels used the periphery of openings both for foraging and travel, and occasionally travelled across openings (Figure 8). However, core territories (where 30% of the outermost locations have been deleted) (Figure 9) seldom included openings and were largely restricted to forested habitat. In the 20% patch-removal treatment where most of this study was conducted, much of the treatment unit remains forested and therefore this type of harvest appears to have only a small effect on behaviour and population size (see Figure 2).

I examined the use or avoidance of habitat in openings, near edges, and in the adjacent forest by red squirrels while they were foraging (Table 1). Within their home ranges, red squirrels avoided the interior of openings greater than 5 m from the forested edge (11.8% of area vs. 2.0% of observations), but did not appear either attracted to or to avoid edges (14.5% of area vs. 13.8% of observations). More use was made of forested habitat 5–15 m into the forest than was available (21.8% of area vs. 30.0% of observations).

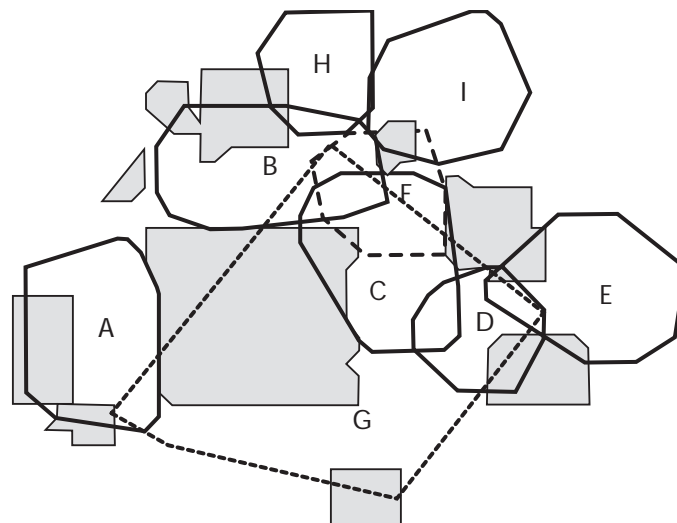


FIGURE 8 Location of red squirrel home ranges, outlined as minimum convex polygons, with 5% of outermost observations deleted. Harvested patches are grey.

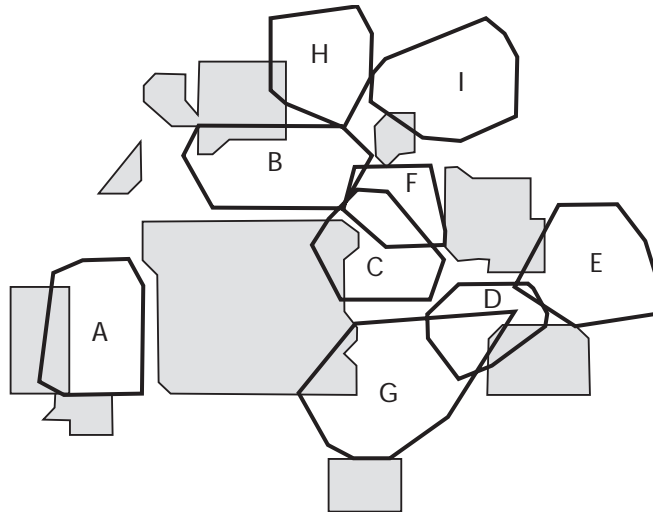


FIGURE 9 Location of red squirrel core territories, outlined as minimum convex polygon, with 30% of outermost observations deleted. Harvested patches are grey.

#### SUMMARY

Red squirrels, northern flying squirrels, and chipmunks at the Opax Mountain study area demonstrated three different responses to the experimental harvesting treatments. The abundance of red squirrels declined moderately (to approximately 50% of the population density of control) across the range of treatments, with the greatest decrease in the 50% patch-cut areas. Northern flying squirrel population size declined strongly (to approximately 25% of the control), and the density of chipmunks increased about sixfold on the 50% patch-cut treatment as compared to the control. When population density was scaled to the amount of timber removed, red squirrel population density decreased in proportion to the amount of timber removed, while that of flying squirrels decreased and chipmunks increased at a greater rate than expected from the amount of timber removed. In the analysis of survival, I was not able to differentiate between losses attributed to emigration and those attributed to mortality, but the similar population survival rates of red squirrels and northern flying squirrels across treatments suggest that the remaining individuals were able to select suitable habitat after harvesting.

TABLE 1 Mean (+ 2 SE) percentage of available area and percentage use by nine red squirrels within their home ranges

Distance from opening	95% points used		70% points used	
	% of area	% of observations	% of area	% of observations
> 5 m in opening	11.8 ± 6.2	2.0 ± 1.6	2.9 ± 1.9	1.7 ± 1.9
On edge	14.5 ± 3.4	13.8 ± 4.4	11.9 ± 3.0	13.0 ± 4.7
5–15 m in forest	21.8 ± 5.6	30.0 ± 7.5	22.0 ± 4.3	28.9 ± 6.8

Telemetry monitoring of red squirrels indicated that animals largely avoided the interior of openings, and appeared to favour forested habitat greater than 5 m from openings. On the patch-cut area, the core areas of territories showed little overlap with the openings, which suggests that leave strips between openings should be sufficiently wide to accommodate squirrel territories.

The different responses by the three sciurid species at Opax Mountain indicate that suitable management of Interior Douglas-fir forests will require the application of a range of treatments across landscapes. Both patch-cut and individual-tree selection partial-cutting harvest systems affected sciurid population density. While red squirrel and chipmunk population density showed either a moderate decline or a strong increase with the amount of timber harvested, the density of northern flying squirrels decreased markedly. To maintain high populations of these small mammals for predators (red squirrels and chipmunks are diurnal, northern flying squirrels are nocturnal), a variety of management treatments should be distributed across the landscape in order to provide the habitats that maintain all species at high population levels.

#### ACKNOWLEDGEMENTS

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#### REFERENCES

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- Buchanan, J.B., R.W. Lindquist, and K.B. Aubry. 1990. Winter populations of Douglas' squirrels in different-aged Douglas-fir forests. *Journal of Wildlife Management* 54:577–81.
- Carey, A.B. 1995. Sciurids in Pacific Northwest: managed and old-growth forests. *Ecological Applications* 5:648–61.
- Carey, A.B., S.P. Horton, and B.L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecology Monographs* 62:223–50.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammal Review* 13:133–48.
- \_\_\_\_\_. 1987. *The natural history of squirrels*. Christopher Helm Ltd., Bromley, Kent, U.K.

- McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in Aspen mixedwood forests in Alberta. J.B. Stelfox (editor). Alberta Environmental Centre and Canadian Forest Service, Edmonton, Alta. pp. 227–40.
- Maser, C. and Z. Maser. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. *Great Basin Naturalist* 48:358–69.
- Maser, C., Z. Maser, J.W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Canadian Journal of Zoology* 64:2086–9.
- Medin, D.E. 1986. Small mammal responses to diameter-cut logging in an Idaho Douglas-fir forest. U.S. Department of Agriculture, Forest Service, Ogden, Utah. Research Note INT-362.
- Patton, D.R., R.L. Wadleigh, and H.G. Hudak. 1985. The effects of timber harvesting on the Kaibab squirrel. *Journal of Wildlife Management* 49:14–9.
- Rosenberg, D.K. and R.G. Anthony. 1992. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. *Journal of Wildlife Management* 57:365–73.
- Rudnicki, T.C. and M.L. Hunter. 1993. Avian nest predation in clearcuts, forests and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358–64.
- Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400–20.
- Smith, C.C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. *Ecological Monographs* 38:31–63.
- Sullivan, T.P., A.S. Harestad, and B.M. Wikeem. 1990. Control of mammal damage. *In* Regenerating British Columbia's forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston (editors). University of British Columbia Press, Vancouver, B.C. pp. 302–18.
- Sullivan, T.P. and R.A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. *Journal of Wildlife Management* 50:595–601.
- Walters, B.B. 1989. Small mammals in a subalpine old-growth forest and clearcuts. *Northwest Science* 65:27–31.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–4.

# Nesting and Foraging Habitat Requirements of Woodpeckers in Relation to Experimental Harvesting Treatments at Opax Mountain

WALT KLENNER AND DAVE HUGGARD

## INTRODUCTION

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Woodpeckers and small, cavity-nesting birds, such as chickadees and nuthatches, are an important and highly visible component of biodiversity in forests. These species play a key role in forest ecosystems, providing nest holes for other cavity-nesting birds, and roosts for a wide range of birds and mammals (e.g., Bull et al. 1986; Backhouse and Lousier 1991). Woodpecker foraging activity may also provide feeding opportunities for several other species (Miller and Nero 1983). These relationships between woodpeckers and many other species have led to the identification of woodpeckers as a “keystone species” (Daily et al. 1993) whose loss would seriously disrupt forest ecosystems. In addition, woodpeckers and the smaller cavity-nesters feed extensively on several forest insect “pests,” and may limit the damage these insects cause (Knight 1958; McCambridge and Knight 1972; Holmes 1990).

Unfortunately, woodpeckers and other cavity-nesting birds are among the wildlife species most likely to decline in managed forests. Woodpeckers rely on several forest attributes that may be reduced in managed forests, such as snags, large deciduous trees, diseased trees, trees with insect infestations, and coarse woody debris. The possibility that woodpeckers will suffer from intensive forest management is supported by experience in other areas with a longer history of forest use than British Columbia. Swedish forestry is known for its intensive silviculture and high level of timber production, but one woodpecker species is almost extinct in the country (Aulen 1988) and several are declining seriously (Angelstam and Mikusinski 1994). The same situation is reported in Finland (Tiainen 1985). In both countries, the decline of these birds is attributed to the loss of old-forest characteristics such as snags and reductions in deciduous trees caused by intensive forest management. Sweden has increasingly attempted to restore some habitat features necessary for the conservation of woodpeckers (Aulen 1991). In the southeastern United States, extensive logging of older forests has caused the extinction of one species (ivory-billed woodpecker) and has endangered another (red-cockaded woodpecker) (Walters 1991), leading to expensive restoration projects. In the Pacific Northwest, special management areas are being established for pileated woodpeckers, which are considered vulnerable in intensively managed landscapes (Bull and Holthausen 1993). Managing forests to maintain cavity-nesters, based on a sound knowledge of their ecology, will hopefully prevent these situations from occurring in British Columbia’s forests.

The trees characteristically used by woodpeckers for nesting have been described in many studies (e.g., over 300 references in Fischer and McClelland 1983), but great variability exists among the different study areas, which suggests that local studies are needed to guide management in the Kamloops Forest Region (Kiesker 1987). More importantly, several studies suggest that nest sites are not limiting for cavity-nesters, and that foraging habitat is critical (Goggans et al. 1988; Walankiewicz 1991; Welsh and Capen 1992). Management guidelines based solely on providing nesting habitat will likely fail to provide adequate foraging habitat to sustain cavity-nester populations. However, the habitat used by cavity-nesters for foraging is only poorly documented, or not documented at all for some species. Because of this, we do not know how forestry affects foraging habitat. Additionally, the effects of landscape-level changes on these birds (e.g., creation of edge and thin leave strips, the interspersed of harvested and old forest) are unknown. Finally, the winter ecology of cavity-nesters has not been studied in this region, even though winter is a critical time for cavity-nesters in other areas (e.g., Scandinavia) (Nilsson 1987).

The current study provides information on the nesting and foraging habitat of woodpeckers and other cavity-nesters at the Opax Mountain Silvicultural Systems site, and investigates the effects of landscape changes (e.g., the influence of edges around patch cuts) in both summer and winter. This information will be used to develop guidelines for the maintenance of the habitat structures and patterns that provide important nesting and foraging habitat for cavity-nesting birds in managed Interior Douglas-fir zone forests.

## STUDY AREA AND METHODS

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The Opax Mountain Silvicultural Systems Project consists of two replicates of each of the following treatments in a randomized block design (Figure 1):

- 20% merchantable volume removal using individual-tree selection (units F, L in Figure 1);
- 50% merchantable volume removal using individual-tree selection (units B, G);
- 35% merchantable volume removal, consisting of 75% of the treatment unit area harvested as 50% merchantable volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H);
- patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K);
- patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); and
- uncut controls (units D, I).

Each replicate block is 20–25 ha and was harvested in winter 1993–1994. For a more complete description of the Opax Mountain site, see Klenner and Vyse (these proceedings).

Study methods were designed to provide information about four areas of woodpecker and small cavity-nester ecology that are relevant to forest management:

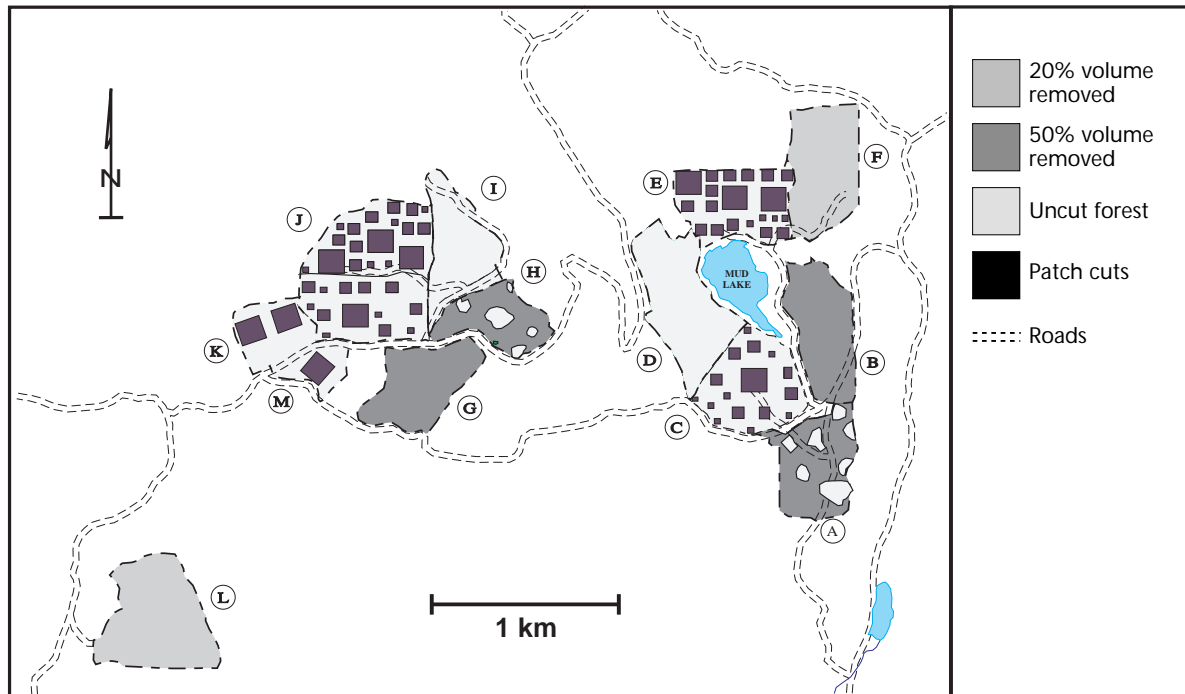


FIGURE 1 Harvesting treatments at the Opax Mountain research site: 20% volume removal using individual-tree selection (units F, L); 35% volume removal; consisting of 75% of the treatment unit area harvested as 50% volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H); 50% volume removal using individual-tree selection (units B, G); patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K); patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); uncut controls (units D, I).

1. relative densities in the different silvicultural systems treatments;
2. habitat and landscape characteristics of foraging sites, and comparison to sites available at several spatial scales;
3. habitat and landscape features of nest sites; and
4. size of territories or home ranges of breeding woodpeckers in summer and of overwintering adults.

#### Relative Density in Silvicultural Systems Treatments

We established transects across the study site at 100-m intervals. Observers walked the transects in the morning at a slow speed (100 m in 10 minutes), recording the time and distance along the transect when they entered and left the study blocks. For any woodpeckers seen or heard along the transect, the observers recorded the time, how the bird was detected, and the distance at detection. The bird was then located, its species and sex recorded, and foraging observations made whenever possible (see below under “Foraging Habitat”). At the end of the transect, the time and distance spent surveying each block was calculated. Each transect was surveyed at least three times per season, including early and later in the morning. We also walked the transects systematically in the breeding season to find nests.

#### Foraging Habitat

For every bird found during the systematic transect surveys or encountered during general searches for woodpeckers, we attempted to observe foraging activities as the bird used a series of consecutive foraging trees. For each tree

in which we observed the bird foraging, we recorded the following information.

- Location of the tree, including which study block it was in and how far it was from edges, both natural (e.g., marshes) and managed (e.g., cutblocks or roads).
- Behaviour: the bird's behaviour was recorded as: pecking/drilling, probing, flaking bark, gleaning, excavating, hawking, drumming, rest/alert, preening, or feeding young.
- Tree characteristics: tree species, diameter at breast height (dbh), height, decay class (following Thomas [1979]), and noting if the top is broken), and evidence of insects or disease.
- Bird position in the tree: whether the bird was in the bottom, middle, or top third of the tree; foraging substrate (bark, bare wood, foliage, or lichen); foraging location (bole or branch).
- Duration of foraging in the tree.

For birds foraging on coarse woody debris, we recorded the location, behaviour, and duration as above and the following characteristics of the log: species, decay class (following Thomas 1979), and diameter where the bird was foraging. Foraging trees were marked with chalk or numbered cards to enable us to return to the site to assess local habitat characteristics with a 5.6 m radius (0.01 ha) plot. When the bird left a tree or log, we recorded the distance to the next foraging site. The series of foraging observations continued until the bird disappeared from view or we had followed for a period of over 1 hour.

**Plots around Foraging Trees and Coarse Woody Debris** After a foraging series ended, we returned to each tree and surveyed a 5.6 m radius plot centred on the foraging tree, and recorded the following information.

- For trees over 7.5 cm dbh, the species, dbh, height, decay class, evidence of insects or disease, and feeding sign or nest holes.
- Canopy cover (estimated).
- Slope, direction of slope, and a brief description of topography.

For birds foraging on coarse woody debris, we estimated coarse woody debris volumes around the log using a triangular intercept transect, with 5-m sides, centred on the foraging site (Van Wagner 1968). For each log that was over 7.5 cm diameter where intercepted by the transect, we recorded the species, decay class, and diameter of the log.

**Random Plots** To determine if woodpeckers and small cavity-nesters were selecting certain types of trees for foraging or nesting, or for certain local habitat characteristics (within a 5.6 m radius of the foraging tree), we evaluated the characteristics of the trees and local area around the trees that birds used (from observations, see "Foraging Habitat"), as well as what was available to the birds. The availability of trees and the characteristics of the local area around these trees was measured using three types of random plots.

1. Plots centred on random trees throughout the study site: The first approximation random plot centres were distributed at 150-m intervals along the transects that were used to census birds. A random angle was then chosen

and the  $n$ th tree in that direction (a random number between 1 and 10) was selected as the plot centre by counting trees within a 10 m wide strip. This procedure helps to avoid possible bias in the selection of plot centre trees (C. Krebs, University of British Columbia, Zoology Department, pers. comm.).

2. Plots centred on random trees within 100 m of a foraging tree: These were selected by choosing a random distance between 10 and 100 m, and a random direction from a random numbers table. To avoid bias in selecting trees that are in more open areas (C. Krebs, University of British Columbia, Zoology Department, pers. comm.), we continued on in the chosen direction to the  $n$ th tree (chosen as a random number between 1 and 10), counting trees in a 10 m wide strip.
3. Plots centred on trees within 100 m of a foraging tree that have similar characteristics to the foraging tree: These are referred to as “matched tree” (e.g., for species, decay class, and size) random foraging plots. Plot centre trees were selected by a process similar to that described above (see 2) except that only trees similar to the foraging tree (with respect to species, dbh, decay class) were counted to arrive at the  $n$ th tree. The same habitat characteristics were measured in the random and foraging habitat plots.

These random plots allowed us to compare the habitat and landscape characteristics of the trees and plots on which the birds were foraging compared to those available in the area in which they were foraging, as well as across the overall study area.

#### Habitat and Landscape Characteristics of Nest Sites

Nests of cavity-nesting birds were found by walking the transect in the study areas during the breeding season, or while following birds at this time of year. The characteristics of the nest tree and the surrounding 5.6 m radius plot were recorded, as described for foraging trees above. The height of the nest and tree diameter at the nest were also recorded. These characteristics were compared to those of random plots, using the same approach as described for foraging plots.

Dates of excavating, incubating, hatching, and fledging were recorded as accurately as possible for each nest. Observations in the nest hole were generally not possible, since the height of most nests and generally unsafe condition of trees precluded climbing to investigate nest chambers. When young were fed at the nest, we recorded the time between feeding visits by the adults during several 2-hour observation sessions.

#### Radiotelemetry Studies

We attached radio-transmitters (Holohil Systems, Carp, Ontario, model BD-2G) to ten hairy woodpeckers and one three-toed woodpecker, and traced the movement patterns of these birds during the May and June breeding season. Radio-transmitters were used primarily to locate birds and then to observe foraging behaviour (more effectively and with less bias than through visual or acoustic searching alone), and to assess home range area. We attempted to locate birds fitted with radio-transmitters each day, and then to observe foraging behaviour for a 1-hour period.

In this report, we present and discuss results on foraging and nesting habitat use, and preliminary information on the spatial use of habitats within the study site during the 1994–1996 period. We do not present results on the relative density of woodpeckers in the experimental treatment blocks, or on the spatial characteristics of woodpecker foraging and nesting in relation to the openings and leaf strips in the treatment units. This work will be presented in a subsequent report. The analysis will focus on woodpeckers, and does not address the foraging and nesting ecology of small cavity-nesting species, such as chickadees and nuthatches.

#### Foraging Habitat

We observed hairy (*Picoides villosus*), three-toed (*P. tridactylus*), black-backed (*P. arcticus*), pileated (*Dryocopus pileatus*), and downy (*P. pubescens*) woodpeckers at the Opax Mountain site, along with red-naped sapsuckers (*Sphyrapicus nuchalis*), Williamson's sapsuckers (*S. thyroideus*), and common flickers (*Colaptes auratus*). Because of their abundance and year-long residency, most of the emphasis in data collection and analysis was placed on hairy and pileated woodpeckers. From 1994 to 1996, we recorded 1976 observations on hairy, three-toed, black-backed, pileated, and downy woodpeckers. Of these, 906 observations were of foraging behaviour. We assessed a total of 282 woodpecker foraging plots in summer and 598 in winter (Figure 2), and compared these to 640 random habitat plots and 579 matched-tree habitat plots (Figure 3).

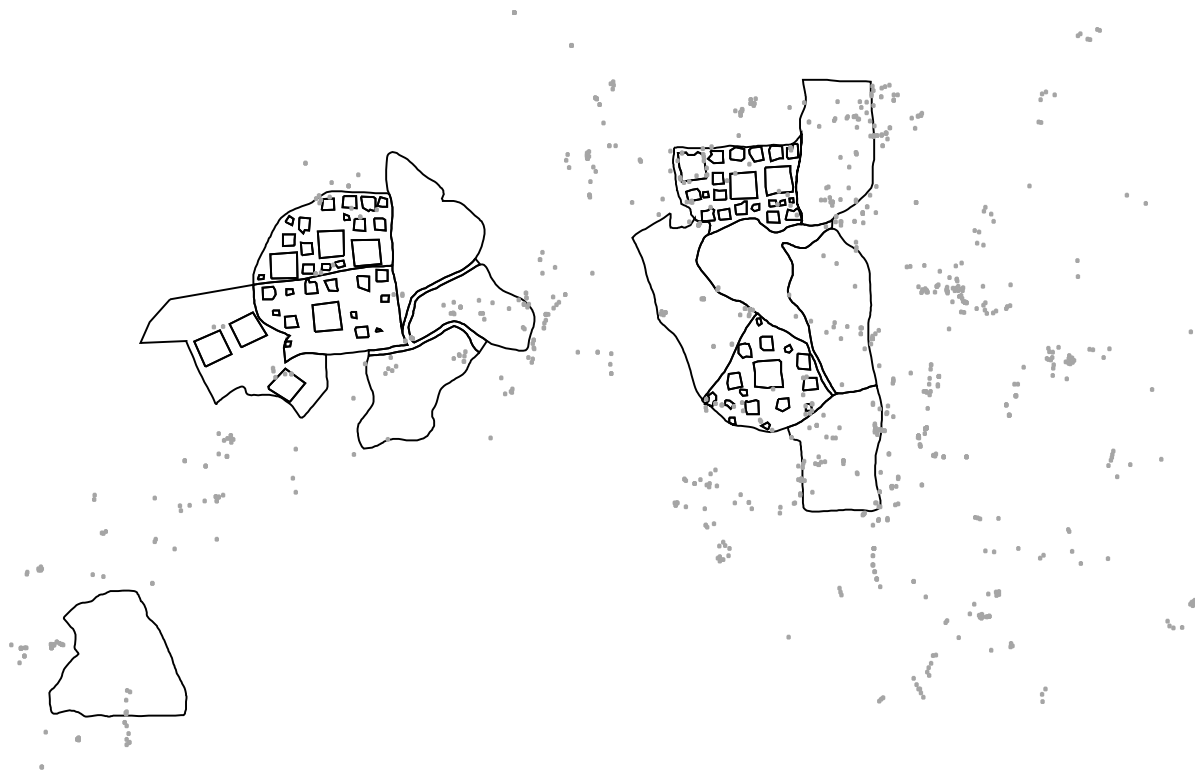


FIGURE 2 Locations of woodpecker foraging observations and the associated 5.6 m radius habitat plots at the Opax Mountain study site from 1994 to 1996.

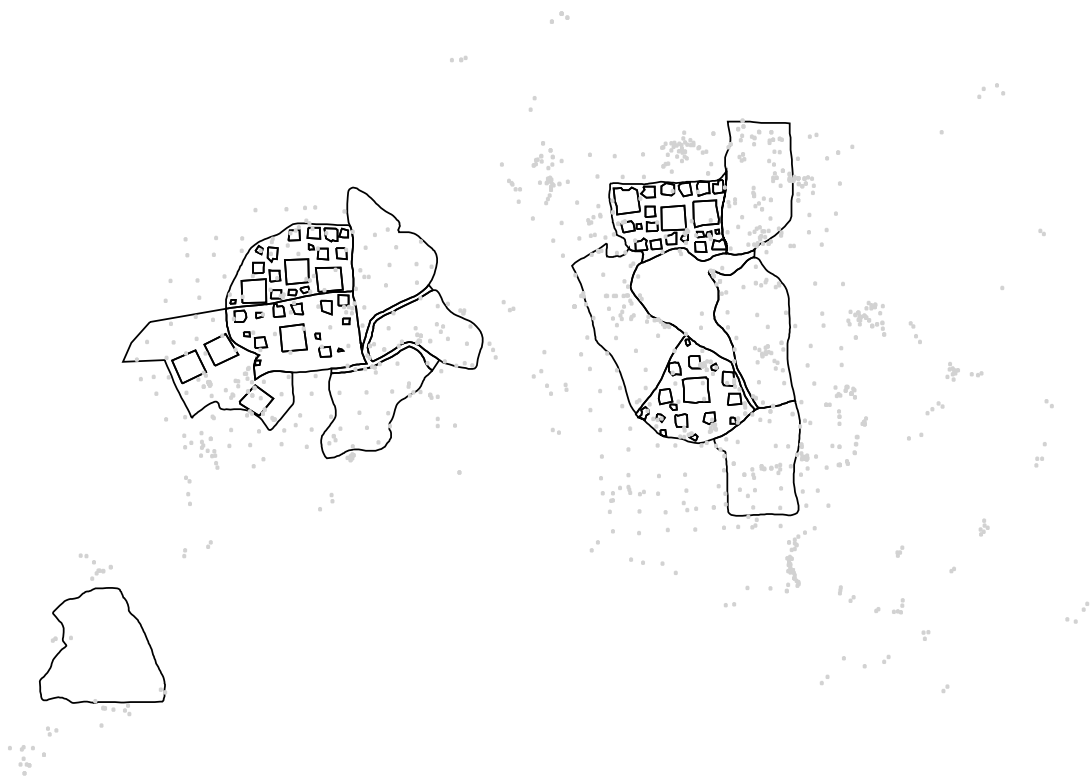


FIGURE 3 Locations of random 5.6 m radius vegetation plots at the Opax Mountain site.

TABLE 1 Percentage distribution of foraging trees used by all woodpecker species by dbh and tree decay class at the Opax Mountain research site, based on 906 foraging observations

Tree species	dbh class	Tree decay class <sup>1</sup>					
		1	2	3	4	5	6+
Douglas-fir	< 10 cm	1	1	2	1	0	0
	10–20 cm	6	2	15	1	0	0
	20–30 cm	8	3	7	2	0	1
	30–50 cm	16	3	9	3	0	1
	> 50 cm	8	1	3	1	0	2
Aspen	< 10 cm	7	1	1	0	0	0
	10–20 cm	34	6	2	2	1	1
	20–30 cm	19	7	2	1	0	0
	30–50 cm	10	1	1	0	0	0
	> 50 cm	4	1	0	0	0	0
Lodgepole pine	< 10 cm	0	0	2	0	0	0
	10–20 cm	24	7	21	0	0	2
	20–30 cm	24	5	5	2	0	0
	30–50 cm	5	2	0	0	0	0
	> 50 cm	0	0	0	0	0	0
Spruce	< 10 cm	0	0	1	3	0	0
	10–20 cm	1	1	23	7	0	1
	20–30 cm	7	5	16	3	0	1
	30–50 cm	11	3	14	1	0	1
	> 50 cm	0	0	0	0	0	0

<sup>1</sup> Tree decay classes follow description in Thomas (1979). 1. Live, 2. Declining, 3. Dead with firm bark, 4. Dead with loose bark, 5. Dead, no bark, 6.+ Dead, no bark and broken.

TABLE 2 Percentage distribution of random trees by dbh and tree decay class at the Opax Mountain research site, based on 640 randomly located trees

Tree species	dbh class	Tree decay class <sup>1</sup>					
		1	2	3	4	5	6+
Douglas-fir	< 10 cm	4	2	2	0	0	1
	10–20 cm	33	8	4	1	0	1
	20–30 cm	17	1	2	0	0	1
	30–50 cm	13	1	2	0	0	1
	> 50 cm	3	0	0	1	0	1
Aspen	< 10 cm	11	0	0	0	0	0
	10–20 cm	23	9	3	3	3	1
	20–30 cm	21	6	3	1	0	0
	30–50 cm	10	1	0	1	0	1
	> 50 cm	0	0	0	0	0	0
Lodgepole pine	< 10 cm	3	2	0	0	0	0
	10–20 cm	48	7	7	0	0	0
	20–30 cm	22	2	0	0	0	0
	30–50 cm	9	0	0	0	0	0
	> 50 cm	0	0	0	0	0	0
Spruce	< 10 cm	8	2	2	2	0	0
	10–20 cm	34	8	11	0	0	0
	20–30 cm	26	0	0	0	0	0
	30–50 cm	8	0	0	0	0	0
	> 50 cm	0	0	0	0	0	0

<sup>1</sup> See tree decay class description in Table 1.

We observed woodpeckers foraging on all species of trees found in the Opax Mountain study area (Table 1). When compared to the species and decay class of trees available (Table 2), woodpeckers clearly used decay class 3 trees more than would be expected from their availability. To determine whether woodpeckers were selecting foraging trees with certain characteristics, we used Ivlev's selectivity index (Krebs 1989). For these analyses, we only used data for hairy and pileated woodpeckers, since other species were either not common enough or were not sampled intensively. Selectivity was analyzed at the within-plot (i.e., determining whether the foraging tree is different from the rest of the trees in the 5.6 m radius plot) and overall scales for tree characteristics, and overall for plot characteristics. Selectivity for tree characteristics (species, dbh, and decay) was almost identical between males and females for both hairy and pileated woodpeckers, so the results were pooled by sex. Selectivity at the within-plot and overall scale was very similar because the composition of the foraging plots did not differ much from random plots and the forest composition was fairly uniform across the site. Only within-plot selectivity data are presented here.

In both winter and summer, and across years, hairy woodpeckers generally selected larger stems, usually trees greater than 30 cm dbh (Figure 4). They also usually avoided stems smaller than 30 cm dbh, except in the winter of 1993–1994 when small-diameter stems were selected. Such annual differences may reflect the sporadic occurrence of insect infestations in specific types of trees. Hairy woodpeckers also preferred trees in decay class 3 (recently dead)

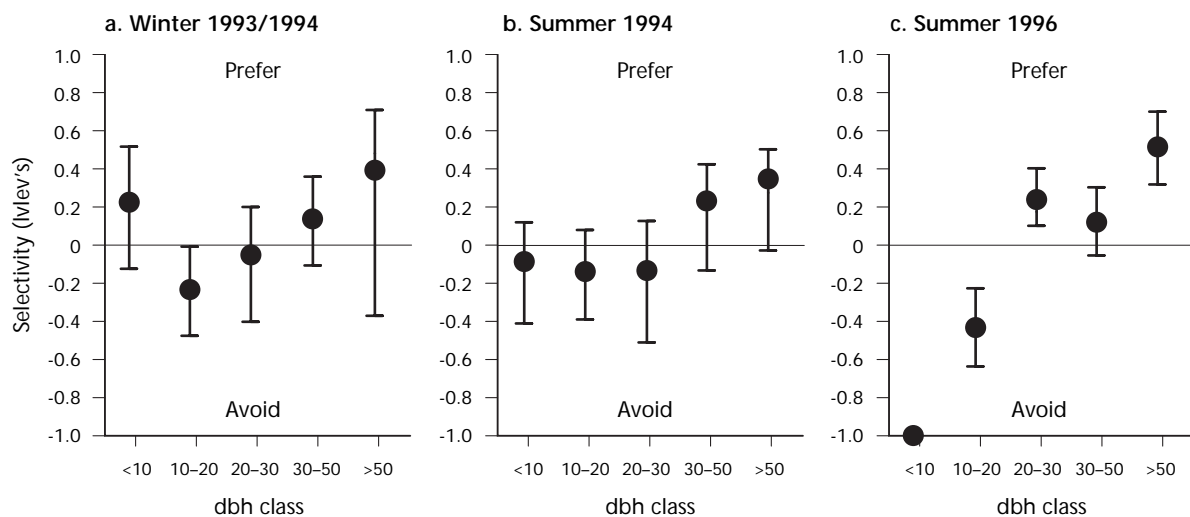


FIGURE 4 Within-plot foraging selectivity (with 95% CI) by hairy woodpeckers (both sexes) by tree diameter class at the Opax Mountain research site.

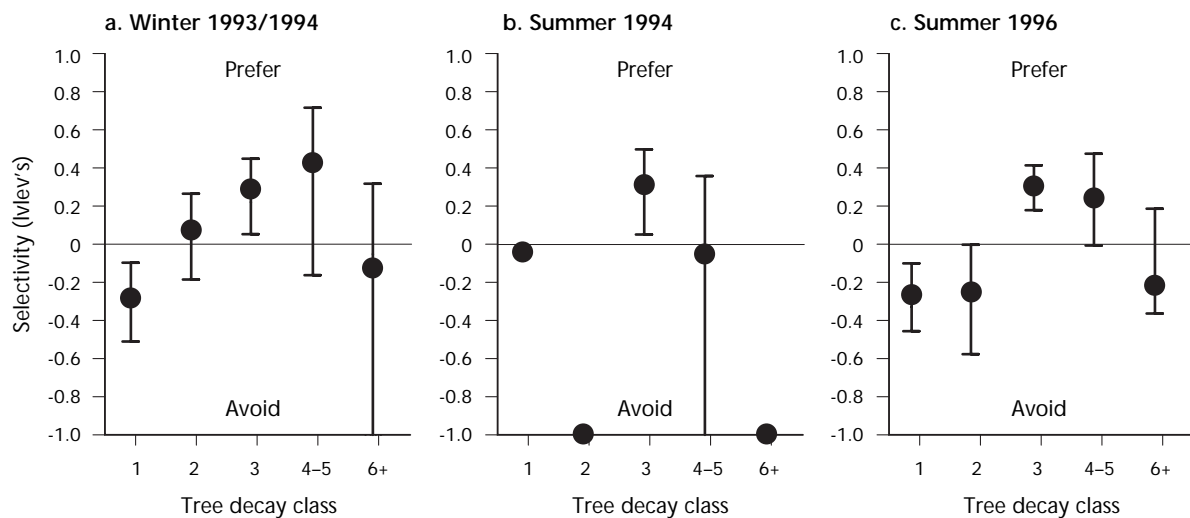


FIGURE 5 Within-plot foraging selectivity (with 95% CI) by hairy woodpeckers (both sexes) by tree decay class (see Table 1) at the Opax Mountain research site.

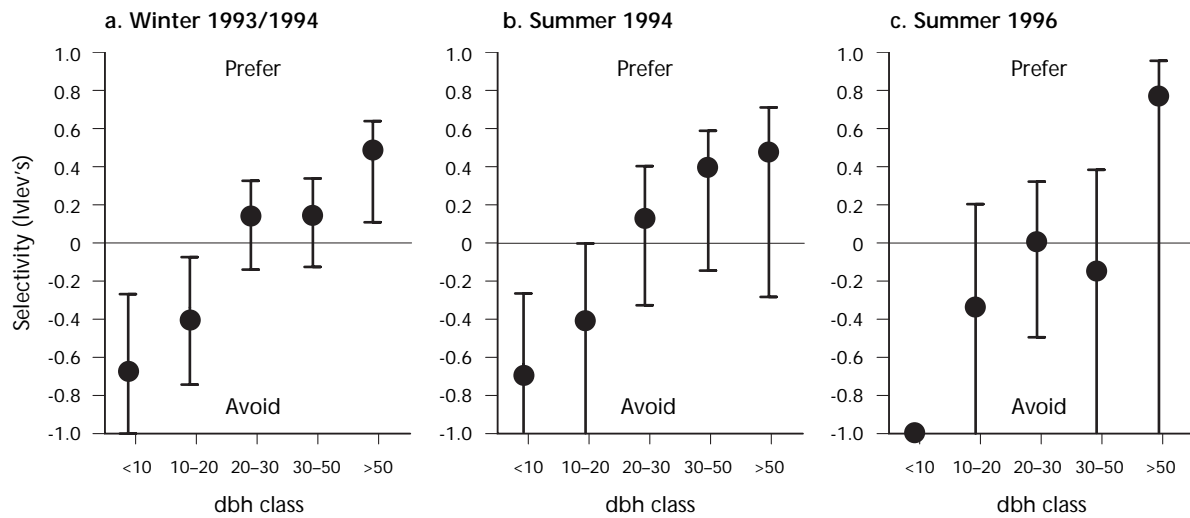


FIGURE 6 Within-plot foraging selectivity (with 95% CI) by pileated woodpeckers (both sexes) by tree diameter class at the Opax Mountain research site.

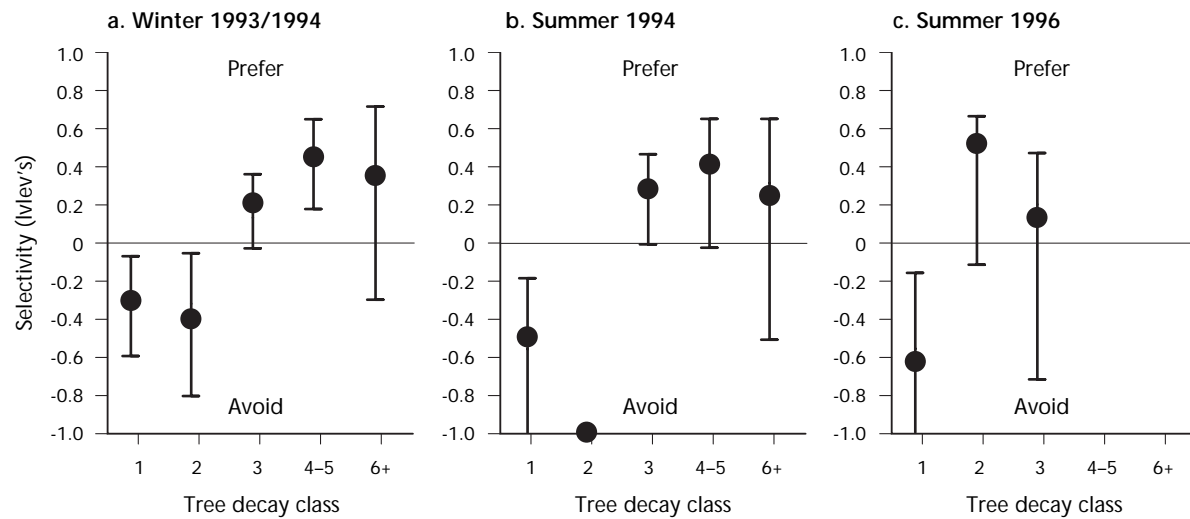


FIGURE 7 Within-plot foraging selectivity (with 95% CI) by pileated woodpeckers (both sexes) by tree decay class (see Table 1) at the Opax Mountain research site.

TABLE 3 Tree diameter at breast height (dbh) and tree decay characteristics of the number of Douglas-fir and aspen trees used for nesting by all species at the Opax Mountain research site (note: of the other active nests found, four were in birch and one was in spruce)

Tree species	dbh class	Tree decay class <sup>1</sup>					
		1	2	3	4	5	6+
Douglas-fir	< 10 cm	0	0	0	0	0	0
	10–20 cm	0	0	6	0	0	0
	20–30 cm	0	0	2	0	0	0
	30–50 cm	2	1	3	1	2	0
	> 50 cm	0	0	2	0	0	0
Aspen	< 10 cm	0	0	0	0	0	0
	10–20 cm	5	2	1	0	0	0
	20–30 cm	12	3	2	2	0	1
	30–50 cm	13	6	3	0	0	0
	> 50 cm	1	0	2	0	0	0

<sup>1</sup> See tree decay class description in Table 1.

and 4–5 (somewhat decayed). They avoided green trees and well-decayed stems in decay class 6 or greater (Figure 5).

Pileated woodpeckers followed much the same pattern as hairy woodpeckers in their selection of larger, recently dead trees, but they also selected well-decayed snags (Figures 6 and 7). Selection for larger, recently dead trees was consistent between seasons, even though hairy woodpeckers often foraged by gleaning foliage insects in the summer, and pileated woodpeckers spent considerable time foraging on downed wood.

#### Habitat Characteristics of Nest Sites

From 1994 to 1996, we located 79 active nests (Table 3). Most of these nests (67%) were in aspen (*Populus tremuloides*), even though aspen represents less than 10% of the trees in the study area. Aspen without any signs of decay were used most often, in contrast to the nests found in Douglas-fir, which were usually in recently dead trees. In the Opax Mountain study area, many of the aspen larger than 30 cm have centre rot, and this feature likely facilitates nest and roost site excavation. Woodpeckers did not appear to select specific habitat features other than tree type for their nests, except for the repeated use of marsh or lake edges (Figure 8).

#### Radiotelemetry Studies

Eleven woodpeckers (10 hairy, one three-toed) were fitted with radio-transmitters in 1996 and located a total of 1149 times. Of the 11 birds fitted with radios, eight hairy woodpeckers were located over a sufficiently long period of time (i.e., greater than 3 weeks) and often enough (more than 100 observations per bird) to have confidence in the home range estimate. These data indicate that hairy woodpeckers had very large home ranges during the summer breeding season in 1996, with an average size of 203.3 ha (1 SE = 61.5 ha; range = 74.6–300.7 ha) (Figure 9). Observations of the wide-ranging movements of colour-banded birds, and brief periods of radiotelemetry monitoring in 1994 and 1995, support the large home range estimates recorded in 1996.

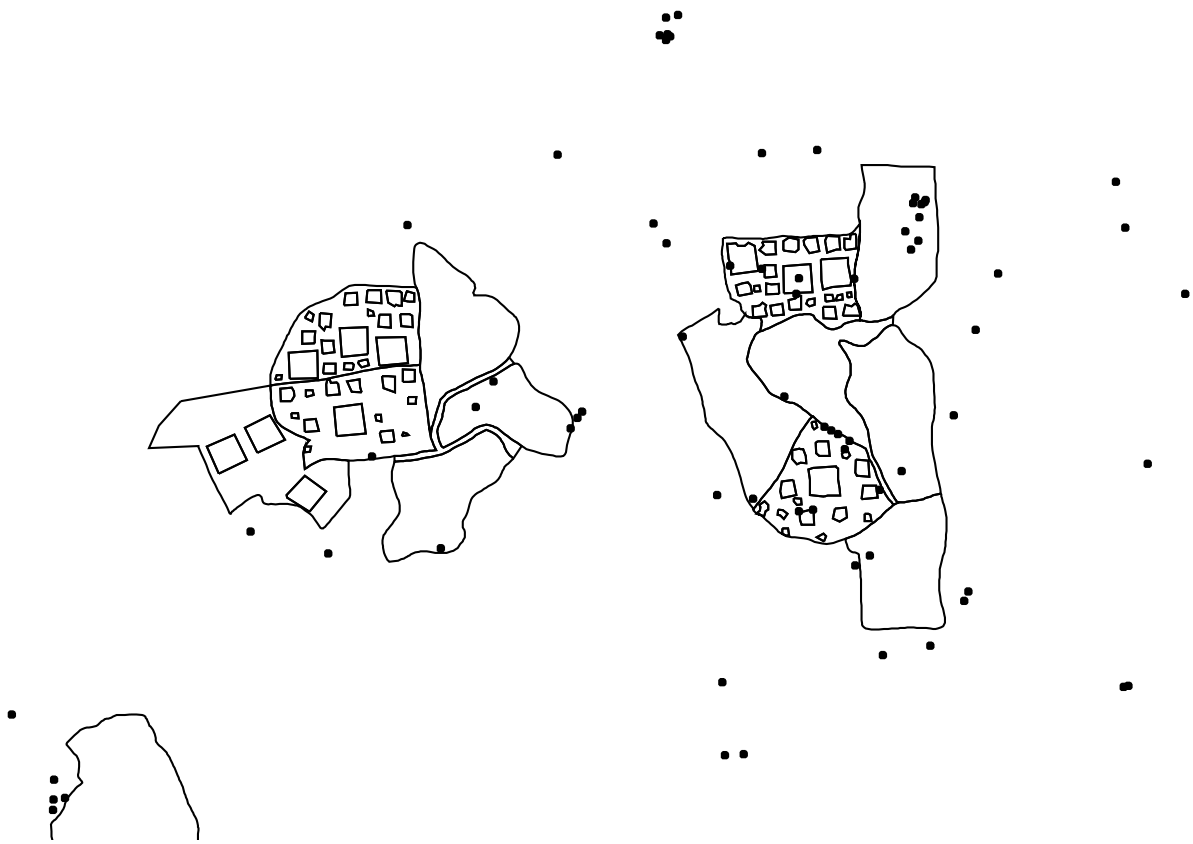


FIGURE 8 Location of woodpecker nests at the Opax Mountain site from 1994 to 1996.

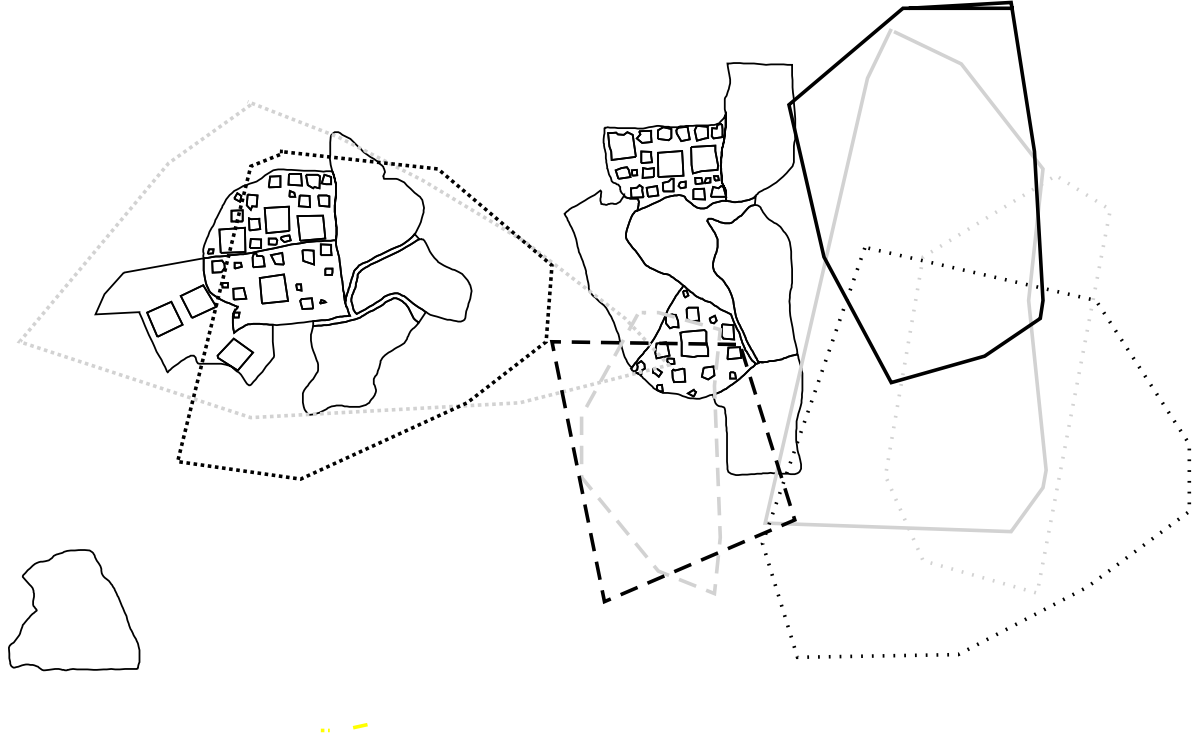


FIGURE 9 Home ranges of four pairs of radio-tagged hairy woodpeckers at the Opax Mountain site. Pairs have common line patterns, and female home ranges are represented by darker lines.

Both hairy and pileated woodpeckers preferred large trees (i.e., greater than 30 cm dbh) and trees that had recently died. The limited number of observations on black-backed and downy woodpeckers suggests a similar need for dead or declining trees, although downy woodpeckers often feed on smaller-diameter trees or at the tips of branches. Sapsuckers, and to a lesser extent common flickers, are migratory in the Interior of British Columbia. In summer, these species forage on insects in living trees, or on the ground (common flicker) and depend less on dead and declining trees than do the other species of woodpeckers. As a consequence, sapsuckers and common flickers are less likely to be adversely affected by forest management practices that promote vigorously growing trees.

From the large home ranges described above, the woodpeckers being monitored at the Opax Mountain site do not appear limited by the availability of nesting habitat. Within their home ranges, each pair of hairy woodpeckers likely had more than a thousand snags, and an equal number of aspen trees, that could be used as potential nest sites. Why such large home ranges are used is not clear. However, only a small percentage of the snags within a bird's home range likely become suitable foraging habitat in any one season. Maintaining hairy and pileated woodpeckers in managed forests will be a challenge to forest managers. These species require management prescriptions that maintain snags or patches of large trees and snags over large areas on an ongoing basis.

Conventional forest management in Interior Douglas-fir forests on an extensive basis can severely diminish the number of large, recently dead snags, and this will have an influence over time on foraging habitat and, to a lesser extent, on nesting habitat. Several management activities that affect the habitat structures used for foraging include:

- the removal of snags for safety reasons during periodic, partial cutting harvest entries;
- the removal of insect-killed trees during salvage operations;
- firewood cutting;
- replacing Douglas-fir and ponderosa pine with lodgepole pine during planting; and
- stand-tending activities that remove deciduous trees such as aspen and promote a uniform cover of evenly spaced conifers, thereby reducing ongoing, suppression-related mortality of trees in dense thickets.

Most of the above issues can be addressed by planning for a range of management practices at the landscape level, and access management to limit the area accessible to firewood cutters. Traditional individual-tree selection partial-cutting systems make it difficult to maintain a long-term supply of large-diameter living, dying, and dead trees. Where large areas (e.g., 50+ ha) are managed as individual-tree selection partial-cutting systems, retaining patches of mature timber within the harvested area (i.e., similar to treatment units A and H) will help provide a long-term supply of foraging and nesting habitat. The loss of important foraging habitat structures over time is not restricted to individual-tree selection partial-cutting systems. A similar constraint will develop in patch-cutting systems after the second or third entry. Therefore, a system of deferred leave areas of mature timber should

probably be incorporated into the patch-cutting rotation to maintain foraging habitat over time.

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#### REFERENCES

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- Angelstam, P. and G. Mikusinski. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest—a review. *Annales Zoologici Fennici* 31:157–72.
- Aulen, G. 1988. Ecology and distribution history of the white-backed woodpecker *Dendrocopos leucotos* in Sweden. Swedish University of Agricultural Science, Department of Wildlife. Report 14.
- \_\_\_\_\_. 1991. Increasing insect abundance by killing deciduous trees: a method of improving the food situation for endangered woodpeckers. *Holarctic Ecology* 14:68–80.
- Backhouse, F. and J.D. Lousier. 1991. Silviculture systems research: wildlife tree problem analysis. B.C. Ministry of Forests and B.C. Ministry of Environment, Wildlife Tree Committee, Victoria, B.C.
- Bull, E.L. and R.S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. *Journal of Wildlife Management* 57:335–45.
- Bull, E.L., S.R. Peterson, and J.W. Thomas. 1986. Resource partitioning among woodpeckers in northeastern Oregon. U.S. Department of Agriculture, Forest Service, Portland, Ore. Research Note PNW-444.
- Daily, G.C., P.R. Ehrlich, and N.M. Haddad. 1993. Double keystone bird in a keystone species complex. *Proceedings of the National Academy of Sciences* 90:592–4.
- Fischer, W.C. and B.R. McClelland. 1983. A cavity-nesting bird bibliography: including related titles on forest snags, fire, insects, disease, and decay. U.S. Department of Agriculture, Forest Service, Ogden, Utah. General Technical Report INT-40.
- Goggans, R., R.D. Dixon, and C. Seminara. 1988. Habitat use by three-toed and black-backed woodpeckers, Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife, Salem, Ore. Nongame Report 87-3-02.

- Holmes, R.T. 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. *Studies in Avian Biology* 13:6–13.
- Kiesker, D.G. 1987. Nest tree selection by primary cavity-nesting birds in south-central British Columbia. B.C. Ministry Environment, Victoria, B.C. Wildlife Report R-13.
- Knight, F.B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. *Journal of Economic Entomology* 51:603–7.
- Krebs, C.J. 1989. *Ecological methodology*. Harper and Row, New York, N.Y.
- McCambridge, W.F. and F.B. Knight. 1972. Factors affecting spruce beetles during a small outbreak. *Ecology* 53:830–9.
- Miller, R.S. and R.W. Nero. 1983. Hummingbird-sapsucker associations in northern climates. *Canadian Journal of Zoology* 61:1540–6.
- Nilsson, S.G. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56:921–37.
- Thomas, J.W. 1979. Wildlife habitats in managed forests in the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, Forest Service, Washington, D.C. Agriculture Handbook No. 553.
- Tiainen, J. 1985. Monitoring bird populations in Finland. *Ornis Fennica* 62:80–9.
- Van Wagner, C.E. 1968. The line intercept method in forest fuel sampling. *Forest Science* 14:20–6.
- Walankiewicz, W. 1991. Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? *Natural Areas Journal* 11:203–12.
- Walters, J.R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Annual Review of Ecology and Systematics* 22:505–23.
- Welsh, C.J.E. and D.E. Capen. 1992. Availability of nesting sites as a limit to woodpecker populations. *Forest Ecology and Management* 48:31–41.

# Winter Use of the Opax Mountain Silvicultural Systems Site by Ungulates, Squirrels, Hares, and Grouse

DAVID HUGGARD AND WALT KLENNER

## INTRODUCTION

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As one component of biodiversity research in the multidisciplinary Opax Mountain Silvicultural Systems study, winter track transect surveys provide information on three groups of vertebrates using the Opax Mountain site: ungulates, carnivores, and others (red squirrel, snowshoe hare, ruffed grouse). Because of the difficulty in distinguishing between the tracks of the two main carnivore species (red fox and coyote) and the rarity or patchy distribution of other carnivores, this paper discusses only the results for ungulates and “other” species.

### Ungulates

Mule deer and moose have received more applied research attention than any other species that inhabit forests in British Columbia. Consequently, they have the most developed set of management guidelines, which reflects their resource value as a hunted species. Handbooks detailing forest management techniques for mule deer are available for the Cariboo Region (Armleder et al. 1986) and the Southern Interior (B.C. Environment 1994). These handbooks generally recommend light partial cutting as the most appropriate means of harvesting forests to retain winter habitat value for deer, and also indicate specific stand structures that should be created. Moose seem to tolerate or benefit from more extensive forest modification (Tomm et al. 1981). These recommendations for ungulate management have been applied over large areas in the dry Interior, and have been incorporated into land management plans (e.g., the Kamloops Land and Resource Management Plan). However, controlled, experimental tests of the value of these management recommendations are rare because of the difficulty and expense of manipulating the forest on an appropriate scale. Most scientific studies of the effects of forestry on deer in the British Columbia Interior come from the Cariboo Forest Region.

Additionally, most deer management has assumed that partial cutting in the Interior’s dry forest would use the traditional individual-tree selection system (Armleder et al. 1986). Recently, however, managers have been increasingly interested in small patch-cut systems of partial cutting because of concerns about regeneration difficulties, insect and pathogen problems, workers’ safety, and the economic costs of individual-tree selection. The high interspersion of young and old forest caused by small patch cuts is a traditional management tool for ungulates in eastern forests (Alverson et al. 1988), but its value is largely untested in Interior dry forests.

Other Species Track surveys also provide information on the winter distribution of red squirrels, snowshoe hares, and ruffed grouse. These medium-sized species are a component of forest-dwelling vertebrate diversity, and are also important prey for predators that are of current direct management concern, such as northern goshawks, marten, and lynx.

## METHODS

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Track Surveys Surveyed transects 100 m apart covering the Opax Mountain site (harvested blocks, controls, and uncut adjacent forest) were walked by experienced observers when the most recent snowfall had finished 24–120 hours previously, with no substantial melt, winds, or flurries during that period. Where tracks crossed the transect, the observer recorded the following:

- distance along the transect,
- harvest type,
- distance from harvested edges,
- species of animal,
- estimated number of animals,
- snow depth where the tracks crossed the transect,
- depth to which the tracks sank into the snow, and
- behaviour indicated by the tracks (e.g., travelling, foraging).

The transects were mapped to relate locations along the transect to other mapped features (e.g., position of openings, topography, and biogeoclimatic site series) in future analyses. Snow depth was also recorded every 100 m along the transects to sample available snow conditions.

Summary Analysis The number of tracks of a species intersecting a transect is a function of the relative abundance of the species in the area, the length of the transect, and the time since the last snowfall. An index of abundance was therefore obtained from the transect data by dividing the number of tracks by the length of the transect (in km), and the time since snowfall (in days). Mean “tracks per km-day” and standard errors were calculated for each study species for:

1. Both areas (Opax Mountain and Mud Lake);
2. Six treatments (control, 20% partial cut, 50% partial cut, 50% partial cut with reserves, 20% patch cut, and 50% patch cut); and
3. Different cut types (uncut, 20% partial cut, 50% partial cut, and “clearcut,” representing sites within the patch cuts). Uncut forest was also divided into “contiguous uncut” in control or adjacent blocks, and uncut “leave strips” within the patch-cut arrays.

Standard errors were calculated based on means of the replicate blocks, which recognizes the non-independence of adjacent transects within a block.

Sessions, Number of Tracks, and Species

Two complete tracking sessions (all transects walked after the same snowfall) were completed in 1994/1995, the Mud Lake transects only were completed once in 1995/1996, and three complete sessions and one half-session were completed in 1996/1997. The yearly variation in effort reflects variation in available funding.

A total of 2401 track intersections and 1935 systematic snow depth measurements were recorded. Species recorded, in decreasing order of abundance, were: red squirrel, mule deer, canids, weasels, small mammals, grouse, snowshoe hare, moose, marten, cougar, lynx, and black bear. Only results for squirrels, deer, grouse, hares, and moose are reported here.

Snow Depths

Snow depths in the winter of 1996/1997 were considerably greater than in the previous two winters (Figure 1). Snow depths were consistently much higher in patch-cut openings, and were somewhat elevated in the partial cuts at Mud Lake, but not at Opax Mountain. The 20 and 50% removal partial cuts did not differ at either site. Snow depths were generally 20–30 cm deeper at the higher-elevation Opax Mountain site than at the Mud Lake site.

Mule Deer

Mule deer are hindered by snow depths greater than 40 cm (Trottier et al. 1983). This is the average depth of snow at Mud Lake in normal winters in areas that have some cover, while the average snow depth at Opax Mountain is somewhat deeper. By exercising some habitat selectivity, mule deer can therefore find acceptable snow levels at both sites in average winters. In 1996/1997, however, average snow depths in all blocks considerably exceeded the 40-cm threshold. The distribution of mule deer showed that the deer responded to this snow-depth threshold in time and space. In 1994/1995, deer tracks were abundant at both sites, with considerably more tracks in the uncut and lightly partial-cut treatment units, moderate numbers in the heavier partial cuts, and almost no tracks in the deep snow in clearcuts (Figure 2). The uncut forest in leave strips was also used considerably less than contiguous uncut forest, although the large annual variability and herding of deer produced wide error bars on estimates. With deep snow in the winter of

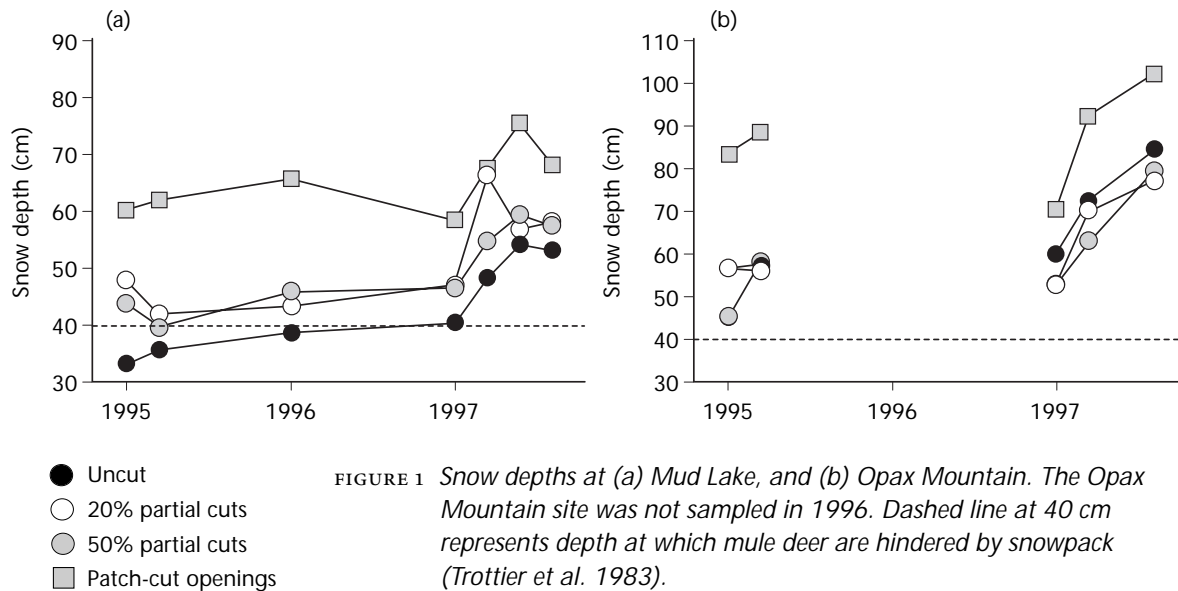


FIGURE 1 Snow depths at (a) Mud Lake, and (b) Opax Mountain. The Opax Mountain site was not sampled in 1996. Dashed line at 40 cm represents depth at which mule deer are hindered by snowpack (Trottier et al. 1983).

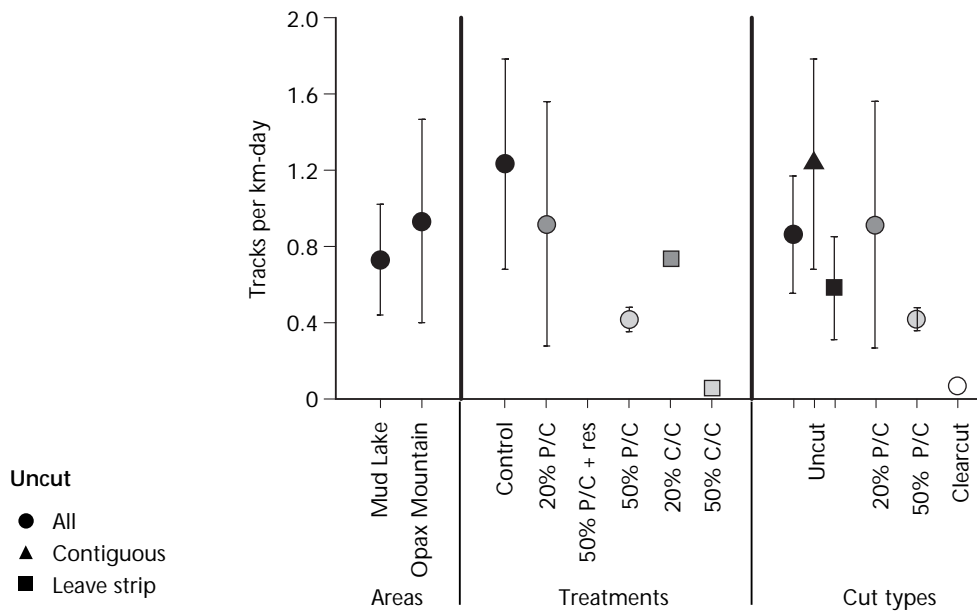


FIGURE 2 Abundance of mule deer tracks by study area, treatment unit, and cut type. Error bars are 1 SE.

1996/1997, deer tracks were seen only in the first two sessions before peak snow accumulation, and were only in the densest forest and the lowest-elevation parts of the Mud Lake site. No deer tracks were found at the Opax Mountain site in 1996/1997 or at either site during peak snow depth in March.

These results are in accord with deer winter range guidelines that allow light-entry partial cutting in low-elevation forests. They also suggest that the alternative system of small patch cuts is not favourable for deer in this forest type. In these areas, deer do not use the openings with deep snow accumulations and appear to prefer contiguous cover to leave strips. Summer use, of course, may differ, but is beyond the scope of this small project. The disappearance of deer from the study area when the snowpack was exceptionally deep emphasizes the importance of broad-scale landscape management for deer, particularly by providing low-elevation dry sites with canopy cover for extreme winters.

Moose in winter can travel in much deeper snow than mule deer (Trottier et al. 1983), but because their preferred habitat is more common at the higher-elevation Opax Mountain site, they may also have to select habitat to avoid excessive snow depths in this area. Moose tracks were more abundant in winter at the Opax Mountain site (Figure 3), and were most common in uncut sites. Light partial cutting reduced moose abundance slightly. They strongly avoided 50% partial cuts and clearcut openings in winter (Figure 3). Unlike deer, moose used the uncut leave strips as much as the contiguous forest, which means that overall the patch-cut treatments were used more than the heavy partial cuts (Figure 3). Moose were present throughout the deep snow in 1996/1997, but their abundance was lower than during 1994/1995.

Moose management guidelines currently allow extensive clearcutting (more than standard management in most places), with some retention of closed-canopy forest as summer thermal cover. The unsuitability of openings

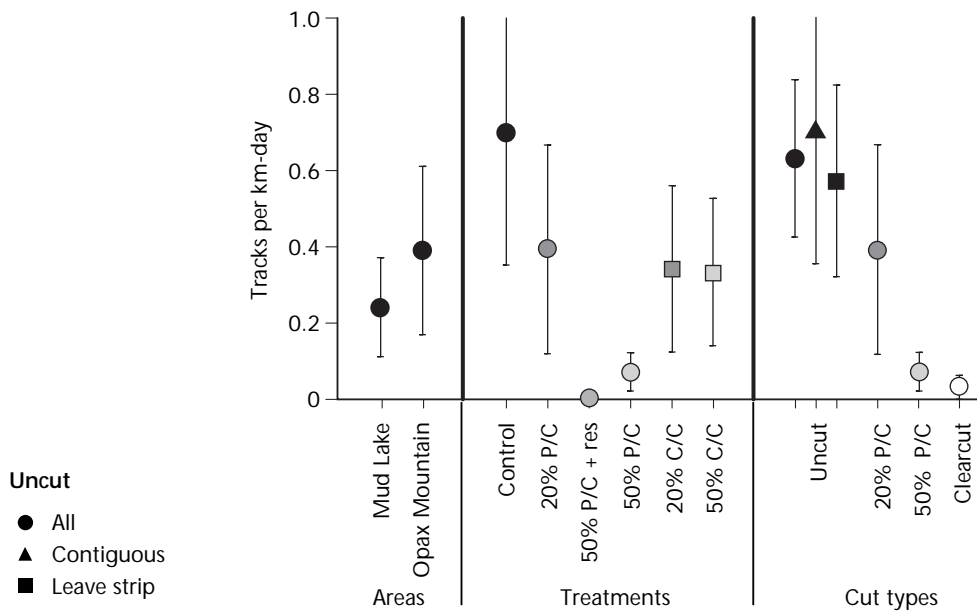


FIGURE 3 Abundance of moose tracks by study area, treatment unit, and cut type. Error bars are 1 SE.

for moose during the winter suggests that leave-strip corridors should be provided for moose in the winter.

#### Red Squirrels

Although red squirrels are arboreal, they do travel on the snow to gain access to their middens on the ground, and to travel between more isolated trees in the open forest. Tracks should therefore reflect both the abundance of squirrels and the proportion of time they spend on the ground. The abundance of tracks (Figure 4a) showed the same pattern of treatment unit effects as the density estimates from a mark-recapture study of squirrels at Opax Mountain (see Klenner, these proceedings, p. 264)(Figure 4b), except for the 50% partial cut with reserve patches, which had more tracks than expected from overall densities. This might reflect more frequent travel on snow when squirrels move through the open forest between reserve patches.

Red squirrels used uncut leave strips as much as contiguous uncut forest (Figure 4a). This was reflected in the overall abundance of squirrels in the patch-cut treatments, where numbers of tracks and summer mark-recapture estimates were proportional to the amount of uncut forest (i.e., track density in the 20% patch cuts was 80% of the density observed in the uncut forest, and was 50% of the density observed in the 50% patch cuts). Both types of partial cut showed reduced levels of use, and squirrels rarely travelled into clearcuts in the winter (Figure 4a).

#### Snowshoe Hares

Snowshoe hares rarely leave areas with dense cover, although they are sometimes thought to benefit from edges, which may enhance the shrubs they feed on. Winter tracking showed that hares were much more abundant at the Opax Mountain site than at the Mud Lake site (Figure 5), probably because they are more frequently associated with higher, montane spruce forests than low-elevation dry forests. At both sites, hares were found almost exclusively in uncut forest areas, particularly in the contiguous uncut forest. Leave strips were used by hares to a lesser extent, which allowed them to occupy the

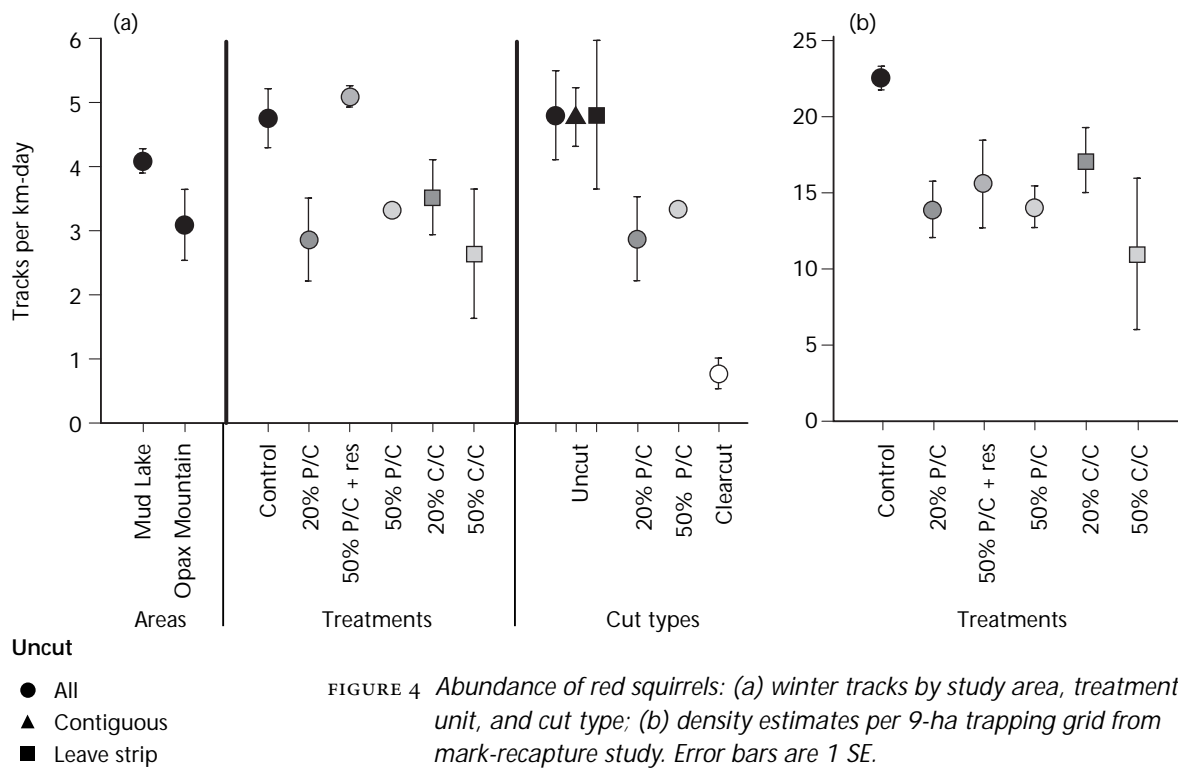


FIGURE 4 Abundance of red squirrels: (a) winter tracks by study area, treatment unit, and cut type; (b) density estimates per 9-ha trapping grid from mark-recapture study. Error bars are 1 SE.

patch-cut treatments, even though they were never found in open clearcuts. The strong association of hares with uncut forest emphasizes the importance of retaining some dense patches of forest in the landscape.

#### Grouse

Most of the grouse tracks in the study area were made by ruffed grouse, although the lowest block, adjacent to the grasslands, supported sharp-tailed grouse at times during the winter. Grouse tracks were rare in clearcut openings and were considerably reduced in the 50% partial-cut treatment units, but were at the same levels in uncut contiguous forest, leave strips, and 20% partial cuts (Figure 6). The 50% partial cut with reserves treatment had more grouse tracks than would be expected from the cut type results because this treatment type included the block adjacent to the grasslands with a wintering flock of sharp-tailed grouse. Ruffed grouse often feed on the exposed branches of shrubs during the winter, and probably benefit from the lower snowpack in the uncut and lighter partial-cut types. Both grouse species are also associated with deciduous trees in winter, and were noticeably more abundant in riparian areas.

#### IMPLICATIONS

This limited research project presents only a small part of the biology of any of the animal groups studied, and should therefore be interpreted with caution. However, it suggests that the light partial cutting used to maintain mule deer winter range in Interior forests is more successful than heavier partial cuts, or the patch-cut and leave-strip harvest systems. However, light partial cutting affects a much larger area than more intensive harvesting systems and makes uncut reserves less feasible. This would be detrimental to species such

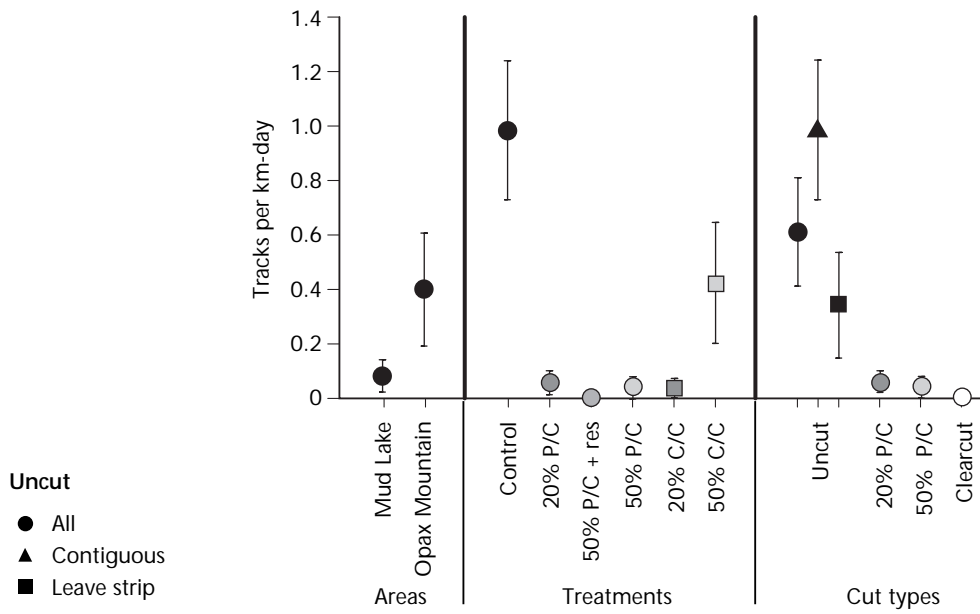


FIGURE 5 Abundance of snowshoe hare tracks by study area, treatment unit, and cut type. Error bars are 1 SE.

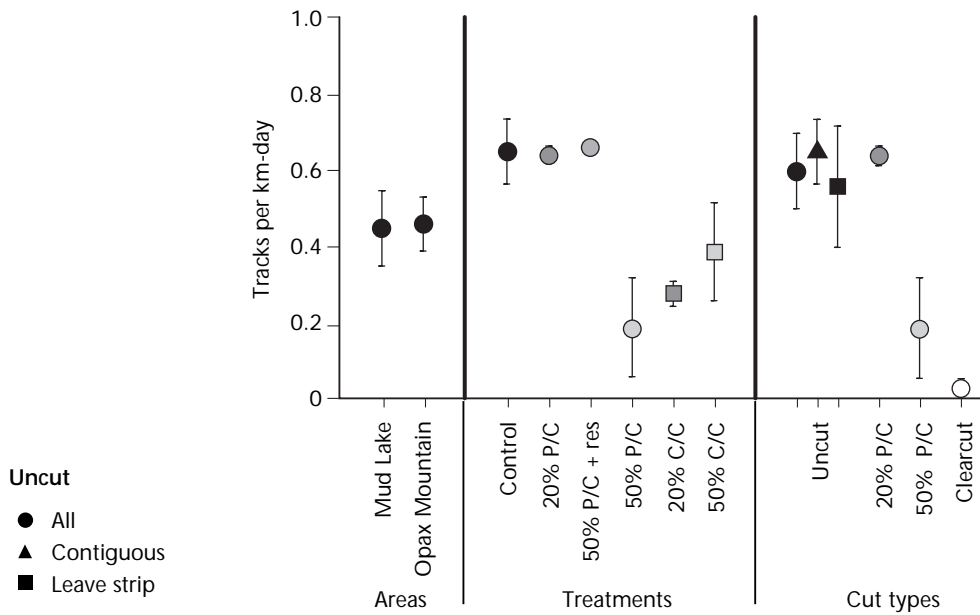


FIGURE 6 Abundance of grouse tracks by study area, treatment unit, and cut type. Error bars are 1 SE.

as snowshoe hares that are negatively affected by any harvesting. Additionally, the effects of the silvicultural treatments on ungulates depends on snow depths. In winters with deep snow, preserving uncut low-elevation sites with low snow cover is critical to maintain ungulate populations at a larger landscape scale.

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#### REFERENCES

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- Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: edge effects in Northern Wisconsin. *Conservation Biology* 2:348–58.
- Armleder, H.M., R.J. Dawson, and R.N. Thomson. 1986. Handbook for timber and mule deer management co-ordination on winter ranges in the Cariboo Forest Region. B.C. Ministry of Forests, Victoria, B.C. Land Management Handbook No. 13.
- British Columbia Environment 1994. Southern Interior mule deer management handbook. B.C. Ministry of Environment, Victoria, B.C.
- Tomm, H.O., J.A. Beck, Jr., and R.J. Hudson. 1981. Responses of wild ungulates to logging practices in Alberta. *Canadian Journal of Forest Research* 11:606–14.
- Trottier, G.C., S.R. Rollans, and R.C. Hutchison. 1983. Range, habitat and foraging relationships of ungulates in Riding Mountain National Park. Canadian Wildlife Service, Ottawa, Ont. Large Mammal Systems Studies Report No. 14.