Bats and Forests Symposium
October 19–21, 1995
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Robert M. R. Barclay and R. Mark Brigham (editors)

Bats and Forests Symposium

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Bats and Forests

R. MARK BRIGHAM AND ROBERT M. R. BARCLAY

ABSTRACT

Until recently, the majority of ecological research on microchiropteran bats, and in particular vespertilionids in temperate parts of the world, was biased towards species and situations where aggregations occurred in human-made structures (buildings and mines). However, significant progress has been made to address questions about the ecology of temperate, insect-eating bats living in more "natural" situations. Even so, our knowledge about how bats use and interact with forest ecosystems is still in its infancy.

In the last five years, intrinsic interest and concern about the impacts of timber harvest and forest management has stimulated various studies of bats in forest ecosystems. Studies of bats have also become a focus for a variety of agencies, especially those who are mandated to manage natural resources on public lands. Therefore, we felt it was appropriate to convene a symposium bringing together biologists, foresters, and land managers with an interest in bat–forest interactions to determine where we stand and to try to identify some common questions for further study. Our original idea was to have a small meeting. It quickly became apparent that there was interest from all over the continent, and indeed other parts of the world. The "small" meeting expanded to include over 100 participants and we could not accommodate everyone interested in attending. On the one hand, we were amazed and impressed by the number and diversity of people who were interested in the topic, but on the other we were disappointed that we had to turn some people away.

This volume presents the results of the symposium that took place from October 19–21, 1995 in Victoria, British Columbia, Canada. In all, 24 speakers gave presentations and there were three poster papers. We received manuscripts from the authors of almost all the papers, and they appear in this volume. In general, the presentations can be subdivided on the basis of what are acknowledged to be the two most important resources for bats: roost sites and foraging areas.

The three presentations at the beginning of the meeting were by individuals with forestry and/or wildlife expertise. These papers were designed to set the stage from a broad perspective. It became clear that forest management issues are complex and can be controversial. The message to biologists studying bats is that we have to be prepared to make recommendations about the best way to manage forests, knowing that

our understanding of the complexity of the system is incomplete and that modifications may be necessary as more information becomes available.

A recurring theme was emphasized by Brad Stelfox: bats have large home ranges for their size and travel considerable distances between roosts and foraging areas. This means that bats link habitats together, and we need to keep in mind the potential ecological and management implications of this. We need to know, for example, at what scale bats view the landscape. Our focus tends to be in terms of smaller scales, but given the movement patterns of bats they may well view things at the landscape scale, and this has important implications regarding the recommendations we make.

What follows is our impression of some of the important themes to come out of the symposium, with respect to the biology of bats in forest ecosystems, and where further work should be focused. This represents our opinions, although these were certainly modified and shaped during the excellent, two-hour discussion session at the conclusion of the formal part of the meeting. It speaks highly of the interest and dedication of those who attended this session that after eight hours of presentations and with a hot meal in the offing, most participants spent over two hours trying to bring everything together.

SPEAKING THE SAME LANGUAGE

To communicate effectively, scientists must speak the same "language," and it was evident during the meeting that even among bat biologists, some terms are used in different ways. The problem becomes worse when biologists try to use forestry terminology! We must become more aware of the correct use of "jargon," and work hard to use terms that transcend provincial, state, and national boundaries. What do we mean by "canopy" or "edge," and what attributes define "over-mature forest stands"?

ROOSTING

A large number of papers on a variety of species and geographical areas dealt with the roosting requirements of forest-dwelling bats. Two aspects in particular emerged from these talks. First, it is clear that tree-roosting bats typically select large (tall) trees in early stages of decay that are more open (uncluttered) than random (available) wildlife trees (see Betts; Crampton and Barclay; Kurta et al.; Sasse and Pekins; Vonhof). Although specific species of roost-trees differ from place to place, general attributes are similar, and one result is higher densities of roosting bats in older forest stands. Second, individual bats switch roosts on a regular basis (Betts; Crampton and Barclay; Kalcounis and Hecker; Kurta et al.; Ormsbee; Vonhof). Our concept of a "colony" may well have to change from the one we have developed by studying bats faithful to a building or cave. Although movement distances between roosts vary with the species of bat and the geographical area, individuals (including lactating females) use

several day-roosts and have larger home ranges than we would have expected. This has clear management implications and we must take a broader, landscape view of bat habitat. What is not clear is why bats switch roosts, and answering this question will be an important area for future research.

Several papers pointed out the need to understand not only the day-roost ecology of forest bats, but also the requirements for night roosts, and the use of roosts other than trees (Perlmeter; Pierson et al.). Especially in managed forests, roosts in bridges may play a key role as alternative night-roosts for bats. Information is lacking on the use of natural night-roosts and their importance.

Participants agreed that future studies of tree-roosting bats should attempt to measure the same set of roost, tree, and site characteristics so that studies will be comparable and a general picture can be developed, if it exists. At a minimum, the following should be measured: roost entrance height and aspect, tree height, DBH, decay stage, percentage of bark remaining, horizontal distance to and height of the nearest tree, horizontal distance to the nearest wildlife tree, horizontal distance to and height of the nearest tree of the same height or taller, canopy height, horizontal distance to the nearest edge (opening), horizontal distance to the nearest water, live-tree density, wildlife-tree density, and percentage of canopy closure.

FORAGING

Almost without exception, papers dealing with habitat selection by foraging bats used some type of ultrasonic detector to monitor echolocation activity. There was considerable debate as to the level of species identification that can be achieved using detection systems, and the caution must be that identification needs to take into account the natural variation of calls used by each species. Within a species, calls differ between individuals, foraging situations, and geographical areas. In particular, calls recorded from known individuals for use in identifying unknown bats must come from free-flying individuals. Calls produced by captive bats in enclosed spaces are unlikely to accurately reflect calls produced in the wild.

Various papers illustrated that bats prefer certain habitats for foraging. Edges (vertical and horizontal) seem to be important, both as commuting and foraging corridors (see Bradshaw; Grindal; Krusic and Neefus; Parker et al.), and riparian zones are areas of high bat activity (see Hayes and Adam; Parker et al.). Harvesting creates edges used by bats, but several papers indicated that bats were not abundant in large openings, including clearcuts (see Crampton and Barclay; Grindal; Hayes and Adam; Perdue et al.). Stand age also influences bat activity, with young stands usually having low activity and more heterogeneous, open, older stands having higher activity (Crampton and Barclay; Erickson), although some of this results from bats commuting from roosts in old stands.

Aside from the aspects mentioned above, several important areas for future work came to light as the meeting progressed. Not only should we experimentally test the various hypotheses to explain roost switching, we also need to consider the ecological and management consequences of switching. What is the social structure of colonial bats in the forest? Are individuals faithful to a series of roosts within and between years? Why do individuals travel as far as they do between roost sites and foraging areas, and what are the ecological consequences of this behaviour?

Information regarding the abundance and diversity of insects in different types and ages of forests or in different habitat types was lacking. We need to know not only what is available to bats in different areas, and whether this influences where they feed, but also the impact that bats have on forest pest species. Although we say that bats are the major predators of nocturnal, flying insects, and assume they have a significant impact on pests, we need hard evidence of this. Likewise we need further research on the effect that bats have on nutrient dynamics within forests. Elucidating these roles will help to place bats in perspective in forest ecosystems.

Finally, participants agreed that we need to follow up on recommendations and to monitor the effectiveness of management practices. As a greater diversity of forest harvesting regimes are used, it is essential to determine how bats respond so that we can "adaptively manage" and adjust recommendations as the gaps in our knowledge are filled. We have come a long way in a relatively short time, and with the interest shown at this meeting, progress should be rapid and we will hopefully need to meet again in a few years.

SECTION I THE BIG PICTURE

Natural Disturbance Regimes as Templates for Boreal Forest Harvest

D. WALKER, J. BRAD STELFOX, S. WASEL, AND D. HEBERT

ABSTRACT

The importance of natural disturbance events (e.g., fires, floods, blowdowns, insect outbreaks) to forest structure and function is generally accepted by ecologists. Accordingly, forest harvest strategies that reasonably approximate the variability in stand structure created by natural disturbances may offer a preferred risk management strategy for maintaining forest integrity. A critical task confronting managers who adopt a coarse-filter (e.g., disturbance regime) approach to forest management is the identification and measurement of variables that most meaningfully define disturbances. In Alberta and elsewhere in North America, variance in stand size, age, and structure created by wildfires is presently being considered by the forest sector, academia, and government as a general model for logging. Alberta-Pacific Forest Industries (AlPac), a large (~6 million ha) Forest Management Area (FMA) holder in northeast Alberta, is evaluating a forest harvest strategy based on a natural disturbance model. Specifically, variation in harvest rotation ages, cutblock sizes, and cutblock residuals (green trees, snags, downed woody material) would approximate fire return intervals, fire sizes, and post-fire residuals, respectively. Justification for this shift in forest harvest planning is the potential for traditional two-pass, 20–30 ha, short-rotation, clearcut harvest in boreal mixedwood forests to alter stand- and landscape-level heterogeneity and thus impair ecological function and wildlife habitat. To evaluate this potential change in landscape pattern, a series of stand metrics (patch size, shape, and interspersion) were used to compare pre-harvest landscapes to those created by a conventional two-pass harvest and modified type-cut harvest regime proposed by Alberta-Pacific Forest Industries. Relative to pre-harvest forest landscapes, traditional two-pass, clear-cut logging resulted in a landscape comprised of stands that had increased edge density, decreased shape complexity (double-log fractal dimension), decreased core area, and increased interspersion of patch types. Relative to the traditional two-pass logging strategy, the modified type-cut logging strategy created a forest mosaic more similar to the pre-harvested landscape. The analyses indicated that changes to landscape patterns caused by different forest harvest strategies were strongly influenced by existing patch configurations (e.g., variances between townships) that occur prior to logging. These preliminary results suggest that modified "type-cut"

logging may maintain pre-harvest forest landscape patterns better than a conventional two-pass logging strategy where cutblocks are spatially constrained to 40–60 ha.

INTRODUCTION

As societal expectations concerning North American forests broaden, so does the need to identify and implement a broader set of objectives that direct management policy (Maser 1994). Past management frequently focused on few forest attributes, primarily tree-fiber production, creating forest landscapes with altered structure and function, which were less able to provide non-fiber benefits to society. Recently, due to large hardwood-fiber allocations, the boreal mixedwood forests of North America have become a focus of national and international controversy involving the forestry sector and environmental groups (Nikiforuk and Struzik 1989). Relative to Alberta's total available Annual Allowable Cut (AAC) for trembling aspen (*Populus tremuloides*), harvest has increased from 2% (1971) to 15% (1988) to ~80% (1990) according to Karaim et al. (1990) and Peterson and Peterson (1992). Current harvest strategies for Alberta's aspen mixedwood forests are dominated by short-rotation (70-year) clearcut (20–30 ha) logging involving two or three passes. Cutblocks are spatially constrained in that average size should not exceed 40 ha and cutblock width cannot exceed 400 m. The ecological issues concerning forest age, forest structure, landscape fragmentation, and sustainable harvest levels that dominated the Pacific Northwest conflict in recent decades have become topical and relevant to the boreal mixedwood forest sector.

Boreal mixedwood forests are a mosaic landscape comprised of countless stands that vary in age, size, shape, and dispersion (Peterson and Peterson 1992). Additional variation is apparent at the stand level for species composition of canopy trees, understorey structure, and levels of snags and downed woody material (Lee et al. 1995). Although much of the variability found in forest communities can be explained by soil type, elevation, and topography (Rowe 1972; Corns 1983; Swanson and Franklin 1992), natural disturbances occurring since the retreat of continental glaciers have contributed significantly to boreal forest heterogeneity (Pickett and White 1985; Attiwill 1994). Boreal forests have experienced a number of natural perturbations (e.g., floods, insect outbreaks, windstorms) during the Holocene epoch (past 10,000 years); however, fire is considered to have been the primary disturbance that shaped these communities (Rowe and Scotter 1973; Kelsall et al. 1977; Barney and Stocks 1983; Johnson 1992). The vegetative patterns created by fire on boreal landscapes are both complex and dynamic, as fire cycles vary both in space (Payette et al. 1989) and time (Bradshaw and Zackrisson 1990; Clark 1990; Bergeron 1991).

Variability created by natural disturbances in forest systems may be essential to plants and animals since biota are adapted to biophysical structures created by disturbances. In Alberta, boreal mixedwood forests support a diverse assemblage of organisms, including 40 fish species (Nelson and Paetz 1992), five amphibians (Russell and Bauer 1993), one

reptile (Russell and Bauer 1993), 236 birds (Francis and Lumbis 1979; Semenchuk 1992), 45 mammals (Pattie and Hoffmann 1992; Smith 1993), and thousands of arthropods (Danks and Foottit 1989). Based on distribution maps in Moss (1983) and Vitt et al. (1988), conservative estimates indicate a rich diversity of plants in Alberta's boreal mixedwood forests, including 600 vascular species, 17 ferns, 104 mosses, 13 liverworts, and 118 lichens. Conservation of these organisms, and the communities to which they belong, may be constrained by the capacity for land-uses to maintain adequate variability in stand and landscape structure.

Current knowledge of the autecology of boreal forest biota is decidedly sparse and directed primarily at species of privileged recreational, conservational, or commercial status. From the better-known vertebrates, forest companies commonly select "feature" or "umbrella" species as models to guide harvest strategies for habitat purposes. Given our information vacuum, it remains uncertain whether forest management strategies built on habitat requirements of selected "umbrella" vertebrate species will adequately conserve entire biotic assemblages and associated forest processes. Concerns about the "fine-filter" approach to forest management include biased selection of taxal groups to which feature species belong, and the uncertainty of this approach to maintaining ecological processes (e.g., soil decomposition, nutrient pathways, successional pathways).

During recent decades, the role of natural disturbances in boreal forest systems has arguably changed as human attitudes and actions towards flooding, fire, and insects have altered the intensity, recurrence, and geographic extent of natural perturbations. Flood-control measures, insect-abatement campaigns, and fire-suppression programs have likely influenced the nature and extent of natural disturbances. In Alberta's boreal forests, research by Murphy (1985) indicates that fire return intervals increased from 38 years in pre-settlement times to 90 years by the late 1960s. In sharp contrast, anthropogenic disturbances are now conspicuous and growing in prevalence in northern forests (Anonymous 1991). Some land-use disturbances, such as agriculture, seismic activity, urban expansion, and transportation corridors, permanently excise patches or corridors of forests from the mixedwood forest mosaic. Others, like commercial clear-cut logging, permit the forest to persist, although in a different form and subject to altered ecological processes.

Recently, forest ecologists have suggested that the impacts of forestry on wildlife and ecological processes could be reduced if logging strategies were devised that approximated natural disturbance regimes and maintained variability in ecosystem conditions (Franklin 1993; Hunter 1993; Maser 1994). Elements of natural disturbances that may serve as a stand-level template for "new forestry" include retention and dispersion of live trees, snags, and downed woody material. At the scale of the landscape, the size, shape, rotation age, and interspersion of cutblocks could approximate the frequency distribution of these attributes created by natural disturbances such as fire. If we accept that organisms are adapted to different forest structures and scales, then it is important to ask whether contemporary forest practices maintain adequate heterogeneity within the forest landscape. Such is the intention of this paper. It is a deserving question because guidelines that regulate forest harvest are arguably restrictive and may encourage forest companies to reduce environmental variability as

they seek to create an "acceptable" forest directed by the regulatory process. Monotypic approaches to forest harvest and regeneration are unlikely to accommodate the variable and dynamic nature of the boreal mixedwood forest mosaic. They are, however, perceived to facilitate less costly and less complicated planning, harvest, and regeneration.

To date, there exist few studies examining spatial patterns of forest stands created by harvest within the boreal mixedwood forest. The advent of geographic information systems (GIS) and availability of remote photometric data permit exploration of spatial patterns (size, shape, interspersion) that are important to forest ecosystem management. Simulation models of forest structure and development allow forecasting of future forest attributes following defined forest successional trajectories and management practices. Together, these analytical techniques can be used to explore spatial and temporal patterns of forest communities subjected to commercial logging. In this paper we quantitatively examine the frequency distribution of stand size, stand age, and stand shape of pre-harvest forests, and forests of two different harvest strategies in the boreal mixedwood region of northeast Alberta. These analyses focus on eight selected townships within the FMA area of Alberta-Pacific Forest Industries Inc.

METHODS

Digital GIS data for this study were obtained from the Alberta Vegetation Inventory (AVI) through Timberline Forest Industry Consultants and AlPac. AVI is an ongoing initiative to develop a standardized vegetation inventory for forest-dominated areas of Alberta. This inventory is compiled from a combination of 1:20,000, black-and-white aerial photography and ground measurements. AVI data describe multiple-stand variables including canopy species composition, height, crown closure, site productivity rating, soil moisture, decade of stand origin, stand structure/understorey, stand condition, and modifiers describing non-vegetated and anthropogenically disturbed land. AVI organization and availability focused our study design on those areas within the FMA with available data. As AVI data were only available at the township level and not continuous across the FMA, the township (9.6 × 9.6 km) was chosen as the discrete unit of landscape analysis. Township units were chosen using two criteria: (1) digital AVI data were complete, and (2) digital traditional forest harvest plans (standard two-pass, 10–20-year green-up period, 70–80-year rotation) had been generated for the township and were readily available.

A SUN Sparc Station 10 and Arc/Info (1994) software were used to perform initial GIS manipulations of digital landscape coverages. In order to remove erroneous stand boundaries and to group the data to a relevant level, adjacent polygons were pooled by height class and cover type for each township. Stands were first classified into six height classes of five-metre increments (0–5 m, >5–10 m, >10–15 m, >15–20 m, >20–25 m, >25 m) and four cover types (coniferous, deciduous, mixedwood, other). Coniferous polygons were those composed of ≥80% coniferous composition, deciduous polygons were ≥80% deciduous composition, and mixed-

wood polygons were those in which neither deciduous nor coniferous composition was ≥80%. Polygons classed as "other" included aquatic areas (lakes, rivers, streams, ponds, flooded areas), clearings vegetated by herbs, grasses, forbs, and/or shrubs less than six metres, pasture, roads, industrial areas (well sites, microwave towers, transmission lines, gravel pits, farm areas, rail lines, gas and oil development), and urban development and recreation areas. Based on identical species/height classification, boundaries between adjacent polygons of the same type were removed. The resultant coverage of pooled AVI polygons was the base coverage for all other coverages generated, and was labelled as the pre-harvested coverage.

To create traditional harvest coverages, operational harvest plans generated by Timberline were used. First-pass harvest blocks were overlaid on the pre-harvested coverage and those areas scheduled to be cut were reclassified to the lowest height class (0–5 m). Forest cover height data were then projected 10 years using a growth/yield model (data provided by Timberline). Second-pass harvest blocks were overlaid on this new coverage and scheduled polygons reclassified to the lowest height class (0–5 m). Coverages with both first and second pass were again dissolved based on species/height classification to remove old polygon boundaries from within new harvest-block polygons. Because first- and second-pass harvest blocks were not designed to follow pre-harvest stand boundaries, this process created many new polygons, a proportion of which had a high length-to-width ratio (sliver polygons). Because it was determined likely that harvesting would remove many of these sliver polygons rather than leaving them, those smaller that 200 m² and of the same species/ height class as the adjacent scheduled stand were joined with the cutblock polygon.

Coverages for modified type-cut harvest were created using Foreman⁺1 harvest scheduling software (data provided by Timberline). Foreman⁺1 schedules stands to be harvested based on site productivity, stand age, volume, and species composition, but does not consider operational economics or logistics. It was decided to schedule those remote stands where logging costs would be high because criteria now used to determine feasibility may not be relevant with modified type-cut harvest. It is possible that the range of harvest blocks scheduled in a modified type-cut harvest plan may include much larger blocks than are presently harvested. This may result in economic flexibility to pursue smaller, more isolated blocks. All polygons were evaluated for fiber and site attributes by Foreman⁺1 for a 20-year window. For purposes of analyses, all scheduled stands were considered to be harvested during a single, short (one-year) entry. All harvested polygons were then reclassified to the lowest height class (0–5 m), and boundaries removed from between adjacent polygons with the same species/height class.

Each of three landscape coverages (pre-harvested, traditional, and modified type-cut) for each of eight townships was examined using FRAGSTATS (McGarigal and Marks 1994) software. FRAGSTATS generates a number of metrics based on the pattern of polygons composing the landscape, a subset of which were used for these analyses (Table 1). To generate metrics relating to core area, an edge width or edge buffer was defined at 30 metres. This approximated 1–1.5 the height of mature aspen trees.

TABLE 1 *Subset of spatial pattern metrics generated by FRAGSTATS used in these analyses*

	Metrics generated by FRAGSTATS
Number of patches	Number of polygons on the landscape coverage.
Patch density	Number of polygons per unit area.
Perimeter	Total length of polygon boundaries.
Edge density	Length of edge per unit area.
Total core area	Sum of area of all polygons after eliminating the area of a previously defined buffer (30 m for these analyses).
Shape complexity	Double-log fractal dimension calculated using perimeter and area; varies between one and two with one being a simple Euclidean shape and two the theoretical maximum shape complexity.
Interspersion Index	Index describing the extent to which patch types are distributed in relation to other patch types. A high interspersion index defines a patch mosaic whereby each patch is uniformly distributed among other patch types.

From the landscape metrics generated by FRAGSTATS comparisons at the landscape scale were made using area, perimeter, number of patches, total core area, edge density, shape complexity, and interspersion index. Because there was great variation in overall pattern between different townships, comparisons were limited to within-township changes. Percentage change from pre-harvest to traditional harvest, and from pre-harvest to modified type-cut harvest were calculated for each of the landscape metrics, with the exception of area, perimeter, and number of patches. Frequency distributions were generated for polygon area and perimeter, while the number of patches was presented as a mean of the eight townships.

RESULTS

Frequency distributions of polygon area and perimeter describe a similar negative-exponential pattern for all landscapes examined (Figures 1 and 2), with many polygons of small areas or short perimeters, and a few polygons with large areas or long perimeters. In both area and perimeter, the traditional harvest landscapes had more polygons with small areas or short perimeters than did pre-harvest or modified type-cut landscapes. This is due to an increase in the number of polygons in the traditional harvest townships as compared to the pre-harvest and modified type-cut harvest (Figure 3). With traditional harvest, constrained by operating ground rules, many small polygons are created around the edges of cut-blocks and, therefore, the number of polygons with small areas and short perimeters is greater in traditionally harvested landscapes.

Relative to pre-harvest landscape, total core area decreased in traditional harvest landscapes for all eight townships (Figures 4 and 5), indicating an increase in polygon fragmentation. The modified type-cut
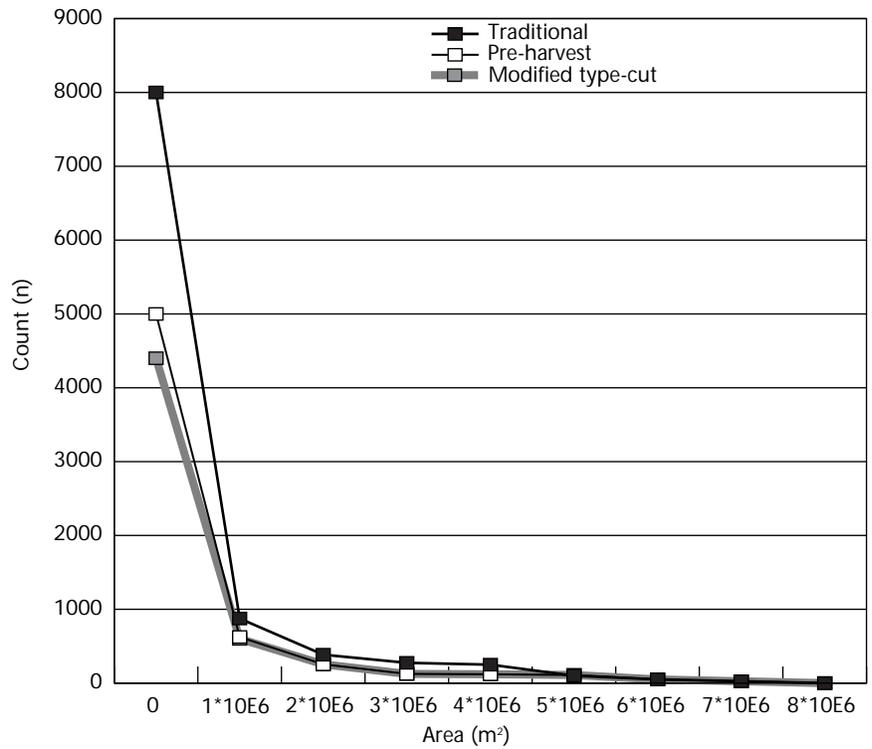
FIGURE 1 *Frequency distribution of patch size in pre-harvest, traditional, and modified type-cut forest landscapes.*
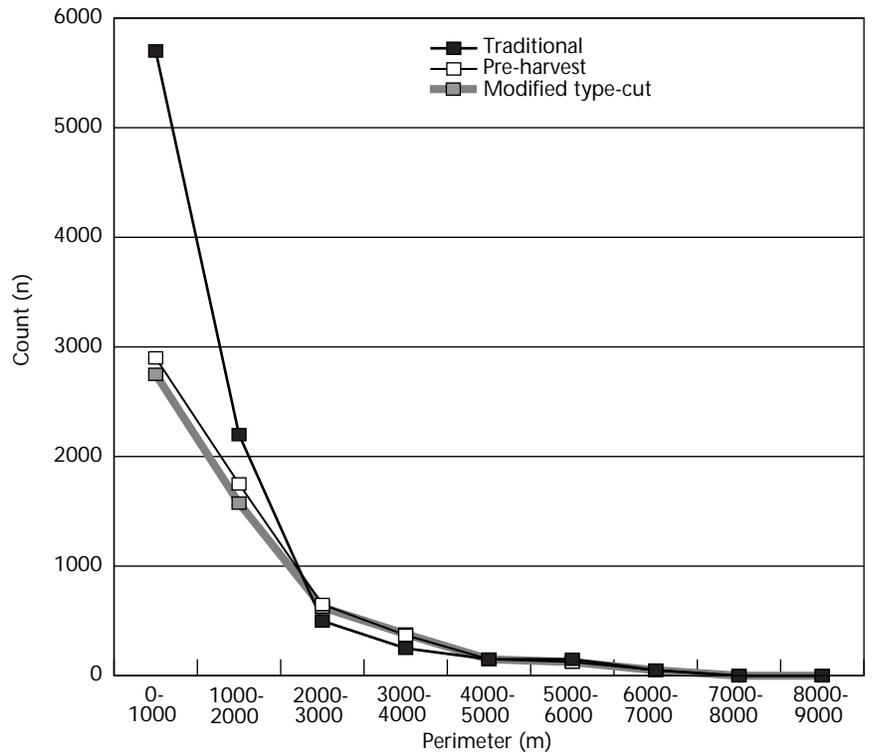
FIGURE 2 *Frequency distribution of patch perimeter in pre-harvest, traditional, and modified type-cut forest landscapes.*
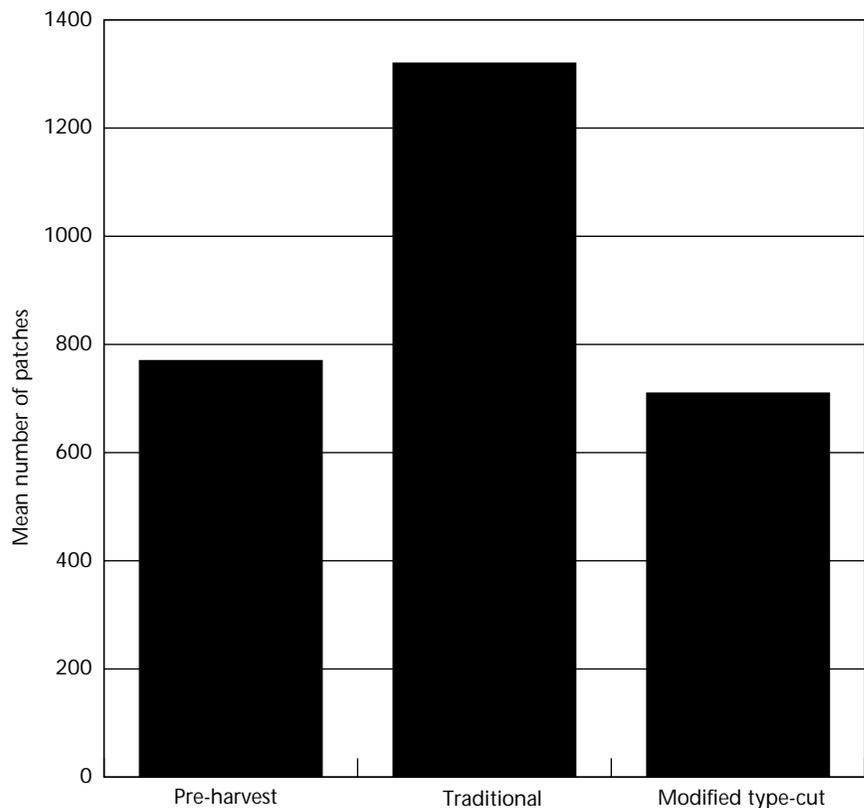
FIGURE 3 *Mean number of forest patches in pre-harvest, traditional, and modified type-cut landscapes.*

landscapes demonstrated an overall increase in core area as a result of the aggregation of polygons ready for harvest in the 20-year window. There were two townships in which the modified type-cut landscapes demonstrated a decrease in total core area (Townships 1 and 6). This is likely due to site productivity differences detected by Foreman[+1] within species/ height defined polygons. This site productivity difference resulted in the partitioning of these polygons based on differences in growth/yield projections, resulting in more edge and, therefore, less core area.

Shape complexity decreased in all eight traditional harvest landscapes relative to the pre-harvest landscapes (Figures 6 and 7). This indicates a change towards simpler, more Euclidean shapes. Relative to pre-harvest landscapes, the modified type-cut harvest exhibited little change in shape complexity ($<1\%$ versus $>22\%$ for modified type-cut and traditional harvest, respectively).

Edge density increased in all traditional landscapes when compared with the pre-harvest landscapes (Figures 8 and 9), due to an increase in the number of polygons and fragmentation of the landscapes with traditional two-pass logging. There was a decrease in edge density for six of the eight modified type-cut townships, reflecting the aggregation of polygons due to scheduling of 20 years of merchantable harvest in one year. The two townships that had increases in edge density (1 and 6) likely reflect the same patch configurations causing the decrease in core area for these townships (Figures 4 and 5).
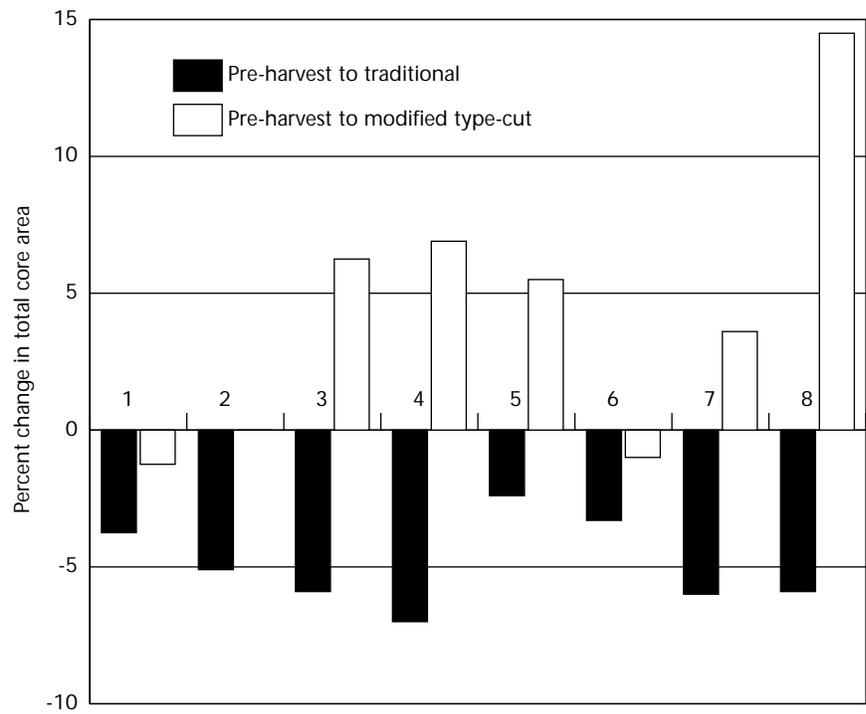
FIGURE 4 *Changes in total core area, relative to pre-harvest landscape, caused by traditional and modified type-cut harvest.*
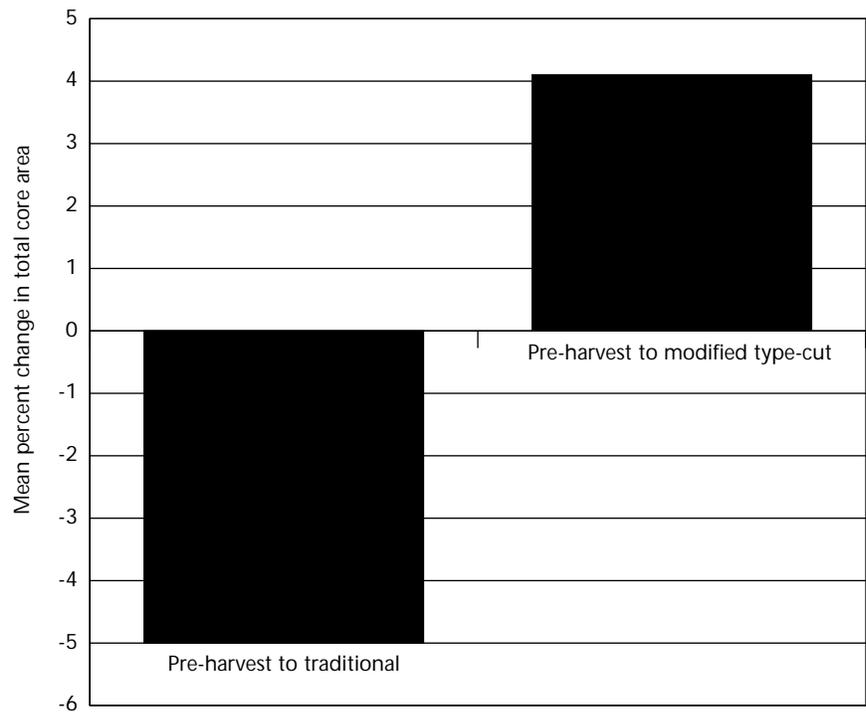
FIGURE 5 *Mean percentage change in total core area comparing three land-scapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut. Positive change indicates an increase in core area and negative change indicates a decrease in core area.*
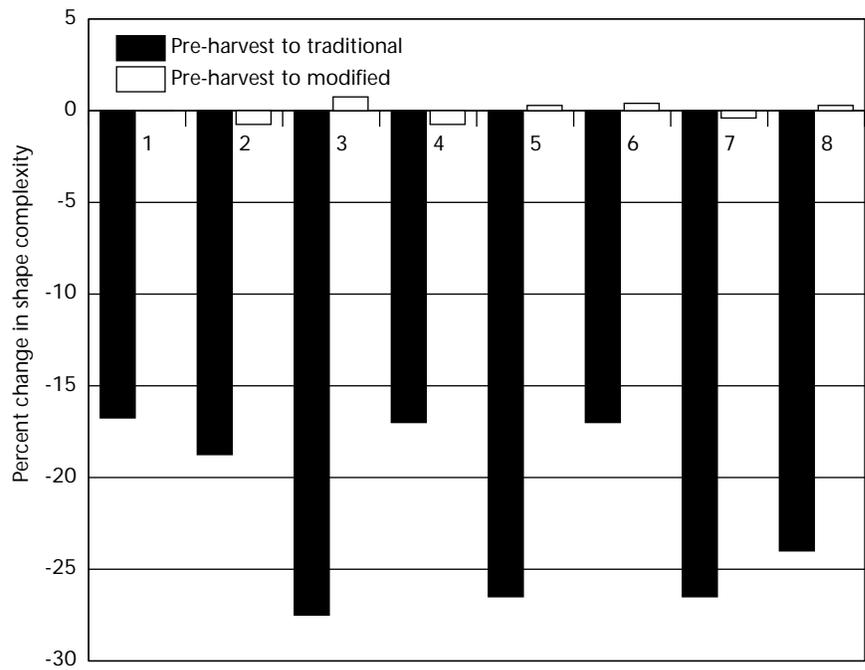
FIGURE 6 *Percentage change in shape complexity (double-log fractal dimension) comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut. Positive change indicates an increase in shape complexity and negative change indicates shape simplification.*
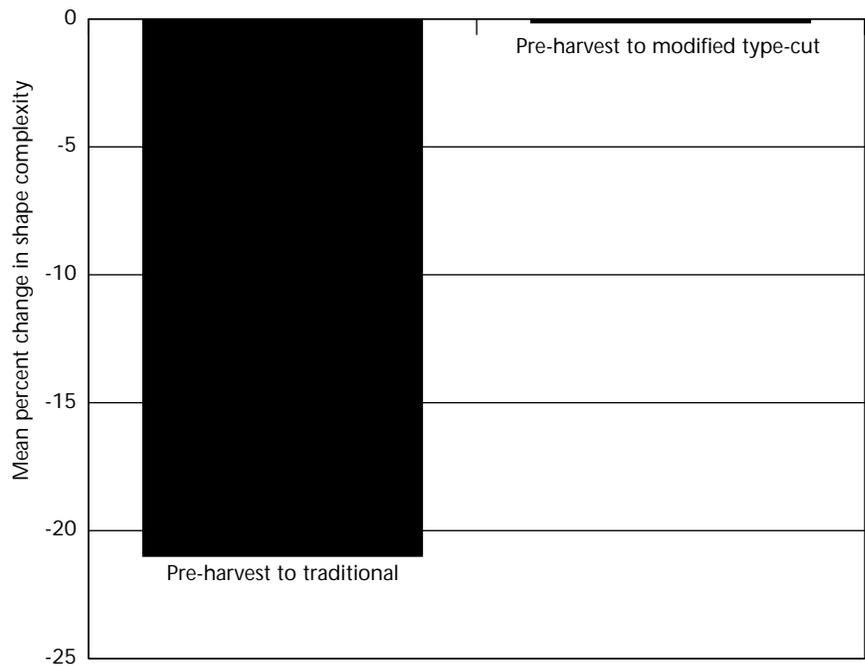
FIGURE 7 *Mean percentage change in stand complexity (double-log fractal dimension) comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut. Positive change indicates an increase in shape complexity and negative change indicates shape simplification.*
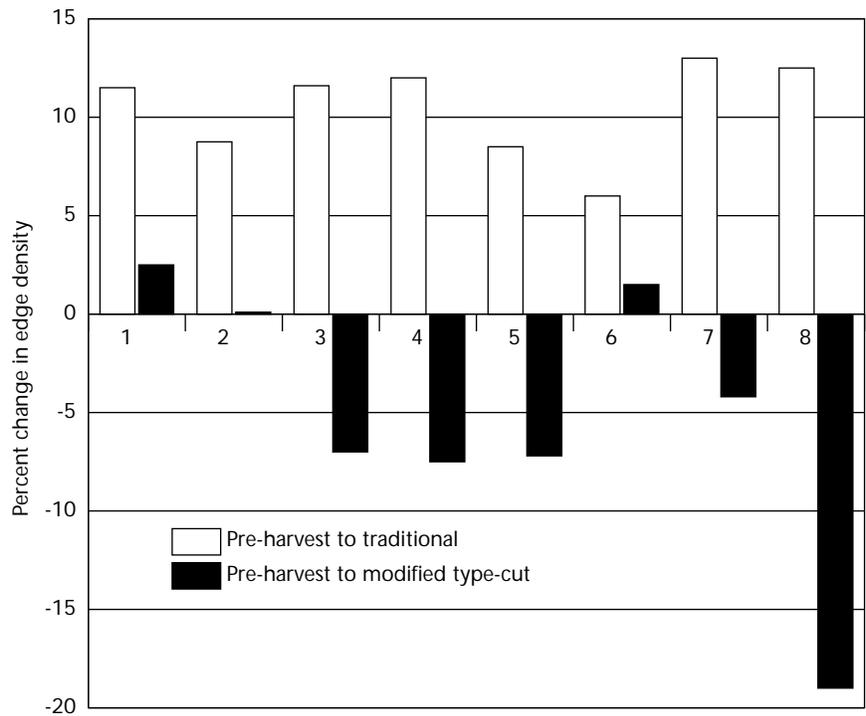
FIGURE 8 *Percentage change in edge density comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut.*
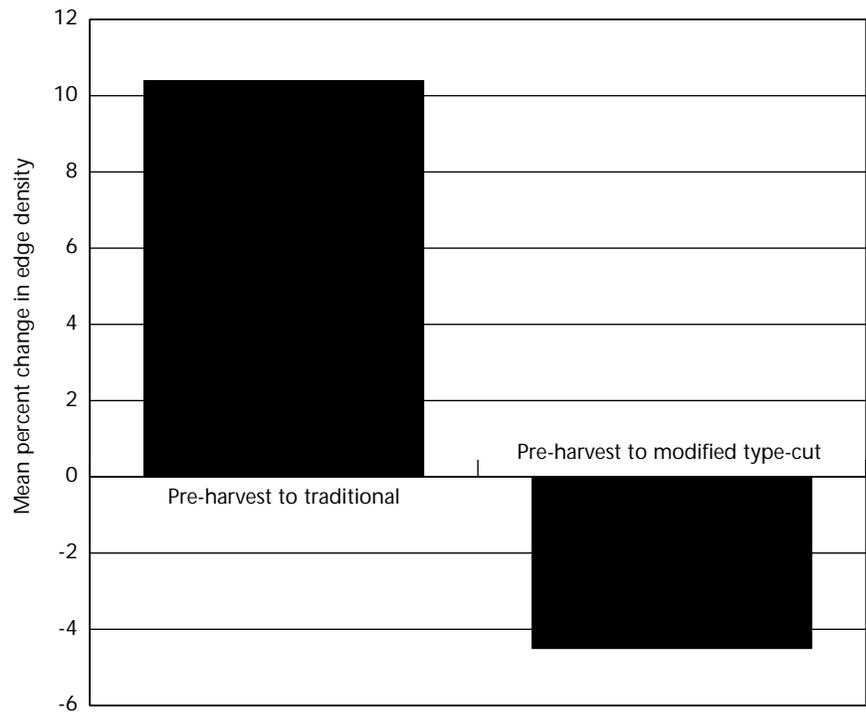
FIGURE 9 *Percentage change in edge density comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut. Positive change indicates an increase in edge per unit area and nega-tive change indicates the opposite.*
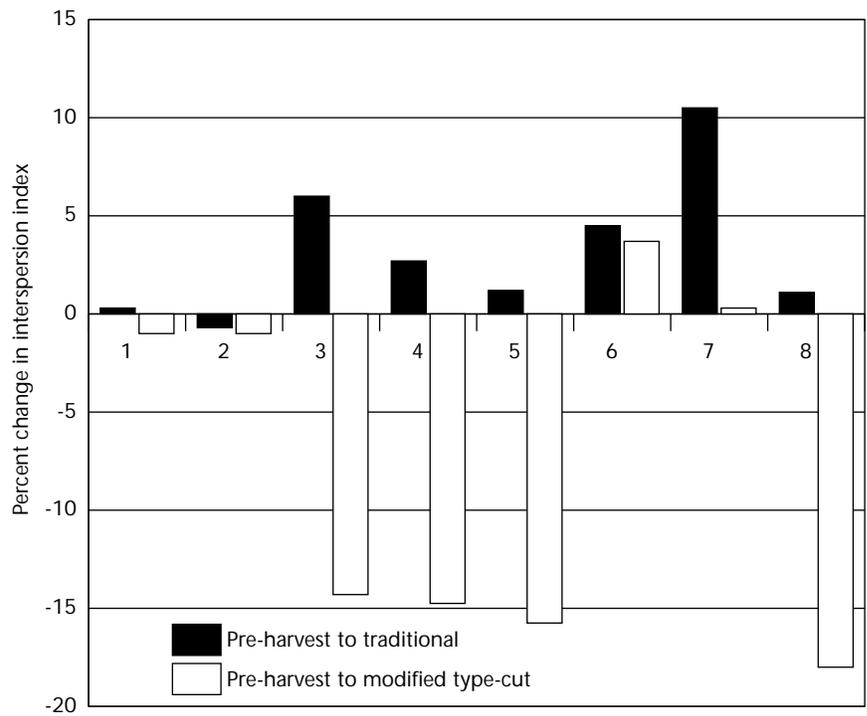
FIGURE 10 *Percentage change in interspersion comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut.*
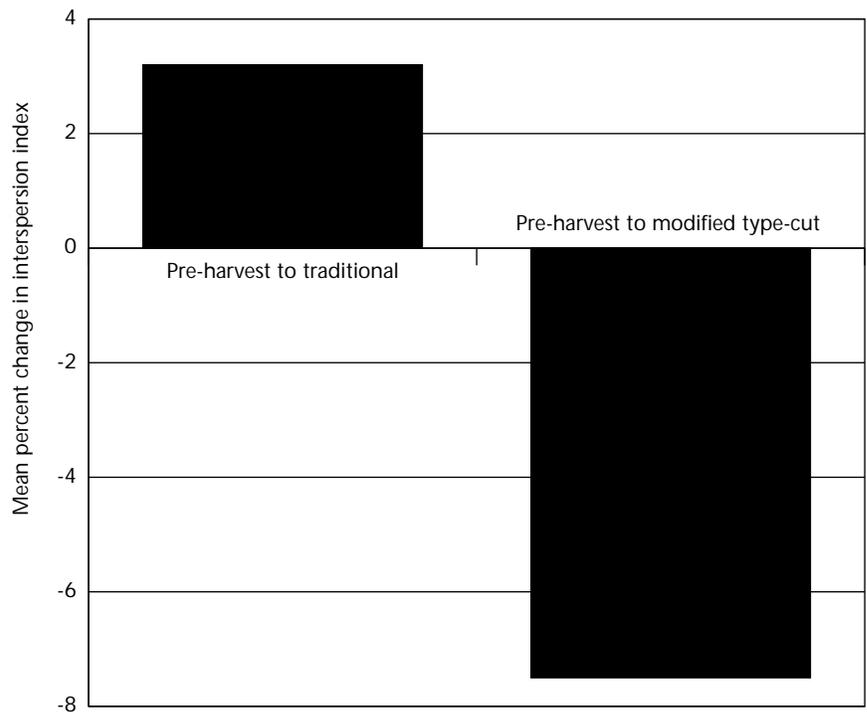
FIGURE 11 *Mean percentage change in the interspersion index comparing three landscapes: (a) pre-harvest to traditional, and (b) pre-harvest to modified type-cut. Positive change indicates an increase in interspersion and negative change indicates the opposite.*

Relative to pre-harvest landscapes, there was an overall increase in the interspersion index in traditional landscapes reflecting the "checkerboard" pattern created by traditional two-pass harvest (Figures 10 and 11). There was a decrease in the interspersion index for the modified type-cut landscape, a result of the aggregation of polygons of different cover/height types.

DISCUSSION

Results of these spatial analyses of landscape pattern in the boreal mixed-wood forests of northeast Alberta support the contention that the pre-harvested landscape is highly variable in patch size, shape, and interspersion. Considerable township-to-township variance indicates that landscape patterns are not uniform at the spatial scale of the township. A comparison of traditional (two-pass, 20–30-ha cutblocks) and progressive (modified type-cut) forest harvest strategies reveal that cutblocks constrained in size and shape by regulations frequently create a landscape dissimilar to the pre-harvest landscape. In contrast, the type-cut approach to forest harvest maintained heterogeneity in stand size, shape, and interspersion found in the pre-harvest townships.

The implicit assumption of this paper is that biota are capable of detecting and responding differently to patches of different composition, canopy height, size, and shape. However, the 5-m canopy height intervals and canopy composition of greater than or less than 80% coverage are arbitrary break-points that may or may not have biological relevance. In contrast, some species may detect and respond differently to patches whose canopy heights differ by less than 5 m. Detecting levels of sensitivity by biota to stand shape, canopy height, stand area, and composition is an important area of evaluation by ecologists if future landscape analyses are to be completed with meaningful biological criteria.

Maintaining a range of natural variability (RNV) (Swanson et al. 1993) in commercial forest landscapes is a recognized goal of the Alberta Forest Conservation Strategy (1995). Rationale for maintaining RNV is based on the assumption that biota are adapted to environmental variation created by disturbances. As such, these findings suggest that government regulatory agencies should consider revisions to timber harvest rules that currently constrain patch size, patch shape, and patch interspersion.

expertise, and advice were invaluable. Discussions with Doug Sklar, Dave Fox, Kim Rymer, Tim Juhlin, Wes Baker, and Pat Gallupe helped to clarify implementation, planning and operations issues.

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An Ecosystem Context for Bat Management: A Case Study of the Interior Columbia River Basin, USA

BRUCE G. MARCOT

ABSTRACT

The ecological role and environmental requirements of 15 species of bats were analyzed in an ecosystem assessment of the interior Columbia River Basin, USA. Ecological roles of bats potentially contribute to nutrient cycling, insect population control, transmission of disease, hosting obligate ectoparasites, and accumulation of pesticides. Such roles can influence ecological processes in forest canopies, soils, and water bodies, and population levels of arthropods and their predators, and of other species of bats. Specific studies are needed on rates of effects. The macroecology and collective environmental requirements of all 15 bat species also provide for a wide range of other species in forest, wetland, riparian, and other settings. Such a systems- and biodiversity-wide approach helps put bat management into an ecosystem context and helps focus needs for further inventory, monitoring, and research.

INTRODUCTION

Federal, state, and provincial land management agencies in Canada and the USA are moving towards ecosystem management of forests and grasslands (Bormann et al. 1994; Pojar et al. 1994). This entails crafting land management activities to better tier the ecological requirements and roles of plant, invertebrate, and vertebrate species, including bats (Kaufman et al. 1994). In such an approach, the collective macroecology, ecological roles, and environmental requirements of bats can be incorporated into an ecosystem management context. This paper illustrates one such approach from an ongoing study of species, biodiversity, and ecosystems in the interior Columbia River Basin. The study is part of a scientific assessment and land-use planning project called the Interior Columbia River Basin Ecosystem Management Project, conducted jointly by USDI Bureau of Land Management (BLM) and USDA Forest Service (FS).

The interior Columbia River Basin (CRB) includes portions of seven western states and covers about 60.9 million ha (Figures 1 and 2). (This area also contains parts of the Klamath Basin and northern Great Basin in southern Oregon, included in the land-use planning area for this project.) BLM and FS lands comprise 52 percent of this area, with the remainder in private, state and local government, tribal, and federal lands.

The CRB area contains nine major landforms ranging from arid grasslands and lowland plains and valleys, to intermontane basins and breaks, to steep mountains and glaciated ranges (Figure 3a). Precipitation, relief, and elevation vary widely throughout the study area (Figures 3b, c, and d).

The CRB area is sparsely inhabited by people as compared with other parts of the USA. However, 63 percent of the area, originally native grasslands, especially *Fescue*/bunchgrass and *Agropyron*, 24 percent of the native shrublands, such as mountain sage and big sage, and 44 percent of old-growth forests, have been greatly altered or eliminated due to agriculture, urbanization, livestock grazing, and timber harvesting.

METHODS

Information on distribution, ecology, and ecological roles of bats and other species was gathered from existing literature (e.g., Christy and West 1993; Nagorsen and Brigham 1993; Thomas 1988), and from conducting modified Delphi surveys of knowledge from panels of species experts (Marcot et al., unpub.; see Acknowledgements). This information, and vegetation cover types and structural stages used by each bat species, were described and coded into a relational database. Such information should be considered a first approximation, and may be useful in building tentative working hypotheses for management. Much further empirical work is needed to validate these hypotheses.

Range distribution maps of each bat species were drawn (scale 1:1,000,000) and digitized in a geographic information system (ArcInfo). Total area of the CRB and each species' range within it were calculated from the maps. Trends of habitat for each species were analyzed by comparing historic (early 1800s) to current area of vegetation cover types and structural stages associated with each species, using vegetation maps from W. Hann et al. (unpub., CRB Ecosystem Management Project, Walla Walla, Washington).

The CRB study area was partitioned into 7,733 sub-watersheds or sixth-level hydrologic units (see Jensen and Bourgeron 1993 for explanation of hydrologic unit coding system). Within the CRB, these sub-watersheds averaged 7,880 ha and ranged from 96 to 86,500 ha. Each was characterized according to total area; percentage of overlap of each bat species' distributional range; historic and current dominant vegetation cover type and structural stage; dominant landform category; highest and lowest annual precipitation (available data from 1989); highest and lowest elevation; and topographic relief (biophysical data from Fire Lab, FS, Missoula, Montana).
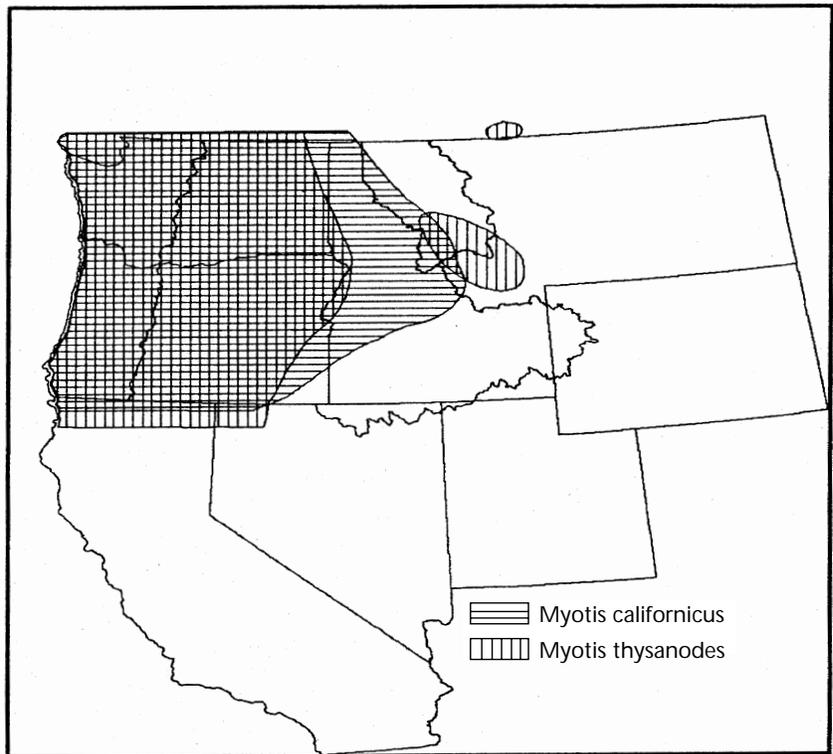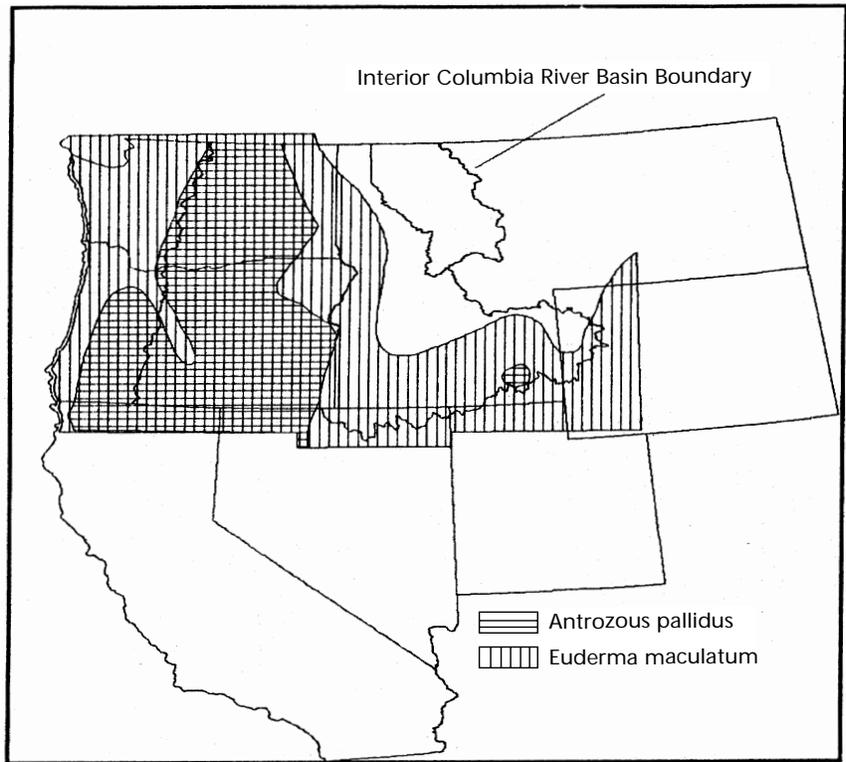
FIGURE 1 *Ranges of eight bat species in the Interior Columbia River Basin. Distributions beyond the general area of the Basin are not shown. An additional seven bat species are ubiquitous throughout the Basin (see text).*

Pipistrellus hesperus
Plecotus townsendii
pallescens

Tadarida brasiliensis
Myotis yumanensis
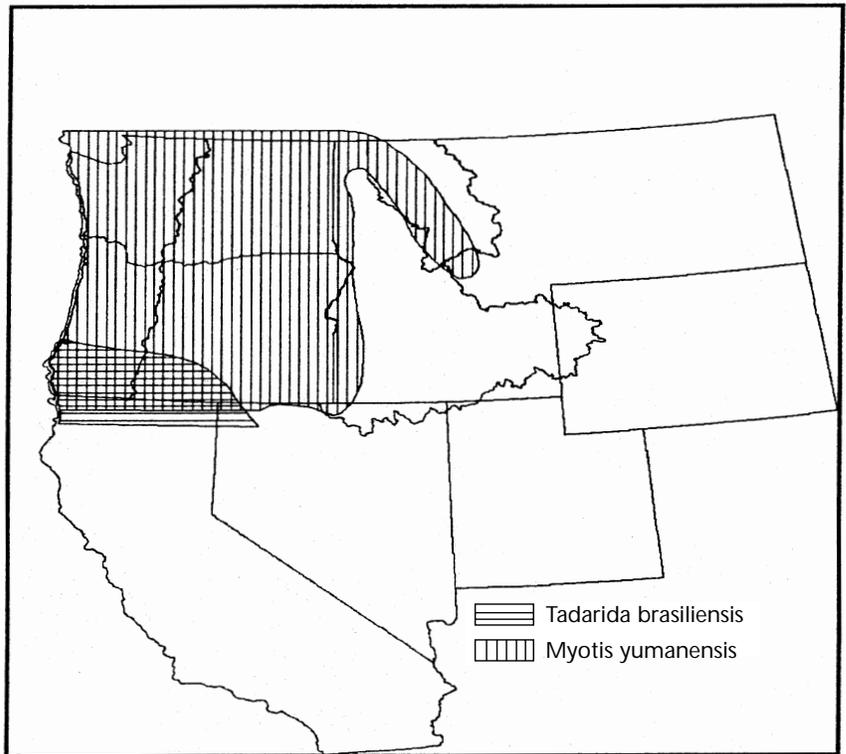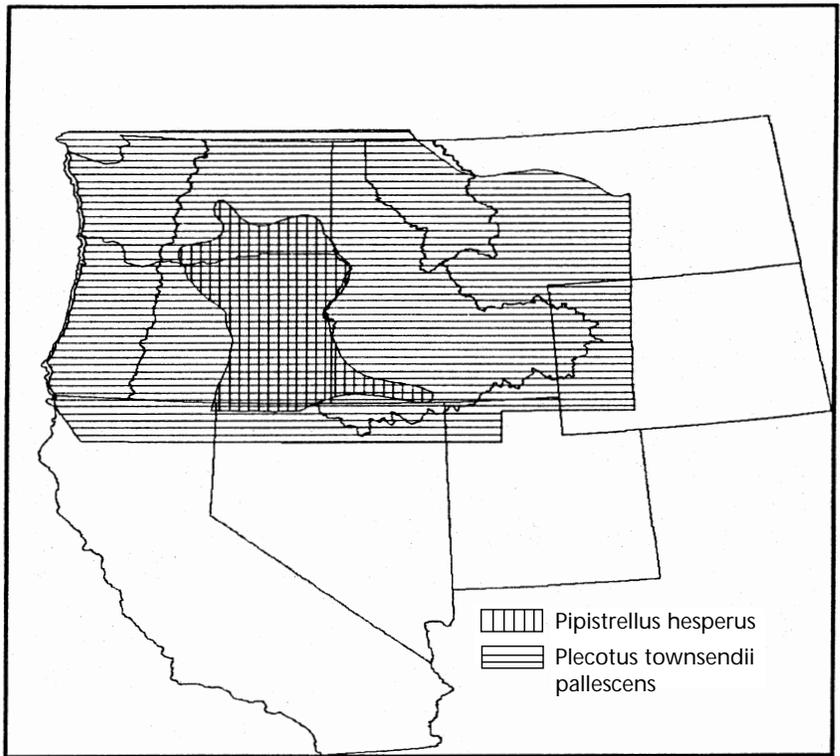
FIGURE 1 *Continued*
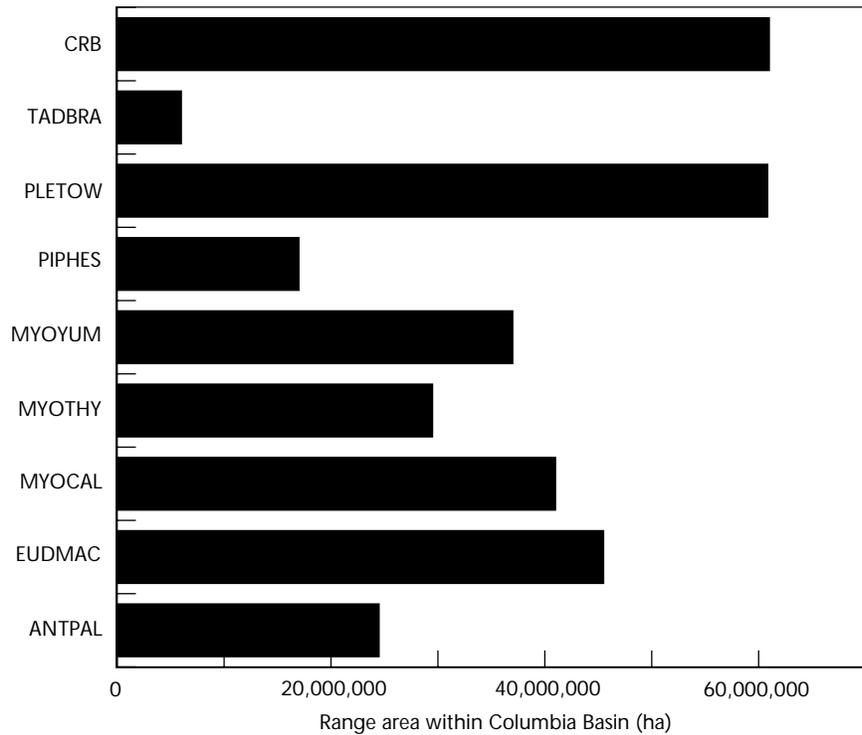
FIGURE 2 *Total range of eight species of bats within the Interior Columbia River Basin, based on the distributional maps in Figure 1. See Table 1 for species codes. CRB = total area of the Basin and ranges of the additional seven ubiquitous species.*

Highest and lowest annual precipitation levels within sub-watersheds were significantly positively correlated ($p < 0.01$, Pearson correlation coefficient r = 0.677, n = 7739 sub-watersheds), as were highest and lowest elevation levels ($p < 0.01$, r = 0.700, n = 7739). Thus, for further analyses only one of each variable pair, highest levels, was used. Also, slope and relief were significantly positively correlated ($p < 0.02$, r = 0.410, n = 7739), so only one of the pair, relief, was carried into further analyses.

The CRB area, and macroecology properties within each bat species' range, then were characterized by tallying the total area within each sub-watershed in each biophysical category of landform, precipitation, elevation, and relief. Data were summarized as percentage of total area, rather than as absolute area, within each bat species' range, because total macrohabitat area likely overestimated true habitat available to each species.

Each bat species was characterized according to its key environmental correlates; that set of microhabitat, substrate, and other environmental factors thought to most influence population fitness and viability. Also listed for each bat species were key ecological functions, the known or hypothesized primary set of activities performed by organisms that affect the ecological function of their ecosystem. Key environmental correlates and key ecological functions of bats were compared with those of all vertebrates in the CRB to determine the degree of similarity.

FIGURE 3A *Landforms.*
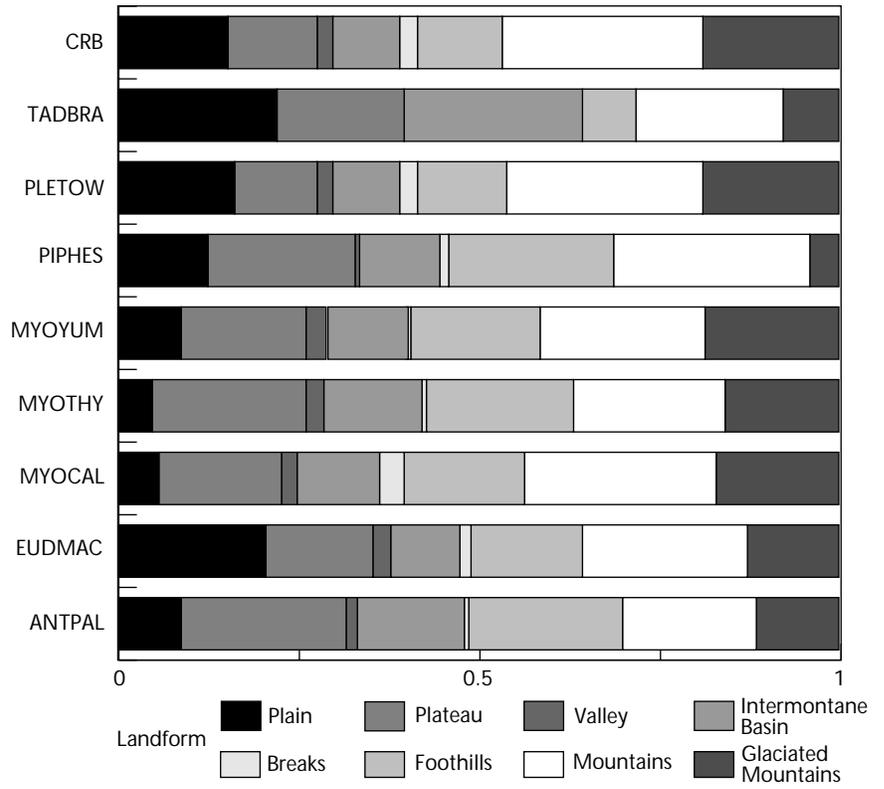
Landform legend: Plain, Plateau, Valley, Intermontane Basin, Breaks, Foothills, Mountains, Glaciated Mountains

FIGURE 3 *Proportions of each bat species' range among biophysical attributes within the 6th level hydrologic unit codes of the interior Columbia River Basin, based on habitat attributes listed in the appendices applied to the entire Basin. (See Table 1 for species codes.) CRB = overall distribution within the Basin and for the additional seven ubiquitous bat species.*

High Ppt legend: VL, LO, MI, HI, VH
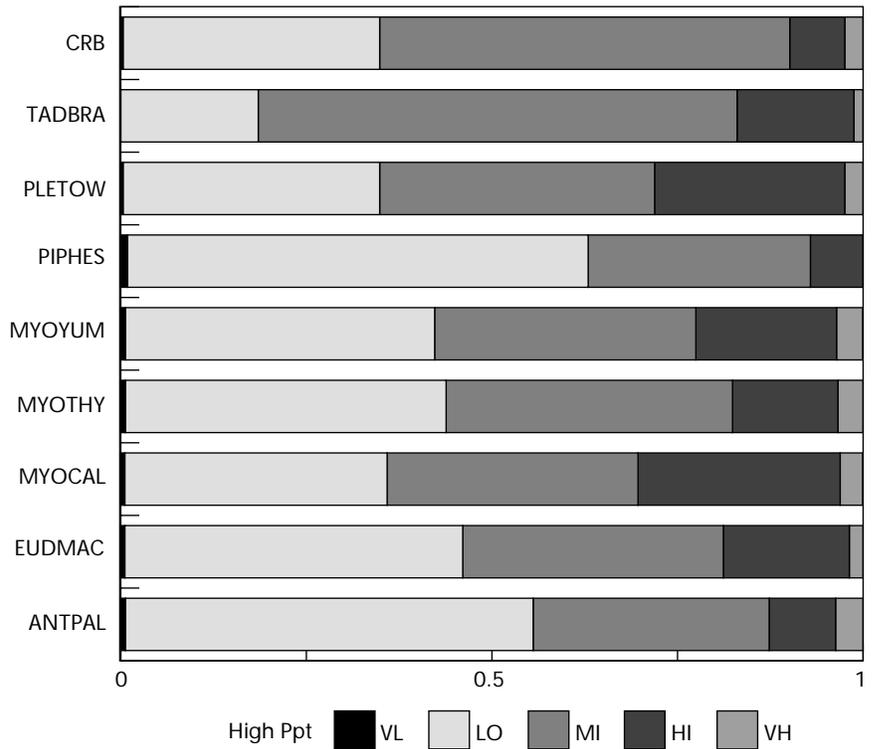
FIGURE 3B *Highest mean annual precipitation. Very low = 0–203 mm, low = 204–508, mid = 509–1016, high = 1017–2032, very high = 2033+m.*
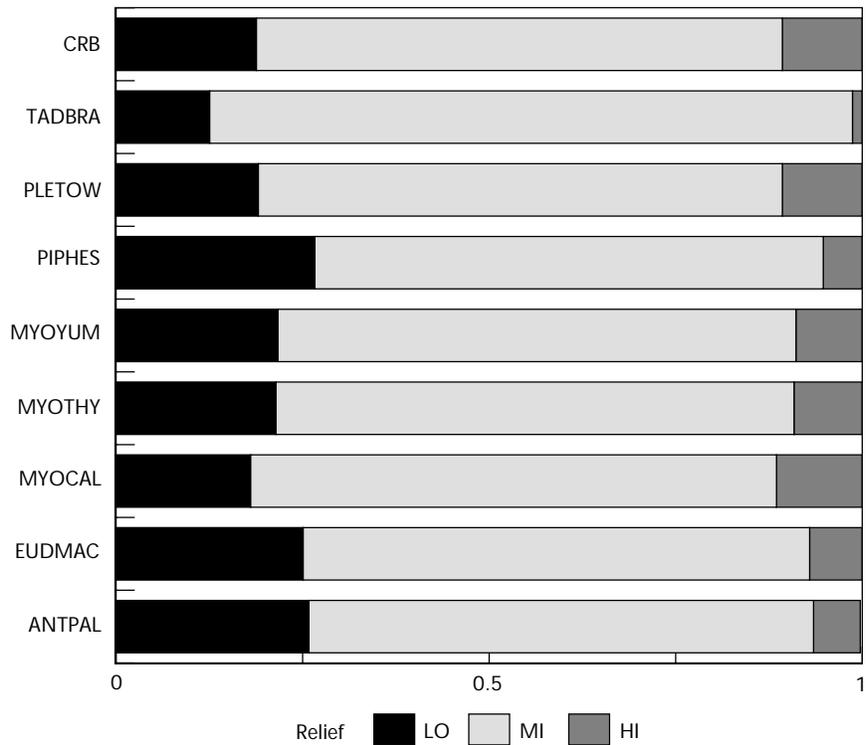
FIGURE 3C   *Topographic relief. Low = 0–305 m, mid = 306–1219 m, high = 1220–2438 m.*
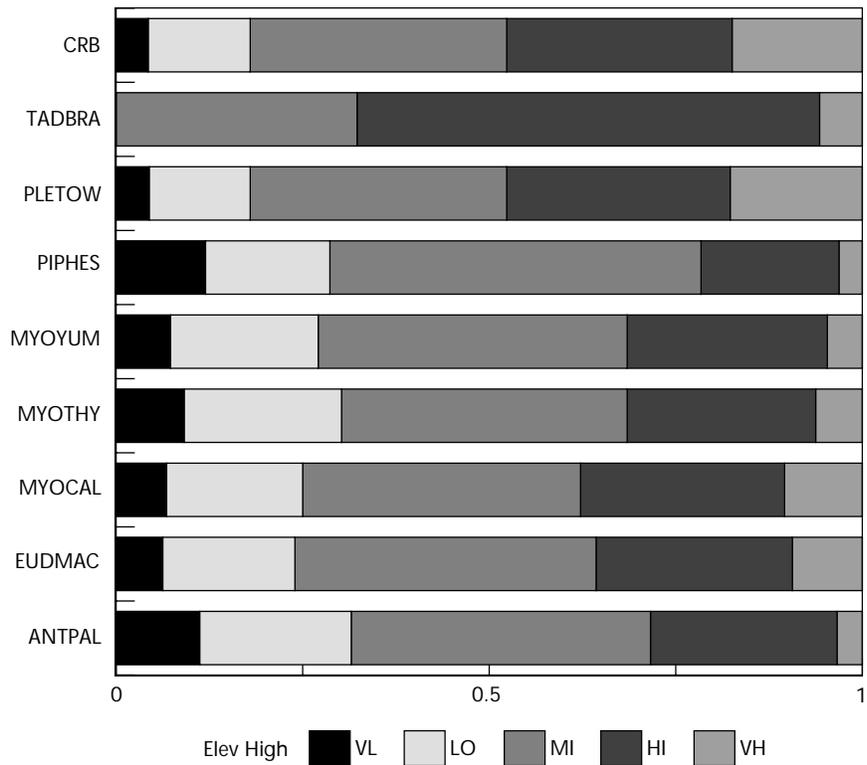
FIGURE 3D   *Highest elevation. Very low = 0–610 m, low = 611–1219 m, mid = 1220–1829 m, high = 1830–2348 m, very high = 2349+ m.*

Distribution of Bat Species

Fifteen species of bats among nine genera regularly occur within the CRB (Table 1). Seven species are ubiquitous in the CRB, although some of these are sparsely distributed. Another eight species occupy less than the full CRB area (Figure 1), in coverage ranging from *Tadarida brasiliensis*, which occurs only in southwestern Oregon, to the nearly ubiquitous *Myotis californicus* (Figure 2). By state within the CRB, bat species' richness decreases north and east, with 15 species in Oregon, 14 in Washington, 13 in Idaho, and 11 in Montana. This trend is likely due to area and heterogeneity of habitats of each state within the CRB.

Vegetation Cover Types and Structural Stages Used

No bat species is requisitely associated with a single vegetation cover type or structural stage (Appendix 1). Of all 36 vegetation cover types within the CRB, those used by most bats (> nine species) are two woodland and five forest types, including interior Douglas-fir forest and interior ponderosa pine forest (12 bat species). Those least used (< three bat species) include three oak and conifer forest cover types peripheral to the CRB area, and two native shrub cover types (Mountain Big Sage and Chokecherry/Serviceberry/Rose) that have suffered substantial historic declines (used by *Lasionycterus noctivagans* and *Corynorhinus townsendii*).

Among the vegetation structural stages, Closed Tall Shrub and Open Tall Shrub stages are the least used (< six bat species), whereas various woodland and forest stages are most used (>11 bat species) (Appendix 2). Old Single-stratum Forests and Old Multi-strata Forests—the old-growth forests of the CRB, which have suffered historic declines—are among the stages most used, each with an associated 13 bat species. Individual species probably vary in their response. *C. noctivagans* is closely associated with old forest stages in general. *C. townsendii* is likely affected by loss of

TABLE 1 *The fifteen species of bats regularly found within the interior Columbia River Basin, U.S.A.*

SPPCODE	Scientific name	Common name
ANTPAL	*Antrozous pallidus*	Pallid bat
EPTFUS	*Eptesicus fuscus*[1]	Big brown bat
EUDMAC	*Euderma maculatum*	Spotted bat
LASCIN	*Lasiurus cinereus*[1]	Hoary bat
LASNOC	*Lasionycteris noctivagans*[1]	Silver-haired bat
MYOCAL	*Myotis californicus*	California myotis
MYOCIL	*Myotis ciliolabrum*[1]	Western small-footed myotis
MYOEVO	*Myotis evotis*[1]	Long-eared myotis
MYOLUC	*Myotis lucifugus*[1]	Little brown myotis
MYOTHY	*Myotis thysanodes*	Fringed myotis
MYOVOL	*Myotis volans*[1]	Long-legged myotis
MYOYUM	*Myotis yumanensis*	Yuma myotis
PIPHES	*Pipistrellus hesperus*	Western pipistrelle
PLETOW	*Corynorhinus townsendii*	Pale western big-eared bat
TADBRA	*Tadarida brasiliensis*	Brazilian free-tailed bat

[1] Ubiquitous in the interior Columbia River Basin, U.S.A.

old-growth ponderosa pine (*Pinus ponderosa*) forests. *Myotis thysanodes* selects large (>58 cm diameter at breast height) snags in remaining old forests.

Myotis californicus and *Tadarida brasiliensis* can be thought of as the most specialized on macrohabitats, each using the fewest vegetation cover types (< six cover types, compared with a median of 14 cover types used per bat species). *M. californicus* is closely associated with forest cover types and *T. brasiliensis* with grassland cover types. *Pipistrellus hesperus* and *T. brasiliensis* are the most specialized on vegetation structural stages, each using < six stages (compared with a median of 10 structural stages used per bat species); they are closely associated with herb and shrub stages. *Eptesicus fuscus* and *Lasionycterus noctivagans* are the most generalized (each using >24 cover types and >12 structural stages) (Appendices 1 and 2).

Historic Trends of Habitat

All but three of the bat species have suffered declines in total area of their native habitats (vegetation cover types and structural stages) in the CRB since early historic times (Figure 4). Some of these declines may have occurred outside the historic ranges of individual species within the CRB, and these estimates do not account for changes in microhabitats and specific substrates used for roosting and breeding. Habitat of *Lasionycteris noctivagans* has declined the greatest in absolute area. Habitat has increased for two habitat generalists (*Eptesicus fuscus* and *Corynorhinus townsendii*) and one specialist (*Tadarida brasiliensis*, but this species occurs only in a small corner of the CRB).
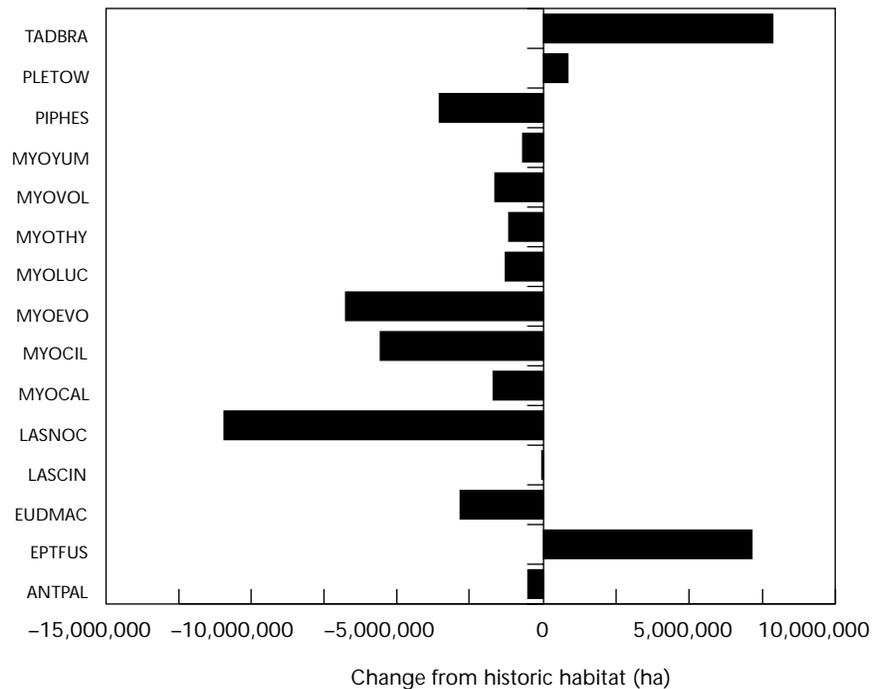
FIGURE 4 *Change in the amount of habitat from early historic (early 1800s) to current times for each of the 15 bat species of the Interior Columbia River Basin. Habitat amounts were based on vegetation cover types and structural stages listed in the appendices, applied to the entire Basin. See Table 1 for species codes.*

Declines in specific vegetation cover types, including native herblands, grasslands, sagebrush, and old forests, may have been accompanied by local declines in associated bat species, although data on bat population trends are lacking. Correlations are likely to be poor between some local bat populations and amount of habitat, defined here as gross vegetation cover types and structural stages. For example, although total area of habitat of *Corynorhinus townsendii* has increased, populations have declined. This is because microhabitats and specific substrates, as for roosting, and human disturbance, need to be additionally considered. However, provision of habitat is the first and most important need for conservation.

Macroecology

As a whole, bats within the CRB occur in all landforms (Figure 3a). However, *Tadarida brasiliensis* seems more associated with valleys and plains and less with mountainous landforms (Figure 3a), and with areas of somewhat higher precipitation (Figure 3b) and lower relief (Figure 3c) than generally available in the CRB. *Pipistrellus hesperus*, *Euderma maculatum*, and *Antrozous pallidus* also are somewhat less associated with mountains and are species more of drier valleys, plains, and foothills (Figures 3a and b) of moderate to low relief and elevation (Figures 3c and d). Species more associated with mountainous landforms include the seven ubiquitous species (Table 1), as well as *Myotis californicus* and *M. thysanodes* (neither associated with plains landforms), and *M. yumanensis* and *C. townsendii*.

Key Environmental Correlates

General associations with macrohabitats and biophysical characteristics, of course, are only part of the ecological story. Such associations are being used within the CRB to guide land-use planning on a broad scale. However, when broad-scale planning guidelines rank site-specific management actions, finer descriptions of habitats for conservation are needed. These are found in the listing of key environmental correlates (KECs) for each species (Table 2). KECs of the 15 bat species of the CRB were categorized into vegetation elements, biological non-vegetation elements, non-vegetation terrestrial substrates, riparian and aquatic bodies, and human disturbance elements.

The key forest vegetation elements for bats include snags (eight bat species out of 65 total vertebrate species often or primarily use snags); foliage and dead parts of live trees, as for roosting (four bat species out of 36 vertebrates); and exfoliating bark (four bat species out of six vertebrates). Also important to bat ecology are lithic substrates, used primarily by 13 bat species (out of 113 vertebrates). Specific lithic substrates used by bats are cliffs, talus, boulders, caves, outcrops/crevices, lava tubes, and canyons. Riparian and aquatic bodies used by bats include rivers, streams, ponds, and wetlands; these are used primarily by 10 bat species (out of 278 vertebrates) largely as foraging habitat.

Planning ecosystem management guidelines for bats also means addressing human disturbance elements, which can provide some (but not all) foraging and roosting requirements. These human disturbance elements used by some bats include little-used roads or trails (providing forest openings for aerial insect feeding), developments, buildings, bridges, agricultural developments, mines, and livestock guzzlers. However, it is as important to determine if such developments reduce KECs or habitats for

TABLE 2   *Key environmental correlates for bat species found in the interior Columbia River Basin, U.S.A. See Table 1 for species name codes. [] = total number of all vertebrate species within the Basin closely associated with the correlate. (Data and outline of correlates taken from a much longer classification system designed for all species [Marcot et al., in prep.].)*

1. Vegetation elements
    a. forest or woodland vegetation substrates
        i. snags (entire tree dead)—ANTPAL, EPTFUS, LASNOC, MYOCIL, MYOEVO, MYOLUC, MYOVOL, PLETOW [65]
        ii. live trees (as for roosting)—ANTPAL, LASCIN, MYOEVO, PLETOW [36]
            (1) exfoliating bark—LASNOC, MYOCAL, MYOLUC, MYOYUM [6]

2. Biological (non-vegetation) elements
    a. presence of nesting structures
        i. cavities (includes in structures, rocks, tree bark)—MYOCAL, MYOYUM [39]

3. Non-vegetation terrestrial substrates
    a. lithic (rock) substrates
        i. cliff—ANTPAL, EPTFUS, EUDMAC, MYOCIL, MYOEVO, PIPHES, PLETOW [55]
        ii. talus—MYOEVO [49]
        iii. boulder, large rocks—PLETOW [8]
        iv. cave—ANTPAL, EPTFUS, LASNOC, MYOCIL, MYOEVO, MYOLUC, MYOVOL, MYOYUM, PLETOW, TADBRA [26]
        v. rock outcrops/crevices—ANTPAL, EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOLUC, MYOVOL, MYOYUM, PIPHES [38]
        vi. lava tubes—TADBRA [2]
        vii. canyons—PIPHES [9]
    b. forages above tree canopy—LASCIN [11]

4. Riparian and aquatic bodies—EPTFUS, EUDMAC, LASCIN, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOYUM, PIPHES [278]
    a. rivers—ANTPAL, EPTFUS, MYOLUC [69]
    b. streams (permanent or seasonal)—LASCIN, MYOLUC [74]
    c. lakes or reservoirs (lacustrine)—ANTPAL, EPTFUS, LASCIN, MYOCAL, MYOLUC, MYOYUM [134]
    d. ponds (permanent or seasonal)—ANTPAL, EPTFUS, EUDMAC, LASCIN, MYOCAL, MYOLUC, MYOVOL, MYOYUM [96]
    e. wetlands, marshes, or wet meadows (palustrine)—EUDMAC, LASNOC [90]
    f. swamps—MYOCIL [7]

5. Human disturbance elements
    a. roads or trails (positive effect)—ANTPAL [6]
    b. residential development (positive effect)—MYOCAL, TADBRA [15]
    c. buildings (positive effect)—EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOVOL, MYOYUM, PLETOW, TADBRA [27]
    d. bridges (positive effect)—ANTPAL, EPTFUS, MYOEVO, PLETOW [9]
    e. agriculture and croplands (positive effect)—TABRA [84]
    f. mines and mining activities (positive effect)—EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOYUM, PLETOW [10]
    g. guzzlers (positive effect)—ANTPAL [1]

other bat and non-bat species, such as reduction in old forest stages. Also, direct disturbance of bat colonies in nurseries and hibernacula, particularly in caves, is of concern and should be regulated by management (White and Seginak 1987).

<div style="float:left; font-weight:bold; text-align:right;">Key Ecological
Functions</div>

Species, including bats, are more than just a function of their environment. Their ecological roles often affect the productivity and diversity of the ecosystems they inhabit. One key ecological function of all 15 bats of the CRB is predation of invertebrates, particularly insects. Although insectivory is shared among 225 vertebrate species of the CRB, seven of the bat species in particular might play key roles in controlling some forest and agricultural insect pests (Table 3).

Another key ecological function likely shared by all 15 bats of the CRB is that of aiding dispersal or concentration of nutrients. *Tadarida brasiliensis* produces guano so copiously that it can create and modify its own ecosystem. *Eptesicus fuscus* likely is important in aiding nutrient transport into subterranean environments; sometimes it is the only bat species occupying caves and mines in Idaho and Montana within the CRB, whereas elsewhere in the CRB *Corynorhinus townsendii* and *Myotis evotis* also play this role. *Lasionycteris noctivagans* may be an important agent for distributing riparian nutrients to upland environments as it travels from wetland foraging sites to forest roost sites. *L. noctivagans and L. cinereus* might aid in long-distance nutrient movement, as feeding and roosting sites can be separated by as far as 20 km.

Another key ecological function of *Eptesicus fuscus* and *L. noctivagans* is that of disease transmission, particularly rabies. *E. fuscus* is a potential threat as there are many contacts with humans and bites are known to draw blood.

In cave roosts, *Myotis evotis*, *Corynorhinus townsendii*, and possibly other species (from personal observation in northwestern California) also act as hosts in a coevolved relationship with a small group of specialized insects. These are the wingless, obligate ectoparasitic bat flies (Streblidae and Nycteribiidae: Diptera) and the bed bug *Cimex latipennis* (Cimicidae: Hemiptera).

The relation with *C. latipennis* bears further telling. In all its stages, it feeds on bats usually at roosts; it is an obligate sanguinivore, a blood-feeder. Like its Dipteran bat fly brethren, it is completely flightless and depends on bats for dispersal. It likely overwinters at roost sites whether or not bats are present, ensuring that it has ready access to the next arrivals. It is known to be associated only with *Myotis* and may control bat populations by excessive feeding on young bats, but there are no studies testing this hypothesis. It is not known to be a vector of disease as it is little studied.

Another key ecological function associated with bats is accumulation of pesticides (Clark 1981, 1988). *T. brasiliensis* may be more susceptible to pesticides than the other bat species due to its foraging in agricultural and rangeland habitats (Appendix 1). *Eptesicus fuscus* also may be susceptible. Use of selected pesticides is sometimes part of federal land management activities; for example, on federal lands of the CRB, use of any registered material to control western spruce budworm (*Choristoneura occidentalis*) is legal.

TABLE 3

TABLE 3   *Key ecological functions of bat species found in the interior Columbia River Basin, U.S.A. See Table 1 for species name codes. [] = total number of all vertebrate species within the Basin with the ecological function. (Outline of functions taken from a much longer classification system designed for all species [Marcot et al., in prep.].)*

I. Trophic relationships
  A. heterotrophic consumer
    1. secondary consumer (primary predator or carnivore)
      a. consumer or predator of invertebrates, including insects (insectivorous)—ALL 15 SPECIES [225]

II. Nutrient cycling relationships
  A. aids in physical transfer of substances for nutrient cycling (C,N,P, other)—ALL 15 SPECIES [33]

III. Interspecies relationships
  A. insect control[1]—EPTFUS, EUDMAC, LASNOC, MYOEVO, MYOLUC, MYOVOL, PLETOW [22]
  B. commensal or mutualist with other species[2]—MYOVOL [4, as affecting management]
  C. competitor[3]—EPTFUS [46, as affecting management]

IV. Disease, pathogen, parasite, and toxins relationships
  A. carrier, transmitter, or reservoir of vertebrate diseases (including rabies)[4]—EPTFUS, LASNOC [52]
  B. host for invertebrate obligate ectoparasites[5]—MYOTIS? OTHERS?
  C. accumulation of pesticides—ALL 15 SPECIES?

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[1] Interspecies relationships—insect control:
EPTFUS—Important consumer of agricultural pests; insect/predation control (e.g., pine beetles [*Dendroctonus* spp.: Scolytidae] and cucumber beetles [*Diabrotica* spp., *Acalymma* spp.: Chrysomelidae).
EUDMAC—May affect community structure of noctuid moths by selective pressure.
LASNOC—Important predator of forest pests. Moth and beetle strategist.
MYOEVO—Insect predator/controller. Important due to relatively large numbers and wide distribution at higher elevations.
MYOLUC—Insect control.
MYOVOL—Important insect predator/control agent due to sheer numbers.
PLETOW—Predator/control agent of agricultural and forest pests.
[2] Commensal or mutualist with other species:
MYOVOL—Communal rooster. Will share roost with other species.
[3] Competitor:
EPTFUS—May affect local distribution and habitat use by other bats. Known to chase off other bats.
[4] Carrier, transmitter, or reservoir of vertebrate diseases:
EPTFUS—Potential threat of rabies to humans. Have frequent contact with humans and are known to draw blood.
LASNOC—Higher incidence of rabies than other bats.
[5] Host for invertebrate obligate ectoparasites:
Myotis and others probably serve as host for wingless, invertebrate obligate ectoparasites (bat flies of Streblidae and Nycteribiidae, and the bed bug *Cimex latipennis* of Cimicidae).

Habitats and possibly populations of bats have mostly declined in the CRB since early historic times, the declines associated with conversion of native grasslands, shrublands, wetlands, and old forests. Current population viability of the 15 bat species in the CRB is largely unknown.

Bats of the CRB occupy a wide range of vegetation cover types and structural stages, but some species are closely associated with grassland/herbland and old forests for roosting, with riparian and aquatic bodies for foraging, and with lithic, crevice, and cave environments for roosting and nurseries. Others use a variety of human-built structures and human-altered environments.

Ecological roles of bats potentially contribute to nutrient cycling, insect population control, transmission of disease, and accumulation of pesticides. Bats also have the capacity to influence population levels of other species, including other bats and coevolved ectoparasites. They might play a key role in controlling population levels of insects, including forest and rangeland lepidoptera and agricultural and forest insect pests, although much of this needs greater study.

Such roles can influence ecological processes in a variety of ecological subsystems, including forest canopies, soils, subterranean environments, wetlands, and riparian areas. Bats might play a major but largely invisible role in enhancing productivity and trophic health, and affecting species diversity of these subsystems. Research is needed to determine specific rates to test this working hypothesis.

Integrating Bats into Ecosystem Management

One aim of ecosystem management is to consider the collective needs of multiple species. For bats, this means considering (1) their macrohabitat uses, depicted as vegetation cover types and structural stages; (2) their microhabitat requirements, depicted as KECs; (3) the range of ecosystems in which habitat management guidelines should be applied; and (4) how such guidelines also can serve to meet the needs of all other species (in this paper, I considered all other vertebrates; the current CRB planning project is also considering specific management needs for rare fungi, lichens, bryophytes, vascular plants, and selected invertebrates as well as all vertebrates).

Knowledge of bat ecology, such as snag and live-tree use, can help devise silvicultural activities in managed forests to meet needs of bats and other species simultaneously. Also likely important to managing population viability and long-term evolutionary potential of bats is maintaining seemingly marginal habitats (Gates et al. 1984). This would entail maintaining the full array of vegetation cover types, vegetation structural stages, and terrestrial, riparian, and aquatic substrates and environments used by the full array of bat species in the CRB.

The macroecology and collective environmental requirements of all 15 bat species also likely provides for a wide range of other species in forest, wetland, riparian, and other settings. Bats provide part, but not all, of the needs for all biota of the CRB. Of further interest in ecosystem management is knowledge of how disturbance dynamics of habitats influence suitability for bats and other species; this is little understood for bats of

the CRB. Coupled with an understanding of the key ecological functions that bats play in their sundry environments, and the fuller array of habitat conditions and disturbance conditions used by other species, a systems- and biodiversity-wide approach puts bat management into an ecosystem context.

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Veg. Code	ANT PAL	EPT FUS	EUD MAC	LAS CIN	LAS NOC	MYO CAL	MYO CIL	MYO EVO	MYO LUC	MYO THY	MYO VOL	MYO YUM	PIP HES	PLE TOW	TAD BRA
CRB003	×	×	×												×
CRB008		×	×	×	×			×						×	
CRBS01	×	×	×		×		×	×		×	×	×		×	
CRBS02	×	×	×		×	×	×		×	×				×	
CRBS03	×	×	×		×		×	×		×	×	×		×	
CRBS04			×		×		×	×			×		×	×	
CRBS05		×		×	×		×								
CRBS06	×		×		×		×	×							
CRBS07	×		×		×		×	×							
CRBS08	×	×	×											×	×
CRBS09		×		×	×			×			×				
CRBS10		×			×			×							
CRBS11		×		×	×			×							
CRBS12	×	×	×											×	×
CRBS13	×		×		×										
SAF205		×	×	×	×	×		×	×		×	×		×	
SAF206			×		×			×	×		×				
SAF208		×			×			×							
SAF210		×	×	×	×	×	×	×	×	×	×	×		×	
SAF212		×		×	×			×							
SAF215		×		×	×			×							
SAF217		×		×	×										
SAF218		×		×	×		×	×							
SAF219	×	×	×		×		×	×		×	×	×		×	
SAF227		×	×	×	×	×		×	×		×	×		×	
SAF233		×			×										
SAF235		×		×	×	×									
SAF237	×	×	×	×	×	×		×	×	×	×	×		×	
SAF243		×			×										
SAF245		×			×										
SRM104	×		×		×		×			×				×	
SRM322	×		×		×		×			×				×	
SRM402					×									×	
SRM406			×		×		×	×			×		×	×	
SRM414	×		×		×								×	×	×
SRM421					×										

Vegetation codes: CRB003 Shrub or Herb/Tree Regen, CRB008 Pacific Silver Fir/Mt Hemlock, CRBS01 Juniper Woodlands, CRBS02 Mixed Conifer Woodlands, CRBS03 Juniper/Sagebrush, CRBS04 Big Sagebrush, CRBS05 Shrub Wetlands, CRBS06 Agropyron Bunchgrass, CRBS07 Native Forbs, CRBS08 Exotic Forbs/Annual Grass, CRBS09 Grand Fir/White Fir, CRBS10 White Bark Pine/Alpine Larch, CRBS11 Red Fir, CRBS12 Cropland/Hay/Pasture, CRBS13 Fescue-Bunchgrass, SAF205 Mountain Hemlock, SAF206 Engelmann Spruce/Subalpine Fir, SAF208 Whitebark Pine, SAF210 Interior Douglas-fir, SAF212 Western Larch, SAF215 Western White Pine, SAF217 Aspen, SAF218 Lodgepole Pine, SAF219 Limber Pine, SAF227 Western Redcedar/Western Hemlock, SAF233 Oregon White Oak, SAF235 Cottonwood/Willow, SAF237 Interior Ponderosa Pine, SAF243 Sierra Nevada Mixed Conifer, SAF245 Pacific Ponderosa Pine, SRM104 Antelope Bitterbrush/Bluebunch Wheatgrass, SRM322 Mountain Mahogany, SRM402 Mountain Big Sagebrush, SRM406 Low Sage, SRM414 Salt Desert Shrub, SRM421 Chokecherry/Serviceberry/Rose.

APPENDIX 2 Occurrence (×) of 15 bat species of the interior Columbia River Basin, U.S.A., by vegetation structural stage (STR). See Table 1 for bat species name codes, and below for structure codes.

STR	ANT PAL	EPT FUS	EUD MAC	LAS CIN	LAS NOC	MYO CAL	MYO CIL	MYO EVO	MYO LUC	MYO THY	MYO VOL	MYO YUM	PIP HES	PLE TOW	TAD BRA
Ch	×	×	×		×		×	×		×			×	×	×
Clms	×	×	×	×	×		×	×		×	×		×	×	×
Ctss		×		×	×		×								
Ofm	×	×	×	×	×	×	×	×	×	×	×	×		×	
Ofs	×	×	×	×	×	×	×	×	×	×	×	×		×	
Oh	×	×	×		×		×	×		×			×	×	×
Olms	×	×	×	×	×		×	×		×	×		×	×	×
Ots	×	×	×		×										×
Sec		×	×	×	×	×	×	×	×	×	×	×		×	
Si	×	×	×	×	×	×	×	×	×	×	×	×		×	
Ur	×	×	×	×	×	×	×	×	×	×	×	×		×	
Wdl	×	×	×		×	×	×	×	×	×	×	×		×	
Yf		×	×	×	×	×	×	×	×	×	×	×		×	

Vegetation structural stages: Ch Closed Herbland, Clms Closed Low Shrub, Ctss Closed Tall Shrub, Ofm Old Multi-strata Forest, Ofs Old Single-strata Forest, Oh Open Herbland, Olms Open Low Shrub or Open Mid Shrub, Ots Open Tall Shrub, Sec Stem Exclusion Closed Canopy Forest, Si Stand Initiation Forest, Ur Understorey Reinitiation Forest, Wdl Woodland (Stand Initiation, Stem Exclusion, Understorey Reinitiation, Young Multi-strata, Old Multi-strata, or Old Single-strata), Yf Young Multi-strata Forest.

SECTION II BATS IN FORESTS

The Role of Research in Conserving Bats in Managed Forests

M. J. LACKI

ABSTRACT

Awareness of bats as an important component of forest ecosystems has only recently begun to receive attention by both research biologists and forest land managers. Data collection has focused primarily on identifying species composition, roost selection, and frequency of use among habitats, with the latter data usually not species specific. Co-ordinated efforts between research and management are now needed to answer questions related to the impacts of intended management programs on bats in forests, particularly the application of silvicultural prescriptions. Conserving populations of bats while achieving other forest management goals needs to be a primary focus. I present examples from Kentucky on how research biologists and forest land managers have co-ordinated efforts to enhance habitat for bats.

INTRODUCTION

Since the seminal work by Thomas (1988) that examined activity levels of bats among forest seral stages of varying age, a number of studies addressing questions on bats in forests have appeared. Research has emphasized identification of bat species (Miller 1990; Crampton 1994; Perkins et al. 1994); location of roosts (Kalcounis 1994; Morrell et al. 1994; Peterson and Perkins 1994; Rainey and Pierson 1994; Sasse and Pekins 1994; Vonhof 1994), and activity levels of bats among habitats (Helmer et al. 1990; Thomas 1991; Navo et al. 1992; Erickson 1993; Holroyd 1993; Stevens et al. 1993; Grindal 1994; Storz 1994; Burford and Lacki 1995), with activity levels used as a measure of habitat use. With a few exceptions (Navo et al. 1992; Storz 1994; Burford and Lacki 1995), most attempts to measure activity levels have not been species specific.

Co-ordinated efforts are now needed between research scientists and forest land management agencies to improve the quality of data collected and apply the information so that maximum benefits in habitat conservation for bats can be achieved. In this paper I review the present state of habitat management for bats in Kentucky, USA, and provide examples

of how combined efforts between research scientists and management personnel of the Daniel Boone National Forest, Kentucky, have enhanced habitat for bats in forests in eastern Kentucky.

METHODS

To determine the extent to which forest lands in Kentucky are being managed to promote the conservation of bats, I surveyed by telephone from June to September 1995, representatives of municipal, state, and federal agencies responsible for the management of public lands in Kentucky. I asked two basic questions of each respondent. First, has any land management action been implemented to enhance habitat suitability for bats? Second, was there any research completed to justify the proposed management action(s) taken? Respondents were permitted to elaborate to the extent that they felt was appropriate, and any additional information they provided was recorded.

I contacted a total of 12 agencies for information, including two municipal (Otter Creek Park, Raven Run Sanctuary), six state (Kentucky Chapter of the Nature Conservancy, Kentucky Department of Fish and Wildlife Resources, Kentucky Department of Parks, Kentucky Department of Transportation, Kentucky Division of Forestry, Kentucky State Nature Preserves Commission), and four federal (National Park Service, Tennessee Valley Authority, U.S. Department of Defense, U.S. Forest Service). With the exception of the Kentucky Chapter of the Nature Conservancy ($n = 2$), I contacted only one representative for information from each municipal and state agency; however, due to differences in management policies among federal land holdings within agencies, I contacted a separate representative of each federal land holding to ensure completeness and accuracy of the data.

I organized management actions as those pertaining directly to roosting habitat or to commuting and foraging habitat, and evaluated them separately. I divided research efforts into two categories, monitoring and original research. Original research projects were then categorized as either field studies, natural experiments, field experiments, or laboratory experiments, following Ratti and Garton (1994, pp. 16–17). I made no attempt to compare management and research actions taken among municipal, state, and federal agencies. Instead, my objective was to make an overall assessment of what was being accomplished statewide for the management and conservation of bats.

RESULTS AND DISCUSSION

Management of Bats in Kentucky

Kentucky is inhabited by 15 species of insectivorous bats, with the families Vespertilionidae ($n = 14$) and Molossidae ($n = 1$) represented (Barbour and Davis 1974). The sole molossid, *Tadarida brasiliensis*, is known only from one modern record and Pleistocene deposits in Mammoth Cave (Barbour and Davis 1974). Three species, *Myotis sodalis*, *M. grisescens*, and

Corynorhinus townsendii virginianus, are listed as federally endangered (United States Fish and Wildlife Service 1991), and an additional four species, *C. rafinesquii*, *M. austroriparius*, *M. leibii*, and *Nycticeius humeralis*, are listed as threatened or endangered in Kentucky by the state heritage program (Kentucky State Nature Preserves Commission 1994).

Of the agencies surveyed, 66.7% ($n = 8$) actively manage roosting habitat (e.g., caves and mines) for bats (Table 1). A total of 65 roosts receive some form of active management to regulate human intrusion, including gating ($n = 28$), fencing ($n = 2$), or posted signs ($n = 35$), with the latter category referring to roosts not gated or fenced; almost all gated or fenced roosts also have posted signs. The Daniel Boone National Forest (USFS) has closed several roads, and in one case re-routed a road to increase the level of protection at roosts. With the exception ($n = 15$ mine portals) of Big South Fork National River and Recreation Area (NPS), all roosts that have been gated or fenced contain at least one federally endangered bat at some time during the year. Several respondents indicated that plans are underway to gate or fence additional roosts.

Other structures used as roosts are wells and cisterns located on Land Between the Lakes (TVA). These structures are left open depending on consultation with the U.S. Fish and Wildlife Service. Three agencies actively put up bat boxes: Raven Run Sanctuary, Kentucky Department of Fish and Wildlife Resources, and the Daniel Boone National Forest.

TABLE 1   *Management for bats and research programs by public land agencies in Kentucky, U.S.A.*

Agency[a]	Management roosting habitat	Number cave/mine roosts	Population monitoring	Management foraging habitat	Original research
Municipal					
OCP	yes	1	yes	none	none
RRS	none	—	none	none	none
State					
KCNC	yes	2	yes	yes	yes
KDFWR	yes	1	none	yes	none
KDP	yes	2	yes	none	none
KDT	none	—	yes	yes	none
KDF	none	—	none	yes	none
KSNPC	yes	2	none	yes	none
Federal					
NPS	yes	22	yes	yes	yes
TVA	none	—	none	yes	yes
USDD	yes	1	none	yes	yes
USFS	yes	34	yes	yes	yes

[a] Abbreviations for land agencies are Otter Creek Park (OCP), Raven Run Sanctuary (RRS), Kentucky Chapter of the Nature Conservancy (KCNC), Kentucky Department of Fish and Wildlife Resources (KDFWR), Kentucky Department of Parks (KDP), Kentucky Department of Transportation (KDT), Kentucky Division of Forestry (KDF), Kentucky State Nature Preserves Commission (KSNPC), National Park Service (NPS), Tennessee Valley Authority (TVA), U.S. Department of Defense (USDD), and U.S. Forest Service (USFS).

Among those agencies responsible for the management of bat roosts, 62.5% ($n = 5$) monitor population levels (Table 1). In addition, the Kentucky Department of Transportation monitors summer roost trees harbouring maternity colonies of bats in construction-zone rights-of-way, with removal of roost trees taking place outside the maternity season. In a few instances the Department of Transportation altered site selection to avoid loss of roost trees.

Nine agencies (75%) manage their forest lands, at least in part, to provide commuting, foraging, or summer roosting habitat (Table 2). Establishment of no-timber-harvest zones and protection of stream corridors are the most common management practices. The Kentucky Division of Forestry maintains a co-operative relationship with Carter Caves State Resort Park and has established a no-timber-removal policy on the adjacent Tygarts State Forest to protect foraging habitat for the colony of *M. sodalis* that hibernates in a cave in the park. Interestingly, no comparable program for management of foraging habitat is in place for Carter Caves State Resort Park. Cumberland Gap National Historical Park (NPS) has established a moratorium on timber removal, one aim of which is to protect summer roosting habitat of *M. sodalis*. The Daniel Boone National Forest maintains a Cliffline Management Policy to protect roosting and foraging habitat of *C. townsendii virginianus* and *C. rafinesquii*, along with other sensitive animal and plant species. Under this policy, a 92-metre-wide strip of forest, 61 m below cliffs and 31 m above cliffs, is protected within the known range of *C. townsendii virginianus* and within 1.6 km of roosts of *C. rafinesquii*. Further, no timber harvest is permitted within a 0.4-km radius, no-disturbance zone surrounding any known roost of either of these two species. The Daniel Boone National Forest is in the process of developing a summer habitat management policy for *M. sodalis*, with this policy to be based primarily upon the Habitat Suitability Index model for *M. sodalis* developed by 3D/Environmental in co-operation with the Indiana Department of Natural Resources for the U.S. Fish and Wildlife Service (Romme et al. 1995).

TABLE 2   *Forest management practices for bats applied by public land agencies in Kentucky, U.S.A.*

Agency[a]	No-harvest zones	Midstorey removal	Burning	Streamside management	Snag management	Woodland ponds	Wildlife openings
State							
KDFWR	—	—	—	—	—	—	yes
KCNC	—	—	—	—	—	—	yes
KDT	—	—	—	yes	roosts	—	—
KDF	1 site	—	—	—	—	—	—
KSNPC	yes	—	—	—	—	—	—
Federal							
NPS	1 park	—	—	—	—	—	—
TVA	—	—	—	yes	—	—	—
USDD	—	—	—	yes	—	—	—
USFS	yes	73 ha	364 ha	yes	14/ha	328	120 ha

[a] Abbreviations for land agencies are as in Table 1.

Respondents indicated that management of stream corridors is based on the U.S. Fish and Wildlife Service's guidelines for protecting habitat of *M. sodalis* (U.S. Fish and Wildlife Service 1983). Other management practices that have been implemented for bats include midstory removal, burning, maintaining snags, construction of woodland ponds, and maintaining wildlife openings, with the preponderance of activity taking place in the Daniel Boone National Forest (Table 2). Midstory removal and burning in stands of timber on the Daniel Boone National Forest has occurred on the southern ranger districts where the federally endangered, red-cockaded woodpecker (*Picoides borealis*) coexists with *C. rafinesquii*, a species that is threatened in Kentucky (Kentucky State Nature Preserves Commission 1994). These practices are designed to reduce predation at nest cavities of *P. borealis* and to enhance foraging habitat for both species.

Research on Bats in Kentucky Forests

Respondents from five agencies (41.7%), the Kentucky Chapter of the Nature Conservancy, National Park Service, Tennessee Valley Authority, U.S. Department of Defense, and U.S. Forest Service, indicated that original research was supported on some facet of bat ecology, distribution, or association with a management practice. All projects qualified as field studies based on Ratti and Garton's criteria (1994), with the possible exception of an analysis of metal loadings in guano of *M. grisescens* that required laboratory analyses (Lacki 1994). No study was based on a natural experiment or a field experiment.

Mist netting surveys were funded by all five agencies, except the National Park Service where survey efforts focused on inventory of bats using mine portals as hibernacula. The Daniel Boone National Forest was the only land agency to finance more than one project ($n = 4$) and the only agency to examine the suitability of current management practices for bats (Adam et al. 1994; Burford and Lacki 1995; K. Huie-Netting, EKU, unpubl. data; J. Kiser, EKU, unpubl. data). Extensive surveys of cliffs and adjacent habitats were also completed by U.S. Forest Service personnel in each ranger district of the Daniel Boone National Forest.

Coordinated Research and Management of Bats

The Daniel Boone National Forest encompasses approximately 271,000 ha and is located in the Cumberland Plateau physiographic region in eastern Kentucky. The terrain is rugged with an extensive series of cliffs present in much of the region. Mixed mesophytic forest is the predominant vegetative cover, and due to past logging practices is composed of stands of timber of varying age.

The U.S. Forest Service began supporting externally funded research on bats in the Daniel Boone National Forest in 1990. Initial efforts focused on foraging habitat requirements of maternity and bachelor colonies of *C. townsendii virginianus*, a federally endangered species that hibernates primarily in a single cave in Kentucky (Lacki et al. 1994). The initial research phase had two objectives. First, to establish the size of foraging areas used by the bats in these colonies and, second, to identify habitats important to foraging bats. The overall goal was to evaluate the appropriateness of the Cliffline Management Policy, described previously, for protecting habitat of *C. townsendii virginianus*. Studies of radio-tagged bats demonstrated considerable movement, with bats observed up to 8.4 km

from roosts, and wide variation in foraging area size tracking periods (Adam et al. 1994). Evaluation of habitat use by radio-tagged bats demonstrated extensive use of cliffs (Adam et al. 1994) reinforcing the need for a Cliffline Management Policy; however, the analysis chosen also showed forest habitat to be important, but did not resolve differences in the condition of forest habitat (e.g., stand age or silvicultural prescription).

A subsequent project examined activity of bats in five habitats using ultrasonic detectors, with all sites selected within the known foraging areas of *C. townsendii virginianus*, and detectors set at the frequency best suited to detect this species. Results showed low activity in stands of timber <30 years of age, in stands of timber ≥30 years of age, and at the bases of cliffs, with high levels of activity on clifftops and in old fields (Burford and Lacki 1995). These results further supported the need for the Cliffline Management Policy and identified openings (e.g., old fields) as foraging habitat of *C. townsendii virginianus*. This research supported an existing management program on the Daniel Boone National Forest of maintaining wildlife openings as habitat for game species, and provided a solid research base to extend the creation of more openings forest-wide as foraging habitat for bats (Table 2). The importance of openings was further substantiated by a simultaneous investigation of food habits of *C. townsendii virginianus* (Shoemaker 1994) that demonstrated consumption by this bat of moths whose larvae feed on agricultural and old field plants, as well as moths whose larvae feed on woody plants.

These research efforts were supplemented with mist netting near the entrance to roosts. Placement of mist nets over road-rut ponds and adjacent to woodland ponds proved to be extremely successful locations for capturing bats, including *C. townsendii virginianus* (J. MacGregor, USFS, unpubl. data). Consequently, a program of constructing woodland ponds and maintaining road-rut ponds was established in the forest to provide drinking sites for bats as well as habitat for amphibians. Considerable progress has been made in the construction of woodland ponds (Table 2), with an expected increase in pond placement such that no pond is more than 0.4 to 0.8 km from an adjacent pond (S. Bonney, KDFWR, pers. comm.). A research project contracted out to Eastern Kentucky University is now examining use of woodland ponds by bats in the forest (K. Huie-Netting, EKU, unpubl. data).

Concern was expressed by management staff of the Daniel Boone National Forest over the need to increase the level of protection at the hibernaculum of *C. townsendii virginianus*. Gating the cave was discussed, but was viewed as potentially harmful as bats occupy the cave year-round. A concurrent phase of monitoring population levels of *C. townsendii virginianus* in the cave over a period of three years (1990–92) showed seasonal fluctuation in population levels, with consistently low numbers of bats inside the cave in August (Lacki et al. 1994). The cave was gated during 11 to 14 August 1993, despite higher numbers present than were recorded previously in mid-August (J. MacGregor, USFS, unpubl. data). Subsequent monitoring efforts in winter months show the population of *C. townsendii virginianus* to remain stable (Figure 1). This cave is also used as a hibernaculum by *M. sodalis*, with this population also remaining unchanged (Figure 1).
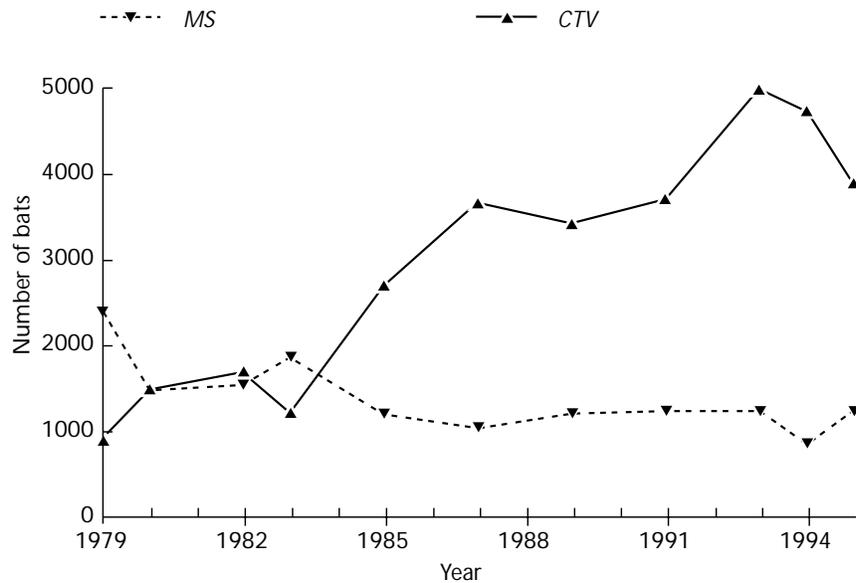
FIGURE 1 *Population estimates for hibernating* Corynorhinus townsendii virgin-
ianus *and* Myotis sodalis *in a cave in Lee County, Kentucky, USA. The
entrance was gated from 11 to 14 August 1993.*

**Management
Implications**

These examples demonstrate that research and management can be co-
ordinated to enhance habitat conditions for bats in forests. Research
results have been important in the development of management policies
on the Daniel Boone National Forest targeting habitat enhancement for
bats, including construction of woodland ponds, creation and mainte-
nance of wildlife openings, and protection of cliffs and roosts. Additional
research projects are underway to evaluate autumn foraging and roost
requirements of *M. sodalis* (J. Kiser, EKU, unpubl. data) and summer for-
aging requirements of *C. rafinesquii* (T. Hurst, UK, unpubl. data). Com-
munication is the key to this process as research biologists and land
managers have different agendas, and may not always agree on the inter-
pretation and meaning of the data. I believe it is extremely important for
research biologists to clearly convey the assumptions and limitations
behind the research methods chosen, especially in written research pro-
posals, as these have a significant bearing on interpretation and eventual
application of data to the management process.

Survey data clearly demonstrate that, although bats receive some atten-
tion by most land management agencies in Kentucky, there is a consider-
able need for improvement (Tables 1 and 2). With the exception of the
Daniel Boone National Forest, limited research into the habitat require-
ments of most bat species on public forest lands in Kentucky has been
completed. Further, the relationship between silvicultural prescription and
habitat suitability has been largely ignored. There are few data to substan-
tiate the establishment of no-harvest zones as a management option for
enhancing habitat for bats, a common silvicultural prescription for bats in
Kentucky (Table 2). The one possible exception to this would be stands of
timber in the immediate vicinity of caves used as roosts (Adam et al. 1994;
J. Kiser, EKU, unpubl. data; T. Hurst, UK, unpubl. data). Clearly, more
data are needed to determine habitat use of bats in relation to silvicultural

prescriptions. Due to shifts in the preferred choice of silvicultural prescription over the past several decades, managed forests have undergone extensive change in plant species composition, distribution and frequency of stand age classes, and structural characteristics within stands. Suppression of fire, prescribed burning, clearcutting, shelterwood cutting, selective logging, highgrading, and patch cuts have all been used in Kentucky. Given that historical patterns of habitat use by bats are unknown, neither the present conditions or the observed patterns of use are likely to be representative of what constituted habitat for bats under presettlement conditions. Determining whether managed forests can support populations of bats at higher densities will require experimentation into several available silvicultural options.

Survey results indicated that field studies were the predominant research approach taken for identifying habitat needs of bats in forests in Kentucky. Field studies are limited in their inference because they are based on comparisons between groups that already possess the characteristics of interest (Ratti and Garton 1994). I suggest that field experiments, where treatments (e.g., silvicultural prescriptions) are randomly assigned within the known distribution of roosts and foraging areas of bat species, would strengthen our understanding of habitat requirements of bats in forests. Achievement of successfully designed field experiments will require co-operation between research biologists and land managers. This approach has the advantage of an established baseline, against which long-term monitoring of responses by bats can be compared.

ACKNOWLEDGEMENTS

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Bats and Trees in Britain

MIKE HOLMES

In Britain, all species of bats are protected. Any structure that they use as a shelter, whether the bats are actually using it at the time or not, is also protected. This means buildings, but must also include trees. Unfortunately the "law can be an ass," and as we shall see, this one is meaningless in many ways.

There are 14 species of bats listed for the British Isles and all are dependent on trees in some way, at some period of the year, although for two only as hunting habitat. These are the Greater and Lesser Horseshoe (*Rhinolophus* spp.). Others are almost totally tree-dependent. They are the Noctule (*Nyctalus noctula*), its smaller cousin the Leislers (*Nyctalus leisleri*), plus the very rare Bechsteins (*Myotis bechsteinii*) and Barbastelle (*Barbastella barbastellus*).

As in other parts of the world, hollow trunks provide hibernation sites whilst old woodpecker holes and cracks in branches are excellent for other roost requirements. If you cut these trees down, you destroy the bats' homes. Various insect species are symbiotic with native tree species. Four hundred species are associated with the English oak (*Quercus robur*). The insects are the bats' food, and when the trees are cut down, you take away the food source. Home and food have gone, so that is the end of the bats. It is happening all over the world. Since 1945, about 35% of the remaining woodland has been cleared for agriculture throughout Britain. One agricultural industrialist who causes habitat destruction in a really bad way told me that oak trees were no longer necessary as the British Navy no longer builds wooden ships!

Many estates have an overpowering desire to tidy up the countryside and turn it into a city park landscape. Old trees have to come down just because they look untidy. The Royal Family recently decided that all the ancient oaks at Windsor, their home just outside London, should come down. The idea is extraordinary. My Royalist loyalties get further stretched! Luckily they were saved because of the force of public opinion.

Trees are thought to be dangerous, often quite incorrectly, and sentenced to death. Highways departments are the most pernicious on this score. Old trees by the roadside are being steadily removed.

Even some trees that are home to bats are not saved entirely. They are just lopped back instead of being felled. Unfortunately, the lopping may include the limb that contained the bats. The safety laws—if you like to call them that—are higher up the pecking order than the laws looking after bats. The old trees in question are, of course, the ones that provide roost sites and food sources.

The destruction is not only in woodland; tree lines and hedgerows throughout lowland Britain are being cleared to make larger field systems as dictated by modern agriculture. Tree lines are essential for bats. Many species follow them as a navigation system and will not cross open country. They provide protection from predators, such as owls, and are a shelter from wind. The wind shelter is essential for insects; without it, they will not fly. So—no shelter—no food for bats.

Since the Second World War, almost all species of bats in Britain have decreased by over 60%. The continuing destruction of habitat (that means trees) must be a major reason. There are others of course, but at present, this could be the worst.

In the Bronze Age, a system of woodland management was developed that was highly friendly to wildlife; known as coppice and standards, it allowed light to reach the forest floor and neighbouring areas in rotation; thus, the ground plants could flourish and consequently, insects also flourished: a food chain was created.

The Second World War changed all the old ways of working the countryside, including forestry. Woodland was left to grow; a 100% canopy cover stopped floor growth. Clear felling of quick-growth, non-native conifers prevailed. Insect numbers were greatly reduced.

Poor Old Bats

I worked partly in woodland management. Now and again I heard horrific stories of chain-saw massacres and the death of colonies as old, broadleaved trees were felled. These happenings were usually hushed up, but I picked up whispers. Bats in torpor cannot wake up and escape quickly enough to avoid these operations. Though some cutters showed concern, the work is cost-high and time cannot be lost looking after bats.

A number of us are now trying to tackle the problem. The actual clear felling of deciduous native woodland has pretty well stopped in the U.K. There are widespread replanting schemes, but it will be a long time before these young forests fill the requirements for bat habitat.

What has not stopped is the widespread destruction of old, overmature trees, and I see little hope on this score. As ever, the basic problem is the lack of knowledge, understanding, and interest in bats, which, of course, boils down to education.

A lot of us work with schools. The interest shown by children at the primary stage is really great. I walk into a number of schools and am greeted with excited friendly cries of "Hello, Batman," but it will be a long time before these children can do any more than influence their parents through their enthusiasm.

But the people to get to are those actually working with trees. In the southeast of England last February, we held a symposium. We invited about 150 people who were responsible in one way or another for the management of forests, woodland both private and public, and work on individual trees.

We were not preaching to the converted. We tried to raise people's awareness of and their interest in bats, and to give an idea of guidelines that should be followed. In fact, we were successful in many quarters and did generate a lot of co-operation. Our necessary work is to keep that co-operation and interest going and spread it through the country without getting people fed up with our attentions.

A number of organizations have asked for co-operation in producing guidelines for their work when there is a danger of it clashing with bat interests. The Bat Conservation Trust is working to produce a leaflet, *Bats and Trees*. Other conservation organizations are interested in producing their own—the more the merrier—more people will be made aware.

There are, though, many obstacles, one of which is the law. The Act that protects bats is badly worded and way down the pecking order. Even if it can be proved that bats use a tree for shelter, as it is termed, that tree has to come down, if it is said to be in a dangerous state where people may be endangered. Also, the law's wording states that one may not intentionally do anything to harm bats. "Intentionally" is not possible to prove, in practice, in a court of law.

I will end on a more hopeful note—we are trying and are having some success in making people think about bats and their use of trees, together with the danger that exists for bats in those trees.

But, . . . it is hard work.

SECTION III   ROOSTING

Roosting Behaviour of Silver-haired Bats (*Lasionycteris noctivagans*) and Big Brown Bats (*Eptesicus fuscus*) in Northeast Oregon

BURR J. BETTS

ABSTRACT

I used telemetry to locate maternity roost sites of four *Eptesicus fuscus* and five *Lasionycteris noctivagans* in northeast Oregon, and I measured characteristics of the roost tree, roost site itself, and surrounding habitat. I also recorded the frequency and distance of roost shifts and the size of some maternity colonies. Both species used large live and dead trees with the diameter of the trees used by *E. fuscus* being significantly larger than those used by *L. noctivagans*. Roost sites were high, uncluttered, and faced no particular direction. None of these features differed significantly between the two species. Trees used by *E. fuscus* were in significantly more open forest on flat terrain than those used by *L. noctivagans*. *E. fuscus* tended to have larger maternity colonies than *L. noctivagans*. Bats of both species changed roost trees frequently. *E. fuscus* moved farther between trees than did *L. noctivagans*, most of which remained in the same drainage. Because of roost-tree lability and the need for large trees as maternity roosts, it is important that forest planners retain large trees when laying out salvage and green timber sales.

INTRODUCTION

Until a few years ago most of the information we had on bat roosts and roosting behaviour came from observations made at artificial structures or at mines and caves. Other than occasional serendipitous observations, little was known about the use of trees as roost sites. As the miniaturization of radio transmitters has progressed, we have applied telemetry to filling this knowledge gap. The first detailed telemetry studies on roost sites in Nearctic forests were by Brigham (1991) and six speakers at the 24th Annual North American Symposium on Bat Research in Ixtapa, Mexico in October 1994 (Crampton 1994; Kalcounis 1994; Morrell et al. 1994; Rainey and Pierson 1994; Sasse and Pekins 1994; Vonhof 1994). In addition, there are eight papers in this volume that address Nearctic forest roost sites and behaviour.

Studies of the same species in different locales and of different species in the same locale are valuable for identifying intraspecific and interspecific variations in roost-site selection and behaviour. Such comparative studies should allow us to identify generalizations regarding the important characteristics of roost trees and surrounding habitat. They also should enable us to identify differences in roost choice and fidelity and the ecological conditions producing this variation. Forest maternity roost trees of big brown bats (*Eptesicus fuscus*) and/or silver-haired bats (*Lasionycteris noctivagans*) have been described in studies from Saskatchewan (Kalcounis 1994), British Columbia (Brigham 1991; Vonhof 1994), Alberta (Crampton 1994), and northern California (Rainey and Pierson 1994). The purposes of my study were (1) to describe the characteristics of maternity roost trees and the surrounding habitat, and (2) to document roost fidelity and the frequency and distance of roost shifts of *E. fuscus* and *L. noctivagans* in northeast Oregon.

MATERIALS AND METHODS

I conducted this study in the Spring Creek area approximately 20 km west of La Grande, Oregon. This area (45° 19′N, 118° 19′W), which is heavily managed by the United States Forest Service, is a mosaic of pine and fir forest patches of differing age, species composition, and openness, and contains several artificial stock ponds. Summers in northeast Oregon are typically hot and dry. Over the last 10 years maximum temperature, minimum temperature, and total precipitation have averaged 27.3°C, 10.9°C, and 26.9 mm, respectively, for June to August.

In 1994, six *E. fuscus* were captured in mist nets at Upper Hunter Pond on 20–21 June. To the back of each I glued a radio transmitter (model BD-1, Holohil Systems Ltd., 112 John Cavanagh Road, Carp, Ontario, KOA 1L0, Canada) with Skin-Bond cement (Smith & Nephew United, Inc., Largo, FL 34643, USA). Palpation indicated that all six bats were pregnant and near parturition. The signals from two of these bats were not detected after the night of release, and because of equipment problems none of the bats were located until 29 June. Thereafter the position of each transmitter was determined daily with a Telonics TR-2 receiver and a two-element antenna (Telonics, 932 E. Impala Avenue, Mesa, AZ 85204, USA) until it no longer moved during two successive nights, which occurred on 8 July for the last transmitter. Bats continued to emerge from two of the trees in which there were non-moving transmitters. The four bats carried the transmitters an average of 15 days.

In 1995, I caught five *L. noctivagans* and attached transmitters in the same manner as described above. These bats were captured on 17 July at Tip Top Pond, approximately 1.5 km south of Upper Hunter Pond. Presumably, because of the cold, rainy spring and early summer in 1995, parturition was delayed. Two of the bats were lactating and three were pregnant. I followed them until 2 August. They carried their radios for an average of 10 days.

I observed bats emerging from seven trees on 13 nights to determine the exact location of the roost site and to count the colony size. Roost

sites in five other trees were identified with telemetry. I determined the species, condition (live, snag), height, and diameter at breast height (DBH) of each roost tree. If the specific location of the roost site was known, I noted the compass direction it faced and the openness of the habitat around it. To determine the latter, I imagined a half-sphere, 6 m in diameter, centred on the roost site, and then estimated the percentage of this area unobstructed by limbs or other obstacles. At the location of each tree I measured the gradient and aspect of the slope and average canopy cover (taken 3 m N, E, S, and W of the tree). As an indicator of forest density near each roost tree, I measured the diameter of each tree >5 cm DBH and calculated the total stem area within a 0.1 ha circular plot centred on each tree. Finally, I used large-scale maps to measure the distance between successive roost trees.

I used non-parametric statistics in all analyses to avoid making assumptions about data distribution. Average values are reported as mean ± 1 sd.

RESULTS

Seven and 11 roost trees were located for *E. fuscus* and *L. noctivagans*, respectively (Table 1). All the live trees used as roosts had some defect, such as dead branches, a broken top, or a split trunk that indicated internal decay. A cavity or crack was visible in the area of the defect for five of the six live roost trees. All the snags had cracks and cavities; most had some branches and loose bark. The two species of bats differed primarily in the use of live trees versus snags, but this difference was not significant (Table 1). Also, *L. noctivagans* used several grand fir (*Abies grandis*) as well as ponderosa pine (*Pinus ponderosa*), while *E. fuscus* used ponderosa pine almost exclusively. Two *E. fuscus* used the same cottonwood (*Populus trichocarpa*) and two *L. noctivagans* used the same western larch (*Larix occidentalis*).

TABLE 1 *Characteristics of roost trees used by* Eptesicus fuscus *and* Lasionycteris noctivagans *in northeast Oregon, 1994–95.*

Tree	*E. fuscus*	*L. noctivagans*	*P*
Species			
Ponderosa pine (live)	4	1	—
Ponderosa pine (snag)	2	5	—
Grand fir (snag)	0	4	—
Western larch (live)	0	1	—
Cottonwood (snag)	1	0	—
Total live, dead	4, 3	2, 9	>0.05[a]
Height (m)	18.0 ± 6.5	24.0 ± 9.2	>0.05[b]
DBH (cm)	76.3 ± 12.2	59.6 ± 13.9	0.037[b]

[a] Fisher Exact Probability Test.
[b] Mann-Whitney U Test.

The trees used by *L. noctivagans* were significantly smaller in diameter than those used by *E. fuscus*, but they did not differ significantly in height (Table 1). *E. fuscus* roost sites included a broken top, a woodpecker cavity, a split cavity next to a dead limb, and the top of a lightning-split trunk. Of the eight roost locations determined for *L. noctivagans*, one was under bark and the other seven were woodpecker cavities. The direction of the roost opening varied considerably within each species, ranging from 5°–350° for *E. fuscus* and from 25°–270° for *L. noctivagans*. There were no significant interspecific differences in the height of the roost site or the openness of the habitat around it (Table 2). Between 30 July–2 August, 1995 I determined the time at which sunlight first reached the roost site in the morning and left it in the evening for six *L. noctivagans* roosts sites. The average elapsed time between first morning and last evening solar exposure was 12.7 ± 0.6 h. Exposure time earlier in the season, when young were small, would have been even longer.

The roost trees used by *E. fuscus* were mostly on ridge tops in open pine forest, whereas those used by *L. noctivagans* were on denser forested slopes. This subjective evaluation is supported by significant differences between the two species in slope gradient, canopy cover, and stem area in the surrounding 0.1 ha (Table 3). Slope aspect varied considerably, ranging from 20°–340° for each species.

Two of the *E. fuscus* used at least four different trees each during the study period and were together in two of them. These six trees formed a fairly linear group across three ridges with the greatest distance between trees being 2.1 km. These trees ranged from 0.45–2.4 km from the capture site at Upper Hunter Pond. The other two *E. fuscus* remained in the same tree the entire time that they carried transmitters. This tree was a barkless, cottonwood snag in a broad, flat creek bottom 3.8 km from Upper Hunter Pond. The five *L. noctivagans* occupied at least 2, 4, 4, 2, and 2 trees, respectively. These are minimum numbers because I could not determine

TABLE 2 *Height and habitat openness of roost sites used by* Eptesicus fuscus *and* Lasionycteris noctivagans *in northeast Oregon, 1994–95.*

	E. fuscus	*L. noctivagans*	*P*[a]
Height (m)	10.5 ± 2.4	13.3 ± 5.5	> 0.05
Openness (%)	93.0 ± 8.8	98.0 ± 2.3	> 0.05

[a] Mann-Whitney U Test.

TABLE 3 *Habitat characteristics around roost trees used by* Eptesicus fuscus *and* Lasionycteris noctivagans *in northeast Oregon, 1994–95.*

	E. fuscus	*L. noctivagans*	*P*[a]
Sample size	7	11	—
Slope gradient (%)	12.3 ± 8.9	3.5 ± 12.7	0.0372
Canopy cover (%)	25.0 ± 16.7	42.2 ± 12.9	0.0236
Stem area (m²)/0.1 ha	1.1 ± 0.2	2.6 ± 1.1	0.0008

[a] Mann-Whitney U Test.

their locations every day. One of the bats that used four different trees twice moved back and forth between two of them. One bat spent three days at a site more than 5 km from the capture site at Tip Top Pond, and then moved to a tree only 0.2 km from the pond. With this exception, all the *L. noctivagans* stayed within the same drainage. The average distance moved between successive trees was significantly different for the two species (*E. fuscus*: 0.83 ± 0.81 km, n = 5; *L. noctivagans*: 0.12 ± 0.05 km, n = 8; Mann-Whitney U = 3, *p* = 0.016).

Although the data are limited, I found more *E. fuscus* roosting together than *L. noctivagans*. I observed 69 *E. fuscus*, including two carrying transmitters, emerge from one roost tree, but only five emerged from this tree on each of the following two evenings. A week later, I observed 46 *E. fuscus* exit another tree, again including the same two bats carrying transmitters. No bats emerged from this tree four days later. Three groups of *L. noctivagans* were observed exiting five trees on eight nights. Each group contained one bat with a transmitter. Group size ranged from 3 to 16 individuals.

DISCUSSION

In her review of roost fidelity of bats, Lewis (1995) identified five benefits of roost lability, including predator avoidance, escape from disturbance, parasite load reduction, avoidance of unfavourable microclimate, and reduction of commuting distance between roost and changing foraging locations. Neither *E. fuscus* nor *L. noctivagans* in this study showed strong fidelity to specific maternity roost trees, which is contrary to the generalization reached by Lewis (1995) that cavity-dwellers in large trees tend to be site-faithful compared to those roosting in small trees. However, the bats in my study did remain in the same general area, and it thus seems unlikely that reduction of commuting distance is a probable explanation, especially given the extra energy expenditure that must accompany movement of the young. Brigham (1991) provided evidence that tree-roosting *E. fuscus* in British Columbia also did not minimize commuting distance. I noticed no disturbance that would explain the frequent roost shifts of some individuals compared to those that moved less often. The relative importance of potential predators, parasites, and microclimate is harder to discern and is an area ripe for study.

Both *E. fuscus* and *L. noctivagans* exhibited variation in the species and condition of trees selected as maternity roost sites, but this seems largely dependent upon what is available. In this study, *E. fuscus* used mostly ponderosa pine, similar to the results of Brigham (1991). However, in his study all the bats used snags, while four of the six pines used in my study were alive. In another part of southern British Columbia (Vonhof 1994), *E. fuscus* used dead white pine (*Pinus strobus*), and in Saskatchewan (Kalcounis 1994) they used both live and dead trembling aspen (*Populus tremuloides*). The *L. noctivagans* in this study used mostly snags of three species. They used white pine snags in Vonhof's (1994) study, snags of eight species in northern California (Rainey and Pierson 1994), and both live and dead trembling aspen in Alberta (Crampton 1994, this volume).

Parsons et al. (1986) found a small maternity colony in a hollow, dead section of a living basswood (*Tilia americana*). Although *E. fuscus* seems to prefer cavities, *L. noctivagans* occasionally roosts under bark (this study; Pierson and Rainey 1994).

The most consistent characteristic of the maternity roost trees used by these two species, as well as other bat species, is tree size. Both diameter and height, which are generally correlated, have been used as measures of size. Large diameter has been reported as an important requirement for *E. fuscus* (Brigham 1991; this study), *L. noctivagans* (Parsons et al. 1986; Rainey and Pierson 1994; this study), and several *Myotis* species (Sasse and Pekins, this volume). Obviously, trees must be large enough to contain cavities if they are to be used by cavity-roosting bats, but large diameter may also be important because of the insulatory value of the wood around the cavity. Roost trees have also been reported as being taller than average (Crampton 1994; Kalcounis 1994; Vonhof 1994; Sasse and Pekins 1994). The value of height may reflect the need for the cavity to be high enough to provide adequate solar exposure and avoid the clutter of understorey vegetation (Kalcounis 1994; this study).

Regardless of the reasons that these bats need big trees and regardless of the reasons for roost site lability, it is clear that individuals use several large trees each breeding season. Unfortunately, large trees, both live and dead, are often the most valued by humans for lumber, other wood products, and firewood. There is tremendous political pressure in our study region to increase the salvage logging of large tracts of timber killed by recent insect attacks and drought before the trees lose their value through decay and before they fuel a devastating fire. Lumber companies want large trees as well as small, but even if only the smaller ones are removed the remaining isolated ones are more likely to fall in a windstorm. It is important that forest managers recognize the value of large trees to bats as well as other species as they plan salvage and green timber sales. Hopefully, the information coming out of this conference will help provide the documentation that they will need to plan wisely.

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Roost-site Preferences of Big Brown Bats (*Eptesicus fuscus*) and Silver-haired Bats (*Lasionycteris noctivagans*) in the Pend d'Oreille Valley in Southern British Columbia

MAARTEN J. VONHOF

ABSTRACT

I examined the roost-site preferences of big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) in the Pend d'Oreille River Valley (POV) in southern British Columbia during the summer of 1995. Roost trees were located via radio-telemetry, then observed at dusk to confirm use and determine colony sizes. I found a total of 27 roost trees used by the two species. Both big brown bats and silver-haired bats preferred large trees (either tall or with a large DBH) that were uncluttered by surrounding trees relative to available trees in the immediate vicinity of the roost, and in other areas of the same stand. Both species preferred trembling aspen. Big brown bats preferred trees in decay stages two and six, whereas silver-haired bats exhibited no decay-stage preferences. When the tree and site characteristics of roost trees used by big brown bats and silver-haired bats were compared, only the height of the tree relative to canopy height discriminated between them. Big brown bats prefer trees that are higher relative to the canopy than silver-haired bats. This information was used to develop a set of management recommendations for maintaining bat roosting habitat in the POV.

INTRODUCTION

The POV occurs in the Southern Interior Mountains Ecoprovince in southern British Columbia, just north of the U.S. border. The valley is unique because it has an east-west orientation, which results in an abundance of south-facing slopes and associated dry, warm climate. Forests in the POV have been modified both by conventional logging practices and hydroelectric developments, including dams and associated power lines. Surveys for bats in the POV have found that the valley contains large numbers of at least 10 species (Rasheed and Holroyd 1995; Vonhof 1995a, b). Of particular interest was the extremely high abundance of relatively large bat species, such as big brown bats (*Eptesicus fuscus*) and silver-

haired bats (*Lasionycteris noctivagans*), which can be difficult to capture and are caught in low numbers in other regions of British Columbia (M. Vonhof, pers. obs.; Rasheed and Holroyd 1995).

The apparent abundance of bats in the POV provided an excellent opportunity to examine the roosting requirements of forest-dwelling bats. In summer, bats spend over half of each day in a roost site, and because of this, roosts play a vital role in the lives of bats. Roosts may provide bats with a thermally stable environment or space in which they receive protection from the elements (Vaughan 1987), and in which individuals can cluster together, thereby reducing the energetic costs of thermoregulation (Trune and Slobodchikoff 1976; Kurta 1985). Roosts may also provide protection from predators (Fenton 1983; Tidemann and Flavel 1987), and serve as sites for social interactions with conspecifics (Morrison 1980). The choices made by bats with respect to the type and location of roost sites likely have a strong influence on their survival and fitness.

Much of the detailed work on the roosting ecology of bats has centred on bats roosting in caves or man-made structures, as these locations are often relatively accessible to humans and easy to find (see Kunz 1982). In contrast, few studies have examined the ecology of bats roosting in trees. Most records of tree-roost sites are simply descriptions or anecdotes of single colonies in trees (e.g., Barclay and Cash 1985; Parsons et al. 1986; Kurta et al. 1993a, b; see references in Kunz 1982). A few studies have examined specific tree characteristics and compared them to random samples of available trees to gain some indication of site-selection by bats (e.g., Barclay et al. 1988; Taylor and Savva 1988; Lunney et al. 1988). However, these studies only examined small numbers of characteristics and could not provide a complete picture of the specific tree or site characteristics selected by bats.

Recently, Vonhof and Barclay (in press) provided an in-depth look at the roosting requirements of forest-dwelling bats. Out of 22 tree and site characteristics that they measured, only three significantly discriminated between roost and available trees: tree height, distance to the nearest available wildlife tree, and percentage of canopy closure. Bats preferred tall trees close to other wildlife trees situated in areas with open canopies. Furthermore, bats preferred western white pine trees, and to a lesser extent, ponderosa pine trees, in intermediate stages of decay. The results provided testable predictions for the roost-site preferences of bats, and further studies in other areas with different forest types may determine the generality of their results.

This paper summarizes the results of a study to investigate the roost-site preferences of forest-dwelling bats in the POV. Reproductive female *Eptesicus fuscus* and *Lasionycteris noctivagans* were outfitted with radio-transmitters in order to locate roost sites. The tree and site characteristics of the roost trees used by the two species could then be compared to each other, as well as to randomly selected trees, to determine which characteristics bats select. This information was then used to develop management recommendations for the maintenance of bat-roosting habitat in the POV.

Roost sites were located using radio-telemetry. Bats were captured in mist nets set across marshes, small ponds, edges of a dam reservoir, clearcut edges, and across roads at various locations and elevations throughout the valley. Captured bats were identified to species, sexed, and aged as adults or juveniles (young of the year) based on the degree of ossification of the metacarpal-phalange joints (Racey 1974). I measured mass and forearm length and assessed reproductive condition (Racey 1974) for all captured individuals.

I attached small (0.53–0.73 g; Model BD2, Holohil Systems Ltd., Wood-lawn, Ontario) radio-transmitters to pregnant or lactating female *Eptesicus fuscus* ($n = 8$) and *Lasionycteris noctivagans* ($n = 10$). Transmitters were attached between the scapulae of individual bats using Skin-Bond® (Cana-dian Howmedica, Guelph, Ontario) surgical adhesive. I located roost sites during the day by tracking radio signals with at least two receivers (Lotek STR 1000, Lotek Engineering Inc., Newmarket, Ontario) and two- or three-element Yagi antennae. All but three of the roosts found by radio-telemetry were verified by watching the tree at dusk for emerging bats.

Once roosting sites had been located, I measured a range of tree char-acteristics for all roosts (Appendix 1). I measured diameter at breast height (DBH), and determined all tree heights, entrance heights, and slopes with a clinometer and entrance aspect with a compass corrected to true north. Two observers independently estimated the percentage of bark remaining on the tree, and the mean was taken. In addition, I measured the horizontal distance to and height of the nearest tree of the same or greater height, which is defined as the closest tree to the roost in a 90° arc extending out from the roost entrance.

I classified each roost tree into one of nine decay stages, based on the British Columbia Wildlife Tree Classification System (Backhouse and Lousier 1991; Vonhof 1995a), which takes into account characteristics of the tree, such as the percentage of bark remaining, number of limbs pre-sent, condition of the top, and condition of the heartwood and sapwood. I only measured trees falling into decay stages two to seven, as by defini-tion decay-stage one trees and decay-stage eight to nine trees provide no suitable roosting opportunities for bats.

I established a 17.8 m radius (0.1 ha) plot around each roost tree, and within it measured two randomly selected available trees, defined as trees in decay stages two to seven not known to contain bats. If the plot con-tained less than two available trees, the closest available trees outside the plot were measured. I also measured site characteristics within the plot. The percentage of canopy closure within the plot was visually estimated by at least two observers and the mean was taken. I measured the height of at least two trees (range two to five) within the canopy using a clino-meter, and took the mean to estimate canopy height within the plot.

I also established two plots located in other areas of the same stand. I located plots by selecting a random point between 100 and 300 m from the roost tree along each of two transects established in randomly selected directions that differed by greater than 90°, and determined the nearest available tree to the random point (focal tree). If this random point lay

outside the stand, I chose another random direction and distance, and located the nearest available tree. I established a 17.8 m radius (0.1 ha) plot around the focal tree and measured the tree characteristics of the focal tree in the same fashion as for roost trees, and measured the site characteristics of the plot.

I performed a series of stepwise discriminant function analyses, including the variables outlined in Appendix 1, to determine whether the tree and site characteristics of roost trees used by the various bat species differed, and to determine which tree and site characteristics the bat species select relative to available trees. All roost trees were considered together in all comparisons of roost trees regardless of the reproductive condition of the bats, because sample sizes did not permit separate analyses for pregnant and lactating bats. In all cases I then applied a canonical discriminant function analysis to the same data with the significant variables from the stepwise analysis to determine the placement of these variables along the discriminant function. This analysis provided the total sample standardized canonical coefficients (TSSCC) for each variable, and classification error rates based on cross-validation. The relative magnitude of the TSSCC is a measure of the contribution of each variable to the discrimination, and its sign indicates to which group individual trees belong as their value for the particular variable increases. Separate analyses were performed between roost trees and available trees from two geographic scales: available trees from the immediate vicinity of the roost tree (within the 0.1 ha circular plot around each roost tree), and available trees from other areas of the same stand. Because tree species and decay stage are categorical and could not be included in the discriminant function analyses, I analyzed them separately using randomization tests, comparing the roost trees used by *E. fuscus* and *L. noctivagans*, and comparing roost trees with available trees.

RESULTS

I found a total of 27 roost trees using radio-telemetry. Fifteen roosts were used by *E. fuscus*, and 12 by *L. noctivagans*. *Eptesicus fuscus* roosted in natural hollows and abandoned primary cavity excavator (PCE) hollows in almost equal numbers ($n = 5$ and 6, respectively), and in one instance also roosted in a crack caused by a lightning strike. I could not identify the nature of the roost for three of the roosts used by *E. fuscus*. *Lasionycteris noctivagans* tended to roost more often in abandoned PCE hollows ($n = 8$) than natural hollows ($n = 4$), but did not roost in cracks. Colony sizes varied widely both within and between the two bat species, but *E. fuscus* colonies (mean: 34; range: 2–61) were significantly larger than *L. noctivagans* (mean: 12; range: 1–35) colonies (ANOVA: $F_{1,24} = 13.54$, $P < 0.01$). Colony size was not significantly correlated with either tree height or DBH for either *E. fuscus* or *L. noctivagans* ($P > 0.05$ in all cases).

Eptesicus fuscus **Roost-Tree Preferences**

Of the 19 variables initially entered into the stepwise discriminant function analysis, only two significantly discriminated between *E. fuscus* roost trees and available trees in the immediate vicinity of the roost tree (Table 1).

TABLE 1 *Summary of the stepwise discriminant function analysis on tree and site characteristics, comparing roost trees used by* E. fuscus *with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. The centroids for roost trees and available trees lie at the positive and negative ends of the discriminant axis, respectively.*

| | | Partial | | | |
Variable	Order included	*F*	*P*	R^2	TSSCC
Immediate vicinity					
Horizontal distance to nearest tree					
of same or greater height	1	17.84	0.0001	0.29	0.75
DBH	2	4.93	0.0318	0.11	0.67
Stand					
Tree height	1	25.12	0.0001	0.40	1.32
Number limbs remaining	2	9.19	0.0045	0.20	−0.71
Percent bark remaining	3	8.64	0.0058	0.20	0.70
DBH	4	5.94	0.0202	0.15	0.53

The horizontal distance to the nearest tree of the same or greater height accounted for 29% of the variation between roost and available trees, and DBH accounted for 11%. Based on the canonical discriminant function analysis, in this and subsequent analyses, the centroid for roost trees was at the positive end of the discriminant axis, and the centroid for available trees was at the negative end. The TSSCC's for both horizontal distance to the nearest tree of the same or greater height and DBH were positive, indicating that roost trees tend to be further away from other tall trees and have a greater DBH than available trees from the immediate vicinity of the roost. The classification error rates for roost trees was relatively high (53%), whereas that for available trees was relatively low (13%). The overall classification error rate was 33%.

Four variables significantly discriminated between *E. fuscus* roost trees and available trees from other areas of the same stand: tree height, number of limbs remaining, percentage of bark remaining, and DBH (Table 1). Tree height was by far the strongest discriminating variable, explaining 40% of the variation between roost and available trees. The other three variables each explained between 15–20% of the total variation. Overall, the combination of the four discriminating variables explained 95% of the variation between *E. fuscus* roost and available trees from other areas of the same stand. Based on the canonical discriminant function analysis, the centroid for *E. fuscus* roost trees was at the positive end of the discriminant axis and the centroid for available trees was at the negative end. The TSSCC's for tree height, percentage of bark remaining, and DBH were positive, indicating that *E. fuscus* roost trees tend to be taller, have a greater diameter, and have more bark remaining than available trees from other areas of the same stand. In contrast, the TSSCC for number of limbs remaining was negative, suggesting that *E. fuscus* roost trees have fewer limbs than do available trees from other areas of the same stand. The classification error rates for roost and available trees were low (0% and 7%, respectively), with an overall error classification rate of 4%.

TABLE 2   *Summary of correlations between significant discriminating variables, and between significant discriminating variables and other variables included in the discriminant function analysis comparing roost trees used by* E. fuscus *with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. Values listed in the table are correlation coefficients (*r*). Blank spaces indicate no significant correlation.*

Variable	Variable	Immediate vicinity	Other areas of same stand
Tree height	DBH	0.64***	0.61***
Tree height	Horizontal distance to tree of ≥ height	0.57***	0.55***
DBH	Horizontal distance to tree of ≥ height	0.55***	
DBH	Height of tree of ≥ height	0.35*	
DBH	Tree height relative to canopy height	0.65***	
DBH	Horizontal distance to nearest available tree		0.37*
Horizontal distance to tree of ≥ height	Tree height relative to canopy height	0.51***	
Horizontal distance to tree of ≥ height	Horizontal distance to nearest available tree	0.30*	
Horizontal distance to tree of ≥ height	Horizontal distance to nearest neighbour tree	0.53***	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

I found significant positive correlations between the significant discriminating variables and other measures of tree size and clutter around the roost tree when comparing *E. fuscus* roost trees with both available trees from the immediate vicinity of the roost and available trees from other areas of the same stand (Table 2).

Eptesicus fuscus did not roost at random with respect to the availability of different tree species when compared to either available trees from the immediate vicinity of the roost tree (randomization test; $G = 34.79$, $P < 0.001$; Figure 1) or to available trees from other areas of the same stand ($G = 34.87$, $P < 0.001$; Figure 1). *E. fuscus* preferred trembling aspen (*Populus tremuloides*), and to a lesser extent ponderosa pine (*Pinus ponderosa*). *E. fuscus* roosted less frequently than expected in Douglas-fir (*Pseudotsuga menziesii*), and did not roost at all in any of the other five available tree species. All five natural-cavity roosts and six abandoned PCE hollow roosts were located in trembling aspen. The only crack roost used by *E. fuscus* was located in a ponderosa pine tree. Two of the three roosts for which I could not determine the nature of the cavity were located in trembling aspen, and the third was in a Douglas-fir tree.

Eptesicus fuscus also did not roost at random with respect to the availability of different decay stages when compared to available trees from the immediate vicinity of the roost tree (randomization test; $G = 26.45$, $P < 0.001$; Figure 2) or to available trees from other areas of the same stand ($G = 21.63$, $P < 0.001$; Figure 2). *E. fuscus* roosted in trees of decay stages two, three, five, and six, and roosted more frequently than expected in decay-stage two trees, based on their availability in the immediate vicinity of the roost tree and in other areas of the same stand. *E. fuscus* roosted more frequently in decay-stage six trees based on their availability in the immediate vicinity of the roost tree only. Three natural-cavity roosts were found in trees in decay-stage two, and the other two were found in trees in decay stages five and six. Roosts in abandoned PCE

FIGURE 1   *The proportion of* E. fuscus *roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in the 10 major tree species found in the POV. Tree species notation is as follows: DF = Douglas-fir, GF = grand fir, LP = lodgepole pine, PP = ponderosa pine, WP = western white pine, WC = western redcedar, WL = western larch, DM = Douglas maple, PB = paper birch, TA = trembling aspen.*
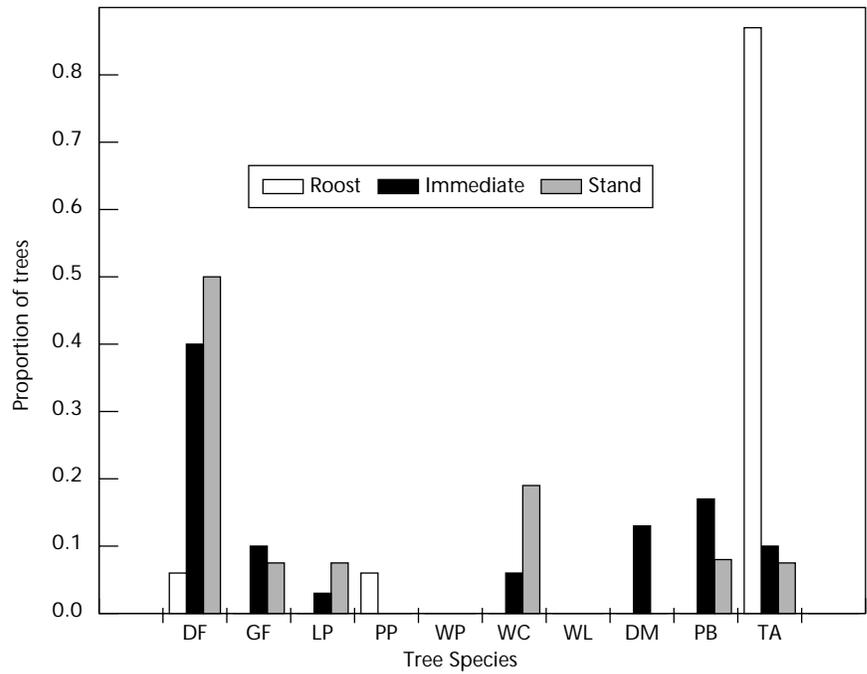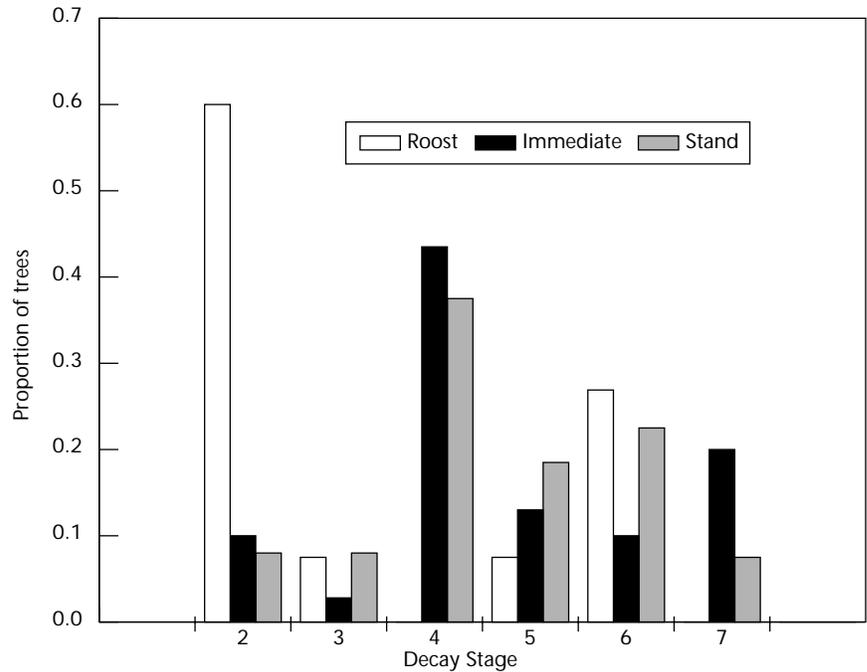

FIGURE 2   *The proportion of* E. fuscus *roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in each of the six decay stages.*

hollows were found most often in decay-stage two trees ($n = 4$), but were also found in decay-stage six trees ($n = 2$). The single crack roost was on a decay-stage two tree.

Lasionycteris noctivagans
Roost-Tree Preferences

Three of the 19 variables that initially entered into the stepwise discriminant function analysis significantly discriminated between *L. noctivagans* roost trees and available trees in the immediate vicinity of the roost tree (Table 3). The horizontal distance to the nearest tree of the same or greater height, the horizontal distance to the nearest neighbouring tree, and tree height all accounted for approximately 17–20% of the variation between roost and available trees. The TSSCCs for both horizontal distance to the nearest tree of the same or greater height and tree height were positive, indicating that roost trees tend to be further away from other tall trees and be taller than available trees in the immediate vicinity of the roost. The TSSCC for horizontal distance to the nearest neighbouring tree was negative, suggesting that roost trees tend to be closer to neighbouring trees than available trees. Based on the magnitude of the TSSCCs, horizontal distance to the nearest tree of the same or greater height was the strongest discriminating variable, followed by horizontal distance to the nearest neighbouring tree, and then tree height. The classification error rates for roost and available trees were 33% and 17%, respectively, with an overall error rate of 25%.

Only one variable (DBH) significantly discriminated between *L. noctivagans'* roost trees and available trees from other areas of the same stand, and it explained over 35% of the variation between roost and available trees (Table 3). The TSSCC for DBH was large and positive, indicating that *L. noctivagans'* roost trees tend to have greater diameters than available trees from other areas of the same stand. The classification error rates for roost and available trees were relatively high (25% and 29%, respectively), with an overall error classification rate of 27%.

When comparing *L. noctivagans'* roost trees with both available trees from the immediate vicinity of the roost and available trees from other

TABLE 3   *Summary of the stepwise discriminant function analysis on tree and site characteristics, comparing roost trees used by* L. noctivagans *with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. The centroids for roost trees and available trees lie at the positive and negative ends of the discriminant axis, respectively.*

Variable	Order included	Partial			
		F	*P*	*R²*	TSSCC
Immediate vicinity					
Horizontal distance to nearest tree of same or greater height	1	6.79	0.0135	0.17	1.02
Horizontal distance to nearest neighbouring tree	2	8.06	0.0077	0.20	−0.84
Tree height	3	7.35	0.0107	0.19	0.70
Stand					
DBH	1	17.80	0.0002	0.36	1.20

TABLE 4 *Summary of correlations between significant discriminating variables, and between significant discriminating variables and other variables included in the discriminant function analysis comparing roost trees used by* L. noctivagans *with available trees from both the immediate vicinity of the roost tree as well as from other areas of the same stand. Values listed in the table are correlation coefficients (*r*). Blank spaces indicate no significant correlation.*

Variable	Variable	Immediate vicinity	Other areas of same stand
Tree height	DBH	0.39*	0.43**
DBH	Horizontal distance to tree of same or greater height	0.35*	0.35*
DBH	Height of tree of same or greater height		0.38*

* $P < 0.05$, ** $P < 0.01$

areas of the same stand, I found significant positive correlations between the significant discriminating variables and other measures of tree size and clutter around the roost tree (Table 4).

L. noctivagans did not roost at random with respect to the availability of different tree species when compared to available trees from other areas of the same stand (randomization test; $G = 19.54$, $P < 0.01$; Figure 3), but did when compared to available trees from the immediate vicinity of the roost tree ($G = 12.22$, $P > 0.05$; Figure 3), although there was a trend
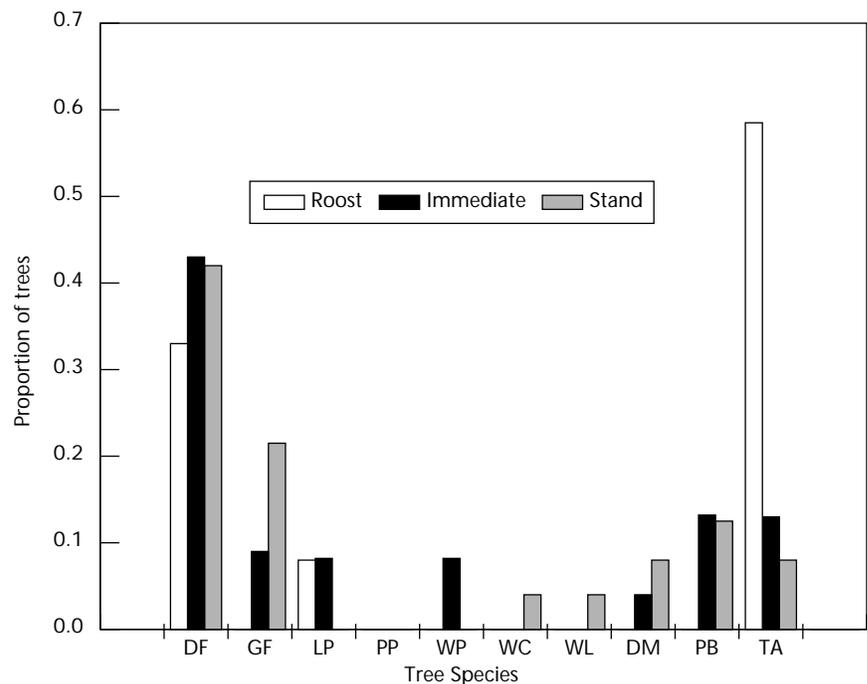

FIGURE 3 *The proportion of* L. noctivagans *roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in the 10 major tree species found in the POV. Tree species notation is as in Figure 1.*

towards preferring particular tree species. Relative to available trees from other areas of the same stand, *L. noctivagans* preferred trembling aspen and lodgepole pine (*Pinus contorta*). *L. noctivagans* used Douglas-fir slightly less frequently than expected, based on its availability in other areas of the same stand. *L. noctivagans* did not roost in any of the other six available tree species. Four of the eight roosts in abandoned PCE hollows were located in Douglas-fir, three in trembling aspen, and one in lodgepole pine. All four natural-cavity roosts were in trembling aspen.

L. noctivagans roosted at random with respect to the availability of different decay stages, whether I considered available trees from the immediate vicinity of the roost (randomization test; $G = 7.53$, $P > 0.25$; Figure 4) or available trees from other areas of the same stand ($G = 8.15$, $P > 0.10$; Figure 4). Roosts in abandoned PCE hollows used by *L. noctivagans* were found in all decay stages except for decay-stage three. Three of the four natural-cavity roosts were found in decay-stage two trees, and the other was found in a decay-stage five tree.

Comparing *Eptesicus fuscus* and *Lasionycteris noctivagans* Roost-Tree Preferences

Only one variable significantly discriminated between roost trees used by *E. fuscus* and *L. noctivagans*: tree height relative to canopy height ($F = 17.84$, $P < 0.001$). This variable explained a relatively low proportion (partial $R^2 = 29\%$) of the variation between the two groups of roost trees. Based on the canonical discriminant function analysis, the centroid for *E. fuscus* roost trees was at the positive end of the discriminant axis and the centroid for *L. noctivagans* roost trees was at the negative end. The TSSCC for tree height relative to canopy height (0.75) was positive, indicating that *L. noctivagans* roost trees tended to be further beneath the
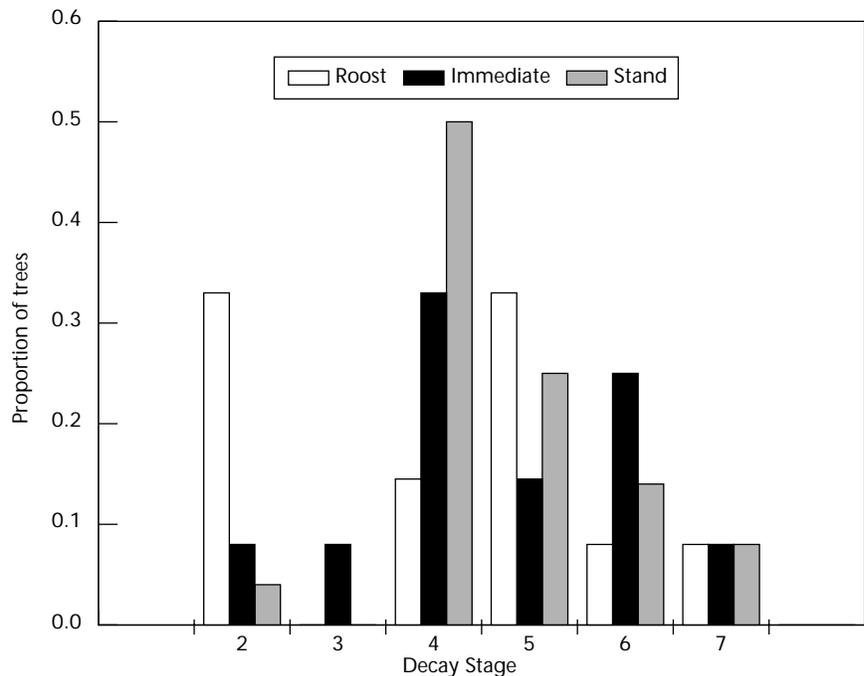

FIGURE 4   *The proportion of* L. noctivagans *roost and available trees from both the immediate vicinity of the roost and other areas of the same stand in each of the six decay stages.*

canopy than *E. fuscus* roost trees. The classification error rates for *E. fuscus* roost trees and *L. noctivagans* roost trees were 27% and 33%, respectively, with an overall error classification rate of 30%.

I found significant positive correlations between tree height relative to canopy height and DBH, and tree height relative to canopy height and tree height, and negative correlations between tree height relative to canopy height and slope, and tree height relative to canopy height and canopy height (Table 5).

I found no significant difference between the species of tree roosts used by *E. fuscus* and *L. noctivagans* (randomization test; $G = 6.19$, $P > 0.05$). However, I did find a significant difference between the decay stages used by the two bat species ($G = 11.04$, $P < 0.05$). *E. fuscus* used decay-stage two and six trees more often than *L. noctivagans*, and, conversely, *L. noctivagans* used decay-stage four and five trees more often than did *E. fuscus*.

TABLE 5 *Summary of correlations between the significant discriminating variable and other variables included in the discriminant function analysis comparing roost trees used by* E. fuscus *and* L. noctivagans.

Variable	Variable	*r*
Tree height relative to canopy height	DBH	0.56**
Tree height relative to canopy height	Tree height	0.93***
Tree height relative to canopy height	Slope	−0.40*
Tree height relative to canopy height	Canopy height	−0.51**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

In general, both big brown bats and silver-haired bats preferred either large-diameter or tall trees that were relatively far away from surrounding trees. Similarly, Vonhof and Barclay (in press) found that bats prefer tall trees close to other available trees that are surrounded by an open canopy, while other studies on tree-roosting bats have shown that bats prefer large-diameter trees (e.g., Barclay et al. 1988; Lunney et al. 1988; Taylor and Savva 1988; Brigham 1991) rather than tall trees. Similarly, in some studies, cavity-nesting birds (Harestad and Keisker 1989; Lundquist and Mariani 1991) prefer large-diameter snags, whereas in other studies a preference for tall trees has been observed (Nilsson 1984; Raphael and White 1984; Rendell and Robertson 1989). In all analyses comparing roost trees with available trees I found that either tree height or DBH, or both, significantly discriminated between the two groups of trees. I also found that tree height and DBH were significantly positively correlated, such that the tree height variable in the discriminant function analysis also included information with respect to DBH, and vice versa. Thus, tree size may be the more appropriate factor selected by bats, rather than any particular measure of tree size. The two measures of tree size also contain information with respect to clutter around the roost tree. Tree height and DBH were generally positively correlated with the measures of clutter around

the roost tree that significantly discriminated between roost and available trees (i.e., horizontal distance to the nearest tree of the same or greater height, and horizontal distance to the nearest neighbouring tree), such that large trees are relatively uncluttered. Therefore, to receive the potential benefits of uncluttered trees, bats need only select large trees, or vice versa.

Bats may select large, uncluttered trees for several reasons. The diameter of a tree may set an upper limit to the size of the colony of bats that can form in a particular cavity. This may be especially important for reproductive females, as colonial bats may experience significant thermal and energetic benefits by clustering (Trune and Slobodchikoff 1976; Kurta 1985). Colony sizes, particularly for big brown bats, were generally large (up to 61 individuals), and small trees would simply not be able to support large colonies of bats. The potential size of cavities would be extremely important around the time of parturition, as the number of individual bats using the same space increases dramatically when females begin to give birth. Clutch size within cavity-nesting bird species increases with increasing cavity size (e.g., Rendell and Robertson 1989), and the size of the cavity may limit the size of maternity colonies of bats in tree roosts. In addition, the larger a tree is at the time of death the longer it will stand (Cline et al. 1980; Newton 1994), and the greater the time it will potentially remain as a useful roost site to bats.

Bats may also gain significant energetic benefits by choosing trees that are exposed to sunlight. Low roost temperatures slow fetal and juvenile development in bats (Racey 1973; Tuttle 1976; Racey and Swift 1981), and seasonal low temperatures reduce the number of reproductive females and the number of young successfully fledged (Grindal et al. 1992; Lewis 1993). Thus, reproductive female bats may benefit energetically by selecting roosts that are heated by the sun for at least part of the day. Tall trees relatively uncluttered by surrounding trees are exposed to sunlight for a greater length of time than are trees with canopy cover. Indeed, nearly all of the roost trees that I found, including all of the maternity colonies, were exposed to direct sunlight for at least part of the day. Although neither big brown bats nor silver-haired bats preferred trees with a particular orientation, a cavity in the centre of a tree exposed to sunlight will be heated via conduction through the walls of the cavity, no matter which side of the tree is exposed to the sunlight (Vonhof and Barclay in press).

Flight is costly (Speakman and Racey 1991), and a clear flight path in front of the roost entrance on a large, uncluttered tree may result in energetic savings. In addition, bats are susceptible to aerial predators, such as hawks, falcons, and owls (Barclay et al. 1982; Fenton et al. 1994) as they enter and leave their roosts. The ease with which bats enter and leave their roosts will determine the length of time they are exposed to predation, and thus bats may select tall, uncluttered trees that provide easy access. It is also likely that large, uncluttered trees are easier to find than trees concealed by the canopy, and may stand out as landmarks to bats flying over the canopy surface, assisting in roost relocation (Vonhof and Barclay in press).

Big brown bats and silver-haired bats preferred roosts in trembling aspen trees. The preference of big brown bats for trees with a greater percentage of bark and fewer limbs remaining in part explains their

preference for trembling aspen, which has these characteristics relative to other available tree species. The tree species and decay-stage preferences of cavity-roosting bats are closely tied to the preferences of PCEs and to the dynamics of natural-cavity formation (Vonhof and Barclay in press). In the northwestern United States and in British Columbia, in areas with similar forest types to those in the POV, PCEs prefer trees with decayed heartwood but relatively hard sapwood, such that there is a hard outer shell surrounding a relatively soft tree core (McClelland et al. 1979; Harestad and Keisker 1989; Lundquist and Mariani 1991). Natural cavities with similar characteristics may form, provided that a path for infection is created through limb detachment, lightning strike, frost cracks, or other trunk wounds, or top-breakage (Newton 1994). Trembling aspen trees over 40 years of age almost always harbour heart rot while they are alive (Winternitz and Cahn 1983; C. Steeger, pers. comm.), and provide excellent conditions for cavity excavation by PCEs and natural-cavity formation. Consequently, PCEs exhibit strong preferences for trembling aspen in many areas (Erskine and McLaren 1972; Winternitz and Cahn 1983; Harestad and Keisker 1989; C. Steeger, pers. comm.), and trembling aspen trees likely provide the greatest number of suitable cavities for roosting bats. In areas where trembling aspen is less abundant, PCEs also exhibit preferences for other tree species, such as western larch (McClelland et al. 1979), western white pine (Lundquist and Mariani 1991), and western hemlock (Zarnowitz and Manuwal 1985), which also harbour heart rot while they are still alive (Cline et al. 1980; see also McClelland et al. 1979; Lundquist and Mariani 1991). However, these tree species occur at low densities in the POV.

Compared to big brown bats, silver-haired bats roosted in Douglas-fir relatively frequently. Although avoidance of Douglas-fir by some PCEs has been noted (Crockett and Hadow 1975; McClelland et al. 1979), species such as red-breasted nuthatches strongly prefer to excavate cavities in Douglas-fir killed by *Armillaria* spp. (C. Steeger, pers. comm.), and it was in these cavities that the silver-haired bats roosted. Douglas-fir tends to decay from the outside in, so that decay softens the sapwood before it affects the heartwood (Cline et al. 1980). Therefore, cavities in Douglas-fir tend to break down relatively quickly and may be available to bats for only a short time. However, the high densities of Douglas-fir snags in the POV likely results in at least some suitable cavities being available to bats for roosting. The relative impermanence of cavities in Douglas-fir may explain why both species preferred to roost in more durable cavities in trembling aspen. In other areas of British Columbia, where greater numbers of alternatives are available, no bats have been found roosting in Douglas-fir, even though it is relatively abundant (Vonhof and Barclay in press).

MANAGEMENT IMPLICATIONS

Current forest-harvesting practices and increased hydroelectric developments, with associated increases in the number of cutlines and increased water fluctuations along reservoirs, may significantly reduce suitable habitat for tree-roosting bats. This practice—common to the POV of putting

in relatively large cutblocks separated by small strips of forest—removes large portions of the available roosting habitat, and because older-aged stands are most often targeted in forest-harvesting operations, the remaining forested areas are often deficient of suitable roosting habitat. Similarly, cutlines remove large tracts of forest, and are often developed with little consideration of the kinds of forest that are removed. Older-aged stands contain a greater abundance of large snags in a variety of decay classes (Cline et al. 1980) and are characterized by reduced tree densities, more canopy gaps, and less clutter (Franklin et al. 1981). Thomas (1988) found that bat activity was high in old-aged forest stands in Oregon for the first fifteen minutes after sunset, and suggested that bats use older stands for roosting. However, similar conditions to older-aged stands may be provided in second-growth stands in which large trees were retained, and bats in this study roosted equally often in large trees in older-aged stands or in remnant trees in second-growth stands. If forest stands are intensively managed or are on a relatively short-rotation cycle, the number of large, older-aged trees that are suitable for roosting will decrease.

Although leaving small numbers of trees within cutblocks has been shown to provide habitat for some cavity-nesting birds (e.g., Morrison et al. 1983), I do not believe that this practice can be applied to the management of tree-roosting bats. I did not find any bats roosting in trees left standing in clearcuts, and roost trees tended to be situated within forest stands, rather than in the open. Tree-roosting bats tend to switch roosts frequently, and subsequent roost trees were situated within a relatively small area (Brigham 1991; Lewis 1995; Vonhof 1995a, b). Providing small numbers of trees in an open cutblock will not provide the range or number of alternative trees necessary to meet the needs of bats, and the trees left standing will likely have very different thermal characteristics and provide different degrees of protection from predators than trees within the forest. Only by providing relatively large areas of intact forest will the requirement of bats for small numbers of suitable alternative roost trees within forest stands be met.

Selection harvesting may be a more suitable approach to integrate forestry and bat habitat than clearcutting. Prescriptions that involve selective removal of understorey trees while maintaining veteran and dominant trees (e.g., diameter-limit cut) could reduce the level of clutter in dense, second-growth stands, while preserving the largest and most valuable wildlife trees, and maintaining some degree of canopy cover and associated microclimate. Periodic, low-intensity burning in these selectively harvested stands would help to maintain a more open habitat over time. Other management techniques that accelerate green-tree decomposition and increase wildlife-tree recruitment rates in forested areas (e.g., tree topping with a feller buncher) may enhance habitat for wildlife-tree-dependent species, including bats.

Bats roosting in cavities depend to a greater extent on the dynamics of cavity formation, and the preferences of PCEs, for roosting sites. Managing for PCEs has been suggested as a means to maintain secondary-cavity-user populations, the idea being that if the requirements of PCEs are met, then so will those of secondary cavity users (Brawn and Balda 1983). However, this may not always be the case, and more attention should be focused on determining the rates of cavity turnover and cavity densities (Sedgewick

and Knopf 1992). Considerably larger numbers of cavities may be required in a given area if competition for cavities among tree-dwelling species is strong. Thus, to ensure an adequate supply of cavities for cavity-roosting bats, it will also be necessary to determine the presence and needs of other secondary cavity users in the same area.

Protecting large patches of trembling aspen trees, which bats (this study, Crampton 1995; Kalcounis, pers. comm.) and PCEs (e.g., Erskine and McLaren 1972; Winternitz and Cahn 1983; Harestad and Keisker 1989) strongly prefer, should be a management priority. The density of available trembling aspen trees in the POV is relatively low, and thus areas that contain this species should be carefully managed. By protecting stands of trembling aspen to promote natural-cavity formation and meet the requirements of PCEs, a reasonable number of available cavities for tree-roosting bats should be maintained. Available Douglas-fir trees occur at high densities in the POV, and the large number of *Armillaria* spp. root-rot centres in the POV should also provide cavities for silver-haired bats.

ACKNOWLEDGEMENTS

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APPENDIX 1 Tree and site characteristics included in the stepwise discriminant function analysis on roost and available trees.

Tree Characteristics
Diameter at Breast Height (DBH)
Tree Height
Tree Height Relative to Canopy Height
Percentage of Bark Remaining
Number of Limbs
Horizontal Distance to Nearest Neighbouring Tree
Height of Nearest Neighbouring Tree
Horizontal Distance to Nearest Tree of the Same or Greater Height
Height of Nearest Tree of the Same or Greater Height
Horizontal Distance to Nearest Available Tree

Site Characteristics
Aspect
Slope
Percentage of Canopy Closure
Canopy Height
Number of Canopy Layers
Horizontal Distance to Nearest Edge
Deciduous Tree Density
Coniferous Tree Density
Available Tree Density