

# The Physical Nature of Vertical Forest Habitat and its Importance in Shaping Bat Species Assemblages

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## ABSTRACT

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Recent work on forest-dwelling bat species has stimulated interest in how the composition of these faunas is derived and maintained. Resource limitation and competition do not appear to be important, but forest structure may be a primary influence in shaping bat communities.

Old-growth forests differ from younger forests in that they exhibit greater structural heterogeneity. They may be perceived as habitat volumes containing discrete layers, each with its own peculiar structural characteristics. For bats, the ability to fly allows movement into different, structurally distinct microhabitats, through vertical shifts between forest layers. Hence, vertical structural complexity may be an important habitat feature for forest-dwelling bats.

I quantified vertical forest structure by measuring profiles of foliage density. Increasing foliage density can be viewed as decreasing uncluttered space within which a flying animal could manoeuvre. Small, interspecific differences in wing morphology should have important implications for manoeuvrability and agility, which may be reflected in interspecific microhabitat associations. I made predictions about bat activity, based on ecomorphology, regarding vertical microhabitat association for sympatric species in three forest types on the west coast of Vancouver Island, British Columbia. Predictions were tested using ultrasonic detectors and mist nets set at three heights, corresponding to the canopy, understory, and shrub layers.

Here, I outline the theoretical framework, and attempt to elucidate how functional relationships between habitat structure and bat community structure may be determined. I also present preliminary results from this ongoing study.

## INTRODUCTION

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Habitat structure may influence the distribution of organisms in three ways: by imposing a physical constraint on movement, by creating a

scattered pattern of resource distribution, or by altering microclimates. The extent to which they influence animal communities can vary as a function of habitat structural complexity (Brown 1991). Bats are the only true flying mammals, and this method of locomotion is sensitive to variations in habitat structural complexity (McKenzie and Rolfe 1986). This sensitivity may be reflected in patterns of microhabitat use. Here, I outline a preliminary study, and propose future work, examining the functional role of vertical habitat structure in influencing the arrangement of bat species assemblages in three coastal, temperate, old-growth forests.

Habitat structure develops in three dimensions. Typically, structure is measured horizontally, quantifying habitat heterogeneity, and vertically, quantifying habitat complexity (Alpert 1991). In terrestrial environments the extent of the vertical dimension of habitat structure may encompass three orders of magnitude. In rock-surface lichen communities this dimension is measured in a few millimetres, while in some temperate coniferous forests, it extends through 100 metres. In forests, particularly old-growth forests, vertical structural complexity is not homogeneous. Stratification is evident in the form of distinct layers, such as the canopy, understorey, and shrub. They can be viewed, simplistically, as having habitat edges that run in the horizontal plane. For forest-dwelling bats, vertical stratification in forest structure may be an exploitable habitat feature. By short, vertical movements into different forest layers, rapid shifts between structurally distinct microhabitats should be possible and may be advantageous. Determining to what extent bats use this dimension of forest structure, and how its use differs between species, is the principal objective of this study. The aim is to elucidate three-dimensional patterns of habitat use by insectivorous bats, be that for the purposes of feeding, roosting, and/or commuting to preferred foraging sites. By viewing forest habitats as a complex volume of space, exploitable in three dimensions, a more pervasive understanding of how bats use this habitat may be developed.

The functional role of habitat structure in shaping community structure is not easily determined. Relationships are complicated by numerous confounding factors, all of which conceivably influence the composition of bat communities. For instance, the physical structure of a habitat is not necessarily the principal determinant of community structure. Competition between organisms for limited resources may be more important. However, there is little evidence that resource competition, particularly for prey, actually occurs in bat communities (Findley 1993). Bat community structures are also influenced by latitudinal effects (Schum 1984; Willig and Selcer 1989), longitude (Heller and Volleth 1995), and by stochastic processes (Willig and Moulton 1989). At smaller spatial scales, additional confounding factors are introduced. For example, not all species within the community are equally sensitive to the same structural variables. Also, different aspects of forest structure may be important during different times of the year. This may vary between species, sexes, and even individuals. Variables of habitat structure are multifarious. Not all are readily quantifiable, and time constraints preclude assessing all of the ones that are. Variables that are important may be ignored, or simply not recognized as being ecologically relevant to bats. In addition, the spatial and temporal scales at which habitat structure is examined may not be appro-

priate to reveal functional relationships. Bats, as important agents in nutrient cycling in the forest, have the potential to modify their surrounding habitat structure.

By focusing on the potentially strong relationship between flying ability, microhabitat association, and vertical habitat structure, the confounding effects of unmeasured and unmeasurable variables can be mitigated. Examining vertical forest structure within an ecomorphological framework may allow functional relationships between habitat structure and community composition to be determined. For flying mammals the ecomorphological premise states that interspecific differences in wing morphology translate into ecological differences, particularly in foraging style. Strong relationships between form and function have been demonstrated in some bat faunas (McKenzie et al. 1995). Detailed studies of flight morphology in bats (e.g., Fenton 1972; Norberg 1981; Aldridge 1986; Norberg and Rayner 1987; Saunders and Barclay 1992) have illustrated how relatively small, interspecific differences in wing morphology and body size can have important implications for flight style and consequently foraging behaviour. By quantifying habitat structure in terms of the amount, or density, of material obstructing flight space (hereafter termed clutter), and determining correlations between bat activity and microhabitats of differing clutter density, functional relationships may be demonstrated. Comparing vertical structure and vertical bat activity between several forest types and exposing patterns and relationships allows an estimation of the general applicability of the findings at larger spatial scales.

#### Defining Habitat Structure

Habitat structure is comprised of abiotic and biotic elements. Abiotic structure affects most bat species on a seasonal time scale, where winter hibernacula are located in caves, and year round for species that use abiotic roosting sites (e.g., *Corynorhinus townsendii*). For the most part, biotic structural influences (i.e., plant material) are more relevant to bat communities. However, abiotic habitat structures, such as soil horizons, topography, and local geology, have indirect effects on animal communities by influencing the growth and distribution of plant species, thereby influencing biotic structure. There are horizontal, vertical, and scale elements to the development of habitat structure (Brown 1991). Here, I focus on vertical structure, and assess differences in bat activity with height in reference to vertical profiles of foliage density.

#### Ecomorphology and Habitat Structure

It is clear that not all bat species are capable of exploiting vertical structural complexity to the same extent. Species differ in wing morphology and body size, which dictate manoeuvrability and flight style. Manoeuvrability can be quantified as the volume of space required for a flying bat to change direction during flight at a constant speed (Norberg and Rayner 1987). Bats display a great variety of wing sizes and shapes, which follow some general trends. Larger, faster-flying species are characterized by long, narrow wings. At the opposite end of the spectrum are smaller, slower-flying species that have short, broad wings. Wing design can be defined mathematically as ratios of certain morphological measurements. Wing loading (body mass divided by total wing area) and aspect ratio (wing span divided by wing area) are mathematically derived indicators of flying ability. They are closely related to agility, stalling speed, and manoeuvrability. Bats with long, narrow

wings typically have high wing loadings and high aspect ratios. They have high relative stalling speeds and are less manoeuvrable. Species with short, broad wings have low wing loadings and low aspect ratios, have low stalling speeds, and are highly manoeuvrable.

Based on this understanding of how morphology reflects manoeuvrability I make predictions regarding microhabitat associations. In essence, this is a test of the theory of ecomorphology, or “morphology as the cast of the ecological mould” (Findley 1976). Data on wing morphology and ear length, for all the bat species known to be present in the study region, were taken from the literature (Norberg and Rayner 1987). An index, composed of the sum of the following values—ear length divided by body mass, wing loading, and aspect ratio—was determined for all species in the sample. This index is an approximation of a species’ ability to negotiate a complex and physically cluttered habitat, what I have termed clutter tolerance. Long ears, relative to body size, are characteristic of species associated with cluttered habitats (e.g., *Myotis evotis*, *Corynorhinus townsendii*). Indices for all species were put in rank order (Figure 1). I assumed in constructing this index that all measured morphological variables are equally important in dictating microhabitat preferences, so that a proportionate change in any one variable would alter with equal significance the ability of a species to cope with clutter. The predictive power of the clutter tolerance index is limited in that it relates purely to possible microhabitat associations. Small, highly manoeuvrable bats would be expected to show an equal association with highly cluttered habitat and open habitat. Furthermore, caution should be employed when relying on simplistic approaches in predicting ecological characteristics based on morphometric data (Norberg and Rayner 1987; Saunders and Barclay 1992). Present designs may not necessarily reflect optimal adaptations to current environments, and phylogenetic constraints should not be discounted in the analysis of flight performance.

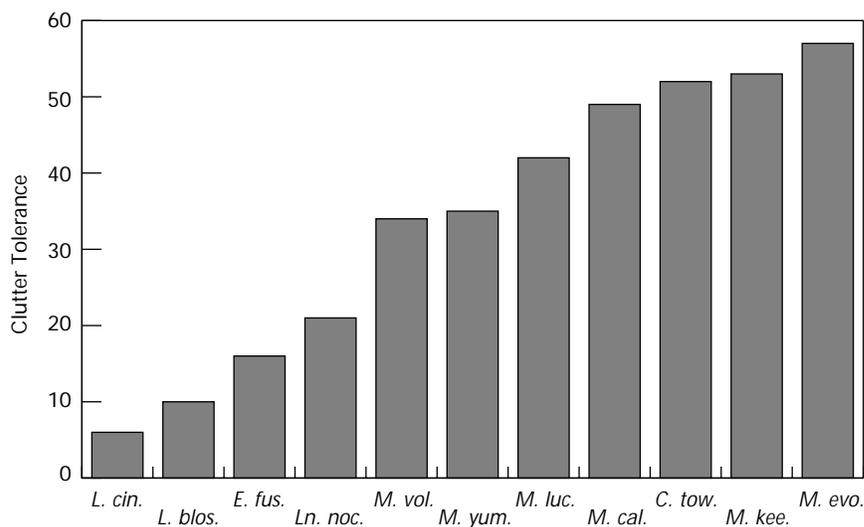


FIGURE 1 Ranked clutter tolerance index for 11 northwestern Nearctic bat species. Indices were determined by summing three morphological variables associated with flight style.

Old-growth forest (over 200 years old, Kirk 1992) is distinct from younger forest in displaying greater vertical structural heterogeneity (Arsenault and Bradfield 1995). This dichotomy is pronounced in the wet, highly productive regions of the Pacific Northwest. In the western hemlock (*Tsuga heterophylla*) forests of coastal British Columbia, small, localized disturbances, the result of winter storms and lightning strikes, characterize the disturbance regime. This is reflected in the uneven age structure of these forests. These localized events, coupled with a successional process that involves a wide diversity of tree species with differing shade tolerances (Terborgh 1985; Hunter 1990), combine to mould the structure of the forest habitat volume, creating vertical stratification in forest structure. Forest stratification is typified by an upper layer of overstorey, or canopy, one or more subdominant layers composed of younger stems of the canopy trees, and mature trees of other species that fail to reach the canopy, constituting the understorey (Spurr and Barnes 1980). In essence, vertical structural complexity results from a combination of factors, including the longevity and large size of the dominant conifers, plant species' richness, and long-rotation, localized disturbance (Arsenault and Bradfield 1995).

Summary of  
Objectives

1. Assess the vertical distribution of foraging activity by vespertilionid bats in three coastal, old-growth forest types on Vancouver Island, British Columbia.
2. Determine habitat structure (in particular vertical structure) differences between the forest types.
3. Determine if vertical habitat structure can be functionally linked to bat community composition, through correlational analysis of microhabitat association and vertical forest structure.
4. Compare predicted, interspecific vertical microhabitat associations with observed distributions.

#### MATERIALS AND METHODS

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This study is being conducted at two main sites: the Carmanah watershed (48° 64'N, 124° 61'W), and Rocky Point (48° 37'N, 123° 72'W). Both study sites are within old-growth forest that has never been logged or managed. Two biogeoclimatic zones are represented (Table 1).

Anabat II ultrasonic detectors, set at three heights in the forest along vertical transects, were used to sample bat activity. Detectors were used in combination with delay switches and tape recorders to enable the automated recording of bat calls.

Five sample trees were selected at each of three old-growth forest sites. The selection of trees was not random. Emergent canopy trees were preferentially selected so that equipment could be raised above the main canopy layer if desired. In addition, trees were selected for their accessibility to static line, or fixed rope, climbing techniques, which precluded a random approach. All sample trees were at least 30 m apart, the maximum distance being 300 m.

Suitable high branches, with adequate clearance to ground level, were selected. Trees were climbed by a professional arborist who attached

TABLE 1 Biogeoclimatic zones, representative flora, and local climatic means for two of the forest types sampled.

Site	Stand type	Biogeoclimatic zone	Mean annual temp. (range)	Mean annual precip. (range)	Representative flora
Carmanah Valley	Sitka spruce ( <i>Picea sitchensis</i> )	Coastal western hemlock (CWH), subzone: very wet; hypermaritime (vh)	8.2°C	2951 mm	Western redcedar ( <i>Thuja plicata</i> ) and western hemlock ( <i>Tsuga heterophylla</i> ) dominate the open canopy. Salal ( <i>Gaultheria shallon</i> ), red huckleberry ( <i>Vaccinium parvifolium</i> ), and salmonberry ( <i>Rubus spectabilis</i> ) dominate the moderately well-developed shrub layer.
Rocky Point	Douglas-fir ( <i>Pseudotsuga menziesii</i> )	Coastal Douglas-fir (CDF)	9.2 to 10.5°C	647 to 1263 mm	Redcedar–Grand fir–Foamflower association. Tree stratum consists of Douglas-fir ( <i>Pseudotsuga menziesii</i> ), grand-fir ( <i>Abies grandis</i> ), western redcedar ( <i>Thuja plicata</i> ), bigleaf maple ( <i>Acer macrophyllum</i> ), and western flowering dogwood ( <i>Cornus nuttallii</i> ). Western redcedar occurs in the understorey.

Source: Meidinger and Pojar, 1991.

pulleys to selected branches, so that equipment could be raised and lowered from the ground. This eliminated any unnecessary damage to the tree from frequent climbing trips to place and retrieve detectors. Pulleys were approximately 45 m above the ground within the forest canopy. Three detectors, enclosed in plastic, watertight containers, with ultrasonic microphones exposed, were set at three levels along each vertical transect: canopy (45 m), understorey (25 m), and shrub (1.5 m, Figure 2). On any night, all detectors were oriented to point in the same direction, although this direction changed from transect to transect. Detectors were left activated for the entire night. The light-sensitive switch, a feature of the Anabat II system, was not used, as it frequently failed to record early and late bat activity due to high relative light levels during twilight. Each Anabat detector and delay switch were powered by a single, 12-volt, sealed, rechargeable battery (Powersonic model PS-1270). This allowed continuous sampling for up to five nights. The detectors were lowered each day and moved to another transect (i.e., a different tree), audio-cassette tapes were replaced, and the digital clocks in the delay switches were re-synchronized. To reduce the influence of sampling bias due to differing sensitivities between individual detectors, all sensitivity dials were set at 6, and detectors were rotated between levels after each sample night.

Mist nets were set over watercourses and within the forest to determine the species composition of the local bat fauna. Bats caught in nets were removed and identified to species, then morphological measurements were taken and an outline of an extended right wing was traced onto graph

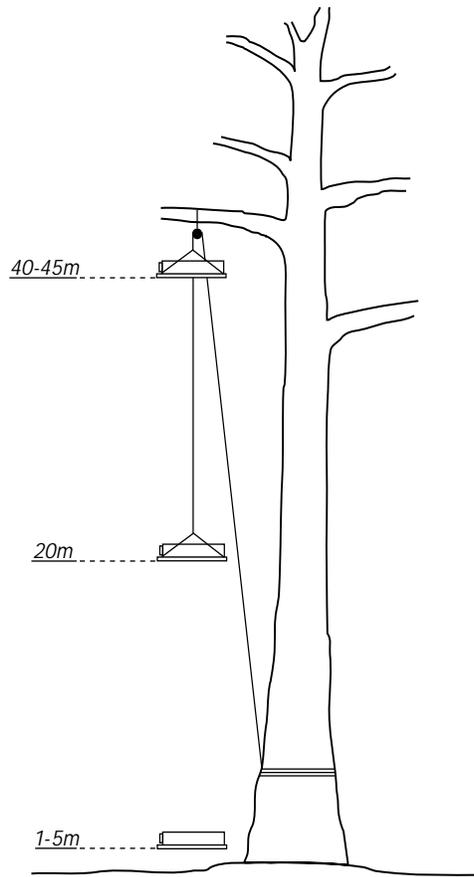


FIGURE 2 Positioning of bat detectors along a vertical transect at each sampling tree.

paper. This allowed measurement of wing area and wingspan. The bats were then weighed and marked with a chemi-luminescent tag (Buchler, 1976) affixed between the scapula with skin cement. Each tagged bat was released in an open area so that recordings of calls could be made using an Anabat detector connected to a tape-recorder. This provided a set of reference calls used to identify species, or species groups.

Vertical profiles of foliage (clutter) density were constructed, following MacArthur and Horn (1969). An SLR camera equipped with a 205-mm zoom lens attached to a tripod was used to generate cross-sections of vertical forest structure. At each sampling point eight transects, separated by increments of  $45^\circ$ , were set from the base of the stem running 30 m into the surrounding forest, creating eight radii of a circle with a diameter of 60 m, the centre being the sample tree. Along each transect a profile was measured every 5 m, producing six profiles per transect and a total of 48 for the sampling plot. All types of plant material, including twigs and branches, were included in the profile. There is no salient reason to consider any type of plant matter less or more important in obstructing bat flight.

Bat activity was measured as the number of bat passes. A bat pass was any call sequence that included two or more pulses (Garcia and Barclay 1993). Call sequences were classified as either a commuting pass or a

foraging pass. Sequences were designated as commuting passes if they lacked the characteristic increasing pulse repetition rate associated with a foraging attempt, or “feeding buzz.”

Recordings of bat calls will be analyzed, using Anabat 5.2 software, and compared with reference recordings made of known species, to determine the species or species group to which the call most closely resembles.

## RESULTS

Sampling was conducted on a total of 55 nights between June and August 1995, resulting in a total of 165 detector-nights. Of these, 25 sampling nights were at Carmanah Valley (69 detector-nights, some detector-nights were excluded due to equipment failure), and 21 nights at Rocky Point (63 detector-nights).

Mean foliage density with height for both Rocky Point and Carmanah (Figure 3) indicate distinct structural differences. At Rocky Point, foliage density is concentrated at the canopy level, approximately 35–50 m, whereas in Carmanah, foliage density is distributed more evenly, with

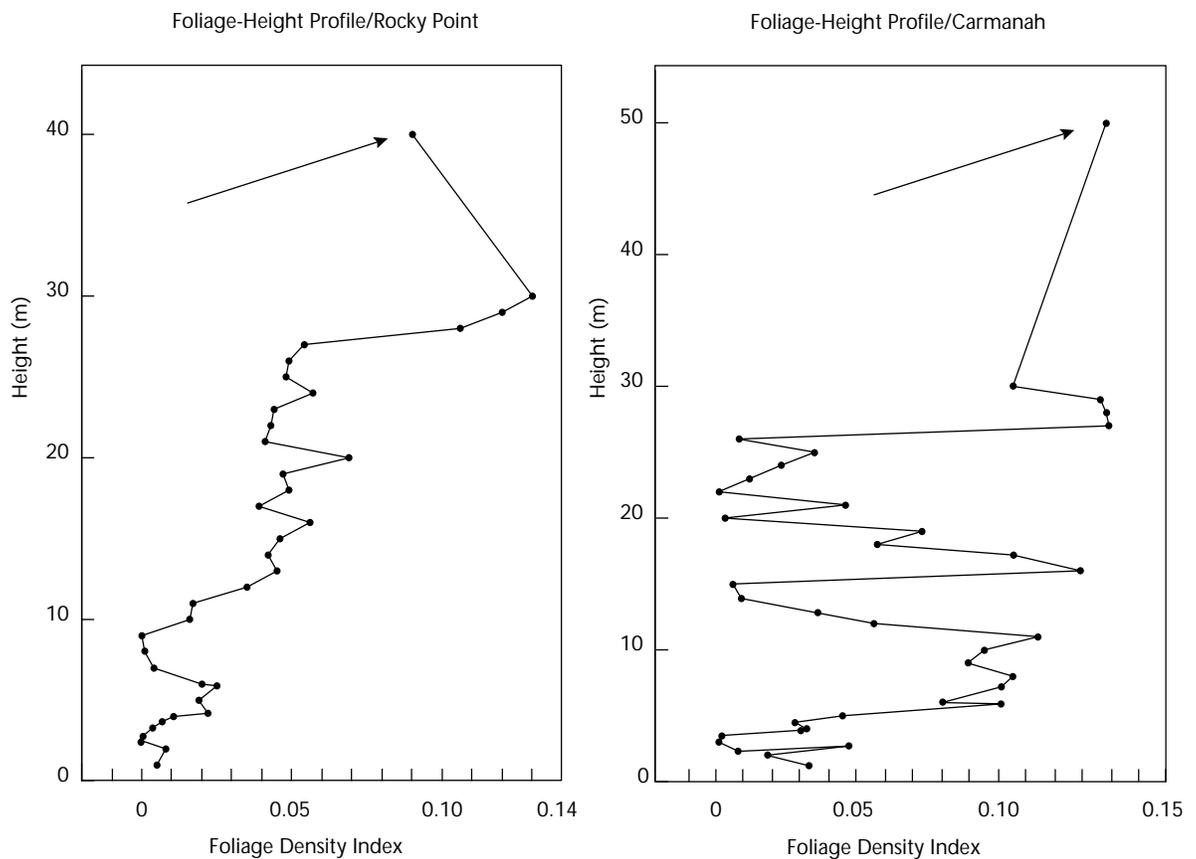


FIGURE 3 Mean foliage density vertical profiles for both forest types ( $n = 16$ ;  $n = 23$ ). Points highlighted by arrows represent approximate mean densities of foliage between 30 and 70 metres.

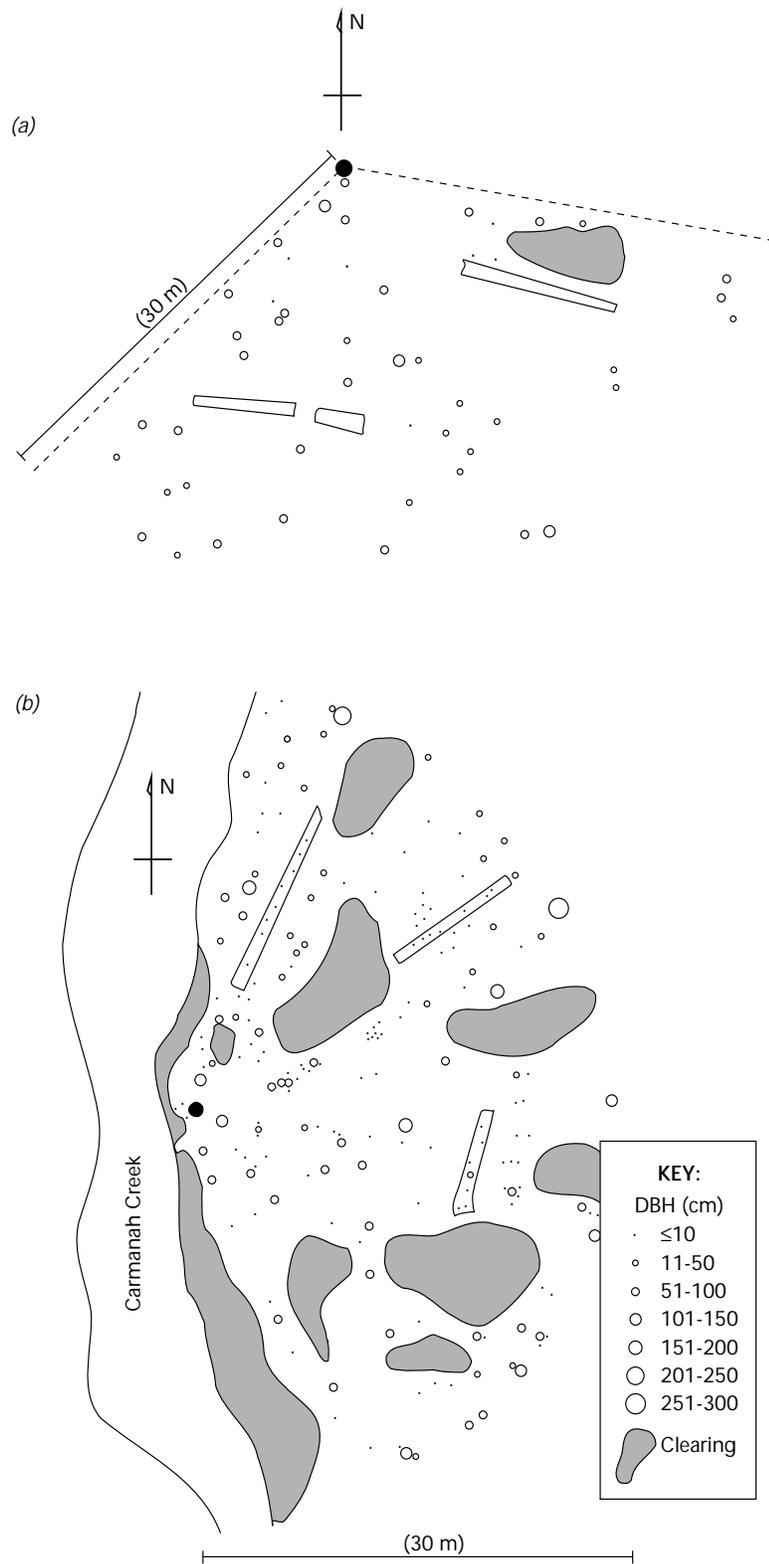


FIGURE 4 Representative 30-m-radius plots for (a) Rocky Point and (b) Carmanah Valley. Filled circles are sampling trees. Open circles are live or dead stems.

peaks of density in the understorey and canopy. This agrees closely with personal observations of the vertical structure of these forest types, and is partly the result of differences in stand age structure between these forest types. Rocky Point sample plots (CDF, Coastal Douglas-fir (*Pseudotsuga menziesii*) zone) are characterized by a marked consistency of stem DBH (diameter at breast height), implying an even age structure (Figure 4a). Carmanah plots (CWH, Coastal Western Hemlock (*Tsuga heterophylla*) zone) display a wide range of stem DBH, and have a higher basal area ( $B = 0.005454 * D^2$ ) per unit area, reflecting the well-developed understorey of this forest (Figure 4b).

Nightly bat activity patterns show marked differences between forest types. At a broad level, when forest types are compared, there is considerably more activity at Rocky Point. If height in the forest is considered, then distinct patterns appear. At Rocky Point, activity is concentrated in

CARMANAH VALLEY (Sitka spruce stand)                      ROCKY POINT (Douglas-fir stand)

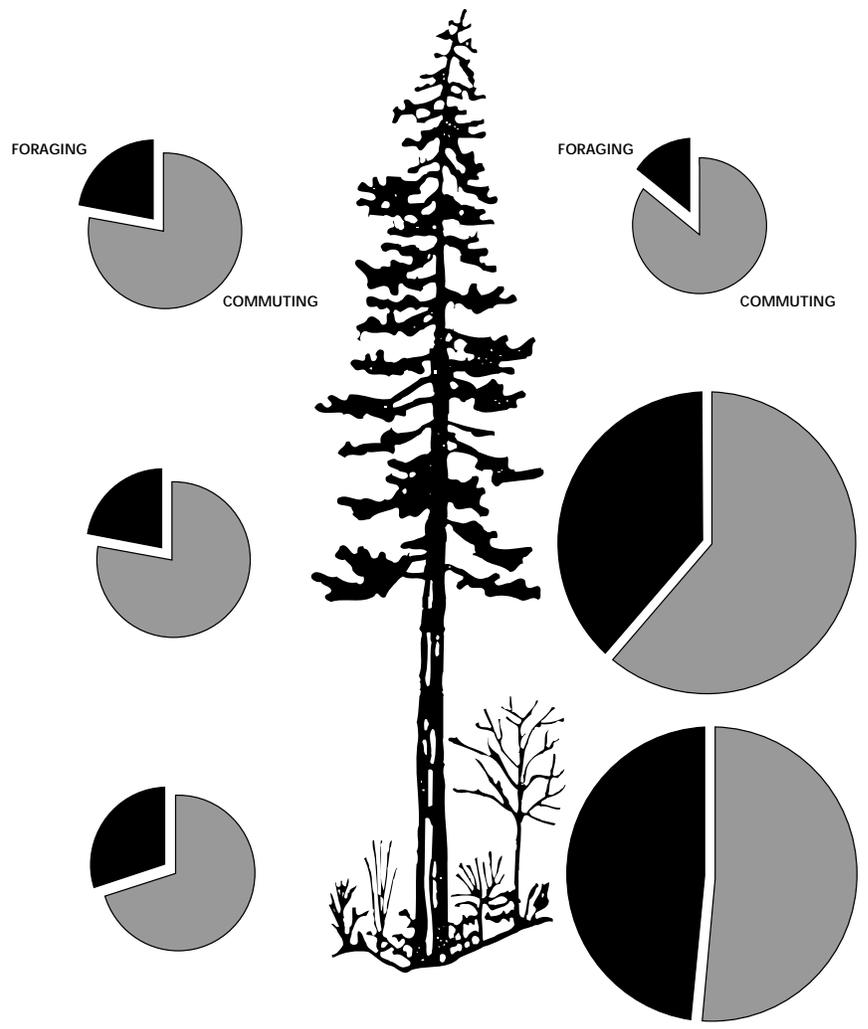


FIGURE 5 Vertical bat activity for both forest types (132 detector-nights). Diameters of pie-charts represent percentage of the total activity for all sites.

the shrub and understorey, with considerably less activity in the canopy. Foraging activity exhibits a general trend of decreasing with increasing height at Rocky Point (Figure 5). Carmanah sites do not display this apparent relationship. Both total activity and foraging activity remain relatively constant with height, although at the same approximate intensity as canopy activity at Rocky Point.

Foraging activity is not constant throughout the night at either site. Distinct peaks appear in the first hour after sunset for both forest types. However, foraging activity drops and remains low in Carmanah, whereas several further successive peaks in activity occur at Rocky Point (Figures 6a, b).

## DISCUSSION

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My results are preliminary and have not been statistically assessed. It would be premature to make any firm conclusions about the patterns of

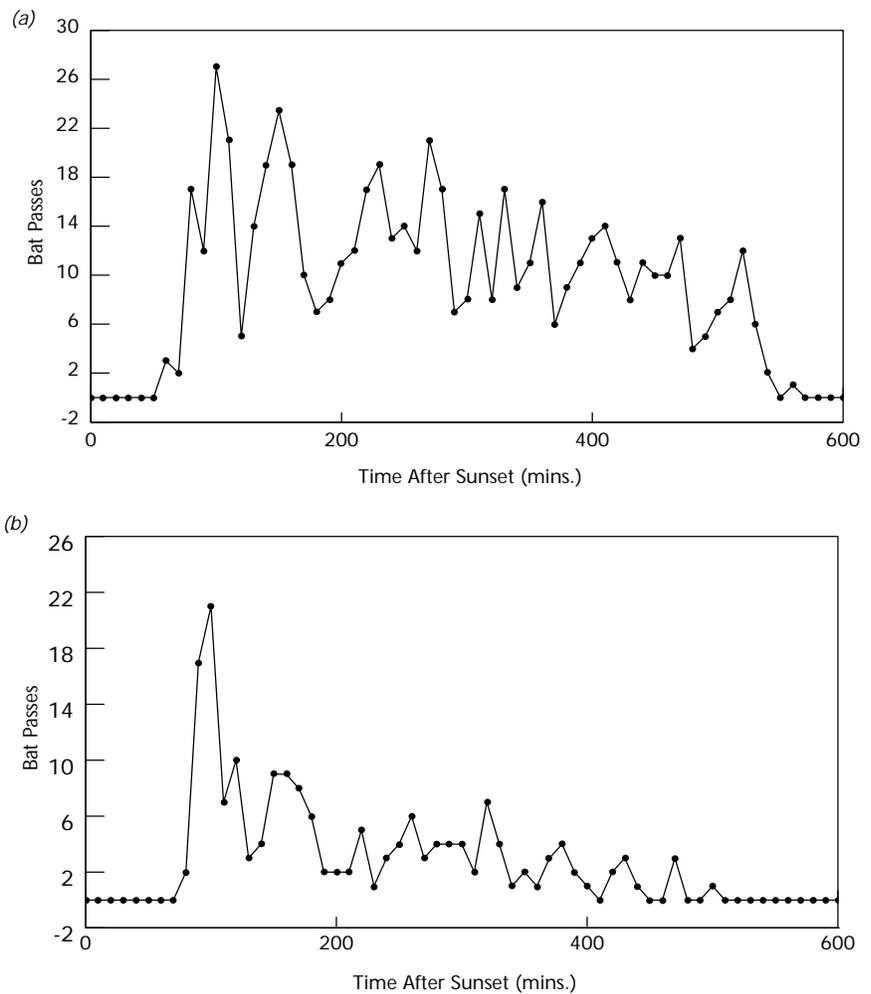


FIGURE 6 Summed foraging passes with time after sunset for (a) Rocky Point and (b) Carmanah Valley.

bat activity that have emerged so far. However, a broad pattern of vertical differences in activity is evident. The open structure of the Douglas-fir forest type harbours more bat activity, whereas the structurally more complex western hemlock forest of the Carmanah Valley has relatively lower levels of bat activity. Whether or not these apparent differences in activity, between and within forest types, reflect differences in bat community structure, is yet to be determined. Two pieces of evidence do, however, corroborate the hypothesis that differences between forest types are the result of different associated bat species assemblages. First, mist netting in both forest types (Rocky Point  $n = 25$  nights; Carmanah  $n = 13$  nights) resulted in the capture of 54 bats (all at ground level), distributed among five species. At Rocky Point the following species were trapped: *Myotis lucifugus*, *Myotis californicus*, *Myotis evotis/keenii*, *Lasionycteris noctivagans*, and *Corynorhinus townsendii*. At Carmanah only two species were trapped: *M. lucifugus* and *M. californicus*. Second, patterns of foraging activity after sunset (Figure 6a) at Rocky Point, typified by an initial large peak in activity followed by successively smaller peaks until dawn, imply the superimposing of nightly activity patterns of several species. Further research and analysis of current data will be undertaken to determine if these findings are consistent.

At present there is a paucity of information regarding the vertical distribution of bat foraging activity with respect to forest structure, for any forest type, but in particular for temperate forests. In the coastal regions of the Pacific Northwest, and for temperate regions in general, this gap in our understanding of habitat use is considerable. Developing a more pervasive, three-dimensional understanding of habitat use is an important research goal. Old-growth forests provide a unique opportunity to construct a "baseline" behavioural and ecological knowledge of minimally disturbed habitats and communities. If, in the future, a fully informed and effective reconstruction of damaged habitats is to be undertaken, or habitat reserves are to be created, this baseline knowledge will be invaluable.

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