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Use of the Forest Canopy by Bats

Abstract

Of the 15 species of bats in the Pacific Northwest, 11 are known to make regular use of the forest canopy for roosting, foraging, and reproduction. This paper reviews roosting requirements, foraging, and the importance of landscape-scale factors to canopy-using species in the Northwest. Many northwest bats use several different types of tree roosts. Common roosting sites are in cavities, crevices, and foliage. Factors that may be important in roost site selection include microclimate, roost structure, crown architecture, canopy tree age and species, bark characteristics, foliage density, and stand and landscape composition. Some representative Pacific Northwest cavity- and crevice/bark-roosting species include the little brown bat (*Myotis lucifugus*), silver-haired bat (*Lasionycteris noctivagans*), and long-legged bat (*M. volans*). Only two Pacific Northwest species are known to roost in foliage. Several species forage in forest gaps, along forest edges, or in riparian areas. Long-eared (*M. evotis*) and Keen's (*M. keenii*) bats may forage within the forest canopy, although foraging behavior of these species in the Pacific Northwest is not well documented. Stand- and landscape-scale complexity may be important in providing bats with the abundance and diversity of roost, foraging, and hibernation sites they require.

Introduction

Little work has been done on forest canopy use by bats in the temperate region, particularly in the Pacific Northwest. Moreover, the understanding of the significance of the forest canopy to bats is complicated by the fact that few temperate species are restricted to any one habitat type for foraging and roosting. Most species meet only some of their requirements within the forest canopy and must go outside the canopy to satisfy the remainder of their needs. The term canopy is used here in the broadest sense to encompass all components (trunks, as well as branches and foliage) of the upper parts or crowns of trees that make up forest stands. A detailed list of canopy attributes of potential significance to bats and other canopy species may be found in Carey (this issue).

About 11 species of Pacific Northwest bats appear to regularly use the forest canopy. An additional two species are occasional canopy users (the fringed bat, *M. thysanodes* and the western small-footed bat, *M. ciliolabrum*) (Table 1). Forest bat communities in the Pacific Northwest are made up of some six to eight *Myotis* species and four non-*Myotis* species. The most frequently encountered species include the little brown bat (*M. lucifugus*), the Yuma bat (*M. yumanensis*), the California bat (*M. californicus*), the long-legged bat (*M. volans*), the long-eared bat (*Myotis evotis*), the big brown bat (*Eptesicus fuscus*), the silver-haired bat (*Lasionycteris noctivagans*) and the hoary bat (*Lasiurus cinereus*) (Christy and West 1993). Townsend's big-eared bat (*Plecotus townsendii*) also forages in forested environments.

Bats use the canopy for a variety of purposes, including roosting, foraging, and reproduction. In this paper, we will examine the use of the forest canopy by Northwest bats for roosting and foraging. The importance of landscape composition to bats, will also be discussed.

Roosting

The roosting ecology of bats has been reviewed by Kunz (1982a). Species diversity and population size of colonial bats appear to increase with increased roost availability and diversity (Humphrey 1975, Findley 1993). Areas that offer a variety of tree, cliff, and cave roosts, often support the largest number of bat species and individuals (Humphrey 1975, Findley 1993).

The specific roost sites selected by various bat species may be determined in part by such factors as morphology, flight and echolocation capabilities, proximity to other resources (food, water, hibernation sites), climatic factors, and roost availability, among others. Vaughan (1970) has reviewed the relation between morphology (skull shape, pelvic girdle, and limb proportions) and roost selection in bats. Shump and Shump (1980) found that hoary and red bats, which roost in exposed locations, have greater pelage insulation than little brown and big brown bats, which roost in more protected sites. These authors related pelage differences to differences in roost condition and gregariousness in these species. Hoary bats have a relatively high aspect ratio and wing-loading and are not well adapted for highly maneuverable flight, which may influence their choice of roost sites (Constantine 1966, Barclay 1985).

TABLE 1. Forest canopy use by Pacific Northwest bat species. Species marked with an asterisk (*) are infrequent canopy users; all others listed are regular canopy users.

Species	Canopy Use	
	Roosting	Foraging
Myotis lucifugus[1]	X	X
Myotis yumanensis[2]	X	X
Myotis californicus[3]	X	X
Myotis volans[4]	X	X
Myotis evotis[5]	X	X
Myotis keenii[6]	X	X
Eptesicus fuscus[7]	X	X
Lasiurus cinereus[8]	X	
Lasiurus borealis[9]	X	
Lasionycteris noctivagans[10]	X	X
Plecotus townsendii[11]		X
*Myotis thysanodes**[12]		X
*Myotis ciliolabrum**[13]		X

[1]Barbour and Davis 1969, LaVal et al. 1977, Fenton et al. 1980, Fenton and Barclay 1980, Barclay and Cash 1985.

[2]Fenton et al. 1980, van Zyll de Jong 1985.

[3] Krutzsch 1954· Fenton and Bell 1979, Fenton et al. 1980.

[4] Baker and Phillips 1965, Whitaker et al. 1977, Fenton and Bell 1979.

[5] Manning and Jones 1989, Barclay 1991.

[6]Cowan and Guiguet 1965.

[7] Fenton et al. 1980, Brigham 1991.

[8] Constantine 1966, Shump and Shump 1982, Barclay 1984, Barclay 1985.

[9]Constantine 1966, Furlonger et al. 1987.

[10] Kunz 1982b, Barclay 1985.

[11]Kunz and Martin 1982.

[12]Barbour and Davis 1969, Whitaker et al. 1977.

[13]Fenton et al. 1980, van Zyll de Jong 1985.

Constantine (1966) found that hoary and red bats generally roost where they could drop down through an unobstructed distance to attain flight speed.

Norberg and Rayner (1987) discuss the relation between morphology, flight, and echolocation capabilities in bats. Tuttle (1976) examined the significance of proximity of maternity roosts to foraging areas and hibernation sites in gray bats (*Myotis grisescens*). Thomas (1988) and Barclay (1991) have suggested that climate and elevation may play a role in the choice of roost location and distribution of the sexes in some bat species.

Choice of roost site may differ with sex, age, reproductive condition, and migratory status of an individual. Constantine (1966) observed that young red bats roost higher in trees than do adults. Fenton (1970) found that reproductive female little brown bats select different roost sites than do males, based upon their thermal requirements.

Most Pacific Northwest species roost in a variety of situations, rather than in only one particular roost type (van Zyll de Jong 1985). The roosting ecology of Pacific Northwest bats has been reviewed by Christy and West (1993).

The major types of tree roosts used by temperate bats include cavities, crevices behind exfoliating bark, crevices formed in rugose bark, cracks in wood, and in foliage. Rarely, bats have been reported roosting in nests of other mammals (squirrels) and in epiphytes (Spanish moss) on trees (Neill 1952, Constantine 1958).

Tree Cavities

Tree cavities used by bats may be in hollows formed in the trunks or branches of snags or damaged live trees. They generally provide a relatively stable microclimate and offer protection from predators (Kunz 1982a, Tidemann and Flavel 1987).

Factors in selecting tree cavities include microclimate, structure, tree age, size, and height.

Microclimate: Microclimate of a cavity can be affected by aspect, entrance height, canopy cover, density of surrounding vegetation, tree status (alive or dead), thickness and insulating properties of the cavity walls, tree diameter, cavity size, and number of bats occupying the cavity. Maeda (1974) found that large noctule bats (*Nyctalus lasiopterus*) in Japan preferentially roost in cavities in live trees, which provides more constant temperatures than cavities in snags. Tideman and Flavel (1987) suggested that the higher water content of live trees increases their insulative value and cavity humidity. Female bats in reproductive condition generally have different breeding-season roosting requirements than males and may roost separately from them. Pregnant or lactating females often roost colonially at more protected roost sites that provide the high temperatures necessary for maximizing growth and development of the young (Barclay 1991). Males and nonreproductive females commonly roost solitarily or in small groups, in less protected and thermally stable environments (Barclay 1991).

Structure: Maeda (1974) reported that large noctule bats select roosts based on the following structural characteristics of the roost cavity: shape, position, entrance height, size, and degree of entrance protection. The position of the entrance has to permit easy flight from the cavity. Tideman and Flavel (1987) studied cavity-roosting bats in Australia and found that bats select cavities with entrance holes that are just larger than the size of the bat. Presumably, small entrances provide greater protection from predators and may reduce competition from birds and other bats. Roost entrances are also oriented to prevent the entry of rain into the cavity.

Tree characteristics: The age of cavity trees is important to bats to the extent that it is a factor in frequency of cavity formation, cavity size, and cavity characteristics (Tideman and Flavel 1987). Tideman and Flavel (1987) failed to find any relation between roost site selection and tree height, for the Australian bats they studied. Lunney et al. (1988), found that the Australian big-eared bat (*Nyctophilus gouldi*) a cavity- and crevice-roosting species, select large diameter trees, of more than 80 cm d.b.h. for roosting.

Some examples of Pacific Northwest bats known to use tree cavities are the little brown bat (Fenton and Barclay 1980), the big brown bat (Brigham 1991), the California bat (Krutzsch 1954), and the silver-haired bat (Kunz 1982b). Some of these species (particularly the little brown bat, the big brown bat, and the California bat) commonly use buildings as roost sites as well. Barbour and Davis (1969) list buildings as the preferred roost sites for these three species.

Tree Crevices

Many tree-roosting bats roost behind exfoliating bark on trunks or branches of dead or live trees. Bark roosts provide a much less permanent, less secure and less thermally stable roosting environment than cavities. Bats that roost under bark must change roosts more frequently than those roosting in cavities because of the more transient nature of their roost sites (Kunz 1982a). They are probably also more vulnerable to predation and weather.

Other types of crevice roosts include cracks in tree trunks and in larger branches, and crevices created by bark rugosity. Perkins and Cross (1988) reported that silver-haired bats prefer roosting in old (> 150 years) Douglas-fir (*Pseudotsuga menziesii*) forests in Oregon, probably because of the bark characteristics of old trees. The bark of old Douglas-fir tend to provide more crevices by separating more widely from the trunk. Old trees also develop more pronounced ridges and crevices in the bark itself. Bats were found to prefer Douglas-fir to ponderosa pine (*Pinus ponderosa*) and true fir (*Abies* spp.), probably because of differences in bark characteristics. The bark of these latter species tended to be less rugose and generally did not form as deeply creviced furrows. Barclay et al. 1988 observed silver-haired bats roosting in spaces behind folds of bark, in split tree trunks, and in depressions on tree trunks. Other Northwest bats that roost under bark or in other tree crevices include the long-legged bat and the long-eared bat (van Zyll de Jong 1985).

Foliage Roosts

Foliage roosts provide the most exposed type discussed thus far. They are used most frequently in tropical regions. Potential foliage roost sites are more abundant than cavity- and crevice-roosts, but their greater exposure makes them more hazardous. Their abundance, however, makes them easy to find near foraging areas, and might help to reduce commuting distance. The abundance of foliage roosts also facilitates the wide distribution of some foliage roosting species. Predation risks are probably higher for foliage roosting bats, and many temperate and tropical foliage roosters are cryptically colored and roost solitarily or in small family groups (Kunz 1982a). One Northwest foliage roosting species, the hoary bat, has a characteristic grizzled appearance that may contribute to its concealment. Temperate foliage roosting species are generally well insulated against cold temperatures (Shump and Shump 1980) and may make long distance latitudinal migrations in response to diminished winter food supplies (Shump and Shump 1982).

Foliage roosting bats tend to change roosts more frequently than other species in response to the transient nature of their roost sites. Within the same season, they may show some fidelity to a general area, however (Kunz 1982a, Lunney et al. 1988).

Bats that roost in foliage may roost high in the canopy, in subcanopy trees, or in understory foliage. Roost sites may be in dense foliage, in relatively exposed locations, among leaves, or on branches. Sites may be concealed from above, but conspicuous from below (Constantine 1966, Kunz 1982a). Hoary bats and red bats (*Lasiurus borealis*) for example, have been found to select roost sites covered by dense foliage above and around the sides, but open below. This arrangement presumably reduces their visibility and accessibility to predators, but permits them to take flight readily (Constantine 1966).

Location of the roost tree relative to surrounding vegetation may also be of importance to some species. Certain species may prefer trees within the forest interior, and other species prefer to roost along a forest edge. Constantine (1966) reported that hoary and red bat roost sites were usually located along a forest edge.

Perkins and Cross (1988) found that hoary bats were primarily associated with old Douglas-fir forests in Oregon and hypothesized that this is due to bats' roosting requirements. The large trees and large and heterogeneous canopies found in such forests may furnish more roost sites available for foliage roosting bats than young forests. Old coniferous forests are more likely to provide the canopy structure, including dense foliage adjacent to uncluttered flight space, required for roosting by these bats. In contrast to younger trees, older trees tend to have crowns that begin higher off the ground and have the needles more concentrated toward the edge of the canopy (Perkins and Cross 1988).

Foraging

Foraging tends to be opportunistic rather than restricted to a particular foraging strategy or habitat for most North American bat species (Vaughan 1980, Barclay 1991, but see Fenton 1982, Furlonger et al. 1987). Furlonger et al. (1987) found that bats in eastern Canada exploit concentrated patches of prey. They suggested that this type of foraging strategy may supersede preference for a particular type of foraging habitat. Some authors (Black 1974, Crome and Richards 1988, Findley 1993) maintain that species of bats may partition foraging habitat by vegetation structure, reflecting differences in their morphology, echolocation call structure, and flight capabilities. Findley (1993) reviews the relation between morphology and community structure in bats.

Foraging Habitat

Aldridge and Rautenbach (1987) divided African insectivorous bats into four major groups according to foraging-habitat preference: (1) clutter foragers, maneuverable species with echolocation calls suited to a cluttered environment and capable of foraging within the forest canopy; (2) intermediate clutter foragers, moderately maneuverable bats capable of foraging in open areas and open woodland, but not within dense vegetation; (3) woodland-edge foragers; and (4) open-air foragers that lack maneuverability. Other authors have used similar classification schemes to describe North American bat species. LaVal et al.(1977) studied bat populations in Missouri and found that hoary and red bats tended to forage in open areas away from forest clutter, including high over the forest canopy and over open fields. Gray bats foraged in riparian areas and over water. Little brown bats foraged along forest edges and within the forest. The northern myotis (*M. septentrionalis*) a close relative of the Keen's myotis, a Pacific Northwest species, was a clutter forager and foraged in forested areas. The Indiana myotis (*M. sodalis*), another clutter forager, foraged primarily in the canopy, but the northern myotis foraged below the canopy but above the understory shrub layer, which suggests that some vertical stratification may occur within bat communities.

Crome and Richards (1988) investigated the differential use by bats of gaps (created by logging) and closed canopy areas in an Australian rain forest. They divided bat species into canopy specialists (clutter foragers), gap incorporators (intermediate clutter foragers), and gap specialists (open-air foragers). Habitat preference of the bats was found to be related to wing morphology and flight maneuverability. Canopy-specialists were highly maneuverable, and gap specialists were capable of faster but less maneuverable flight. Gap incorporators, which foraged in both types of habitats, had wing characteristics and flight capabilities intermediate between the other two types. Crome and Richards (1988) concluded that vegetation structure and wing morphology determine allocation of different habitat types among species.

Many Pacific Northwest species forage in riparian areas (little brown bats and Yuma bats (Kurta 1982, Herd and Fenton 1983, Lunde and Harestad 1986, Brigham et al. 1992), in clearings and roads within forests (California bat, Yuma bat, and long-legged bat (Barbour and Davis 1969, Fenton and Bell 1979, Brigham et al. 1992) or in open areas or along forest edges (hoary bat, red bat) (Constantine 1958, Barclay 1985). Gleaning species, such as the long-eared bat and possibly the Keen's bat, may forage within the canopy (Cowan and Guiguet 1965, Manning and Jones 1989, Barclay 1991). None of these species are known to restrict its foraging to just one habitat type, however. Riparian areas and forest edges are exploited by many bat species to some extent, perhaps because these areas support higher densities of flying insects (Furlonger et al. 1987, Cross 1988, Thomas 1988, Barclay 1991).

Landscape Context

Although several canopy attributes may be of consequence to bats (Carey, this issue), the composition of the surrounding landscape may also play a role in determining the relative importance of specific attributes, and may influence bat distribution. Some landscape-scale considerations are discussed below.

Distribution of Bats

Several authors have looked at the diversity of bat communities in different broad habitat types. In general, topographically complex regions tend to support the most bat species. Jones (1965) studied bats in the Mogollon Mountains of New Mexico and Arizona. He recorded the greatest percentage of captures in higher elevation, mixed-conifer, forest; an intermediate percentage in mid-elevation, pine-oak woodland; and the lowest number of captures in lowland, xeric-shrub, grassland. These differences were presumably related to differences in availability of roost sites, food resources, and water. Jones (1965) found that different species dominate the bat community in each of these habitats. Big brown bats predominate in higher elevation coniferous forest, and hoary bats are most common in the pine-oak woodland.

Thomas (1988) found a disproportionate use of old-growth Douglas-fir stands by bats in the Cascade Range of Washington and Oregon and Coast Ranges of Oregon, compared to young and mature stands. Increased roost availability in old growth stands probably accounted for this difference because bats did not appear to be concentrating foraging activity within the forest stands.

Resource Proximity

Although forest bats may have roosts that meet their primary requirements within a particular forest stand, the composition of the surrounding landscape is important in determining whether roost sites can be used successfully. Proximity of good quality roost sites to foraging and drinking areas, as well as to hibernation sites, can reduce the energetic costs of commuting (Tuttle 1976). Because many bats concentrate their foraging in riparian areas, proximity of roost sites to riparian areas assumes particular importance. Where roost sites are far from foraging areas, juvenile mortality may be higher. Tuttle (1976) found that growth and survival of juvenile gray bats in the southeastern United States is impaired when the distance from the maternity roost site to foraging areas is too great. Optimal maternity-roost conditions, highly productive foraging sites, and nearby hibernation sites can compensate for greater roost-to-foraging site distances, however (Tuttle 1976).

Bats sometimes may require connecting corridors of suitable habitat between critical resources. Tuttle (1976) observed that gray bats, which roost in caves and forage over water, generally fly between these sites within the forest canopy.

The abundance, diversity, and relative proportion of critical resources may also be important to bats. Many bats change roosts frequently and require several different roosts of diverse character to compensate for changes in air temperature, weather, predators, prey patches, and other factors. Humphrey et al. (1977) observed a maternity colony of Indiana bats that used two roost sites about 30 m apart. Each roost site had different thermal properties, and the colony shifted between them depending on temperature and weather conditions. Bats may therefore need a selection of different roost sites (and perhaps different tree species), with a variety of thermal and other properties, distributed across the landscape and located within a fairly constrained area.

Riparian Zones

As is true for many other vertebrates, riparian zones assume disproportionate importance for many bats, which may do most of their foraging in these insect-rich areas (Brigham et al. 1992). Bats frequently use riparian zones as travel corridors as well. Thomas (1988) found that foraging rates for several Pacific Northwest *Myotis* species are significantly higher over water than in the forest where they roost. Roost sites may be more abundant in riparian areas because of an increased number of snags and older trees, as well as rock crevices in eroded stream banks (Cross 1988). For species such as the hoary bat, known to roost in deciduous trees, riparian areas may be preferred because of a preponderance of such trees in the riparian zone (Cross 1988). Riparian areas also provide the open flight space and forest edge conditions required by some species.

Role in Forest Ecosystems

Tree-roosting bats, which deposit large amounts of nitrogen-rich guano at the roost site, may help to provide nutrients in forest ecosystems with nutrient-poor soils. Given their great mobility, bats may be important in transporting nutrients from riparian areas or locations outside the forest ecosystem into forest communities (Cross 1988, Rainey et al. 1992).

Continuous occupation of cavity roosts by bats may modify the roost substrate and environment in ways that affect other cavity dwellers. These effects may include erosion of cavity sides, increased humidity, increased ammonia, increased temperature, and an enhanced rate of deterioration of the roost tree by the accumulation of feces and urine (Kunz 1982a).

Bats consume many insects, such as termites, that are considered to be forest pests (Whitaker et al. 1977). Their role in controlling forest pests remains to be determined, however.

Conclusion

Bats are a highly diversified taxonomic group whose small size, low reproductive rate, high energy demand, and complex needs have made them, perhaps, more vulnerable than many other vertebrate groups. These complex needs require a complex environment. Tall canopies and diverse forest structure, such as those found in late-seral stages of coniferous forests may provide some of the complexity needed by bats (Perkins and Cross 1988). For many bat species, a mosaic of habitat types in close proximity to one another, including a mix of forests, openings, and riparian areas, may provide optimal habitat.

A tremendous amount of research remains to be done to assess the role of forest canopies in Pacific Northwest bat communities. The relative importance of the canopy attributes described in Carey (this issue), including such factors as layering, degree of canopy closure, gaps, canopy volume, and tree species characteristics, need to be investigated. Much of the information currently available is anecdotal, often based on unproven assumptions, or represents generalizations derived from knowledge of bat communities elsewhere. Additional data are needed on roost availability vs. use, insect densities, and prey selection by bats in the canopy and in forest gaps, and effects of landscape composition on bat behavior. Effective management for bats in the Pacific Northwest will require basic research on forest canopy and landscape use. This type of information should prove valuable for making management decisions on cavity tree retention, creation of multilayered canopies, and riparian zone protection.

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