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The Biologically Significant Attributes of Forest Canopies to Small Birds

Abstract

The biologically significant attributes of Pacific Northwest canopies to passerines and other small birds are reviewed. Some evidence suggests that deciduous and coniferous forests represent basic criteria for broadscale habitat selection of PNW birds in this region. However, many species possess rather generalized habitat affinities, and are adapted to a variety of forest types and stand ages. Fine-scale habitat discrimination appears to be associated with structural features such as branch architecture, bark texture, percentage vegetation cover, snag characteristics, and the density and the geometry of foliage. Many species of birds, particularly cavity nesters, reach their greatest abundance in old forest types. Old-growth forests have also been shown to provide important wintering habitat for several birds that reside here permanently. Riparian communities represent another special vegetation type characterized by high avian abundance and species richness.

Introduction

Songbirds are frequently used to characterize forest communities, because they are useful indicators of habitat quality and provide insight into the carrying capacity of various habitats (Graber and Graber 1976, Gilbert and Allwine 1991). Passerines are particularly suited for field censusing because they are diurnal, abundant, easily detected, and possess diverse life histories (Paulson 1992). In the Pacific Northwest, most research on forest avifuana has examined abundance and distributional patterns in various forest types and stand ages, or in relation to structural features such as snags and gaps. In general, however, the basic biology of many species has not been adequately documented, particularly in relation to how birds use canopy environments across the varied topographical, moisture, and vegetational gradients that characterize these forests. The objective of this paper is to provide an overview of how Pacific Northwest canopy ecosystems are relevant to the biology of the region's small, forest-dwelling birds (i. e., passerines, swifts, and woodpeckers). Structural attributes of these systems are emphasized.

Historical Perspective

Forest vegetation has changed dramatically over the last 30,000 years in response to large scale changes in the Earth's climate (Brubaker 1991). Consequently, Douglas-fir (*Pseudotsuga menziesii*) forests probably do not represent a co-evolved complex of species bound together by tightly linked and balanced interactions (Brubaker 1991). This inference provides insight into why most Pacific Northwest birds are generalist foragers, because insufficient time has elapsed for them to segregate into small exclusive niches (Orians and Wilson 1964, Slobodkin and Sanders 1969, Gilbert and Allwine1991). Airola and Barrett (1985) found that permanent residents in the Sierra Nevadas made greater use of substrates that were available year-round, such as conifer foliage, branches, and tree trunks than seasonally available substrates. Presumably this difference reflects their adaptation to northern coniferous landscapes (Mayr 1976), and the need to retain efficient foraging abilities on substrates during the winter when prey is scarce (Sabo and Holmes 1983). In contrast, Airola and Barrett (1985) found that most migrants preferred the more productive, seasonal, deciduous vegetation characteristic of neotropical areas for where they are derived (Mayr 1976). A similar pattern of foliage-type preference was also noted by Alatalo (1982) in northern Finland, who found that migrants used more of deciduous foliage then did residents. Research on the Olympic Peninsula (Sharpe, unpublished data) also supported these foliage-type preferences by demonstrating that most resident species used coniferous forests as their primary habitat, but the region's migrants exhibited a broader use of forest communities including deciduous, mixed and coniferous communities. Such differences in foliage-type preferences, however, are relative (Airola and Barrett 1985), and their several migratory species make extensive use of coniferous forests; the olive-sided flycatcher (*Contopus borealis*), western wood pewee (*Contopus sordidulus*), hermit warbler (*Dendroica occidentalis*).

Tree Species Composition

The factors associated with habitat selection by birds are not well understood. Avian habitat selection may be hierarchically ordered, proceeding from gross physiognomic features at the regional scale to specific vegetation types at more localized scales (Wiens and Rotenberry 1981, Klopfer and Ganzhorn 1985). At fine scales, habitat discrimination appears to be associated with structural features such as branch architecture, bark texture, percentage vegetation cover, snag characteristics, and the density and geometry of foliage (Robinson and Holmes 1982, Raphael and White 1984, Airola and Barrett 1985, Holmes and Schultz 1988). Preferential use of specific tree species is well documented for cavity nesters in the Pacific Northwest (Mannan et al. 1980, Raphael and White 1984, Manuwal and Huff 1987, Holmes and Schultz 1988, Nelson 1988, Manuwal 1991). Several studies in temperate systems also demonstrate that insectivorous birds forage for their prey differentially among the foliage of various tree species (Franzreb 1978, Hunter 1978, Bushby and Sealy 1979, Holmes and Robinson 1981, Airola and Barrett 1985, Morrison et al. 1985). Robinson and Holmes (1984) have also shown that some birds change their search tactics when foraging on different tree species. Holmes and Schultz (1988) have also suggested that the availability of food resources for foraging birds are a function of the type and abundance of prey species present, which varies among tree species; the foliage structure and characteristics of the trees, which influence prey detectability and accessibility; and the morphological and behavioral abilities of each bird species to perceive and capture those prey. The following paragraphs provide some examples of how the structure and substrate of canopies interact with prey and avian morphology to determine food availability for birds.

One of the most obvious differences between conifer and deciduous trees is the type of food resources they produce. Conifers produce seed crops (favored by nuthatches, finches, and crossbills) and broadleaf vegetation generally produces fruits and nuts (favored by such birds as waxwings, tanagers, and thrushes). Perhaps equally important, but more difficult to quantify, is the manner in which the contrasting structural environment of conifers and evergreens influence the foraging activities of songbirds. Compared to deciduous trees, evergreens typically provide continuous cover and a more ameliorated microclimate for both arthropods and foliage-gleaning insectivores (Axelrod 1966, Jackson 1979). In the Sierra Nevada, Airola and Barrett (1985) found that ridged, horizontal limbs of conifers were favored by perch-gleaning insectivores, which could hop along branches, and access large amounts of foliage. The xerophytic nature of conifer needles (Jackson 1979), however, and the presence of secondary compounds in certain conifer species (Wahlenberg 1946) may limit the exploitation of evergreens by phytophagous insects, which may subsequently limit insectivorous birds. For example, Airola and Barrett (1985) found that, during the nesting season, insectivores avoided feeding on incense cedar (*Calocedrus decurrens*), which they attributed to the tree's essential oils, in addition to the small, scale-like needles that mature quickly and reduce the period of susceptibility to phytophagous insects. In contrast, Morrison et al. (1989) found that brown creepers (*Certhia americana*) concentrated their foraging activity on incense cedar during the winter in response to the seasonal availability of scale insects. Ecomorphological studies by Leisler and Thaler (1982) and Keast and Saunders (1991) found that the papillae on the feet of the golden-crowned kinglet (*Regulus satrapa*) penetrated the rugosities of conifer foliage and twigs, allowing the bird to adopt feeding postures and take advantage of foraging opportunities that are more difficult for its smoother-footed congeneric, the ruby-crowned kinglet (*R. calendula*). Several studies have suggested that the foliage structure of deciduous trees can influence how insectivorous birds detect, attack, and capture prey. For example, some deciduous trees may require small, perch-gleaning birds to expend more energy accessing the leaves, which are typically at the ends of branches (Robinson and Holmes 1982). Franzreb (1978) has also suggested the large size and movement of the leaves of quaking aspen (*Populus tremuloides*) may limit the ability of ruby-crowned kinglets to exploit them as a foraging substrate. Birds that are capable of hover-gleaning, however, can probably access larger leaves, and they are therefore less constrained by branch and foliage structure (Holmes and Robinson 1981). Whelan (1989), however found no effect of tree species on the learning rates of two eastern paruline warbler species, suggesting that these birds should be able to respond to prey distribution changes equally well on both sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*).

The surface texture of tree trunks is also important to birds belonging to bark-gleaning and trunk-drilling guilds. In general, the abundance and availability of bark arthropods increases on larger diameter, more heavily furrowed trees (Jackson 1979, Morrison et al. 1985, Nicolai 1986) and is correlated with an increase in brown creepers and, to a lesser extent, red-breasted nuthatches (*Sitta canadensis*) in older stands (Mariani and Manuwal 1990, Huff et al. 1991). In addition, birds such as black-capped chickadees (*Parus atricapilis*) and pine siskins (*Spinus pinus*) have been found to use foliage damage caused by phytophagous insects as cues to locate prey (Heinrich and Collins 1983, Roland et al. 1986).

Gaps

Forest openings caused by natural tree mortality are a conspicuous feature of late-successional forests (Franklin et al. 1981), and are typically characterized by heightened avian richness and abundance. Higher light levels penetrate to the forest floor in gaps, resulting in an increased concentration of resources for birds, such as fruit-bearing deciduous shrubs and insects (Blake and Hoppes 1986). Aerial-sallying insectivores such as flycatchers and tanagers also appear to be influenced by small gaps, since their feeding activities often occur in interior spaces within the canopy (Airola and Barrett 1985, Gilbert and Allwine 1991). Gaps may also influence the vertical distribution of birds in the canopy, as some species that dwell high in the crown move down to lower levels in gaps (Airola and Barrett 1985, Balda 1969).

Canopy Height

As tree height increases, there is a concomitant increase in vertical profiling and selective use of the canopy by birds. Hawking and sallying species such as warblers and flycatchers appear to favor open sites higher in the canopy where there is increased visibility and maneuverability (Airola and Barrett 1985). Foliage gleaners have also been found to focus their foraging activity on leaves that have recently been exposed to sunlight, as these newly-warmed surfaces are presumably sites of increased insect activity (Balda 1969, Airola and Barrett 1985). In contrast, trunk gleaning species such as the red-breasted nuthatch and brown creeper favor lower, older portions of the canopy where furrowed bark is more abundant (Jackson 1979, Airola and Barrett 1985, Morrison et al. 1989).

Snags

Snags are important structural features of Pacific Northwest forests (Cline et al. 1980, Franklin et al. 1981) and are used extensively by resident birds for cavity nests, roosting, perch hunting, and as a foraging substrate. Consequently, the absence of standing deadwood structures can be a major limiting factor for many snag-dependent birds (Haapanen 1965, Balda 1975, Cline et al. 1980, Raphael and White 1984). Nearly all cavity nesting birds in these forests prefer to excavate their nests in dead wood or dying trees rather than live trees (Raphael and White 1984, Lundquist and Mariani 1991). Several studies have also demonstrated that most cavity nesters select the tallest and largest diameter snags within a stand (Mannan et al. 1980, Raphael and White 1984, Zarnowitz and Manuwal 1985, Carey et al. 1991). These larger-diameter snags confer several advantages to nesting birds, including increased thermal insulation, enhanced protection from predators, and more room to house large clutches (Karlsson and Nilsson 1977, Pingjun and Martin 1991). Food resources for birds also increase with larger diameter snags because of their increased surface area for wood boring insects, as well as their greater moisture retention, which is favorable for termites (Blackman and Stage 1924). Larger diameter snags, particularly those species with slower decay rates, tend to persist longer and thus increase their value to birds (Dahms 1949). Nelson (1988) found that the relatively soft, ephemeral snags of western hemlocks were avoided by all species of cavity nesters. Birds may also avoid hemlock, or well-decayed snags of any species, because the soft wood may compromise the integrity of the nest entrance and increase the risk of predation. Soft snags may be more susceptible to breaking at the cavity during high winds (Pingjun and Martin 1991). Birds also tend to favor snags that are clustered on the landscape, because clustering reduces the amount of time spent traveling between food patches, as well increasing the search costs for predators (Raphael and White 1984, Pingjun and Martin 1991).

Non-cavity nesting species such as flycatchers and raptors often use snags rather than live stems for perching and hunting sites. Once snags have toppled, they continue to be used by birds as song perches, plucking posts, and drumming posts. Decaying woody debris also supplies important habitat for invertebrates and small mammals, which in turn provides food for forest birds.

Stand Age

Several studies have examined changes in bird communities across a chronosequence of naturally regenerated stands that include young, mature, and old-growth forests (Manuwal and Huff 1987, Carey et al. 1991, Gilbert and Alwine 1991, Huff and Raley 1991, Lundquist and Mariani 1991, Manuwal 1991). In general, these studies found avian diversity to be relatively consistent across a chronosequence; however, abundance was highest in old-growth stands older than 200 years for many species of birds. Mature stands (80 to 200 years old) generally exhibited lowest abundance, which was attributed to the uniform canopy, poorly developed understories, and the limited availability of large snags. Young stands (about 30 to 90 years old) in contrast, often had snags or large stumps as carry-overs from a previous late-successional forest, and these structures provided nest sites for species such as chestnut-backed chickadees (*Parus rufescens*).

Nesting species that have been found to reach their greatest abundance in old forests types include the hairy woodpecker (*Picoides villosus*), red-breasted sapsucker (*Sphyrapicus ruber*), pileated woodpecker (*Dryocopus pileatus*), Pacific-slope flycatcher (*Empidonax difficilis*), olive-sided flycatcher (*Contopus borealis*), red-breasted nuthatch, winter wren (*Troglodytes troglodytes*), brown creeper, chestnut-backed chickadee, varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), red crossbill (*Loxia curvirostra*), and evening-grosbeak (*Coccothraustes vespertinus*). The Vaux's swift (*Caetura vauxi*), however, is associated exclusively with old-growth forests for nesting and roosting snags (Bull 1991). Franklin et al. (1981) demonstrated that old-growth forests have several ecological attributes limited or absent in younger stands, including large old trees, snags, canopy gaps, increased foliage-height diversity, high foliar biomass, high leaf surface area, and a mixture of tree species and age classes. Stiles (1980) also demonstrated that older forest communities, with their increased vertical profile, permit birds to nest higher above the ground than in younger stands. Consequently, they can have spherical territories, an optimal shape for reducing energy expenditures associated with foraging trips and territorial defense. Old growth also provides critical wintering habitat for the relatively large percentage of permanent residents in the Pacific Northwest (Manuwal 1991). Research on winter birds by Manuwal and Huff (1987) and Huff et al. (1991) in young, middle-aged, and old-growth stands has demonstrated that older forests provide more suitable winter habitat by providing more food resources and an ameliorated microclimate for roost sites. Consequently, more birds survive the winter in older stands and may replenish younger stands in the spring. Western hemlock, a prolific seed producer, is a shade-tolerant species that is dominant in many older stands (Franklin and Dryness 1973, Franklin et al. 1981). Compared to other species, such as Douglas-fir, hemlock becomes important for wintering finches by providing a more stable intra-annual production of cone crops as well as delayed release of seeds, which supplies a food resource lasting into the cold winter months (Isaac 1943, Fowells 1965, Manuwal and Huff 1987).

Riparian Communities

Riparian communities represent another special vegetation type receiving extensive use by birds, particularly in drier regions. These systems occupy a unique link between aquatic and terrestrial habitats and consequently provide a localized abundance of food, water, and cover for birds and other wildlife (Odum 1979, Oakley et al. 1985, Naiman and Decamps 1990). Noteworthy features of riparian areas include the high edge-to-area ratios of stream corridors, and the unique disturbance regime of flowing water, which creates a mosaic of plant communities and stand ages (Campbell and Franklin 1979, Thomas 1979). In addition, riparian communities are frequently characterized by structurally complex vegetation with large snags and live trees because of the optimal growing conditions and year-round availability of water (Campbell and Franklin 1979, Oakley et al. 1985). These conceptual values are well recognized in drier regions where the vegetational gradients between riparian systems and upland communities is very pronounced (McGarigal and McComb 1992). In the moist coniferous forests west of the Cascade Mountains, however, the differences between riparian areas, particularly along small streams, and upland communities is less dramatic, and consequently the changes in avifuana between these two systems is much less obvious (Anthony 1984, Bruce 1985, Carey 1988, McGarigal and McComb 1992). Even along small streams, however, some evidence has been found that songbirds, such as as the black-throated gray warbler (*Dendroica nigrescens*), MacGillivray's warbler (*Oporornis tolmiei*) and the wrentit (*Chamaea fasciata*) are associated with the presence of water (Carey 1988). The value of small streams may be associated with their steep gullies or ravines, which facilitate tree fall and the development of gaps and deciduous understories (Carey 1988). As stream size increases, their value to songbirds also increases significantly. For example, Lock (1991) was able to demonstrate on the Olympic Peninsula that higher avian richness and abundance were found on large-order rivers. Perhaps the importance of riparian communities is best exemplified by the disappearance of the western subspecies of the yellow-billed cuckoo (*Coccyzus americanus occidentalis*), whose disappearance from most of western North America is attributed to loss of contiguous tracts of cottonwood-willow riparian woodland (Laymon and Halterman 1987).

Managed Forests

Avian use of commercial forests often contrasts sharply with use of naturally regenerated stands. Managed forests are typically characterized by much larger areas of disturbance and a simplification of forest structures that includes reduced density of snags, woody debris, and live trees. Initially, some resources are available for forest birds in large clearcuts, and consequently these sites are often used by open-country birds like hummingbirds, nighthawks, shrikes, and sparrows. If critical wildlife features are retained, however, the avian diversity of managed areas may surpass that of the late-successional forest that formerly occupied the site. Note, however, that essentially all of the species that use harvested areas are cup-nesting species belonging to ground-, brush-, or nectar-foraging guilds, and thus do not present the conservation concerns of forest interior species such as the Vaux's swift, spotted owl (*Strix occidentalis*), goshawk (*Accipter gentilis*), and marbled murrelet (*Brachyramphus marmoratus*). Studies by Martin (1981) and Rosenberg and Raphael (1986) in western forests found that resident birds, or birds with large home ranges and restricted habitat requirement were the most sensitive to forest fragmentation. Separating the impacts of timber harvest into those associated with edge effects and those associated with the direct loss of habitat can be difficult, however.

Future Research

Despite the considerable body of research that has been conducted on the region's avifuana, several areas need more study. A more detailed understanding should be developed as to how each bird species modifies its use of canopy environments in response to the complex topographical, moisture, and vegetational gradients that characterize each of the subregions in the Pacific Northwest. Although considerable attention has been devoted to cavity-nesting species, we need more information on the habitat selection, nesting requirements, and foraging behavior of non-excavating passerines. Much remains to be discovered about the population status of neotropical migrants and the relative contribution of habitat loss in the sub-tropical winter areas compared with Pacific Northwest forests. Ecosystem management offers many promising management options that address the conservation needs of the region's avifuana; however, these techniques need to be examined with long-term studies. A better understanding is needed of the effects growing human populations have on avian communities, particularly at the interface between urban/residential areas and forest environments. Attention should be focused on specialized forest types, such as riparian communities and Garry oak systems, where most declines and localized extirpations of Pacific Northwest avifuana have occurred (Hunn 1982, Lewis and Sharpe 1987, Paulson 1992).

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