

Interactions of Northwest Forest Canopies and Arboreal Mammals

Abstract

The interactions among Northwest forest canopies and the mammals that inhabit them have been poorly studied. My purpose was to identify interactions among arboreal mammals and canopies that have implications for managers seeking to conserve biodiversity in the Pacific Northwest. I constructed a comprehensive, but parsimonious list of canopy attributes that could be biologically important. I compiled a list of mammals that routinely enter the canopy and ranked them relative to arboreality. I identified which attributes might be important to each species and how the attributes might contribute to maintaining arboreal rodent communities. Forest canopies have 26 categories of attributes of 5 major types: context, seral stage, community type, canopy dimensions, and tree species character. At least 12 species of mammals (excluding bats) use forest canopies, but only 7 should be considered truly arboreal. All but one of the arboreal rodents are limited zoogeographically, or in local distribution, because of needs for specific habitat elements. Only one species, the red tree vole, is totally arboreal; thus, the composition and structure of the arboreal rodent community is conditioned by both canopy and noncanopy features of the forest. Of the canopy attributes, diversity of tree species and abundance of nontree organisms, including lichens, mosses, and rot-inducing fungi, seem especially important to arboreal rodents. Diversity of tree species provides a variety of food (foliage, seed, fruit, nuts, and truffles and mushrooms of fungi symbiotic with the trees). Rot-inducing (and pathogenic) fungi provide cavities for leaf-lichen-moss nests and platforms for lichen-moss-twig nests. Lichens also serve as food.

Introduction

Forest canopies are less accessible to the biologist than is the forest floor and, thus, have been studied less than lower structures. Nevertheless, canopies are rich in life (Denison 1973, Pike et al. 1977, Schowalter 1989) and, around the world, commonly used by a variety of mammals other than human beings, including marsupials, bats, rodents, carnivores, and primates (Nowak 1991). Old-growth canopies in the Pacific Northwest are especially tall (50-90 m) and complex, with multilayered vegetation and diverse structures (Franklin and Spies 1991). This complexity of canopy structure and composition suggests that an in-depth understanding of canopy function will be necessary to ensure that efforts to conserve biodiversity in the Pacific Northwest will be successful. Of course, canopies are not independent of the forest ecosystem; their use and function depend on their biogeographic and synecologic context.

My goal in this paper is to identify interactions among arboreal mammals and canopies in the Pacific Northwest that have implications for the conservation of biodiversity. First, I constructed a comprehensive, but parsimonious list of biologically important canopy attributes. Next, I compiled a list of mammals (excluding bats; see

Wunder and Carey this issue) that routinely enter the canopy and ranked them according to the degree to which they use canopies (i.e., arboreality), following the method of Carey (1991). Then, I identified which attributes might be important to each species and how the attributes might contribute to maintaining arboreal rodent communities. Finally, I discuss implications for management and for research.

Canopy Attributes of Biological Importance

All attributes of canopies could have biological importance. Because the attributes are numerous and varied, I constructed a hierarchical classification of canopy attributes (Table 1). The hierarchy begins with spatial and temporal scales, including geographic, geomorphic, and landscape location and stage of forest development and age of tree. Where a canopy is found determines the mix of species that can occur in, or use, the canopy (see Table 2 for mammals). The stage in the development of a community also determines the array of species that can potentially inhabit the canopy. The process of forest development is one of accumulation and redistribution of biomass (Bormann and Likens 1979, Oliver and Larson 1990) among living trees, standing dead trees, and

TABLE 1. Attributes of forest canopies of potential biological importance in the Pacific Northwest.

I.	Context
A.	Biogeographic Region
1.	Species Available: plants, animals, and their commonness and rarity
2.	General Climatic Regime: effects on species and processes
B.	Geomorphic Location
1.	Species Abundance Patterns: forest, habitat, and community types
2.	Climatic-Disturbance Regimes: phenology, limiting factors, perturbations
3.	Special Habitat Elements: cliffs, caves, talus, wetlands, rivers, etc.
C.	Landscape Context
1.	Composition: community types and ecotones
2.	Heterogeneity: seral stages, interiors, and edges
3.	Grain: patch size, diversity, contiguity, and frequency
4.	Connectivity and Isolation
II.	Seral Stage or Stand Condition
A.	Stand Initiation: low, open canopies
B.	Stem Exclusion: dense canopies, sometimes thin; small dead trees; lack of diversity
C.	Understory Reinitiation: slightly open canopy, deepening crowns, few snags
D.	Understory Development: open canopy, medium snags, botanical diversity increasing
E.	Old Growth: high canopy texture, multilayered vegetation, high canopy volume, high species diversity, high size diversity, large snags, large gaps, many associates
III.	Community Type
A.	Species Composition of Canopy Trees
1.	Diversity of Seed Source: abundance, minimum consistency of production, palatability, food value, synchronicity of seed crop failure
2.	Variety in Architecture: shape, branchiness, branch size, branch angle, leaf or needle size, leaf or needle density
3.	Variety in Life Form: conifer, deciduous hardwood, evergreen hardwood
B.	Canopy Associates
1.	Epiphytes: mosses, lichens, ferns, mistletoe
2.	Endophytes: diseases and rot fungi (produce cavities, broken tops)
3.	Invertebrates: slugs, snails, spiders, mites, insects (larvae and adults)
4.	Vertebrates: amphibians, reptiles, birds, and mammals
C.	Other Associates
1.	Understory Woody Plants: foliage, fruits, nuts, seeds, insects, mycorrhizae
2.	Understory Forbs, Ferns, Grasses: foliage, fronds, seed
3.	Forest-floor Mosses and Lichens: nest material
4.	Rhizosphere Associates: ectomycorrhizal fungi
5.	Soil Organisms and Microorganisms
IV.	Canopy Dimensions
A.	Volume
1.	Total Height
2.	Height to Live Crown
3.	Areal Extent
B.	Density
1.	Canopy Closure
2.	Interconnectedness of Tree Crowns
3.	Layering
C.	Heterogeneity
1.	Texture of Canopy Surface (rugose old growth vs. smooth young, even-aged)
2.	Gaps: frequency and size
V.	Tree Species Character
A.	Size and Age of Canopy Trees
1.	Branch Size and Shape
2.	Bark Rugosity
3.	Decadence: broken tops and branches: cavities
4.	Biomass of Fruit or Seed
B.	Species-Specific Attributes
1.	Associates: fungi, mosses, lichens
2.	Phenology: bud, leaf, and seed production
3.	Life Form: size, architecture, growth form, shade tolerance, fire resistance
4.	Health and Longevity: root-, butt-, and top-rots; insects; and disease resistance

TABLE 2. Some mammals using forest canopies, the degree to which they use canopies (arboreality, scale of 0-12), and their distribution in the Pacific Northwest.

Species	Geographic Distribution ¹				
	Arboreality	WWA	WOR	EWA	EOR
Red tree vole (<i>Phenacomys longicaudus</i>)	12	-	+	-	-
Western gray squirrel (<i>Sciurus griseus</i>)	8	+	+	p	p
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	7	+	+	+	+
Douglas' squirrel (<i>Tamiasciurus douglasii</i>)	7	+	+	-	-
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	7	-	-	+	+
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	7	-	+	-	-
Bushy-tailed woodrat (<i>Neotoma cinerea</i>)	6	+	+	+	+
Townsend's chipmunk (<i>Tamias townsendii</i>)	4	+	+	-	-
Porcupine (<i>Erethizon dorsatum</i>)	3	+	+	+	+
Marten (<i>Martes americana</i>)	3	+	+	+	+
Fisher (<i>Martes pennanti</i>)	3	p	p	p	p
Raccoon (<i>Procyon lotor</i>)	2	+	+	+	+
Forest deer mouse (<i>Peromyscus oreas</i>)	1	+	-	-	-

¹ Distribution in western Washington (WWA), western Oregon (WOR), eastern Washington (EWA), and eastern Oregon (EOR) expressed as present (+), present, but rare (p), and absent (-).

fallen trees, litter, soil organic matter, and a variety of life forms including cryptogams, ferns, forbs, shrubs, shade-tolerant understory trees, fungi, invertebrates, and vertebrates. The accumulation of biomass and its apportionment among diverse life forms leads to a complex ecosystem that allows niche diversifications and increased species diversity within the community (Whittaker et al. 1973, Hutchinson 1978). Thus, at subsequent, and lower, levels in the hierarchy, apportionment of biomass, increased species diversity, and cumulative species-specific effects begin to assume importance. Although I believe the outline of attributes is comprehensive, it certainly is not exhaustive. I will illustrate how many of these attributes are important to mammals; some of them (and others) will be important to bats (Wunder and Carey this issue) and birds (Sharpe this issue). But, I expect (and hope) others will amend and refine the list.

Arboreal Mammals

Carey (1991) developed a scale to measure the degree to which mammals inhabit or frequent forest canopies and called the scale "arboreality." Arboreality is evaluated by ranking a species' use

of trees (overstory and understory) and shrubs relative to its use of the forest floor for three activities: travel, nesting and denning, and foraging. Ranks range from 0 (no routine use) to 4 (activity confined to trees and shrubs). The three rankings are summed to obtain arboreality, which ranges from 0 to 12. In the Pacific Northwest, the most arboreal mammal is the red tree vole (Table 2), which occurs only in western Oregon and which conducts almost all its activities high in tree canopies (Maser et al. 1981). Indeed, the red tree vole prefers the lower third of the crowns of the largest trees in old-growth forests (Gillesberg and Carey 1991). At the other end of the scale is the forest deer mouse, the most arboreal of the forest-floor mammals, which travels and forages in understory trees and shrubs and whose abundance increases with understory development, but which has not yet been shown to use tree canopies (Carey and Johnson 1995). Mammals that sometimes den in tree cavities and opportunistically forage in trees (marten, fisher, and raccoon; Novak 1991) receive low rankings (2-3). The porcupine, which regularly sleeps in trees, but prefers rock dens (McLean et al. 1993) and which forages for dwarf mistletoe and cambium in trees, but emphasizes intake of herbaceous plants

(Johnson and Carey 1978) also receives a low ranking (3, Table 2). Townsend's chipmunk regularly forages in the understory, sometimes nests in tree cavities, and is only marginally an arboreal mammal (Table 2, Carey 1991). Thus, for the rest of this paper, I will concentrate on interactions between forest canopies and the seven species of mammals that score ≥ 6 points on the 12-point scale.

Interactions Between Arboreal Mammals and Forest Canopies

Red tree vole.—The red tree vole has the narrowest niche of the arboreal mammals. It spends almost all its time in trees (rarely traveling between trees on the ground), eats conifer needles (primarily Douglas-fir, *Pseudotsuga menziesii*, needles), and obtains water from fog drip on needles, moss, and lichens (Maser et al. 1981). Nests of twigs, resin ducts (leftovers from eaten needles), whole needles, and lichens are built on large branches or on whorls of branches. Nests are also excavated in heavy moss layers on large branches, and some nests are in cavities in trees (Gillesberg and Carey 1991). The red tree vole is most abundant in old-growth forests, in large trees, and in areas where crowns interweave (enhancing access to food, facilitating social interactions, and providing numerous escape routes). Limiting factors include crown depth and stability (young tree crowns are constantly moving upward, requiring nest relocation), crown connectedness (contiguity), canopy volume and density, and areal extent and connectivity of mature and older forests. Populations of red tree voles can grow slowly under good conditions; ability to disperse and recolonize vacated habitats is probably low even under favorable conditions (contiguous crowns). The red tree vole seems particularly adapted to the stable conditions of old-growth Douglas-fir (Maser et al. 1981, Carey 1991).

Western gray squirrel.—The western gray squirrel has a broader niche than the red tree vole: it eats conifer seed, oak (*Quercus* spp.) acorns, the seeds, nuts, and fruits of other trees and shrubs, mushrooms, and truffles. It builds its nest of twigs, lichens, and mosses in coniferous trees and will use cavities in coniferous or deciduous trees. Despite its relatively broad niche, it has a narrow habitat in Oregon and Washington, primarily occupying Oregon white oak (*Q. garryana*)-Douglas-fir and Oregon white oak-ponderosa pine

(*Pinus ponderosa*) communities < 1 km from water (streams, ponds, wetlands) and of > 2 ha (Ryan and Carey 1995). In the southern parts of its range, the squirrel occupies the wide array of oak communities available there. In Oregon and Washington, it is sometimes found in plantations of nut-bearing trees. The Oregon white oak communities, however, tend to be ecotonal, merging with native prairies, streamside communities, and wetlands, and easily lost to succession in the absence of wildfire. They are often small in area. Connectivity, in the form of coniferous and riparian forests, seems to be important for travel by gray squirrels and colonization of unoccupied oak-conifer woodlands. Within the oak communities, the presence of large conifers for escape cover, nest sites, and food (seed) is mandatory. Interconnectedness of tree crowns for travel and escape is important. The diversity of nut- and seed-bearing trees and shrubs, for example bigleaf maple (*Acer macrophyllum*), Oregon ash (*Fraxinus latifolia*), California hazel (*Corylus cornuta*), and vine maple (*A. circinatum*), is important for providing high-quality food for the squirrels in years of acorn crop failure.

Northern flying squirrel.—The flying squirrel has a relatively narrow niche as a cavity-dwelling mycophagist, but a broad habitat, occupying a range of conifer, deciduous, and mixed-species forest communities and seral stages (Carey 1991). The flying squirrel is most abundant in old-growth Douglas-fir and mixed-conifer forests (Carey et al. 1992, Carey 1995); their abundance is low in northern forests dominated by western hemlock (*Tsuga heterophylla*) or Pacific silver fir (*Abies amabilis*). The difference in abundance may be due, in part, to the northern forests being colder and more subject to snowfall (with concomitant direct stresses on the lightly built squirrel), but it also appears to be related also to differences in diversity of ectomycorrhizal fungi, which are more diverse in old than young forests and in southern than northern forests in the Pacific Northwest. Fruiting bodies (mushrooms and truffles) of ectomycorrhizal fungi are the primary food of northern flying squirrels, although lichens can be important winter foods (Maser et al. 1986, Carey 1991, Carey et al. 1992, Carey 1995). The flying squirrel uses stick nests of other species, stick-moss-lichen nests it constructs itself, and moss-lichen-cambium nests it constructs in natural cavities and cavities created by woodpeckers. Cavity

nests are more predator-proof, more resistant to wind and precipitation, and thermally superior to stick nests (Carey and Sanderson 1981). Cavities arise out of the interaction in living trees of damage, infection by rot-inducing fungi, and time, with the excavation of rotten wood by woodpeckers and other birds in both living and standing dead trees. Most woodpecker-created cavities are in large, old snags (> 80 cm dbh), and thus are most abundant in old-growth forests (Carey et al. 1991). Arboreal lichens and mosses and terrestrial mosses are important nest materials. Flying squirrel abundance is correlated with understory development, particularly ericaceous shrubs (Carey 1995). These shrubs provide cover for squirrels foraging on the ground for truffles, and may enhance mycorrhizae and truffle production by forming symbiotic relations with the mycorrhizae of trees. Understory composition and abundance reflects both soil moisture and canopy openings (Carey et al. 1991); woody understory development is often greatest in the vicinity of large dead trees or in canopy gaps (Carey 1995). The interactions of canopy openings resulting from the death of large trees and the subsequent development of woody understories, the cavities constructed by woodpeckers in large dead trees, and the diversity of canopy and understory woody plants that promotes fungal diversity make old-growth forests, especially southern Oregon old-growth forests, the optimal environment for flying squirrels. Populations are lower in younger forests and the squirrels adapt to these less hospitable environments by constructing nests from dead twigs and branches, using dens in residual trees and deciduous trees, and moving long distances to forage (unpublished data). Because of their ability to use a range of seral stages, flying squirrels become isolated only by very early stages of forest development and nonforested environments; however, populations in patches of old growth can be substantially reduced through predation (Carey et al. 1992).

Douglas' squirrels and red squirrels.—These two congeners are specialists at exploiting conifer seed as food. The Douglas' squirrel is adapted to western hemlock-Douglas-fir forests (lightly constructed cones), the red squirrel, to forests with ponderosa pine and lodgepole pine (*Pinus contorta*) and heavily constructed or serotinous cones (Smith 1970, 1981). Both species respond to seed abundance with immigration, increased reproduction, and increased juvenile survival and to seed scar-

city by switching to fungi or a limited array of other seed (California hazel, for example), decreased reproduction, emigration, starvation, and decreased survival. Both species will eat mushrooms and truffles when they are available (Maser et al. 1978). In the spring, Douglas' squirrels are equally abundant among young, mature, and old-growth forests (Carey 1989), but in the winter, when food is most scarce, they are most abundant in old forests (Buchanan et al. 1990). The large, old trees and the diversity of tree and shrub species in old forest provide a more dependable supply of food than the young trees, often of one species, in young forests (Carey 1991). Conifers and *Tamiasciurus* have coevolved: trees undergo synchronous failures in cone crops, which reduces squirrel populations, and the squirrels maintain individual territories, which reduces competition for seed and fungi (through spacing), and store food to eat in times of seed scarcity (Smith 1970). Fallen trees and low dead branches provide perch sites from which the squirrels can search for competitors (and predators) while eating. Streams, seeps, and large fallen trees and the moist soil beneath them provide storage sites for fir and hemlock cones (moisture is necessary to keep the cone from opening and spilling its seed). Both squirrels build stick nests lined with mosses, lichens, or grass and build moss-lichen-grass nests in tree cavities. But these squirrels are larger and more robust than flying squirrels and do not seem as tied to cavities. Food seems to be the limiting factor (Carey 1991).

Dusky-footed woodrat.—This species, native to riparian forests in the California chaparral, reaches its northern limits in Oregon, where it inhabits mixed-evergreen and mixed-conifer forests in the Klamath Mountains and interior river valleys. It is most abundant in riparian forest and has a bimodal distribution in upland forests, being most abundant in stand initiation and early stem exclusion stages, rare in stem exclusion and understory reinitiation stages with little understory, and moderately abundant where understory is developed, including old growth (Carey et al. 1992). The dusky-footed woodrat has adapted numerous aspects of its life history to allow it to feed on evergreen sclerophylls high in fiber, tannins, and related polypeptides that are toxic to many mammals (Atsatt and Ingram 1983). This specialization provides the woodrat with a distinct niche; however, it can avail itself of many other

foods, including fungal fruiting bodies. The woodrat makes its houses of sticks and woody debris both on the ground and in trees. It preferentially travels through the understory rather than on the forest floor, where the rustle of dried leaves reveals its presence to predators. It seems to be most limited by the abundance of evergreen sclerophyllous understory, area of suitable stand condition, and connectivity between suitable patches (Carey 1991).

Bushy-tailed woodrat.—The bushy-tailed woodrat is usually an occupant of rock outcrops and talus slopes in shrub and forest communities. Adequate rock shelter is the most important resource for this woodrat in areas with cold weather and heavy snowfall (Escherich 1981). In the relatively warm, low-elevation, transitional and mixed-conifer forests of southwestern Oregon, it also uses cavities in standing and fallen trees and builds houses of sticks and woody debris in tree hollows, on the ground, and on branches in trees. The bushy-tailed woodrat has a broad diet and, in southwestern Oregon, is abundant in streamside forests and other forests with well-developed understories and tree cavities (Carey 1991). Because of its social system of one territorial male with a harem of two or three females, bushy-tailed woodrats occur in small, scattered populations. Thus, area and connectivity of suitable patches of habitat and predation seem to be limiting factors.

Conclusions

Biogeography seems to be the most important determinant of the diversity and abundance of mammals that use canopies in the Pacific Northwest. The southwestern Oregon transition and mixed-conifer forests are characterized by a diversity of plants, fungi, and mammals and a mild

climate. Next, presence of cavities in trees (and the rot that is integral to cavity formation) and the woodpeckers that excavate the cavities are important determinants of abundance of arboreal mammals. Similarly, lichens and mosses in the canopy and on the forest floor are insulating materials and important components of arboreal rodent nests. Tree species diversity and developed understories tend to increase canopy volume, interconnectedness of crowns, and abundance, diversity, and dependability of food sources round out within-stand habitat requirements of the rodents. Volume and extent of the canopy of suitable habitat and connectivity to other patches of suitable habitat also seems important. Other species also benefit from overstory diversity that promotes dependable seed sources (e.g., forest-floor small mammals); cavities for den sites (marten, fisher, raccoon, and many birds); large branches for nesting sites; and canopy openings that promote understory development (e.g., *Strix occidentalis*, Carey et al. 1992).

My review clearly indicates that trees alone do not constitute a forest canopy. Various other organisms associated with trees—including fungi, mosses, lichens and vascular plants in the understory—help determine canopy quality as habitat for arboreal rodents. The presence of arboreal rodents, keystone species, provide a prey base for many vertebrate predators and enhance ecosystem function through fungal spore and seed dissemination (Carey 1991). Research seems especially lacking on the importance of canopy epiphytes and invertebrates (food sources for many mammals and birds) as elements of biodiversity. Management of canopies must be based on knowledge and hypotheses (where data are lacking) about processes, functions, and structure, not on structure alone.

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