

**WILDLIFE USE OF RIPARIAN HABITATS:
A LITERATURE REVIEW**

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INTRODUCTION AND SCOPE OF REVIEW

The Timber Fish and Wildlife (TFW) Agreement of 1987 provides both a framework for forest management practices on the State of Washington's state and private lands to protect natural and cultural resources within the context of the managed forest, and a mechanism to evaluate and modify management practices. The Agreement incorporates recommendations and guidelines for the protection of water, fish, wildlife, and archaeological resources. The representatives of state resource agencies, Native American tribal organizations, timber companies, and conservation organizations who forged this Agreement recognized both the immediate need for new forest management policies to protect these resources and the long-term need for these policies to be flexible and responsive to new information. Thus, a central feature of the TFW Agreement is the introduction of adaptive management to Washington State's natural resources. Adaptive management involves the continual evolution of management practices in response to scientific knowledge gained through careful monitoring of natural resources and well-designed experimental studies to evaluate how resources are impacted by management practices (Walters 1986).

A set of management goals for the different resources provided the starting point for participants to develop the TFW Agreement. For wildlife, the goal "... is to provide the greatest diversity of habitats (particularly riparian, wetlands, and old growth), and to assure the greatest diversity of species within those habitats for the survival and reproduction of enough individuals to maintain the native wildlife of Washington forest lands" (TFW Agreement 1987, p.2). Inherent in this statement is the recognition of the importance of maintaining habitat diversity to ensure wildlife species diversity and of the disproportionate importance of certain habitats, including riparian habitats. Given the importance of riparian habitats for wildlife, it is critical that we understand wildlife response to habitat conditions created by management practices in riparian habitats. In an attempt to balance the wildlife goal with the timber resource goal, the TFW Agreement established Riparian Management Zones (RMZs) for the protection of riparian areas and recommended appropriate sizes, tree densities, and management practices for RMZs associated with several defined water types. These guidelines have been incorporated into the Forest Practices Board Rules and Regulations (1988). The task at hand is to understand and predict wildlife responses to the recommended management procedures. This paper provides a review and synthesis of the literature on wildlife use of riparian habitats in the Pacific Northwest that has served as a cornerstone in the design of an adaptive management study that examines the effectiveness of RMZs in providing habitat for wildlife.

Our literature synthesis is organized around the following components. In our background section we present an overview of riparian ecosystems. In this section we examine the structure and function of riparian zones with respect to the major elements of a riparian zone, the interaction of terrestrial and riparian environments in the riparian zone, and the role of disturbance in shaping riparian habitats. Our overview next addresses general considerations of wildlife use of riparian habitats including features of riparian habitats that enhance the wildlife value of these habitats. We then review theoretical considerations of habitat fragmentation that are relevant to understanding how wildlife species might respond to changing habitat conditions as a result of timber management practices under the RMZ guidelines.

Our second section provides a review of empirical studies on wildlife use of riparian habitats and response to habitat variation in riparian forests. We focus on studies from the Pacific

Northwest (PNW), but include other studies that deal with general considerations of wildlife/riparian relationships. We have examined the literature to address the following types of questions: 1) What are the relative dependencies of PNW species on riparian habitats? 2) What are the critical habitat components that riparian habitats provide for wildlife? 3) How do different silvicultural activities, including road building, in riparian areas affect wildlife? 4) What is the potential response of wildlife species to the establishment of riparian buffer zones?

In our third section we will review the methodologies used to examine these issues. We first consider field methods used to sample vertebrate populations. We next consider the field methods used to describe habitat, determine population parameters of species, and determine community composition. We stress the importance of using multiple metrics to examine wildlife use of riparian areas. Wildlife communities are expected to exhibit temporal and spatial variability. This variability might mask differences between areas if only one metric is used. Furthermore, single metrics might not contain full information to assess wildlife response to habitat changes. For example, one might use species diversity. However, in riparian fragments, species diversity might increase overall due to new opportunities created for weed species, but animals characteristic of the riparian habitat might be lost. Next we will review population and community parameters.

The fourth component develops a ranking system for Washington's riparian wildlife species. Recently, Millsap et al. (1990) developed a system which ranked Florida's wildlife taxa according to biological vulnerability, population status, and management needs to help prioritize conservation efforts. The ranking system was based on a biological score, an action score, and a supplementary set of scores dealing with taxonomic, biogeographic, and political concerns. The biological score was a compilation of 7 variables measuring aspects of a species' distribution, abundance, and life history. The action score was based on 4 variables measuring the current state of knowledge the taxon's distribution, population trend, and limiting factors as well as current conservation efforts. Information used to determine scores was based on the literature and experience of wildlife biologists. Millsap et al. (1990) tested their ranking system by examination of how the system ranked species of known status in Florida and found close agreement. We have modified the methods of Millsap et al. (1990) to rank riparian wildlife species of Washington. We consider the ranking system presented here to be an initial exercise that will be fine-tuned as we collect more information on these riparian species.

We conducted on-line searches on BIOSIS (Biological Abstracts) and Cambridge Life Sciences, AGRICOLA [data base of the National Agricultural Library], CRIS [Current Research in agriculture and related science. Current literature was reviewed by consulting publications such as Current Contents and by reviewing relevant journals. In addition to standard library research procedures, we corresponded with appropriate government agencies and TFW cooperators to obtain relevant reports. We have entered all citations into a bibliographic database. This has allowed sorting of citations by selected keywords and periodic updating through the life of the project. Copies of the database are available to the Wildlife Steering Committee upon request.

RIPARIAN ECOSYSTEMS - GENERAL BACKGROUND

Riparian zones are found adjacent to watercourses such as streams, rivers, springs, ponds, lakes, or tidewaters and represent the interface between terrestrial and aquatic environments. The riparian zone can be variously defined in terms of vegetation, topography, hydrology, or ecosystem function (e.g., Swanson et al. 1982, Kovalchik and Chitwood 1990). The latter approach integrates the former factors and defines the riparian zone as the zone of interaction between the aquatic and terrestrial environments (Swanson et al. 1982, Bilby 1988). This definition encompasses the concept that the terrestrial system influences the aquatic system and, in turn, is influenced by the aquatic system. The zone of interaction can be identified as the water's edge or on a broader scale, as a zone extending from the water through the canopy of the vegetation associated with the zone (Swanson et al. 1982). On the latter scale, riparian zones include the relatively mesic vegetative communities and associated faunas occurring between aquatic and more xeric upland sites (Knopf et al. 1988). Johnson and Haight (1985) divide the zone of interaction into 1) the mesoriparian ecosystem that includes the frequently flooded streambanks, active channel shelves, active floodplains, and overflow channels and 2) the xeroriparian that includes the transitional zone between the mesoriparian and upland ecosystems.

Watercourses associated with riparian zones have been variously classified. A widely adopted system to describe drainages classifies small, headwater channels as first-order streams with each union of first-order streams forming a larger second-order stream, each union of second-order streams forming a still larger third-order stream, and so forth (e.g., Strahler 1957, Everest et al. 1985). For regulatory purposes, The Washington State Forest Practices (1988) recognizes five water types on the basis of size and presence of anadromous fish, with Type 1 corresponding to large rivers and shorelines and Type 5 to small headwaters that do not support fish. From a wildlife perspective, a key element of the riparian zone is the amount of open water, but as Hall (1988) points out, the amount of open water necessary to qualify an area as riparian will depend upon individual species requirements. Wildlife use of riparian areas does not necessarily correspond to the above classifications and it might be preferable to define "operational habitat units" relevant to specific taxa as Bury (1988) does for reptiles and amphibians.

The structure of the riparian zone is closely related to the size of the watercourse. In the Pacific Northwest, most riparian zones are found adjacent to streams and rivers (Oakley et al. 1985) and this is especially true for the forestlands of the region (Swanson et al. 1982, Bury 1988). Given the focus of this review on wildlife use of riparian habitat in managed forests of the Pacific Northwest, we will emphasize the structure and dynamics of riparian zones associated with streams and small rivers. In the following we provide an overview of the structure and dynamics of riparian zones as a foundation for examining wildlife use of these areas.

STRUCTURE AND FUNCTION OF RIPARIAN ZONES

The structure and function of riparian zones are determined by several key elements (Oakley et al. 1985, Swanson et al. 1982, Bilby 1988, Cummins 1980, Brinson et al. 1981). These elements are topography, surface water, soils, microclimate, and vegetation. The interaction between terrestrial and aquatic environments that occurs in the riparian zone is mediated by these elements. On the one hand, they combine to create common features that distinguish riparian

zones from upland areas. For example, riparian zones are characterized by increased primary productivity, higher levels of energy transport, and often, more natural disturbance than upland areas. On the other hand, differences between these key elements result in differences observed among riparian habitats.

Topography

Topography within and adjacent to riparian zones in the Pacific Northwest ranges from narrow, entrenched channels that are typically associated with lower order streams to broad floodplains associated with higher order rivers. Topography determines many other features of the riparian zone (Oakley et al. 1985). Riparian zones surrounded by steep upland slopes, for example, have soils that are typically shallow and coarse textured, are not exposed to direct sunlight for long periods, can be sheltered from winds, have erosion and active transport as dominant processes, and often have associated plant communities that are relatively limited. In contrast, riparian zones associated with broad floodplains have deep and typically fine textured soils, are exposed to sunlight and wind disturbance, have deposition as the dominant process, and have an associated plant community that is diversified in structure and composition. Brinson et al. (1981) distinguish between stream systems with bedrock controlled channels and those with alluvial channels. The former are confined between rock outcrops and have little, if any, developed floodplain. The latter, in contrast, have well-developed floodplains and can adjust dimensions, shape, and gradient in response to changing water conditions. Streams often have alternating sections of both conditions along their entire reach.

Hydrology

A common element in all riparian systems which sets them apart from upland areas is the presence of surface water. The character of this surface water varies from standing to running water and from perennial to intermittent. In the Pacific Northwest perennial streams and rivers exhibit pronounced annual variation in flow levels (Hall 1988). In addition to annual variation in flow, many riparian zones experience periodic catastrophic flooding episodes which might be accompanied by ice flows or debris torrents (Hall 1988, Brinson et al. 1981, Cummins 1980, Oakley et al. 1985). The dynamic nature of the water flow shapes the structure of the riparian zone through erosive downcutting and deposition and is responsible for the high levels of nutrient cycling characteristic of riparian zones. The seasonal variation in water level and flow are important for nutrient recycling in riparian zones (Brinson et al. 1981). The expansion and contraction of stream channels with changing flow levels influences the structure and composition of plant communities (Brinson et al. 1981).

Although the presence of surface water is a conspicuous feature of the riparian zone, an understanding of the hydrology of the riparian zone must also take into consideration the interaction between surface and ground water (Brinson et al. 1981). The ground water is closely associated with the surface water in riparian zones. The water is closer to the surface in riparian than upland areas (Oakley et al. 1985). Under normal conditions, the movement of ground water is toward the surface water, however, during overflow the movement of water can be reversed and water might move into the aquifer (Brinson et al. 1981, Oakley et al. 1985). The topography and substrate characteristics of the riparian zone will determine the extent to which ground water can be stored (Brinson et al. 1981). The interaction between ground and surface determines levels of soil moisture, which can be critical for maintaining riparian vegetation during the dry summer months.

Soils

Both the surface water character and topography of the riparian zone have a direct bearing on the types of soils found in riparian zones. In general, riparian soils differ from upland soils in the origin of soil mineral content, organic content of soils, and amount of soil litter (Bilby 1988). Typically the mineral content of riparian soils is derived from stream deposited sediment whereas that of upland soils is the underlying rock. Consequently, riparian soils can be more heterogeneous in mineral content than upland soils if a drainage basin has a varied geology (Bilby 1988).

A number of factors can contribute to an increase in organic content of riparian soils relative to upland soils. The increased moisture content of riparian soils relative to upland soils generally results in higher decomposition rates and therefore increased organic content. It should be noted, however, that if riparian soils become saturated with stagnant water, decomposition rates will decrease due to lack of oxygen. The organic content of riparian soils is also determined, to some extent, by redistribution during periodic flooding. Large amounts of organic matter will be flushed from areas with high energy flood flows and deposited in other areas where the energy of overflow water is lower (Bilby 1988). The organic content of riparian soils can be greater than upland soils in part because many riparian plants decompose easier than upland plants (Bilby 1988, Edmonds 1980). Decomposition rates can also be affected by the nitrogen content of the litter. Elevated nitrogen content results in more rapid decomposition and, consequently, increased organic turnover (Swanson et al. 1982). In many Pacific Northwest riparian forests, red alder is a common component of the riparian vegetation (Campbell and Franklin 1979). Red alder converts nitrogen gas to reduced or organic nitrogen (Swanson et al. 1982). Consequently red alder litter contains one to four times greater nitrogen than other deciduous or coniferous litters (Swanson et al. 1982, Bilby 1988).

Riparian zones often have exposed soil surfaces whereas upland areas have greater amounts of terrestrial litter. This is due to the combined effects of deposition and flooding in the riparian zones (Bell and Sipp 1975).

Microclimate

Topographic features and presence of surface water can result in microclimatic differences between riparian zones and upland areas. Riparian zones, for example, often have higher humidity, increased rates of transpiration, and greater air movement than upland areas (Thomas et al. 1979).

Vegetation

The hydrological, topographic, substrate, and microclimatic features of riparian zones result in distinctive physiological, compositional, and structural features of riparian vegetation (e.g., Campbell and Franklin 1979, Franklin et al. 1981, Swanson et al. 1982, Oakley et al. 1985). The hydrology of the riparian zone affects the metabolism and growth of vegetation in three primary ways (Brinson et al. 1981). First, increased soil moisture is important in maintaining riparian forest vegetation, especially in the more xeric forests east of the Cascades. Second, the nutrient supply for riparian vegetation depends, in part, on the transport action of streams. Third, flowing water ventilates the soils and roots of riparian plants resulting in more rapid gas exchange. These three factors contribute to faster growth rates and increased primary productivity of riparian plant communities relative to upland communities.

Composition considers both the number of plant species and the abundance of each species. Riparian areas typically have greater species diversity than upland sites. Variation in the diversity of vegetation between riparian sites is related to a site's size, aspect, soil moisture, amount of woody debris, and time since disturbance (e.g., Gawler 1988, Malanson and Butler 1990). The riparian vegetation is composed of generalized species that inhabit both riparian and upslope sites, but are often more abundant in riparian areas because of favorable conditions, as well as specialized species that are found only in the moist riparian habitat. The latter can include species adapted to conditions created by patterns of natural disturbance characteristic of riparian areas (Gawler 1988). Riparian plant species have evolved a variety of strategies in response to flooding and alluvial deposition. Rowe (1983) defined five categories of plants -- invaders, endurers, resisters, evaders, and avoiders -- based on their mode of adaptation to disturbance and Agee (1988) developed these categories in the context of riparian vegetation of Pacific Northwest forests. Invaders (e.g., red alder, black cottonwood, many herbaceous species) are able to quickly colonize disturbed areas after flooding because they produce many reproductive propagules and have rapid growth rates. For example, in Oregon's Central Cascade Range, herbs such as *Circea aplina* and *Montia sibirica* are commonly found on fresh deposits of sand and gravel. Endurers are species that are often damaged during a flooding event but survive in riparian areas through sprouting (e.g., willows) or by production of adventitious roots (e.g., lodgepole pine, coastal redwood). Many riparian plants employ a resister strategy in response to low magnitude flooding. The flexible stems of many willows exemplify this strategy. Evader plants (e.g., *Ribes* sp.) store seeds in the soil and although the plant dies during the flooding disturbance, favorable conditions are created for the stored seeds. Given the nature of flooding disturbance, this strategy is not as widespread in riparian species as in species adapted to fire disturbance. Finally, other species are not well adapted to deposition or inundation during flooding and are categorized as avoiders.

The hydroperiod and the energy of flowing water, especially during catastrophic flooding, affect riparian plant community composition and development in several ways (e.g., Bilby 1988, Brinson et al. 1981, Swanson et al. 1982). The composition of riparian plant communities might be influenced by the dissemination of seeds by stream flow (Daubenmire 1968, Bilby 1988). During periods of heavy flooding the battering action of debris or ice can damage and uproot riparian vegetation. Erosion and bank undercutting of streambanks during flooding events might also eliminate riparian stands. New sites for the establishment of plant communities are thereby created by flooding events. Establishment of streamside vegetation can be retarded in areas where erosion leaves bedrock slopes with little soil or by repeated destruction during successive flooding events.

Classification of riparian vegetation

Given the potential for multi-resource use in riparian habitats, there has been an increase in the number of studies attempting to classify riparian ecosystems (e.g., Cowardin et al. 1979, Ratliff 1982, Youngblood et al. 1985, Pierce and Johnson 1986, Kovalchik 1987). Traditional floristic classification schemes are based on identifying plant associations representative of a site's potential. However, Kovalchik (1987, Kovalchik and Chitwood 1990) suggests that traditional floristic classification theories are inadequate for riparian habitats given the dynamic nature of these habitats. Kovalchik (1987, Kovalchik and Chitwood 1990) recommends combining floristic classification with geomorphic classification to yield a four-level classification that considers physiographic area, watershed characteristics, riparian landforms, and fluvial surfaces/riparian

plant associations. This classification scheme has been applied to riparian habitats in central Oregon (Kovalchik 1987) and the riparian plant associations of northeastern Washington are currently being classified in a similar fashion (Bernard L. Kovalchik, USFS, personal communication).

Characterization of Washington's Riparian Management Zones

The Habitat Management Division of the Washington Department of Wildlife (WDW) recently completed a project characterizing the vegetation of the RMZs and Upland Management Areas (UMAs) in the state. A total of 155 RMZs was sampled on the west side and 29 RMZs were sampled on the east side of the state. Analysis of these data (Andrew Carlson, WDW, personal communication) indicate that the dominant trees in East-side RMZs were hardwoods, red alder, grand fir, western red cedar, and Douglas-fir. The dominant shrubs in East-side RMZs associated with Type 1 waters are black hawthorn, alder, red-osier dogwood, and snowberry. Other common shrubs in these RMZs include serviceberry, mockorange, and bearberry. Dominant herbaceous plants are grasses, horsetails, western yarrow, and sedges. Dominant shrubs in RMZs on Type 3 streams sampled on the East-side include vine maple, red-osier dogwood, alder, and snowberry. Common herbaceous plants in these RMZs are grasses, horsetails, sweetscented bedstraw, coolwort foamflower, and beadleily. The dominant trees in West-side RMZs included red alder, western hemlock, other hardwoods, western red cedar, and Douglas-fir. Dominant shrubs in RMZs associated with Type 1 waters on the West-side are vine maple, salal, salmonberry, trailing blackberry. Red elderberry is also common in these RMZs. Dominant herbaceous plants in these RMZs include grasses, Oregon oxalis, piggyback plant, and swordfern. The shrubs dominant in RMZs associated with Type 2 waters on the West-side are the same as those found in Type 1 RMZs. Dominant herbaceous plants in Type 2 RMZs on the West-side include swordfern, Oregon oxalis, piggyback plant, deerfern, lady-fern and grasses. Dominant shrubs in RMZs on Type 3 streams on the West-side are again similar to those listed above with the exception that red elderberry is not present and stink currant is found in the sampled RMZs. Grasses are less common in RMZs on Type 3 waters than in RMZs on Type 1 or 2 waters. The average cover of shrubs and grasses is greater and the average cover of forbs is less in East-side RMZs associated with both Type 1 and 3 waters than in West-side RMZs on the same water types.

The structure of the vegetation refers to the horizontal and vertical stratification of the plant community. Riparian areas typically have greater structural diversity than upland sites and broader riparian zones have greater structural diversity than narrow, steep-sided riparian areas.

Preliminary results from WDW's RMZ and UMA habitat characterization project indicate that the average number of tree stems/acre is greater for both hardwoods and conifers in East-side (204, 121 trees/acre, respectively) than West-side (100, 86 trees/acre, respectively). This difference is attributed to a greater number of smaller (< 12 in) diameter trees in RMZs sampled on the East-side. The density of larger (> 20 in) trees is similar. Similarly, the average number of both hardwood and conifer snags is similar in RMZs sampled on both sides of the state. Midstream canopy closure over streams was greater West-side than East-side RMZs. Canopy closure was 69%, 71%, and 79% (mean = 76%) for West-side RMZs on water types 1, 2, and 3, respectively and 41%, 49%, and 72% (mean = 65%) for East-side RMZs on water types 1, 2, and 3, respectively.

Influence of vegetation on stream structure and function

Many characteristics of riparian plant species and communities are shaped by the presence and flow of water; however, riparian vegetation, in turn, has a direct effect on stream structure and function. First, roots of riparian vegetation stabilize streambanks and stream beds that help define stream morphology and reduce sedimentation (Brinson et al. 1981, Swanson et al. 1982).

Second, riparian vegetation is an important source of large organic debris (LOD, e.g., tree boles, root masses, large branches) in Pacific Northwest streams. Although such debris was once considered detrimental to stream quality (Triska and Cromack 1980), large organic debris is now recognized as an integral link between terrestrial and aquatic components of forest ecosystems. Indeed, Swanson et al. (1982) suggest that LOD might be the primary influence on lower order mountain streams in forests of the Pacific Northwest. LOD can help define stream structure by retaining gravel and sediment, forming pools, and creating waterfalls (Swanson et al. 1976, 1982, Bilby 1981, 1984, 1988, Triska and Cromack 1980). LOD facilitates deposition of sediments in the stream and consequently affects the morphology and energy transport in lower order streams (Keller and Swanson 1979, Bilby 1988, Swanson et al. 1982). For example, Megahan (1982) found LOD to retain 49% of the sediments in Idaho streams. This retention of sediment can lead to the formation of sediment terraces which form broad, level areas adjacent to the channel, increasing the size of the riparian area (Bilby 1988). With the input of LOD, a stream becomes characterized by long, level portions, in which the gradient is less than the overall gradient of the valley, separated by short, steep falls in which much of the potential energy of the water flow is dissipated (Swanson et al. 1982). Removal of LOD in smaller streams results in a decrease in the percent area of pools and number of waterfalls (Bilby 1981, 1984) and an increase in particle export from a watershed (Bilby 1988). As a result of this pattern of pools and falls, streams with LOD typically have less erosion, slower routing of organic detritus, and greater habitat diversity than straight, even-gradient streams (Swanson et al. 1982). LOD plays a more important role in creating habitat in smaller streams than in larger streams. The woody debris is large relative to stream width and the smaller streams generally do not have strong enough water flow to redistribute LOD. Wood-created habitat is formed by individual pieces of debris or small accumulations. Periodic debris torrents in smaller streams can remove LOD. In larger streams, the greater energy of the water flow and reduced influence of surrounding forests on wider streams results in less LOD and greater clumping of the LOD that is present (Keller and Swanson 1979, Swanson et al. 1982, Triska and Cromack 1980). Preliminary results from WDW's RMZ habitat characterization project suggest that the number of pieces of LOD found in all types of streams on the West-side is greater than for comparable East-side streams.

Third, standing riparian vegetation has an important effect on stream function. Riparian vegetation influences the chemistry of the stream through nutrient assimilation and transformation. The absence of vegetation in the riparian zone can result in greater export of dissolved materials (Brinson et al. 1981, Bilby 1988).

Fourth, the shading of streams by riparian vegetation can affect water temperature, and the magnitude of the effect is directly related to stream size. In smaller streams, riparian vegetation can completely shade the water from sunlight and these streams typically exhibit stable, cool temperatures year-round. Larger streams are too wide to be completely shaded so that riparian vegetation has minimal effect on water temperature. Stream size and the degree to which streams are shaded by riparian vegetation also influences whether the energy source supporting the biotic community of streams is primary production in the stream or detritus from surrounding

vegetation. In smaller streams, shading by riparian vegetation blocks the sunlight reaching the water, thereby reducing primary production by algae. Organic material from the surrounding vegetation represents the main source of energy in these streams. For example, Swanson et al. (1982) report that 95% of the organic matter in lower order streams in Pacific Northwest forests is detritus derived from terrestrial sources. This detritus represents the main food source for many aquatic invertebrates, which in turn, provide food sources for other aquatic and terrestrial species (Bilby 1988). In contrast, primary production by algae and diatoms in larger streams represents the primary energy source for the aquatic community (Swanson et al. 1982, Cummins 1980).

The interaction between the terrestrial and aquatic environment which occurs in the riparian zone changes with stream size. On the one hand, stream size is one of the main factors determining the size of the riparian zone. Small streams produce smaller riparian zones than larger streams. On the other hand, the effect of the terrestrial system on the aquatic system is inversely related to stream size. The forest dominates in small streams, controlling the physical structure and energy base. As Bilby (1988) stresses, understanding this relationship between stream size and interaction between aquatic and terrestrial systems is important when we examine the effects of disturbance in the riparian zone.

Disturbance in riparian zones

Riparian zones are a product of disturbance (Agee 1988) and an understanding of how natural disturbance affects riparian zone structure and function provides insight into how human activities can alter riparian zones. In Pacific Northwest forests natural disturbances such as flooding, fire, and wind, vary in frequency, magnitude, and relative importance in upland versus riparian areas.

Fluvial disturbances in Pacific Northwest forests, as discussed above, can occur as seasonal small-scale events or episodic large-scale events. The effects of fluvial disturbance are typically greatest at the center of the riparian zone and diminish towards the edges. Annual variations in flow make portions of riparian zones available for plants each dry season as channel width decreases 16 to 60% (Swanson et al. 1982). Large-scale flooding has a much greater impact on riparian vegetation, especially in small streams. If a channel is scoured to bedrock by a debris torrent, re-establishment of vegetation must generally be preceded by LOD input and sedimentation. Deciduous trees (e.g., willows, red alder, aspen) dominate post-disturbance riparian zones within 5 to 10 years. Canopy closure by upslope conifers eventually suppresses the shade-intolerant deciduous species (Swanson et al. 1982). Because the forest dominates the riparian zone in smaller streams, development of upslope stands determines that of riparian zones (Agee 1988). In larger streams, fluvial disturbance might result in a stepped progression of successional stages from the channel to the upslope forest (Agee 1988). Deciduous trees colonize recent gravel bars and dominate lower (younger) terraces. Older terraces support conifer stands.

Activity of beavers in the riparian system can alter effects of fluvial disturbance and therefore affect plant succession in riparian zones. Damming of streams by beavers can raise terrestrial water tables to the detriment of some tree species. Removal of canopy cover can promote conditions favorable for invasion of shade intolerant deciduous species. However, beavers further affect riparian vegetation through selection of food sources. Over utilization of deciduous species can lead to the creation of sedge-grass meadows.

Fire is an important disturbance in upland Pacific Northwest forests. Although riparian zones are not immune to fires, their higher humidity, greater fuel moisture, and larger proportion

of less flammable deciduous vegetation, result in less likelihood that fires will start and in lower intensity of fires that do enter riparian zones. These protective factors are less pronounced in smaller stream systems and fires are therefore more likely to burn across riparian zones associated with smaller streams than those of larger streams.

The susceptibility of a riparian zone to wind disturbance is specific and dependent upon local topography, stream size, soil conditions, and forest structure and composition (Agee 1988). Conditions that increase the likelihood of blowdown in a riparian area include 1) little topographic depression of the riparian area, 2) poorly drained soils, 3) orientation of the riparian zone across the direction of prevailing winds, and 4) presence of species (e.g., western hemlock) prone to windthrow.

Agee (1988) modeled the disturbance probabilities of fluvial, wind, and fire disturbance relative to position in the riparian zone for small, medium, and large streams in Pacific Northwest forests. In small streams there is a high probability of fluvial disturbance in the center of the riparian zone and the probability of fire or wind disturbance at the center of the zone is equal to, and under some conditions, greater than, that in surrounding forest. Consequently, the combined probabilities of disturbance are greater in the center of the riparian zone rather than on the edges. Frequent disturbances result in a mixture of patches of invader species with upslope vegetation. The probability of water-based disturbance in riparian zones associated with medium-sized streams is also greatest at the center and decreases towards the edges of the riparian zone. However, the probabilities of fire or wind disturbance are decreased because of higher moisture conditions and more protected topography, respectively. Therefore, the combined disturbance probabilities tend to be reduced at the edges of medium-sized streams. The probability of water-based disturbance relative to position in the riparian zone is similar in large streams to that discussed above for smaller streams. The probability of wind disturbance is relatively great in larger riparian zones because valleys can be corridors of wind movement and saturated soils make trees susceptible to blowdown. High moisture conditions reduce the probability of fire. Combined disturbance probabilities indicate that in larger streams water-based disturbances are the primary disturbance, leading to establishment of invader species.

Agee's (1988) model of disturbance probabilities relative to stream size and position in the riparian zone has implications for assessing impacts of human disturbances in riparian zones and in the design of riparian buffer zones to protect against these disturbances.

Although riparian habitats are the products of disturbance, they can also be especially susceptible to human disturbance because 1) humans are attracted to and therefore concentrate many activities in riparian habitats, 2) riparian habitats constitute a relatively smaller amount of area than upland areas, 3) the long, thin shape of riparian areas creates extensive interface with upland areas and makes riparian areas vulnerable to upland disturbances, 4) riparian habitats support a unique flora that is often sensitive to disturbance (Oakley et al. 1985). Human impacts on riparian habitats are varied and include timber harvesting, livestock grazing, road building, impoundments, channelization, introduction of toxic compounds, hunting and fishing, and non-consumptive recreation (e.g., Brinson et al. 1981, Hall 1988). Given the scope of this review, we will focus primarily the effects of timber harvest, but will also consider those of road building and livestock grazing.

The impact of timber harvesting in riparian and adjacent upland habitats varies with the type of harvest and characteristics of the watershed. Clear-cutting, for example, might have a greater negative impact on riparian habitats than single tree selection (e.g., Oakley et al. 1985).

Research concerning the effects of logging in watersheds has suggested varying levels of impact on riparian zones from little or no impact to substantial impact. Much of the variation reflects the initial definition of the riparian zone, the variables measured, and the design of the studies. For example, a comparative study of logged versus undisturbed sites in northeastern Oregon (Carlson et al. 1990) suggests little differences in LOD and pool volume between sites. In contrast, other studies have identified several major stream-habitat changes associated with logging (e.g., Harr 1976, Harr et al. 1979, Swanson 1980). Water temperatures increase after tree harvesting due to the reduction of shading. Increased sedimentation often results from logging because 1) logging activities (i.e., timber felling, yarding) increase input of soil and detritus into streams, 2) sediments trapped by LOD prior to logging can be released into the channel if LOD is removed, and 3) a reduction in ground cover adjacent to streams increases erosion of soils. Stream flow, especially in smaller streams, can significantly increase following timber harvests. Timber harvest in riparian areas can alter the composition and structure of both the overstory and understory plant communities. Finally, removal of vegetation from small streams can alter the dynamics of the food chain because, as discussed above, terrestrial vegetation represents the primary source of organic input in these streams. Maintenance of vegetative buffer zones adjacent to streams and retention of LOD in stream channels can decrease many of these negative impacts (e.g., Franklin et al. 1981).

Road construction is often associated with logging activities and can have a lasting impact on riparian habitats (e.g., Thomas et al. 1979). The construction of roads in riparian habitats changes vegetation structure, alters microclimate conditions, can result in debris torrents due to increased erosion, and reduces the size of the riparian zone (Oakley et al. 1985).

Livestock grazing in managed forests is more common east of the Cascade Range than on the coastal side. Grazing can remove plant biomass, alter the age structure of plant populations, reduce tree and shrub reproduction by seedling browsal, and change the species composition of plant communities (e.g., Brinson et al. 1981). Although these effects are not limited to riparian areas, livestock often concentrate in riparian areas, especially during hotter, drier times of the year. Heavy livestock grazing in riparian zones has additional negative impacts including soil compaction, break down of streambanks and alterations of channel morphology, increased erosion, lowered water tables, and deterioration of water quality (e.g., Thomas et al. 1979, Oakley et al. 1985, Brinson et al. 1981, Hall 1988).

Timber harvesting, road building, and livestock grazing potentially reduce the value of riparian habitat for native wildlife. In the remainder of this background section we discuss the characteristics of riparian habitats which make them of high wildlife value, wildlife use of these areas, and how buffer zones designed to mitigate the effects of human disturbances in managed forests might affect wildlife.

WILDLIFE USE OF RIPARIAN HABITAT

The high value of riparian habitats to wildlife has long been recognized by naturalists. Quantitative studies conducted during the past several decades have supported observations and have identified biological and physical attributes of riparian habitats which enhance their value to wildlife. Brinson et al. (1981) and Oakley et al. (1985) provide summaries of these biological and physical features.

First, the presence of surface water provides a critical habitat component for wildlife and the abundance of soil moisture creates habitat conditions favorable to many wildlife species. Second, the increased humidity, higher rates of transpiration, and greater air movement often found in riparian zones create microclimate conditions that differ from surrounding uplands and are preferred by some wildlife during hot weather. Third, riparian habitats tend to be complex wildlife habitats because of the interspersed nature of many biological and physical features. Plant communities in riparian habitats are more diverse in their composition and structure than in uplands. Associated with this complexity is an increase in internal edges at the interface between stream channel and riparian vegetation and in the transition between riparian and upland vegetation. A developed deciduous component in riparian plant communities creates additional habitat complexity because of changes in habitat conditions at different times of the year (Thomas et al. 1979). Fourth, the linear shape typical of riparian habitats creates maximum edge effect with adjacent upland forests which is beneficial for some wildlife species. Finally, the shape and habitat conditions of riparian zones make them natural migration routes and travel corridors for many wildlife species (e.g., Thomas et al. 1979, Oakley et al. 1985, Brinson et al. 1981) and therefore might represent routes of gene flow (West 1988).

Brinson et al. (1981) and Johnson (1977) provide extensive reviews of wildlife resources in various regions of the US and Thomas et al. (1979), Oakley et al. (1985), and Raedeke (1988) review wildlife use of Pacific Northwest forests. Most surveys indicate that wildlife species use riparian habitats disproportionately more than other types of habitat. Although especially true in the more arid regions of the US (Johnson and Jones 1977, Brinson et al. 1981), this pattern is generally found in the forests of the Pacific Northwest. Thomas et al. (1979) report that 278 of the 285 terrestrial wildlife species in the Blue Mountains are found exclusively or more commonly in riparian areas and Oakley et al. (1985) report similar patterns for 359 of the 414 wildlife species of western Washington and Oregon forests. In contrast, McGarigal and McComb (1992) report little difference in species diversity between riparian and upland habitats along lower order streams in the coastal mountains of Oregon. The general disproportionate use of some riparian habitats by wildlife species reflects their response to the biological and physical features outlined above. In the following paragraphs we introduce habitat functions that attract wildlife species to riparian areas. Each of these habitat functions will be discussed in more detail in the sections on specific vertebrate taxa.

Riparian habitats provide the water and food requirements for many wildlife species (Oakley et al. 1985, Thomas et al. 1979, Brinson et al. 1981). Clearly, those species dependent upon free water will utilize the surface water present in riparian habitats, especially during the hotter, drier times of the year. Surface water is also required by many species for feeding (e.g., waterfowl, fish-eating birds, some shrews, Pacific giant salamander). Other species will preferentially feed in riparian habitats because the productivity of riparian plant communities provide abundant seeds (e.g., seed-eating birds and mammals) and herbaceous vegetation (e.g., grouse, deer). The structural complexity of riparian plant communities provides many strata for foraging by different wildlife species. Insect eaters such as bats, shrews, flycatchers, swallows, and some salamanders, often forage preferentially in riparian areas because of increased insect abundance. Predators (e.g., coyotes, hawks, owls) are in turn attracted to the abundance of prey in riparian habitats.

Riparian areas provide habitat for many wildlife species for breeding and rearing young. Amphibians require standing water or greater moisture of riparian soils for reproduction. Aquatic

mammals such as beaver and muskrat require water for their dens. Many waterfowl and other birds nest on floating platforms, in trees or snags adjacent to or in streams, and ponds. Fawning and calving grounds of ungulates are often near riparian areas because of the quality of food and cover.

The water and dense vegetation which characterize riparian areas provide many wildlife species with escape, hiding, and resting cover. Aquatic species such as frogs, beaver, and muskrat utilize water for escape from predators. Waterfowl use sheltered areas at the edges of streams and ponds for hiding and resting cover. Many terrestrial vertebrate species use hollow logs and trees, cavities in logs and trees, and dense foliage in riparian areas for hiding and resting cover. The abundance of shrubs and trees in riparian areas provide perches for many bird species.

The linear shape, extension from lowland to higher elevations, and habitat features of riparian areas make them natural travel corridors for many wildlife species (Thomas et al. 1979, Brinson et al. 1981, Stevens et al. 1977). For some species these travel corridors might be used on an annual basis. For example, ungulate species utilize riparian areas between high elevation summer and low elevation winter ranges (Thomas et al. 1979). Riparian areas can be important to bird species during migration (Rappole and Warner 1976, Stevens et al. 1977). As Brinson et al. (1981) point out, many birds seek riparian habitats during migration that are similar to habitats on nesting grounds. During winter months riparian areas can be used by both residents and migrants from northern areas. In addition to providing habitat for annual movements, riparian areas often provide habitat critical for successful dispersal of terrestrial vertebrate species (Brinson et al. 1981). Finally, surface water in riparian areas provide required travel habitat for many aquatic species (e.g., beaver, muskrat).

Although there are common environmental attributes of riparian ecosystems which enhance the wildlife value of these areas, other ecological characteristics vary between riparian areas and further determine the value of these wildlife habitats. These ecological variables have been reviewed by Brinson et al. (1981) and include vegetation type, size and shape of riparian area, stream type and hydrologic pattern, adjacent land use, and elevation.

The structural form of the riparian vegetation has a significant impact on wildlife abundance and community composition. Many species require specific structural attributes (e.g., many songbirds, deer, bald eagles, black bear) (Brinson et al. 1981, Landers et al. 1979, Steenhof 1978). The variety of wildlife habitats is typically greatest in structurally diverse riparian habitats which can support both specialized as well as more generalist species. In addition to structural form, the species composition of riparian plant communities can influence wildlife communities in riparian areas. This is especially true if there are distinct differences in the food value of riparian versus upland vegetation, for example, the presence of deciduous trees along streams in coniferous forests or of mast producing trees in bottomland communities. In addition, riparian plant species might host different invertebrate species further distinguishing the food value of riparian plant communities. The absence of vegetation due to continual erosion and deposition can provide nesting habitat for some species (e.g., belted kingfishers nest on steeply sloped streambanks; spotted sandpipers nest on sandy shoals) and resting habitat for other species (e.g., migrating birds and turtles rest on sandbars).

The size and shape of the riparian area has a direct bearing on its value as wildlife habitat. Narrow strips of vegetation can be sufficient for instream aquatic communities and some terrestrial wildlife (e.g., belted kingfisher; Curtis and Ripley 1975). However, for species requiring large areas of forest or minimal disturbance from humans (e.g., black bear, great blue herons, and

many forest dwelling songbirds; Landers et al. 1979, Brinson et al. 1981), narrow strips are insufficient. The width of the riparian habitat will also influence how land use patterns in adjacent areas will impact water quality and the overall wildlife value of the area. In addition to width of riparian areas, the overall size is an important aspect of the wildlife value of the riparian area and is relative to the space requirements of different species (e.g., home range size, territory size). The question of what constitutes an adequate size for riparian areas is addressed below in the section on buffer zones.

As discussed above, stream type has a direct influence on the riparian habitat and its associated wildlife communities. In the smaller headwater streams, the impact of the upstream riparian vegetation on the stream is greater than downstream where flow volume increases, flooding is more widespread, and the impact of riparian vegetation on the stream is less. Brinson et al. (1981) suggest that middle order perennial streams and associated riparian areas have the greatest wildlife use. Periodic flooding impacts the wildlife value of riparian habitats in a variety of ways. In some cases flooding enhances the availability of food for wildlife by increasing fish production (e.g., Brinson et al. 1981) or by creating new feeding areas. Flooding can also make riparian habitat unsuitable for other species. Species abundance of riparian mammal communities can be related to the timing of recent hydrologic events; impoverished mammal populations have been attributed to recent flooding whereas more abundant populations have been observed in areas not subject to recent flooding (Brinson et al. 1981).

The wildlife value of riparian habitats can also be affected by adjacent land use. If land use practices in adjacent areas result in increased food supplies, some species can be found at higher densities in the riparian area if the riparian habitat provides nesting or resting habitat (e.g., Carothers et al. 1974, Glasgow and Noble 1971). This is often most pronounced in agricultural rather than timber areas (Brinson et al. 1981). The effects of adjacent land use patterns on wildlife use of riparian areas are inversely related to the size of the riparian area.

Elevation can have an influence on composition of riparian wildlife communities. The abundance and diversity of bird communities is often greater in lowland rather than higher elevation riparian areas (Stevens et al. 1977, Burkhard 1978, Knopf 1985). This is in part because the greater availability of moisture in nonriparian habitats at higher elevations reduces birds' dependency on the riparian zone. A similar trend in the abundance and diversity of other wildlife species with elevation awaits confirmation (Brinson et al. 1981)

In sum, riparian areas provide habitat for many wildlife species, but assessing the relative value of a particular riparian area for wildlife must take into account a variety of ecological characteristics. Therefore, habitat management of riparian areas becomes a critical element of wildlife management. To mitigate the effects of timber harvesting in managed forests many states have adopted the use of buffer zones along streams. In Washington state, for example, the Forest Practices Board (1988) prescribed the creation of Riparian Management Zones (RMZs) for managed forests on state and private lands. These RMZs vary in width and number of trees left in the buffer depending upon water type and region of the state. The primary intent of mandating buffer zones along streams has often been the preservation of water quality and fisheries habitat. The maintenance of buffer zones can also benefit terrestrial wildlife species, but the effectiveness of these buffers must take into account a variety of factors. In the following paragraphs we examine these factors from a broad perspective and in the sections on specific vertebrate taxa examine the importance of buffer zones for each group.

WILDLIFE USE OF RIPARIAN BUFFERS - GENERAL CONSIDERATIONS

In the managed forests of the Pacific Northwest buffer zones can serve two distinct roles. Historically, when the prevailing successional stage in PNW was old forest, a function of riparian zones was to provide refugia for species characteristic of early successional stages. Aside from the presence of water, the unique features of riparian zones centered on the admixing of early successional characteristics within old forests. The presence of such areas was especially important for the continued existence of species with limited powers of dispersal. For example, the small strips of open ground supporting grasses and herbs were needed by herbivorous small mammals, which survived at low population densities in such areas, and from which they could rapidly colonize large areas after forest disturbance. With the maintenance of riparian buffer zones in managed forests, a second function envisioned for riparian zones is in providing elements of old forest in a predominantly young forest landscape. Forest harvest, which creates riparian buffer zones in managed forests, however, results in the fragmentation of existing habitat. This leads to the creation of a mosaic of forest patches which are scattered over the landscape and which vary spatially and temporally. Fragmentation of forest habitats results in a reduction in total area of forest habitat, an increase in the amount of edge between previous and newly created habitats, and an increase in isolation of remaining forest patches (Lehmkuhl and Ruggiero 1991). Forest patches created by the retention of riparian buffers are unique in their linear shape and because of the special features inherent to riparian zones. Examination of the effectiveness of riparian buffer zones in the two above mentioned functions must therefore take into consideration the effects of forest fragmentation on wildlife. Excellent reviews of this topic are available (e.g., Harris 1984) and our intent is only to briefly summarize pertinent aspects.

The positive relationship between area size and species abundance has long been recognized for island situations (e.g., MacArthur and Wilson 1967) and has been applied to forest landscapes (e.g., Harris 1984). Larger areas support greater species abundance because of greater habitat diversity and likelihood of colonization from surrounding areas. The maintenance of buffer zones along streams creates forest fragments of potentially different sizes. Studies of terrestrial vertebrates (Rudolf and Dickson 1990, Stauffer and Best 1980, Dobkin and Wilcox 1986) indicate that wider buffer zones (i.e., larger area) often support greater species diversity. Although maintenance of species diversity is a primary goal of current conservation strategies, maximizing species diversity without regard to differences between species is not always a desirable management goal (e.g., Lehmkuhl and Ruggiero 1991, Van Horne 1983, Murphy 1989). Considering the potential dual function of riparian buffer zones in providing habitat for both early and late successional species, managing for species diversity becomes a complex issue. For example, in pine plantations of eastern Texas Dickson and Williamson (1988) found that narrow (< 25 m) streamside management zones supported more small mammals than medium (30-40 m) or wide (50-90 m) zones but that only the wider zones provided habitat for species associated with mature forest stands.

As background it might be helpful to realize that a riparian zone will be inhabited by three sorts of wildlife species. The first group, riparian obligates, are those species that require free water for some aspect of their natural history and must inhabit the riparian zone. They will reach maximum abundance within the riparian zone, and decline in abundance with distance from it. The second, and larger group of species, are those that are characteristic of the old successional stages. Numbers of these species will increase as the area of old forest available to them in the

riparian zone increases, resulting in relatively few of these species in small forest blocks and generally a full complement of species in large blocks. These species might not require the resources of the riparian zone to survive, but will inhabit it and might even have more productive populations within the zone than in the adjacent uplands. The third group of species consists of those characteristic of early successional stages. They have an interesting relationship to riparian zones in that, as previously mentioned, riparian zones almost always provide some level of resources to support these species. This is the result of the periodic disturbance regimes characteristic of riparian zones. They will inhabit riparian zones embedded within old forest in small but persistent numbers. Should the adjacent forest be harvested, the forest successional sequence will be initiated, and these species will rapidly colonize these areas. Given this scenario, they might exert considerable pressure on the resources available to species characteristic of old forest which might be trying to exist within the riparian management zone. How much pressure they exert will be related to the width of the zone.

As discussed above, riparian habitats are characterized by high levels of inherent (natural edge) and maximum edge effect. The creation of riparian buffer zones in managed forests results in equally high levels of induced (disturbance created) edge. "Edge" can be defined as an ecotone or transition between two habitat types. In the managed forest, for example, edge could be found where a forest patch abuts a clear-cut or along the boundary of a riparian buffer. Wildlife biologists have long recognized that the abundance and diversity of some species is greater along edges because of the presence of species adapted to the two adjacent habitat types as well as those specifically adapted to edge conditions. This is known as "edge effect" (Leopold 1933). Wildlife habitat management has traditionally sought to maximize edge effect in managed forests. This has benefited species such as white-tailed deer, elk, and ruffed grouse. Fragmentation of habitat and creation of forest patches with increased edge, however, is detrimental to other wildlife species. A substantial literature examines the impacts of increased edge on wildlife (e.g., Harris 1989, Yahner 1989, Soulé 1986, Temple and Carey 1988, Laudenslayer 1986, Janzen 1986). Lehmkuhl and Ruggiero (1991), for example, summarize seven detrimental edge effects: 1) competition between forest interior and edge species might occur which could reduce the viability of interior species populations; 2) generalist species found in forest patches at time of fragmentation might benefit from the altered environmental conditions outside the patches (a "cross boundary subsidy") and increase in population size or viability to the potential detriment of interior species (e.g., Raedeke and Lehmkuhl 1986); 3) nest predation and nest parasitism can increase in forest patches with substantial edge (Wilcove 1985, Temple and Carey 1988); 4) the forest edge might be a "unidirectional filter" that animals will pass out of but cannot return, for example some species are more vulnerable to predation outside of forest patches; 5) elimination of interior species as a result of forest fragmentation might lead to secondary extinctions because of altered community interactions; 6) extrinsic processes such as blowdown or ground fire, can reduce forest patch size or quality through "edge creep"; and 7) forest patch edges are subject microclimatic changes which alter conditions for interior plant and animal species - in the PNW, for examples, these microclimatic changes are thought to extend up to two tree lengths (160 m) inside a forest patch (Harris 1984, Franklin and Forman 1987).

The potential negative impacts of forest fragmentation on wildlife, the unique features of the riparian habitat, and the dual function envisioned for riparian zones in providing wildlife habitat, require that careful attention be given to the design of buffer zones if they are to be effective in providing that habitat. Although there is general consensus for the need to provide

riparian buffers in managed forests, there is much less agreement as to the size and desired characteristics of these buffers. In part this is because riparian buffers have been designed for a variety of purposes. At one end of the spectrum, if the function of the riparian buffer strip is to protect water quality from logging, a narrow buffer (e.g., 8 m; Trimble 1959, Washington Forest Practices 1988) might suffice, but at the other end, wider buffers are recommended if these strips are designed to maintain wild or scenic values of river corridors (e.g., 400 m; Wild and Scenic Rivers Act P.L. 90-542).

WILDLIFE USE OF RIPARIAN FOREST HABITATS - REVIEW OF EMPIRICAL STUDIES

AMPHIBIANS

During the last ten years there has been a dramatic increase in research to evaluate the extent to which amphibians are associated with various forest and riparian habitats and the impact of logging practices on these communities. This work has grown out of controversy regarding the status of amphibian communities as well as out of studies examining timber harvest impacts on stream water quality and salmonid communities. Many amphibians rely on streams and associated pools to provide foraging areas, cover, reproductive sites, and habitat for aquatic larvae. Some never enter streams or ponds yet depend on moist and cool environmental conditions. In general, amphibians tend to be more active at night when humidity is high and temperatures are low. Many stay underground or in rotting logs during summer droughts and cold winters and are physically and morphologically adapted to function with a low flow of energy (Pough 1980). Thus, they are able to survive long periods when resources are limited.

The ecological significance of amphibians is a function of their use of the environment to regulate body temperatures (Pough 1980). As ectothermic vertebrates, they require less energy because they do not work to maintain a constant body temperature as do birds and mammals. Consequently, an amphibian is much more efficient in transforming food energy to biomass than an endothermic animal. Amphibian biomass is available to other trophic levels and makes them important components of aquatic and terrestrial ecosystems (Pough 1980). Comparisons of amphibian biomass to that of other vertebrates demonstrate the significance of amphibians within certain ecosystems. The biomass of terrestrial and aquatic salamanders in a New Hampshire deciduous forest was twice that of the breeding birds and equal to the biomass of small mammals (Burton and Likens 1975). In old-growth redwood forests in northern California, Bury (1983) estimated over 400 salamanders per hectare. The estimated mean density of plethodontid salamanders associated with downed woody debris ranged from 364 per hectare in 40-75 year old Douglas-fir forest to 744 per hectare in old-growth Douglas-fir forest in Western Oregon (Corn and Bury 1991).

Washington state amphibian communities are notably different on the west and east sides of the Cascade Crest (Table 1). The salamanders, Order Urodela, are moist forest species primarily found west of the Cascade Crest where rainfall is higher and temperatures more moderate. Exceptions include the tiger salamander (*Ambystoma tigrinum*) which is only found east of the Cascade Crest and the long-toed salamander (*Ambystoma macrodactylum*) which is found on both sides of the crest. Both the tiger and long-toed salamander are found in a wider range of habitats than the western Washington species of salamander.

Frog species, Order Anura, are more widespread across the state. Six species are found on both the east and west sides of the Cascade Crest: bullfrog (*Rana catesbeiana*), green frog (*Rana clamitans*), tailed frog (*Ascaphus truei*), spotted frog (*Rana pretiosa*), Pacific chorus frog (*Pseudacris regilla*), and the Western toad (*Bufo boreas*). The spotted frog is currently listed as a state species of concern due to its disappearance from most of the verified historical sites west of the Cascade Crest (McAllister and Leonard 1990, 1991). The Washington Department of Wildlife has implemented a program to determine the status of the spotted frog in Washington.

Table 1. Amphibians of Washington state and their affinities for riparian habitats during different life history stages. Habitat codes: 0 = upland, 1 = riparian, 2 = aquatic. Ranking of dependency on aquatic or riparian habitat: 0-3 = somewhat dependent, 4-7 = moderately dependent, 8+ = highly dependent. Information compiled from Nussbaum et al. (1983), Licht (1986a, b), Good (1989), Welsh (1990), McAllister and Leonard (1991).

	Repro- duction	Neoteny	Adult Feeding	Adult Escape	Over- wintering	Preferred Habitat	Rank Total	Important Forest Structures
Order Urodela								
Cope's salamander	2	2	2	2	2	2	12	8-14°C streams; rocks and LWD
Northwestern salamander	2	2	0 or 2	0 or 2	0 or 2	0 or 2	4 or 12*	LWD; humid coniferous forest
Pacific giant salamander	2	2	0 or 2	0 or 2	0 or 2	0 or 2	4 or 12	mountain streams; rocks; CWD; little siltation; humid forests
Tiger salamander	2	2	0 or 2	0 or 2	0 or 2	0 or 2	4 or 12	ponds; burrows
Torrent salamander	2	NA	2	2	2	2	10	8-12°C headwater streams, splash zones; gravel, moss, CWD
Dunn's salamander	1	NA	1	1	1	1	5	streamside rocks; moist talus; 4- 17°C substrate temperature
Van Dyke's salamander	1	NA	1	1	1	1	5	seepages; streamside talus; talus slopes
Long-toed salamander	2	NA	0	0	0	0	2	ponds, lakes
Roughskin newt	2	NA	0	0	0	0	2	ponds, lakes, slow streams
Ensatina salamander	0	NA	0	0	0	0	0	litter; woody debris
Larch mountain salamander	0	NA	0	0	0	0	0	lava talus slopes of Columbia River Gorge
Western redback salamander	0	NA	0	0	0	0	0	litter, CWD; well-drained talus slopes; 5-19°C substrate temperature

Table 1. Continued. Habitat codes: 0 = upland, 1 = riparian, 2 = aquatic. Ranking of dependency on aquatic or riparian habitat: 0-3 = somewhat dependent, 4-7 = moderately dependent, 8+ = highly dependent.

	Repro- duction	Neoteny	Adult Feeding	Adult Escape	Over- wintering	Preferred Habitat	Rank Total	Important Forest Structures
Order Anura								
Bullfrog	2	NA	2	2	2	2	10	permanent water except cold, high mountain streams
Green frog	2	NA	2	2	2	2	10	permanent quiet water with abundant vegetation
Tailed frog	2	NA	2	2	2	2	10	cold, clear fast-flowing streams; no siltation; rock
Cascade frog	2	NA	2	2	?	2	8	damp meadows; open marsh along ponds and lakes
Spotted frog	2	NA	2	2	?	2	8	ponds, lakes, marshes; surface debris; algae-grown pools
Wood frog	2	NA	2	2	1	2	8	ponds, quiet streams; damp ground litter
Leopard frog	2	NA	2	2	2	1	6	marshes with abundant vegetation
Red-legged frog	2	NA	1	2	?	1	5	still water (permanent or temperature); moist, humid area temperature or permanent ponds; arid, open areas
Great basin spadefoot	2	NA	0	0	0	0	2	shallow, quiet water; emergent vegetation; open areas
Pacific chorus frog	2	NA	0	0	?	0	2	mammal burrows; loose soil for burrowing
Western toad	2	NA	0	0	?	0	2	permanent water; surface debris; rodent burrows
Woodhouse's toad	2	NA	0	0	0	0	2	

* Adults score 4 and neotenic adults score 12.

The importance of riparian zones to amphibian communities in Washington varies with the life history characteristics of each species. Nearly 80% of all species in Washington require aquatic habitat for breeding and development of larvae. Riparian zones are critical for maintaining the water quality of these breeding sites whether they are streams, pools, or ponds.

Habitat associations of adult amphibians are not understood for all species. Trapping in unmanaged Douglas-fir forests in western Washington in the early 1980's has revealed upland habitat associations for ensatina (*Ensatina eschscholtzii*), western redback salamander, northwestern salamander (*Ambystoma gracile*), roughskin newt (*Taricha granulosa*), red-legged frog (*Rana aurora*), Cascades frog (*Rana cascadae*), and tailed frog (*Ascaphus truei*) species (Aubry and Hall 1991). Aubry and Hall (1991) question whether their data reflect true habitat associations or proximity to breeding sites. Most Washington amphibians are believed to occupy a very limited range, however there is little documentation to support this. Movement is most frequently observed on rainy nights but little is known about the movement patterns or distances traveled. Ovaska (1988) estimates the average range of the Western redback salamander (*Plethodon vehiculum*) to be only three meters. Wilson and Larsen (1988) estimated travel distances of seepage dwelling Van Dyke's salamanders to be 5 m.

The following discussion attempts to synthesize and summarize the state of knowledge on amphibian associations within riparian and upland habitats in Washington state. The first section presents details on amphibian species' use of riparian habitats based on life history information. The second section discusses studies examining the effects of timber harvest on amphibians. The third section brings together information on riparian buffer strips and amphibian responses to them. As mentioned above, eastern and western Washington forests and amphibian communities are quite different. Management strategies and sampling techniques must take these differences into account.

Use of riparian habitats

Relative dependency

Obligate inhabitants of riparian zones

Amphibians which can be considered obligate riparian species are: 1) those which are most frequently found adjacent to or in streams or ponds throughout their adult lives; 2) paedomorphic adults that have retained larval gills and cannot survive out of water; 3) those which require aquatic habitat for breeding. These three categories include 80% of all Washington amphibian species (Table 1).

Washington salamanders which are usually found in or near streams are the torrent salamander (*Rhyacotriton cascadae*, *R. kezeri*, *R. olympicus*) and Dunn's salamander (*Plethodon dunni*). Torrent salamanders are considered the most aquatic of all Washington salamanders. Larvae and adults are found in small streams and seeps and adults are also found alongside the stream. Dunn's salamander is most commonly found in rocks alongside streams and waterfalls but is not usually found in the stream. Washington frogs which are most frequently found around streams and ponds are the tailed frog and all of the Ranid species: bullfrog, cascade frog, green frog (*Rana clamitans*), leopard frog (*Rana pipiens*), red-legged frog, spotted frog, and wood frog (*Rana sylvatica*). The tailed frog is found in and along fast moving, mountain streams. The Ranids are found at the edge of marshes, streams, and ponds or in the water.

Paedomorphism has been observed in four species of salamanders in Washington: Cope's salamander (*Dicamptodon copei*), Pacific giant salamander (*Dicamptodon tenebrosus*), Northwestern salamander (*Ambystoma gracile*), and tiger salamander. Paedomorphic individuals are completely aquatic adults due to the retention of larval gills. The preservation of streams or ponds and associated riparian zone is essential to the survival of paedomorphic individuals. The Cope's salamander is rarely found as a terrestrial adult (Jones and Corn 1989) and is therefore considered a truly obligate riparian species. The Pacific giant salamander exhibits facultative paedomorphism (Nussbaum 1976). In areas where breeding streams seasonally dry up, metamorphosis is the rule. Northwestern and tiger salamanders are more commonly found as terrestrial adults although populations of paedomorphic individuals have been observed (Eagleson 1976).

Amphibian species which breed in the water can be considered obligate riparian zone inhabitants for without suitable breeding waters, the species will disappear from an area. The riparian breeding obligates are: all Anurans, Cope's salamander, Pacific giant salamander, torrent salamander, long-toed salamander, northwestern salamander, tiger salamander, and roughskin newt. These species produce larvae which metamorphose in the water. The tailed frog, Cope's salamander, Pacific giant salamander, and torrent salamander breed only in mountain streams and are sensitive to changes in stream temperature, sediment load, and substrate composition.

Riparian vegetation helps maintain the integrity and water quality of the stream. To provide appropriate habitat for obligate species, riparian vegetation must 1) effectively shade the stream in summer and winter; 2) provide a continuous supply of large woody debris to the stream and organic litter to the forest floor; 3) prevent extensive soil erosion along the stream bank; 4) provide refuges for overwintering and escape from hot, dry summer days. The importance of these structures to amphibian communities is discussed throughout this review.

Habitat generalists that use riparian zones primarily while breeding

After breeding in aquatic habitat, many amphibian species migrate to adjacent forest beyond the riparian zone. This upland habitat with its closed canopy offers greater protection from the environmental extremes of summer and winter. These species are Pacific giant salamander, long-toed salamander, northwestern salamander, tiger salamander, and roughskin newt. Van Dyke's salamander (*Plethodon vandykei*) breeds on land and is commonly found under and between rocks alongside streams and in splash zones of seepages and waterfalls and sometimes in forest debris or damp talus far from water. Anuran species which migrate away from riparian zones after breeding are Pacific chorus frog (*Pseudacris regilla*), western toad (*Bufo boreas*), Woodhouse's toad (*Bufo woodhousei*), and Great Basin spadefoot toad (*Spea intermontana*). The Pacific chorus frog, western toad, and Woodhouse's toad are found in upland forests as well as open areas. The Great Basin spadefoot toad is found in arid regions where it survives dry periods by burrowing in sandy soil.

Infrequent inhabitants of riparian zones

Members of the salamander family Plethodontidae are considered forest salamanders because they do not require aquatic habitat for breeding. Consequently, proximity to water does not determine their distribution. They may be found in riparian zones or in upland forests. In Washington these species are the Larch Mountain salamander (*Plethodon larselli*), western redback salamander (*Plethodon vehiculum*), and the ensatina salamander (*Ensatina eschscholtzii*).

Species requirements provided by riparian habitats

Foraging

Foraging strategies vary with life history patterns. Aquatic salamanders, either as juveniles or as paedomorphic adults feed primarily on aquatic invertebrates, zooplankton, fish and amphibian eggs, and tadpoles whereas anuran larvae are generally herbivorous (Nussbaum et al. 1983). Tailed frog tadpoles (*Ascaphus truei*) are filter feeders with mouths that are adapted to cling to rocks in fast-moving streams. They feed by inching across smooth rocks but avoid moss and silt deposits (Nussbaum et al. 1983). Transformed tailed frogs feed on flying or crawling invertebrates along streams or on the forest floor adjacent to the stream (Bury and Corn 1988a).

Paedomorphic salamanders (e.g., Pacific giant salamander and Cope's salamander), have been observed feeding on nearly every type of small, aquatic organism (Nussbaum et al. 1983). Paedomorphic Pacific giant salamanders replace salmonid fishes as the primary vertebrate predator in headwater creeks (Murphy and Hall 1981) feeding on aquatic arthropods as well as snails, other amphibians, and juvenile small mammals (Bury 1972, Nussbaum et al. 1983). Stomach content analysis of Van Dyke's salamanders revealed the presence of aquatic prey species (Wilson and Larsen 1988).

Terrestrial salamanders and anurans feed primarily on aquatic, terrestrial, and flying invertebrates (Nussbaum et al. 1983). Periods of general surface activity have been associated with wet or rainy conditions and cooler temperatures (Smits 1984). Wilson and Larsen (1988) found Van Dyke's salamander activity to be almost entirely nocturnal and positively correlated with substrate temperature. Licht (1986a) compared the feeding behavior of spotted frogs and red-legged frogs. Spotted frog adults fed predominantly in water while floating on the surface or clinging to aquatic vegetation. Only on wet days were they observed feeding on land. Red-legged frogs relied more on terrestrial prey, feeding almost exclusively on land.

Breeding

Seventy-nine percent (19/24) of Washington amphibian species use streams, ponds, and temporary waters for mating, egg deposition, and larval development (Nussbaum et al. 1983). Maintaining the integrity of breeding sites is essential to the continued reproductive success of these species. Characteristics of suitable breeding sites are species specific and determined by a combination of life history traits, predation avoidance, and niche selection strategies. For example, tailed frogs show a strong tendency to return to natal streams during the breeding season (Metter 1964, Daugherty and Sheldon 1982). Red-legged frogs were observed using intermittent waters (Hayes and Jennings 1986) possibly to reduce the vulnerability of eggs and larvae to predators.

Aquatic egg masses are typically surrounded by gelatinous coats and attached to aquatic vegetation, or placed under logs, between rocks, or in crevices (Nussbaum et al. 1983). None of the Northwest anurans exhibits egg-guarding or parental-care behaviors (Nussbaum et al. 1983). Female Pacific and Cope's giant salamanders guard their eggs in aquatic nests until the eggs hatch (Nussbaum et al. 1983). Giant salamanders, torrent salamanders (*Rhyacotriton olympicus*), and tailed frogs deposit eggs in cracks and crevices found in and between submerged rocks and logs (Nussbaum et al. 1983). These nest sites disappear when silt and sedimentation in streams increase.

Recent declines in amphibian populations have been attributed to increased risks of predation from introduced fishes and aquatic habitat alteration (Hayes and Jennings 1986). Longer larval periods increase the chances of predation or habitat loss. In Washington, the length

of the larval period varies with species and region. Anuran larvae generally metamorphose in one season. Exceptions include tadpoles hatched late in the season or in cold, high altitude waters, e.g., bullfrog and tailed frog tadpoles (Brown 1990, Nussbaum et al. 1983, Metter 1967). This indicates a dependence on permanent water sources.

Lungless, terrestrial salamanders (family Plethodontidae) do not depend on aquatic breeding sites; they deposit eggs in moist, cool microsites. Nests have been found in rotting logs, rock crevices, talus slopes, soil cavities, and under bark or litter (Nussbaum et al. 1983, Jones 1989). Young emerge as fully-formed juveniles with no larval stage. The humid conditions associated with riparian areas provide a favorable microclimate for Plethodontids to breed if suitable nest structures are available.

Cover

In stream environments, aquatic amphibians frequently occur under cobble, rocks, boulders, and woody debris (Corn and Bury 1989). Davic and Orr (1987) found a significant positive association between stream salamander population density and the density of pebbles and cobbles. Streams with high silt loads do not provide high quality habitat (Jones 1986). This may be due to depressed aquatic insect populations as well as loss of cover and egg oviposition sites when crevices are filled with silt and sediment. Larval amphibians that develop in streams, including giant salamanders, torrent salamanders, and tailed frog tadpoles, hide under rocks and in gravel during the day where water temperature ranges from 8 - 15°C (Nussbaum et al. 1983).

The marsh edges, emergent vegetation, and muddy bottoms of pond environments provide cover for pond-breeding amphibians and their larvae. All Washington frogs of the genus *Rana* are frequently found at pond and marsh edges during hot, dry summers (Nussbaum et al. 1983). Some species seek escape cover on land and in the water. Licht (1986b) reported that spotted frogs escape by diving into water whereas red-legged frogs escape more frequently by land. Marsh edges and tall grass cover were strongly associated with northern leopard frog (*R. pipiens*) density (Beauregard and LeClair 1988).

Terrestrial anurans occur under vegetation, bark, and logs (Nussbaum et al. 1983). Terrestrial salamanders occur in talus and subterranean cavities, burrows, rotting logs, and under bark (Nussbaum et al. 1983). In a study of naturally regenerated Douglas-fir forests in western Oregon and Washington, Bury and Corn (1988b) and Bury et al. (1991a) found no significant difference in amphibian species richness or abundance related to forest age or old-growth forest moisture gradients. Presumably these forests contain similar structural characteristics (e.g., snags, downed wood, diversity of tree sizes and ages, multi-layered crown canopy) to account for similarities in amphibian abundance. Physiographic variables may be more important than vegetative features in determining amphibian abundance. Bury et al. (1991a) describe three variables associated with amphibian abundance: proximity to streams and ponds, presence of coarse woody debris, and occurrence of talus. Coarse woody debris and talus provide important cover sites for terrestrial salamanders.

Plethodontid salamanders require humid sites for cover. They are often found in moist logs, wet, dense litter, or under rocks of talus slopes where cutaneous respiration is possible (Nussbaum et al. 1983, Stebbins 1985). *Ensatina* and western redback salamander abundance was positively correlated with amounts of coarse woody debris in western Washington forests (Aubry et al. 1988, Aubry and Hall 1991). *Ensatina*s were found most often under pieces of bark; western redback salamanders were found primarily under logs. The Larch Mountain salamander is

restricted to the lava talus slopes of the Columbia River Gorge and retreats to great depths to escape extreme weather conditions (Herrington and Larsen 1985).

Winter cover sites are not well known but include floodplain soil, decaying wood and logs, live trees with heart rot or cavities, and snags (Ohmart and Anderson 1986). Northern leopard frogs overwinter under rubble, 13-40 cm in diameter, in streams with temperatures from 0.5-2.1°C, water depths >85 cm, and mean mid-depth water velocities of 22.5 cm/s (Cunjak 1986).

Riparian areas provide a cool, moist environment necessary for the survival of Pacific Northwest amphibians. They provide continuous sources of coarse woody debris. Trees and smaller vegetation hold soils in place, maintaining talus and subterranean burrows used by amphibians to escape severe weather conditions.

Effects of timber harvest

Two types of approaches are most frequently used to document effects of forest management on amphibians: 1) sampling is done on a variety of sites differing in successional stage; data are correlated between species abundance or richness and habitat characteristics including environmental and successional parameters; 2) sampling is done at similar sites before and after a specified forest management technique is applied. Both methods have advantages and disadvantages associated with them.

Sampling numerous sites of different successional stages carries inherent biases. Little information is available to describe the amphibian fauna prior to the event which initiated regeneration of the stand. Conclusions may be erroneous if they attribute a difference in the amphibian community solely to stand characteristics. These studies can suggest possible relationships but not prove them. Furthermore, site-specific parameters such as amounts of coarse woody debris present appear to have more influence on amphibian communities than broader habitat characteristics associated with successional stage (Irwin et al. 1989, Bury et al. 1991a). This type of approach is logistically simpler because modifications of treatment sites do not have to be considered.

True experiments which compare amphibian communities before and after a treatment are more difficult to realize. Logistical complications often arise when coordinating scientific methods and timetables with management of private and state lands. They can, however, offer the most conclusive information on the effects of forest management techniques on local fauna. Very few studies of this nature have been published in this region.

Clear-cutting

In general, amphibians are more numerous in forested stands than in clear-cuts (Raphael 1988). Raphael (1988) and Raphael and Barrett (1984) reported increased abundance of salamanders with increasing stand age. They suggest that greater volumes of coarse woody debris and greater litter depth found in older forests contribute to higher densities of salamanders. Retention of class 2 logs in northern California clear-cuts increased the likelihood of clouded salamander (*Aneides ferreus*) persistence (Raphael 1988). Aubry et al. (1988) found ensatina and western redback salamanders most often under pieces of bark and logs respectively in western Washington Douglas-fir stands 55 to 730 years old. The retention of coarse woody debris in managed forests could provide for the habitat needs of plethodontid salamanders.

In a narrow corridor along the Columbia River gorge, relict populations of the Larch Mountain salamander are found in talus slopes (Herrington and Larsen 1985). Clear-cutting to the

talus edge and removal of rock for road building results in severe erosion and alteration of soil properties. Such activity threatens Larch Mountain salamander populations. Current evidence suggests that the salamanders cannot remain for extended periods on exposed slopes (Herrington and Larsen 1985).

Many species are conspicuously absent from clear-cuts. Pacific giant salamanders were not found in 6-10 year old clear-cuts but were present in 50% of old growth redwood forest stands sampled in northern California (Bury 1983). In the Oregon Coast Range nine amphibian species were found in old-growth stands. Of these, only two, the northwestern salamander and the tailed frog, were not found in clear-cut sites paired with the old-growth stands (Corn and Bury 1991). Comparisons of abundance in naturally regenerated young and clear-cut stands in the Oregon Cascades showed Pacific chorus frogs to be nearly three times more abundant in clear-cuts (Bury and Corn 1988b). The tailed frog, ensatina, and roughskin newt were more than twice as abundant in young stands than in clear-cuts (Bury and Corn 1988b).

Riparian vegetation shades the stream or pond, regulating primary production as well as water temperature (Naiman et al. 1991). Shortly after clear-cutting, primary production increases followed by a rise in invertebrate populations (Newbold et al. 1980, Murphy et al. 1981, Hawkins et al. 1982). Pacific giant salamanders were more abundant in streams traversing recent clear-cuts than in densely forested stands (Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983). This may be explained by the higher numbers of invertebrate prey (Bury 1988).

A comparison of mean July temperatures of a second order stream in the Oregon Coast Range showed an increase in stream temperature from 14° to 22°C following clear-cutting (Brown and Krygier 1970). Beschta et al. (1987) suggest that an increase in sunlight as well as an increase in stream temperature lead to reductions in diatoms, a food of tailed frog larvae. Increased stream temperatures are believed to be detrimental to torrent salamander populations. These salamanders are generally found in streams with temperatures from 8° to 12°C (Nussbaum et al. 1983).

In managed forests where replanting occurs shortly after clear-cutting, shading levels along small streams can be restored to original levels quite soon. Five years after clear-cutting along a stream in the Oregon Coast Range shading reached 50% of prelogging levels and original shading levels were restored in ten years (Andrus and Froehlich 1988). After the initial productivity bloom, when shade is reestablished, invertebrate and vertebrate populations decline (Murphy et al. 1981, Hawkins et al. 1982, 1983).

Riparian vegetation inputs large amounts of organic debris in lower order streams, providing bank stability and a diversity of habitats, retaining coarse particulate organic matter, and controlling water flow (Keller and Swanson 1979, Bilby and Likens 1980, Naiman et al. 1991). Lower quality food resources and unstable stream habitats are associated with streams in logged forests as compared to unlogged forests (Sedell and Swanson 1984) due to a reduced input of large organic debris (Swanson and Lienkaemper 1978, Bryant 1985). The presence of large organic debris in small stream channels creates a stair-step profile. A pool forms behind the log where sediments, leaves, and other debris are trapped and decomposition and nutrient cycling processes can occur. On the downstream side a small riffle forms with fast-flowing water until another log blocks the channel. The heterogeneity of such a stream provides for a diversity of habitats, debris and sediment retention, and nutrient cycling beneficial to amphibian communities. Stream-dwelling larvae and adults are adapted to exploit such an environment while foraging, breeding, and finding cover. Clear-cutting to the stream or pond edge removes the source of

organic debris for the period of time it takes riparian vegetation to regenerate. Higher water temperatures, increased sediment loads, decreased bank stability, and loss of habitat diversity will negatively affect the habitat value for amphibians associated with streams and ponds.

Increases in fine streambed sedimentation have been documented at or below clear-cuts (Platts et al. 1989). Corn and Bury (1989) found a significantly greater number of streams in logged forests to have small size class substrate (silt, sand, and gravel) than streams in unlogged forests. As silt and fine sediment fill interstitial cracks and crevices between rocks important breeding sites and habitat for Pacific giant, Cope's, and torrent salamanders and tailed frogs are lost. Stream sediment and substrate size influence macroinvertebrate communities which are an important food source for amphibians. In a study of a woodland stream in North Carolina, Reice (1980) reported that substratum size was a prime determinant of the structure of stream macroinvertebrate communities. Prey abundance can determine whether amphibians are present or absent from a site.

Corn and Bury's (1989) survey of amphibian populations in headwater streams in logged and unlogged forests in the Oregon Coast Range revealed higher species richness, density, and biomass in unlogged forests. Density of Pacific giant salamanders was positively related to stream gradient in logged forests. Hall et al. (1978) also reported a decrease in Pacific giant salamander biomass in streams along clear-cuts with gradients less than 6%. Corn and Bury (1989) suggest that the swift-moving waters in higher gradient streams removes silt and sediment, leaving crevices and cavities between rocks unclogged and available for cover and nest sites. The torrent salamander was absent from all low-gradient logged streams, suggesting that local extinctions may result from logging. Several researchers have noted that the torrent salamander must maintain a low body temperature and may be eliminated or stressed by increased water temperatures (Nussbaum et al. 1983, Bury 1988, Corn and Bury 1989).

Corn and Bury (1989) found a positive relationship between the presence of uncut, upstream timber and abundance of aquatic tailed frogs and Dunn's salamanders in logged areas. This result was not statistically significant but does suggest that upstream forests may provide a source for eventual recolonization of disturbed areas. There was no indication, however, that amphibian populations improved as second-growth forests matured to 40-year-old stands.

The potential for recolonization of clear-cut areas from adjacent forest is highly species specific. Frogs and many adult salamanders are capable of moving several hundred meters (Nussbaum et al. 1983) and could recolonize a previously disturbed forest. Salamanders of the family Plethodontidae are believed to have limited home ranges (Ovaska 1988, Wilson and Larsen 1988) with extensive movement limited to nights when the soil is saturated (Wilson and Larsen 1988). Torrent salamanders are limited to natal streams due to the risk of desiccation they face when leaving a stream (Nussbaum et al. 1983). Tailed frogs occur in disjunct populations with very rare dispersal between them (Metter 1967, Daugherty and Sheldon 1982). Corn and Bury (1990) report seeing some juvenile and adult tailed frogs away from streams on rainy nights, suggesting that there may be limited dispersal of this species.

Selective cutting

Partial cutting and thinning harvest practices are employed more commonly east of the Cascade Crest. Information concerning the effects of this type of harvest on western Washington amphibian communities is not available. In central and eastern Washington forests, wildlife

biologists are beginning to examine the effects of partial cuts on amphibian communities. The information to date is only anecdotal.

Forest fragmentation

Rosenberg and Raphael (1986) reported on a study in northwestern California of amphibian responses to fragmentation in Douglas-fir forests at the plot, stand, and 1000-ha level. Amphibian species richness increased significantly in plots with more edge and in more fragmented stands. In 10-ha plots species richness decreased with increasing distance from clear-cuts and was proportional to the amount of clear-cut edge. At the 1000-ha level, species richness was positively correlated to the amount of edge. Responses of individual species varied. Results indicate that of the species found, (Pacific giant salamander, roughskin newt, ensatina, Del Norte salamander, western toad, and Pacific chorus frog) the Pacific giant salamander is primarily an interior forest species. The others were found in forested areas as small as 10-ha and did not appear to be negatively impacted by adjacent forest fragmentation. Distance to breeding sites may limit the abundance of amphibians in 10-ha plots. The Pacific giant salamander is the only species of the six found for which streams provide breeding habitat. Loss of or changes to this habitat can be detrimental. The roughskin newt, western toad, and Pacific chorus frog use ponds and slow-moving sections of streams for breeding habitat. As these are usually silt laden, logging impacts are less severe.

Successional stage of stand

In a survey of terrestrial amphibian communities in the southern Washington Cascade Range, no significant differences among stand age-classes (young, 55-75 years old; mature, 80-190 years old; old growth, 210-730 years old) of naturally regenerated Douglas-fir forest were found when comparing overall species richness (Aubry and Hall 1991). The results suggest, however, significant relationships between individual species' abundance and stand age. Similar terrestrial surveys in the Oregon Cascade and Coast Ranges did not find any amphibian species significantly associated with old-growth forests (Gilbert and Allwine 1991b, Corn and Bury 1991). Results describe amphibian population associations with different stage forest on unmanaged timber lands and may not be applicable to studies on managed forest lands.

Use of riparian buffer zones

To date little has been reported on the effects of riparian buffer zones on amphibians. Buffers have been shown to be effective at protecting stream and pond habitat and structures which are used by aquatic-breeding amphibians.

Buffer zones which were 30 m from each side of the stream provided substantial protection from logging practices by providing a continuous source of large organic debris (Murphy et al. 1986, Murphy and Koski 1989). Thirty meter buffer strips were also shown to be effective at protecting stream biota and habitat by maintaining shade (Beschta et al. 1987), reducing sedimentation (Moring 1982), and maintaining macroinvertebrate communities (Newbold et al. 1980). Steinblums et al. (1984) point out that poorly designed buffer strips are somewhat prone to failure by blowdown which may render them ineffective.

A recent study in eastern Texas tested the effects of stream buffer strip width on amphibian abundance (Rudolph and Dickson 1990). A significantly greater number of frogs was found in streamside zones 30 to 95-m wide than in narrower zones. Study sites were selected

from loblolly pine (*Pinus taeda*) plantations 2 to 4 years old. The authors described the wider riparian zones as having an intact overstory and midstory, sparse shrub and herbaceous vegetation and abundant leaf litter. The vegetation of narrower strips was more similar to that of the recently planted pine plantation adjacent to the streamside zone. Rudolph and Dickson attributed greater amphibian abundance to a closed canopy and abundant leaf litter ground cover. Frog abundance was significantly lower in the adjacent pine plantation than in riparian zones.

Stream and pond breeding amphibians are most sensitive to increases in water temperature and sedimentation levels. Timber harvest practices which remove trees along stream and pond banks appear to alter habitat and microclimate conditions, leaving these areas unsuitable to amphibians. Effective buffer strips have been shown to protect aquatic habitat and characteristics essential to amphibian survival. If forest managers are concerned about maintaining Washington state amphibian communities, effective riparian buffer strips must be provided.

REPTILES

The use of riparian zones and adjacent upland habitats by reptiles has not been extensively studied in the Pacific Northwest. It is difficult to detect species occurrence and relative abundance because many reptiles are only seasonally active, secretive, not evenly distributed, or specialized in their habitat use (e.g., fossorial, arboreal). Sampling techniques are generally biased in that they can detect the presence of only certain species. Despite these difficulties, reptiles should be included in monitoring studies for several reasons. First, they may compose a major proportion of vertebrates in certain ecosystems. Reptiles may predominate in some arid regions with numbers of individuals and species richness greater than resident birds and mammals (Bury and Raphael 1983). In California, riparian systems provide habitat for approximately 40% of the reptiles (Brode and Bury 1984). Second, they are ecologically important in the transfer of energy between trophic levels (Pough 1980). As ectotherms, a greater percentage of the food they ingest is converted to biomass than in endothermic animals because very little energy is used for thermoregulation.

Differences between the reptilian fauna west and east of the Cascade Crest are dramatic (Table 2). In western Washington, 75% (9 of 12) of all state snake species and less than 30% (2 of 7) of all state lizard species are represented. The cooler, moister forests of western Washington generally do not provide the structures which characterize optimum reptile habitat. Pacific Northwest reptiles are most commonly associated with open areas where woody debris provides basking sites for thermoregulation, cover from predators, and invertebrate habitat to assure adequate food resources. Vegetation along with coarse woody debris offers vertical structure important to some species of reptiles. Reptiles may be found in riparian systems which provide this type of structure.

The following discussion presents an overview of the literature describing reptile use of riparian zones and their responses to timber harvest. The first section, Use of Riparian Habitats, classifies Washington state species according to their relative dependence on riparian zones and details the nature of the dependence. The second section examines the impacts of timber harvest practices on riparian and upland species. The third section summarizes studies describing the influence of maintaining riparian management zones during timber harvest.

Table 2. Reptiles of Washington state and their affinities for riparian habitats during different life history stages. Habitat codes: 0 = upland, 1 = riparian, 2 = aquatic. Ranking of dependency on aquatic or riparian habitat: 0-3 = somewhat dependent, 4-7 = moderately dependent, 8+ = highly dependent. Information compiled from Nussbaum et al. (1983) and Bury (1988).

	Repro- duction	Adult feeding	Adult escape	Over- wintering	Preferred habitat	Rank Total	Important Forest Structures
Order Testudinata							
Painted turtle	2	2	2	2	2	10	ponds, marshes with logs, mud bottoms, aquatic vegetation
Western pond turtle	2	2	2	2	2	10	ponds, marshes, slow streams with LWD, mud bottoms, aquatic vegetation
Order Squamata							
Northern alligator lizard	0	0	0	0	0	0	dry leaves, grass, CWD, talus, humid, cool areas
Sagebrush lizard	0	0	0	0	0	0	open, brushy, understories of juniper, ponderosa, lodgepole pine
Short-horned lizard	0	0	0	0	0	0	loose soil, sand for burrowing
Side-blotched lizard	0	0	0	0	0	0	rocks, boulders, cliffs, sand
Southern alligator lizard	0	0	0	0	0	0	CWD, rock piles, thickets, shrubs, grasses
Western fence lizard	0	0	0	0	0	0	vertical comp: boulders, trees, fence rows, buildings, logs
Western skink	0	0	0	0	0	0	rotting logs, surface litter, rocks

Table 2. Continued. Habitat codes: 0 = upland, 1 = riparian, 2 = aquatic. Ranking of dependency on aquatic or riparian habitat: 0-3 = somewhat dependent, 4-7 = moderately dependent, 8+ = highly dependent.

	Repro- duction	Adult feeding	Adult escape	Over- wintering	Preferred habitat	Rank Total	Important Forest Structures
Western terrestrial garter snake	1	2	2	1	2	8	boulders in and along streams, marshes, damp meadows, ponds
Sharptail snake	1	1	1	1	1	5	moist, rotting logs; talus; moist habitats
Common garter snake	1	1	1	?	1	4	wet meadows, humid forests, litter
California mountain king snake	0	0	0	0	0	1	rotting logs, rocks
Gopher snake	0	0	0	0	0	0	talus, south-facing slopes, brush
Night snake	0	0	0	0	0	0	rocky outcrops
Northwestern garter snake	0	0	0	0	0	0	thickets, talus, brush
Racer	0	0	0	0	0	0	open areas: meadows, sagebrush flats, forest edge, fence rows
Ringneck snake	0	0	0	0	0	0	rocks, rotting logs, talus
Rubber boa	0	0	0	0	0	0	rotting stumps, logs, rocks, forest cuts
Striped whipsnake	0	0	0	0	0	0	rocks, sagebrush, burrows
Western rattlesnake	0	0	0	0	0	0	south-facing, rocky slopes

Use of riparian habitats

Relative dependency

Obligate inhabitants of riparian zones

The most aquatic reptiles in the Pacific Northwest belong to the family Emydidae. They are the western pond turtle (*Clemmys marmorata*), a State-listed threatened species, and the painted turtle (*Chrysemys picta*). These turtles are most frequently found in ponds or slow-moving streams with mud bottoms. The presence of large woody debris provides basking sites for thermoregulation. Western pond turtles have been observed in densities of 425 per ha. in California ponds and streams (Bury 1979). Trapping efforts by the Washington Department of Wildlife identified three western pond turtle populations in the Columbia Gorge and no populations in the Puget Sound area (Washington Department of Wildlife Fact Sheet, Milner 1986). Western pond turtles are found in western Washington while painted turtles are found throughout the state.

The western terrestrial garter snake (*Thamnophis elegans*) is largely aquatic in Washington. They are found near marshes or other waters both east and west of the Cascade Crest.

Habitat generalists that use riparian zones

Snakes which use riparian zones as well as upland habitat include the sharptail snake (*Contia tenuis*) and the common garter snake (*Thamnophis sirtalis*). The sharptail snake is generally found in moist habitats, under rotting logs or talus in western Washington. The common garter snake is most commonly found in wet meadows and humid forests, generally under moist litter throughout Washington. In arid regions, the riparian system may provide the most suitable habitat for both of these snakes.

Infrequent inhabitants of riparian zones

Most of the snakes and all of the lizards in Washington are more common in upland than in riparian areas. The rubber boa (*Charina bottae*), racer (*Coluber constrictor*), ringneck snake (*Diadophis punctatus*), California mountain kingsnake (*Lampropeltis zonata*), gopher snake (*Pituophis melanoleucus*), and northwestern garter snake (*Thamnophis ordinoides*) are found in open forests, along forest edges, meadows, and grasslands. The northwestern garter snake is the only one limited to western Washington. The night snake (*Hypsiglena torquata*), striped whipsnake (*Masticophis taeniatus*), and the western rattlesnake (*Crotalus viridis*) are found in arid regions east of the Cascade Crest though the western rattlesnake is sometimes found in woodland areas.

All of the Washington lizards are more common in upland or arid regions than in riparian zones. The northern alligator lizard (*Elgaria coerulea*) and the western fence lizard (*Sceloporus occidentalis*) are the only lizards found in western Washington. The northern alligator lizard may be found along forest edges, in cut-over areas, or around abandoned buildings. The western fence lizard is found in both desert and wooded areas but avoids dense, humid forests. The southern alligator lizard (*Elgaria multicarinata*), short-horned lizard (*Phrynosoma douglassi*), sagebrush lizard (*Sceloporus graciosus*), side-blotched lizard (*Uta stansburiana*), and western skink

(*Eumeces skiltonianus*) are found in a variety of habitats from forest edges to grasslands to desert regions.

In the arid parts of their range in California, the western skink, northern alligator lizard, and ringneck snake depend on riparian systems. They extend their range into arid regions along riparian corridors (Brode and Bury 1984).

Species requirements provided by riparian habitats

Foraging

The western pond and painted turtles forage in the water and alongside it. Both species are omnivorous and feed on plants and small aquatic animals (Nussbaum et al. 1983).

Moist ground litter provides feeding substrate for lizards which forage for insects and spiders (Ohmart and Anderson 1986). The northern and southern alligator lizards feed on arthropods and small vertebrates with the exception of amphibians. They are quite sensitive to the toxic skin secretions of many amphibians (Brodie et al. 1969). The diet of the western skink consists of small arthropods which are stalked in forests, open woodlands, and desert canyons (Tanner 1943).

The western terrestrial garter snake which is largely aquatic in western Washington feeds opportunistically on aquatic and terrestrial prey (Nussbaum et al. 1983). Common garter snakes are also opportunistic feeders. They prey on small mammals, birds, and occasionally other reptiles as well as aquatic vertebrates (Kephart and Arnold 1982). Most snakes, however, are terrestrial, feeding on terrestrial prey. Northwestern garter snakes feed on earthworms, small slugs and salamanders, and similar species associated with moist forest environments. Sharptail snakes feed exclusively on slugs found in moist forest environments (Nussbaum et al. 1983).

Many of the prey species which reptiles feed on can be found within riparian zones. Although most Washington state reptiles are infrequently found within riparian areas, these areas could become important when surrounding forests are harvested. In eastern Texas, numbers of skinks (*Scincella lateralis*) were greater in riparian zones than in adjacent pine plantations two to four years old (Rudolph and Dickson 1990).

Breeding

Washington reptiles, with a few exceptions, breed primarily in terrestrial environments. Western pond and painted turtles mate in ponds, marshes, or slow moving streams, and deposit eggs in nests dug in loose, sandy soils usually adjacent to ponds where mating occurred (Nussbaum et al. 1983). All reptiles which deposit eggs select oviposition sites in loose, sandy soil. Sites vary from sandy areas adjacent to water to arid sites (Nussbaum et al. 1983). In a comparison of reptile use of different habitats for breeding, Bury (1988) concluded that riparian habitats were two times more important than upland habitats. His rankings are based on observations made in the Oregon Coast Range where he found sharptail snakes, mountain kingsnakes, western terrestrial garter snakes, and western pond turtles are more likely to breed in riparian than in upland habitat. The importance of these riparian breeding areas may increase when adjacent forests are harvested.

Cover

According to Bury (1988), riparian habitats in the Oregon Coast Range are twice as important as upland areas in providing cover for reptiles and three times more important than aquatic habitats. Western pond turtles use water for escape cover (Bury 1988). Partially submerged rocks and logs provide basking sites for western pond and painted turtles (Nussbaum et al. 1983). Riparian vegetation provides large woody debris in streams and ponds which turtles use for cover.

Fallen logs and trees have been identified as important components of lizard habitat because they provide both cover and, when exposed to the sun, basking sites (Ohmart and Anderson 1986, Jones 1988). For example, the western skink (*Eumeces skiltonianus*) can often be found in rotting logs, under surface litter, or in moist soil under large, flat stones (Nussbaum et al. 1983). This species prefers moist cover areas. Western fence lizards are more common where there is a vertical component to the environment. Downed wood, trees, and snags provide this vertical component. The sagebrush lizard hides in rodent burrows, crevices, and under surface litter (Nussbaum et al. 1983).

Gravid western terrestrial garter snakes in northeastern California retreated under rocks of intermediate thickness presumably because of thermoregulatory potential (Huey et al. 1989). Sharptail snakes are most commonly found in moist, rotting logs, near streams or in other damp habitats. Periods of high surface activity coincide with the cool, wet portions of the growing season (Nussbaum et al. 1983). Coniferous forests provide habitat for some gopher snakes, although they are absent from dense forests (Nussbaum et al. 1983).

The diversity of structure within a riparian system can provide cover for many Washington reptiles. Those that are infrequent inhabitants of riparian areas when upland forests are present could find better foraging, cover, and breeding areas in riparian buffers after timber harvest. This idea is supported by Rudolph and Dickson's (1990) findings that the abundance of many lizards and snakes was greater within riparian zones than in adjacent pine plantations.

Effects of timber harvest

Clear-cutting

Clear-cuts and stands prior to canopy closure offer more of the structural components required by many reptiles. Coarse woody debris remaining after logging and increased temperatures appear to favor reptile abundance. Raphael (1988) reported that lizards were more abundant in clear-cuts and early-seral forests than older, mature forests. The northern alligator lizard is most common along margins of coniferous forests or under logs in cut-over areas (Nussbaum et al. 1983). During spring or early summer rains, the rubber boa is commonly found in rotting stumps or logs of clear-cuts in the coast mountains and foothills of western Oregon (Nussbaum et al. 1983).

Partial cuts

There is no literature on reptile responses to selective harvesting techniques in the Pacific Northwest. It is conceivable that reducing canopy closure through partial cuts would increase structures important to reptiles. More sunlight would enter and some downed wood would be dropped during the cutting process.

Forest fragmentation

Little information is available on the response of reptiles to timber harvest. Rosenberg and Raphael (1986) found no correlations between reptile diversity and any of the parameters measured (including stand area, insularity, and proximity to adjacent clear-cuts or pure hardwood patches) in patches of old-growth forest in northwestern California. Responses were examined at the plot, stand, and 1000-ha level. Among 10-ha plots, the distance to clear-cut stands was positively related to abundance of sagebrush lizards. At the stand level, Southern alligator lizards (*Elgaria multicarinata*) were negatively correlated with proximity to adjacent hardwood stands. Western fence lizards and sagebrush lizards were identified as species most sensitive to Douglas-fir forest fragmentation.

Successional stage of stand

Raphael and Barrett (1984) and Raphael (1988) found that reptiles tended to be less abundant in mature forests than in young stands less than 150 years old. Snakes were more abundant in older forested Douglas-fir stands in northern California than younger stands (Raphael 1988). Abundance of western skinks, sagebrush lizards and western fence lizards declined with increasing stand age (Raphael and Barrett 1984, Bury and Corn 1988).

Use of riparian buffer zones

Western pond turtles, aquatic garter snakes, and Western terrestrial garter snakes would probably decline and become locally extinct if aquatic, bank, and riparian zone habitats were eliminated. Bury (1988) suggests that northern alligator lizards, rubber boas, sharptail snakes, and mountain kingsnakes may be more numerous in riparian zones than in upland areas, but these species probably do not depend on riparian habitat for their survival.

In an eastern Texas study of reptile abundance in riparian buffer zones, Rudolph and Dickson (1990) reported a significantly greater number of lizards and snakes in buffer zones 30 to 95-m wide than in narrower zones. They also found significantly more lizards in adjacent pine plantations when 30 to 95-m buffer strips were present. The data indicate that reptiles will use both types of habitat but are more abundant after timber harvest when buffer strips of at least 30-m are present.

BIRDS

Most of the studies pertaining to avian use and composition within riparian habitats of the West have been performed in the arid regions of Arizona, New Mexico, Texas, and Colorado (Carothers et al. 1974, Stevens et al. 1977, Johnson et al. 1977, Anderson and Ohmart 1977, Szaro 1980, Knopf 1985). These riparian systems include well-defined vegetative zones within a much drier surrounding area. One must not assume that what occurs in these riparian environments will coincide with what is found in Pacific Northwest (PNW) riparian areas due to variation in climate and vegetation. In addition, ecological differences exist between the riparian zones of eastern and western Washington, and one would expect differences in avian dependency on and responses to change within riparian zones. Very few studies have been performed in the Pacific Northwest pertaining to avian responses within riparian ecosystems. Therefore, the information from studies performed in the southwestern states will be presented to provide the reader with an overview on the general importance of riparian areas to avian populations.

The significance of riparian zones to avian populations depends on the following: 1) climate conditions, 2) riparian and adjacent upland vegetation, 3) time of year, 4) individual bird species characteristics, and 5) stream size, 6) structure, 7) edge to area ratios, and 8) favorable microclimates. Riparian zones will be of greater importance to all bird species in xeric environments, where water is a limiting resource. Johnson et al. (1977) found that 77% of (127/166) species from southern Arizona, southern New Mexico, and west Texas were dependent on water related habitat and 51% (84/166) were completely dependent on aquatic habitat.

Bird densities in the southwest are often greater in riparian areas than adjacent nonriparian areas (e.g., Strong and Bock 1990, Johnson et al. 1977, and Szaro and Jakle 1985). In Arizona, Stevens et al. (1977) found the total number of migrant birds was up to 10.6 times greater in riparian habitats than in adjacent uplands. Szaro and Jakle (1985) found that bird density ranged from 336-446 birds/40 ha in riparian core and edge habitats and decreased with distance from the riparian zone to a low of between 101-137 birds/40 ha. In Iowa, Stauffer and Best (1980) found that the mean densities of breeding birds on larger (>4 ha) study plots increased from herbaceous habitats (153 ± 33 pairs/40 ha) to upland woodlands (339 ± 31 pairs /40 ha) to floodplain woodland (506 ± 46 pairs/40 ha). A similar trend was noted by Tramer (1969). Along a Sacramento river system, Hehnke and Stone (1978) found 95% fewer birds and 32% fewer species on agricultural lands from which adjacent riparian vegetation had been removed than on agricultural land in association with riparian habitat.

Several studies have found greater bird densities and avian species diversity or richness in riparian zones than in adjacent uplands; however this is not always the case and there is considerable overlap in species composition between riparian and upland sites. In the central Oregon Coast Range, McGarigal and McComb (1992) found species diversity, richness, and total bird abundance were greater along upslope transects. They found five species exhibited greater abundance along upslope transects than along streams: brown creeper, chestnut-backed chickadee, dark-eyed junco, golden-crowned kinglet, and Hammond's flycatcher. Two species were more abundant along streams than along upslope transects: winter wren and Swainson's thrush. However, four of the five bird species associated with upslope areas may have been responding to the distribution of snags and conifers. Anthony (1984) found avian communities within riparian zones to be similar to communities of the forested uplands along low order streams within Douglas-fir forests of Oregon. In northern Colorado, Knopf (1985) found that avian species richness was higher in riparian than adjacent upland sites (15-38 species/riparian vs. 4-19 species/upland). The number of species unique to riparian sites was generally lowest at coniferous sites. Conversely, at higher elevations (2747m), avian diversity was greater in upland than the riparian sites. Szaro (1980) found that although riparian areas had greater diversities and densities of breeding birds, some bird species frequented adjacent nonriparian areas for feeding; 41%-84% of riparian breeders were found to use adjacent upland. In Montana, Manuwal (1983) found that riparian strips included 200 pairs/40 ha more birds than the adjacent upland Douglas-fir (*Pseudotsuga menziesii*) forests.

The information that follows presents an overview of the studies performed on birds within riparian zones and specifically targets information regarding the requirements and responses of typical PNW species. This section is divided into three parts. The first part deals with avian use of riparian zones and distinguishes species that are more dependent on riparian habitats from more generalized species. The second section contains information on the responses of PNW

bird species to timber harvest and forest successional stage. The third part describes studies that address the response of bird populations to changes in the riparian buffer strip widths.

Use of riparian habitats

Relative dependency

Obligate inhabitants of riparian zones

Obligate inhabitants are species that depend on riparian zones for breeding, feeding, nesting, or roosting. These species can, however, be found in other habitats during certain times of the day or year. Birds of the northwest that are obligate inhabitants of wetlands include great blue heron (*Ardea herodias*), American bittern (*Botaurus lentiginosus*), common snipe (*Gallinago gallinago*), belted kingfisher (*Ceryle alcyon*), spotted sandpiper (*Actitis macularia*), willow flycatcher (*Empidonax traillii*), American dipper (*Cinclus mexicanus*), veery (*Catharus fuscescens*), gray catbird (*Dumetella carolinensis*), yellow warbler (*Dendroica petechia*), common yellowthroat (*Geothlypis trichas*), yellow-breasted chat (*Icteria virens*), fox sparrow (*Passerella iliaca*), song sparrow (*Melospiza melodia*), Lincoln's sparrow (*Melospiza lincolni*), and northern oriole (*Icterus galbula*) (Knopf in press). Among these, willow flycatcher, veery, gray catbird, yellow warbler, common yellowthroat, fox sparrow, song sparrow, Lincoln's sparrow and northern oriole are considered as obligate riparian species primarily during the breeding season. The great blue heron, American bittern, common snipe, and belted kingfisher are not restricted to streamside riparian areas, but can be found in a variety of wetlands in general. Within riparian areas, they are most often associated with larger streams. Wood ducks (*Aix sponsa*), harlequin ducks (*Histrionicus histrionicus*), common goldeneyes (*Bucephala clangula*), Barrow's goldeneyes (*B. islandica*), bufflehead (*B. albeola*), and common (*Mergus merganser*) and hooded (*Lophodytes cucullatus*) mergansers (Irwin et al. 1989, Lowney and Hill 1989) are dependent on riparian zones and can be found nesting in forests associated with streams and rivers, as well as, marshes, ponds, and lakes.

Habitat generalists that use riparian zones

Many species of birds occur in both upland and riparian habitats. This group includes the hairy woodpecker (*Picoides villosus*), downy woodpecker (*Picoides pubescens*), *Empidonax* flycatchers, western wood-pewee (*Contopus sordidulus*), black-capped chickadee (*Parus atricapillus*), brown creeper (*Certhia americana*), white-breasted nuthatch (*Sitta carolinensis*), western bluebird (*Sialia mexicana*), Bewick's wren (*Thryomanes bewickii*), hermit thrush (*Catharus guttatus*), Swainson's thrush (*Catharus ustulatus*), solitary vireo (*Vireo solitarius*), warbling vireo (*Vireo gilvus*), red-eyed vireo (*Vireo olivaceus*), yellow-rumped warbler (*Dendroica coronata*), black-throated gray warbler (*Dendroica nigrescens*), MacGillivray's warbler (*Oporornis tolmiei*), Wilson's warbler (*Wilsonia pusilla*), black-headed grosbeak (*Pheucticus melanocephalus*), and rufous-sided towhee (*Pipilo erythrophthalmus*) (Stevens et al. 1977, Stauffer and Best 1980, Meents et al. 1981, Morrison and Meslow 1983). In fact, there are regional variations in response to riparian zones. For example, Swainson's thrush in western Washington is not restricted to riparian areas, although it is most common there. In western Oregon (McGarigal and McComb 1992) and parts of western Montana (Manuwal 1986), this

species is more closely associated with riparian areas. This may simply be a factor of dense shrub cover being present.

Some generalist species tend to use riparian zones more than adjacent uplands during the breeding season. The increased complexity of riparian vegetation, vertical layering and canopy cover, provides abundant niches for nesting and available food for young. Manuwal (1986) found that breeding territories of males of the following species restricted to riparian zones in spring: winter wren (*Troglodytes troglodytes*), MacGillivray's warbler, and American redstart (*Setophaga ruticilla*). Those that extended outside the riparian area (which included both riparian vegetation and upland coniferous vegetation) included: Hammond's flycatcher (*Empidonax hammondi*), black-capped chickadee, Swainson's thrush, orange-crowned warbler (*Vermivora celata*), and yellow-rumped warbler. The winter wren, Swainson's thrush, hermit thrush, varied thrush (*Ixoreus naevius*), and rufous-sided towhee require sufficient ground cover (vegetation and coarse woody debris), typical of PNW riparian areas, for nesting and breeding.

Chipping (*Spizella passerina*) and white-crowned sparrows (*Zonotricha leucophrys*) are attracted to riparian areas if the canopy is open enough to accommodate large flocks (Stevens et al. 1977). The lazuli bunting (*Passerina amoena*) and American robin (*Turdus migratorius*) prefer open riparian habitat to dense, riparian areas (Stevens et al. 1977). Song sparrows and swallows are more numerous in grassy openings of riparian zones as opposed to forested riparian areas.

Some birds tend to avoid riparian areas if the vegetation becomes very dense and are more likely to be found in uplands. These include the dark-eyed (Oregon) junco (*Junco hyemalis*), Townsend's solitaire (*Myadestes townsendi*), American robin, rufous-sided towhee, lazuli bunting (*Passerina amoena*); chipping and white-crowned sparrows, purple finch (*Carpodacus purpureus*), and pine siskin (*Carduelis pinus*) (Stevens et al. 1977). Many of these species are granivorous. Granivorous species are not dependent on riparian zones for feeding but may use riparian vegetation for cover (Strong and Bock 1990).

Species requirements provided by riparian habitats

The most important characteristics of riparian environments for birds seem to be structural features, such as sites for feeding, breeding, nesting, roosting, and perching. Foods and characteristics of breeding habitat used by riparian inhabitants are summarized in Table 3.

Food

During the breeding season, virtually all songbirds are insectivorous and obtain food from the ground, on vegetation, or in the air. More aquatically oriented birds obtain food in or near the water. Food sources exploited by birds in riparian environments include aquatic plants, aquatic invertebrates (insect larvae, mollusks, crustaceans), vertebrates (amphibians, fish), and flying insects. Dispersion of breeding common merganser pairs is dependent on the availability of juvenile Pacific salmon (*Oncorhynchus* spp.) in streams (Wood 1986). Similarly, the number and distribution of raptors within riparian zones depends on the availability of food, including salmon, waterfowl, and carrion (White and Cade 1971, Olendorff 1973, Knight et al. 1982). Raptors feeding primarily in riparian habitat include osprey (*Pandion haliaetus*), bald eagle (*Haliaeetus leucocephalus*) (Frenzel and Anthony 1989), and northern harrier (*Circus cyaneus*). Other raptors may be common in riparian areas simply because these areas attract large numbers of suitable prey. Such raptors include: sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*A. cooperii*),

red-tailed hawk (*B. jamaicensis*), barn owl (*Tyto alba*), western screech-owl (*Otus kennicottii*), barred owl (*Strix varia*), and long-eared owl (*Asio otus*) (Knight 1988).

In Arizona, Strong and Bock (1990) found that avian densities increased in riparian areas in summer due to the increase in food abundance there. The lush vegetation of riparian zones provided greater resources for insectivorous birds than either surrounding grasslands or oak-forests. Insectivorous species, such as flycatchers, swallows (Ehrlich et al. 1988), vireos, warblers, thrushes, and tanagers, benefit from abundant insects found over or near water (Stevens et al. 1977). These species use dense riparian habitats proportionally more than adjacent upland habitats due to the higher insect availability there.

Structural features of habitat

Helle (1985b) argued that the narrow habitat breadths of riparian obligates are most likely the consequence of special habitat requirements rather than interspecific competition. Bull and Skovlin (1982) attributed greater species richness and diversity within riparian habitats to greater structural diversity of the vegetative community and thus the availability of more niches. Strong and Bock (1990) concluded that sparsely forested riparian zones adjacent to upland grasslands have higher local breeding densities of birds due to the presence of trees as focal points for nesting and foraging activities.

Wood ducks, goldeneyes, bufflehead, and mergansers depend on riparian zones or adjacent forest for cavity nests (Irwin et al. 1989, Lowney and Hill 1989). Nests are typically found in deciduous trees of the riparian zone. Virtually all bufflehead nests are located within 650 ft (198 m) of water (Erskine 1972). Raptors also depend on riparian trees for perch sites (White and Cade 1971, Olendorff 1973, Knight et al. 1982).

Many birds use riparian habitats because of the deciduous vegetation found there. The high foliage density associated with deciduous trees protects nests from predation. Martin (1988) found that the number of nests increased with foliage density at nest height due to the corresponding decrease in predation risk. Stauffer and Best (1980) predicted the following species would be dependent on the deciduous component of riparian vegetation for breeding and nesting: hairy woodpecker, downy woodpecker, black-capped chickadee, white-breasted nuthatch, red-eyed vireo, warbling vireo, yellow warbler, rufous-sided towhee, and northern oriole. The willow flycatcher and veery are also typical of riparian zones with substantial amounts of deciduous vegetation (Manuwal 1986). Wilson's warbler, Swainson's thrush, and black-headed grosbeak nests are associated with dense alder stands (Morrison and Meslow 1983). Verner and Larson (1989) classified the following as obligate shrub (but not necessarily riparian) nesters: yellow and MacGillivray's warblers, rufous-sided towhee and fox sparrow.

The density of birds using deciduous vegetation depends on the composition of deciduous species present. Carothers et al. (1974) found up to 847 pairs/40 ha breeding in riparian cottonwood (*Populus* spp.), whereas only 332 pairs/40 ha were bred in mixed broadleaf riparian habitat. Heterogeneous deciduous vegetation offers the greatest variety of niches for migrants and has been shown to be most heavily used by migrating birds for nesting and breeding (Stevens et al. 1977).

Migrant passerine use of riparian habitats is influenced by habitat preferences, plant species composition and diversity, accessibility, and quality of adjacent habitat (Stevens et al. 1977). It is likely that summer habitat specialists select vegetation primarily on the basis of nesting requirements and the availability of food for young. Wintering birds are more likely to be limited

by food resources, and their habitat selection probably reflects food availability (Meents et al. 1981). Anthony (1984) found densities of hairy woodpeckers, chestnut-backed chickadees (*Parus rufescens*), winter wrens, golden-crowned kinglets (*Regulus satrapa*), and evening grosbeaks (*Coccothraustes vespertinus*) in riparian areas were higher in winter than in summer.

Effects of timber harvest

The effects of timber harvest on birds are varied and depend upon species characteristics; type, intensity, and timing of harvest; pre-harvest vegetation; and successional stage remaining after treatment.

Clear-cutting

A number of bird species are attracted to clearcuts for foraging and nesting. Granivorous birds are probably attracted to cleared areas because of the annual plants and scattered shrubs that develop (Anderson and Ohmart 1984). Rufous hummingbirds (*Selasphorus rufus*), willow flycatchers, Swainson's thrushes, rufous-sided towhees, white-crowned and song sparrows; orange-crowned, MacGillivray's, and Wilson's warblers are common in clear-cut or young stands (Buckner et al. 1975, Morrison and Meslow 1983). In addition, dark-eyed (Oregon) juncos, Bewick's wrens (*Thryomanes bewickii*), American robins, black-headed grosbeaks, and American goldfinches (*Carduelis tristis*) are regular inhabitants but uncommon nesters in clear-cuts (Morrison and Meslow 1983).

Cleared areas attract birds that typically occur in open areas, such as loggerhead shrikes (*Lanius ludovicianus*) (Anderson and Ohmart 1984), which typically nest in shrubs or small deciduous trees (Ehrlich et al. 1988). Sharp-shinned, Cooper's, and red-tailed hawks commonly forage over clear-cuts (Morrison and Meslow 1983). Logging may increase habitat heterogeneity and foster population growth in prey species (Hagar 1960).

The increase in the amount of edge habitat available after clear-cutting is beneficial to many birds. For example, some species occur in greater densities in forest edges adjacent to clear-cuts than in forest interiors. At the same time, a number of species are sensitive to edge, including: Pacific-slope flycatcher, Hammond's flycatcher, and hermit and Townsend's warblers. Some birds nest in old growth stands and forage in adjacent logged areas (McClelland 1980). Species that are occasionally sighted in clear-cuts but usually nest in surrounding edge habitats include western wood-pewee, rough-winged swallow (*Stelgidopteryx serripennis*), common bushtit (*Psaltriparus minimus*), winter wren, Townsend's solitaire, warbling and Hutton's (*Vireo huttoni*) vireos, black-throated gray warbler, chipping sparrow, Brewer's blackbird (*Euphagus cyanocephalus*), brown-headed cowbird (*Molothrus ater*), and western tanager (*Piranga ludoviciana*) (Morrison and Meslow 1983).

Edge trees harbor a richer insect fauna than those in deep forest and thus can support a greater abundance of insectivorous species (Ranney et al. 1981). In addition, Ranney et al. (1981) found higher primary productivity in edge belts than in interior forest habitats. Nevertheless, there are no studies in the Pacific Northwest that document bird response to edge microhabitats.

Well supervised clear-cutting programs that leave dead snags and some standing live trees and do not disc or burn slash increase avian abundance and species diversity over the entire area being managed (Conner and Adkisson 1975). Ruffed grouse (*Bonasa umbellus*) are common in deciduous, second growth habitat (Aldrich 1963). Olive-sided flycatchers (*Contopus borealis*), black-headed grosbeaks, and western tanagers benefit from logging, due to increases in numbers

of insects and berries (Hagar 1960). In northern California and Virginia, bird abundance declined after clear-cutting but increased above that of the original forest by 3-7 yrs following harvest (Hagar 1960, Conner and Adkisson 1975), however, Meslow and Wight (1975) found decreased avian diversity in mid-successional stages related to a reduction in both the complexity and layering of vegetation.

Along the lower Colorado River, Anderson and Ohmart (1984) found that birds recolonize sites revegetated with native vegetation rapidly, reaching average or above-average densities and diversities in less than 2 yr. Understory-gleaning insectivores, foliage-gleaning omnivores, and foliage-gleaning insectivores were more abundant in young (42-75 yr) stands than old-growth (250-500 yr) (Manuwal and Huff 1987). However, Hammond's flycatchers, hermit warblers (*Dendroica occidentalis*), and western wood-pewees do not invade recently logged areas in California (Hagar 1960). Winter wrens are common in the weed/brush stage that follows logging (Hagar 1960, Peterson and Peterson 1983).

Changes in avian populations occur as a forest progresses from clear-cut to old-growth. Bird species richness was lowest in clear-cut sites and increased with development of shrub and tree layers, peaking in mature stands with crown cover ranging from 45-55% (Verner 1980). The most important features of forests to birds include large dominant trees, mixed tree species composition, multi-layered canopy, irregular crown structure, patches of dense foliage, large standing dead wood, and abundant woody debris on the forest floor (Manuwal and Huff 1987). These characteristics are typical of late successional forests. The large leaf surface area associated with late successional deciduous forests may result in an increase in insect abundance and consequently in insectivorous birds (Grier and Logan 1977, Manuwal 1983). As the canopy develops, species that forage and nest in canopies (e.g., finches, kinglets, and jays) appear (Manuwal and Huff 1987). In addition, increased vegetative cover around the nest in mature forests and an increase in branches for nest support contribute to nesting success in flycatchers (Murphy 1983).

As a forest approaches climax, the biomass of birds supported increases (Salt 1953, Manuwal and Huff 1987). For example, Vaux's swifts (*Chaetura vauxi*), western flycatchers, chickadees, brown creepers, winter wrens, and varied thrushes are more abundant in old-growth than in young or mature stands (Ramsden et al. 1979, Scoullar 1980, Mannan 1982, Anthony 1984, Manuwal and Huff 1987, Manuwal 1991). In terms of breeding guild response, birds in the bark-drilling insectivore, bark-gleaning insectivore, aerial sallying insectivore, and aerial flying insectivore guilds are more common in old growth than younger forest age classes (Manuwal and Huff 1987).

The availability of snags and large-diameter, old trees with loose bark for bird nesting and arthropod microhabitat probably contributes to the high densities of these species in late successional stages (Thomas 1979, Verner 1980, Mannan 1982, Anthony 1984, Zarnowitz and Manuwal 1985, Lundquist and Manuwal 1990, Mariani and Manuwal 1990). In addition, the large amounts of standing and forest floor woody debris common in moist stands might contribute to high densities of wrens and chickadees. Coarse woody debris provides cover for winter wrens and food for chickadees. Abundant snags, logs, and canopy openings from tree-fall gaps in mature and old-growth forests might also make them more conducive to flycatcher foraging (Manuwal 1991). Increased sun exposure due to gaps in the canopy in old-growth forests causes conifers to produce more cones and hence attract more seed eaters (e.g., finches), particularly in winter (Manuwal and Huff 1987).

In the southern Washington Cascade Range, Manuwal and Huff (1987) found that bird abundance increased with stand age in winter but not in spring. In winter, 3 times more birds were in old-growth than in young stands; winter inhabitants included the: gray jay (*Perisoreus canadensis*), red-breasted nuthatch (*Sitta canadensis*), brown creeper, and red crossbill (*Loxia curvirostris*). Old-growth (250-500 yrs) apparently offers more resources to the birds in winter than young (42-75 yrs) or mature (105-165 yrs) stands. This seasonal abundance pattern may be due to differences in forest structure, tree species composition, foraging and roosting sites, and cone crops.

Selective cutting

Many bird species increase in abundance with thinning or selective cutting, however, there is a great deal of regional and site-specific variation in the response of birds. Thinned 85-year-old managed stands supported more breeding dusky flycatchers (*Empidonax oberholseri*), ruby-crowned kinglets, and chipping sparrows than old growth (Mannan and Meslow 1984). In Arizona, higher breeding densities of non-cavity nesting, foliage-gleaning insectivores occurred in thinned than in uncut stands (Brawn and Balda 1988).

Franzreb (1978) studied the importance to birds of foliage for protection from predators, inclement weather, and shelter sites. Brown creepers were eliminated from a partially cut stand. Mountain chickadees (*Parus gambeli*) were reduced in the partially cut stand, due to the reduction of foliage. Juncos increased in abundance in the logged areas, due to additional substrates provided by coarse woody debris remaining after logging.

Forest fragmentation

The number of birds remaining within a forest fragment may be dependent on territory size. Bird species most sensitive to habitat fragmentation have large territories. In general, smaller birds have smaller territories and can survive in smaller fragments (Helle 1985a). If timber practices result in smaller fragments, many large territorial species will be lost. Species which appear sensitive to fragmentation include spotted owl (*Strix occidentalis*) and pileated woodpecker (*Dryocopus pileatus*) (Rosenberg and Raphael 1986). Other species likely to be reduced by forest fragmentation include: 1) long distance migrants that winter primarily in the New World tropics, 2) obligate inhabitants of forest interior; 3) ground nesters, 4) builders of exposed nests, 5) species that lay small clutches or raise only a single brood per year (Robbins 1980, Anderson and Robbins 1981, Temple and Cary 1988). These studies were conducted in eastern deciduous forest. Similar studies have not been done in the Pacific Northwest. In California, avian species richness increased significantly in fragmented stands due to increased edges (Rosenberg and Raphael 1986). The edge effect was largest in the tree-gleaning species. Ground-feeding, forest thrushes showed no pronounced change in numbers in relation to forest edge (Hansson 1983).

In severely fragmented habitats, virtually all the remaining habitat may be so close to edges that virtually no habitat interior remains. This would have a negative impact on forest interior species. In a Maryland forest, 9 species of long distance migrants disappeared from the breeding populations of a study area reduced from 5,260 ha over time to a present level of 40 ha (Anderson and Robbins 1981).

With fragmentation and reduction of forest unit size, nests of ground-nesters are exposed to potential predation (Wilcove 1985). In Sweden, bird abundance decreased in clear-cut areas

except for species of open habitats (Hansson 1983). This might have been due to ambush predation from forest jays (*Cyanocitta* spp.) or interspecific competition from forest species exploiting clear-cuts close to the forest edge (Hansson 1983). By nesting in forest interiors, taxa such as *Empidonax* reduce nest mortality from predation (Murphy 1983).

Forest fragmentation increases the risk of nest parasitism for some birds. Cowbirds are obligate nest parasites whose distribution depends on host species' availability and distribution of habitat. Gates and Griffen (1991) found brown-headed cowbirds were 4 times more abundant at streams edge than in interior forest. The role of the brown-headed cowbird in reducing populations of riparian birds in the Sacramento Valley, California, is discussed by Gaines (1974b). Cowbird parasitism could lead to a decline in songbirds such as yellow warbler, warbling vireo, willow flycatcher, red-eyed vireo, song sparrow, and Swainson's thrush (Brittingham and Temple 1983). The increase in brown-headed cowbird numbers due to the expansion of agriculture into the Colorado River valley has led to increased parasitism and declining numbers of Bell's vireos (*Vireo bellii*) (Meents et al. 1981).

The combined effects of forest fragmentation and simplification of forest structure through even-aged management in northwest forests will probably lead to declines in 1) cavity-nesting birds (woodpeckers, nuthatches, chickadees, brown creeper, and small owls), 2) species closely associated with complex structure on the forest floor (winter wren, thrushes), and 3) species that utilize mid-story canopy layers (warblers and chickadees) (Manuwal 1991).

Elimination of snags

Intensive timber management with shortened rotations eliminates snags (Meslow and Wight 1975). Species richness, abundance, and diversity are greater in plots with snags than in plots without snags (Dickson et al. 1983). Several authors recommend a minimum of 5-6 snags/ha to maintain nesting populations of most primary and secondary cavity nesters (Morrison and Meslow 1983). The decline in availability of snags contributes to a loss of structural heterogeneity and snags provide important perching and roosting sites as well as cavities for hole-nesting species.

Snags are used by many species. Eagles prefer snags as perching and roosting sites; however, communal bald eagle roosts have been clear-cut along the north fork of the Nooksack River in western Washington (Knight 1988). Tall snags near water are ideal nesting sites for osprey, permitting an unrestricted view of the surrounding area (Miller and Miller 1980). In the eastern U.S., Carolina wrens (*Thryothorus ludovicianus*), yellow-breasted chats, and brown-headed cowbirds perch on snags and increase in clear-cuts that retain snags (Dickson et al. 1983). Western wood-pewees, Hammond's and olive-sided flycatchers, and Townsend's solitaires select dead trees or bare branches instead of foliated ones for perching (Miller and Miller 1980). This may be because branches without foliage provide better visibility for foraging and hawking. Cowbirds use the snags as perches from which they may locate nests of other birds.

Cavities in snags provide protection from predators, precipitation, wind, and extreme temperature fluctuations (Miller and Miller 1980). Birds that use cavity nests are vulnerable to predation, parasites, and disease (Miller and Miller 1980). Densities of hole-nesting bird are positively correlated with mean diameter at breast (DBH) height of snags (Mannan et al. 1980, Zarnowitz and Manuwal 1985). Cavity nesters such as purple martins (*Progne subis*) and other hole-nesting swallows, downy and hairy woodpeckers, northern flickers (*Colaptes auratus*), and chestnut-backed chickadees decline in clear-cuts lacking snags (Dickson et al. 1983, Morrison and

Meslow 1983). Pileated woodpeckers require large (> 58 cm DBH), tall (> 12 m) snags for nesting (Meslow and Wight 1975).

Use of riparian buffer strips

The destruction of vegetation stands along river drainage systems could result in significant losses of avian species. Even where riparian buffer strips are left, pronounced declines in abundance and diversity might occur. For example, Beidleman (1978) reported a fourfold decrease in spring species, a threefold decrease in wintering species, a 50-65% decrease in mourning dove (*Zenaida macroura*), black-billed magpie (*Pica pica*), and house wren (*Troglodytes aedon*) abundance, and the elimination of dark-eyed juncos and black-capped chickadees in a riparian buffer dominated by cottonwood and willow (*Salix* spp.) in eastern Colorado. Klebenow and Oakleaf (1981) reported that avian species richness and abundance in the riparian zone of the Truckee River, Nevada declined between 1868 (Ridgeway 1877) and the present as a result of agriculture, grazing, and flood control efforts.

The width of riparian buffer strips affects their use by birds. Avian species richness increases with the width of wooded riparian habitats (Stauffer and Best 1980). Manuwal (1986) found that a 50% increase in the size of a riparian zone was accompanied by a 58% increase in use. Yellow-billed cuckoos (*Coccyzus americanus*) prefer to breed in thick riparian growth occurring in stands at least 300 m × 100 m (Gaines 1974a).

Clearing of riparian areas has left islands of riparian habitat. The size and diversity of the remaining bird population depends on patch size. For example, in cottonwood (*Populus sargentii*) stands along the Verde River, Arizona, breeding bird densities ranged from 425-847 pairs/40 ha and included 20-26 breeding species (Carothers et al. 1974), while a similar but smaller riparian patch of 1.6 ha supported only 10 breeding species, with a total density of 198 pairs/40 ha (Stevens et al. 1977).

The importance of buffer strips to avian communities in the western Washington Cascades has not yet been investigated. The appropriate size and vegetative composition of the riparian zone prescribed to maintain current avian population structures will vary from the east side to the west side of Washington State due to climate, vegetational differences, silvicultural treatments, and individual avian species characteristics. Some important considerations for the remaining buffer strips should include amount of canopy cover and forest floor material, and number of snags.

Table 3. Bird species whose feeding, nesting, or breeding habitat requirements can be met within riparian zones in Washington state. Obligate inhabitants of riparian zones are shown in bold type; all other species listed are habitat generalists that use riparian zones. (Where not stated, source of information is Ehrlich et al. 1988). AqIn = aquatic invertebrates, AqVeg = aquatic vegetation, DecShr = deciduous shrubs, DeTr = deciduous trees, SmVert = small vertebrates, EmVeg = emergent vegetation, WillTh = willow thickets.

Species	Food	Breeding Habitat	Nest site
American Bittern		EmVeg	
Great Blue Heron	Fish, AqIn, SmVert		
Wood Duck	AqIn	Wooded swamp, flooded forest, pond, marsh	DeTr cavity
Harlequin Duck	AqIn	Mountain stream, fast flowing water	Shrubs < 60-90'
Common Golden-eye	AqIn, fish, crayfish, AqVeg	Wooded marshy habitat, pond, lake, river	DeTr cavity
Barrow's Golden-eye	AqIn, fish, crayfish, AqVeg	Densely vegetated lake and pond	DeTr cavity
Bufflehead	AqIn, AqVeg	Densely vegetated lake and pond	DeTr cavity
Hooded Merganser	Fish, AqIn, SmVert	Forested habitat near water	DeTr cavity
Common Merganser	Fish, AqIn, SmVert	Lake/river in mountainous and forested area	DeTr cavity
Common Snipe	High water consumption		
Belted Kingfisher	Fish, AqIn, Amphibians	Near water	Bank
Willow Flycatcher		Swamp, WillTh	DecShr 2'-10'
American Dipper	AqIn, Fish	Swift mountain stream	Cliff face behind waterfall on midstream rock
Veery		Shaded moist woodland	
Gray Catbird		Dense brush bordering swamp	
Yellow Warbler		WillTh	Shrub
Common Yellowthroat		Freshwater and salt marsh	
Yellow-breasted Chat		Dense brush or scrub stream, swamp margin	Dense shrub tangle (Lindsdale 1938)
Fox Sparrow		Riparian woodland	
Song Sparrow		Dense vegetation along watercourse, coast, and marsh	
Lincoln's Sparrow		Bog, wet meadow, riparian thicket	
Northern Oriole		Riparian woodland, forest edge	

Table 3. Continued. AqIn = aquatic invertebrates, AqVeg = aquatic vegetation, DecShr = deciduous shrubs, DeTr = deciduous trees, SmVert = small vertebrates, EmVeg = emergent vegetation, WillTh = willow thickets.

Species	Food	Breeding Habitat	Nest site
Red-winged Blackbird		Marshes and riparian habitat	Emergent vegetation
Osprey	Fish, SmVert	River, lake, coast	Dead or live deciduous or coniferous trees near water
Bald Eagle	Fish, waterfowl, small mammals	Coast, river, lake	Fork of tall tree
Northern Harrier	Animals associated with wet meadows (Klebenow and Oakleaf 1981)		Wet meadow vegetation (Klebenow and Oakleaf 1981)
Sharp-shinned Hawk	Birds, small mammals, frogs, and lizards		
Cooper's Hawk	Few reptiles/amphibians	Decid forest woodland, esp. riparian	
Red-shouldered Hawk	Rodents, snakes, lizards	Riparian forest, swamp	
Red-tailed Hawk	Rodents, amphibians, crayfish, fish		
Barn Owl	Rodents, amphibians, reptiles, insects		
Western screech owl	Arthropods, amphibians, reptiles, fish	Riparian/oak woodland, scrub, orchard, woodlot	
Barred Owl	Rodents, crayfish, amphibians	Coniferous, coniferous-deciduous forest, wooded swamp, river valley	
Long-eared Owl	Rodents, amphibians, reptiles, fish, insects	Coniferous, coniferous-deciduous forest, esp. near water	
Downy Woodpecker		Deciduous and mixed decid-coniferous woodland, riparian woodland, park and orchard	
Hairy Woodpecker		Deciduous and coniferous forest, wooded swamp, orchard, woodland habitat	

Table 3. Continued. AqIn = aquatic invertebrates, AqVeg = aquatic vegetation, DecShr = deciduous shrubs, DeTr = deciduous trees, SmVert = small vertebrates, EmVeg = emergent vegetation, WillTh = willow thickets.

Species	Food	Breeding Habitat	Nest site
Western Wood-pewee		Coniferous-deciduous forest, forest edge, riparian woodland	
Dusky Flycatcher		Open coniferous forest, aspen grove, WillTh	
Western Flycatcher		Deciduous and coniferous forest and woodlands, esp. near water	
Purple Martin		Open country, savanna, rural area, esp. near water	
Tree Swallow		Open country, woodland edge near water	
Violet-green Swallow	Insects		
Northern Rough-winged Swallow	Insects	Open country, savanna, rural areas, esp. near water	
Cliff Swallow	Insects	Open country, savanna, rural areas, esp. near water	
Barn Swallow		Open country, savanna, rural areas, esp. near water	
Bank Swallow		Open country near running water	
Black-capped Chickadee		Deciduous or mixed decid-coniferous woodland, riparian woodland, or thicket habitat	DeTr cavity
Chestnut-backed Chickadee	Spiders, seeds	Humid forest regions	
Brown Creeper		Cottonwood/willow communities (Meents et al. 1981)	
White-breasted Nuthatch		Deciduous forest, woodland, and forest edge habitat	
Bewick's Wren		Open woodland and shrubland	
Winter Wren	Spiders	Near water in dense coniferous forest	
Western Bluebird		Open, riparian, burned or cutover woodland	

Table 3. Continued. AqIn = aquatic invertebrates, AqVeg = aquatic vegetation, DecShr = deciduous shrubs, DeTr = deciduous trees, SmVert = small vertebrates, EmVeg = emergent vegetation, WillTh = willow thickets.

Species	Food	Breeding Habitat	Nest site
Swainson's Thrush		Woodland, coniferous forest edge esp. where damp), orchards, and riparian thickets	
Hermit Thrush		Coniferous, mixed or deciduous forest and forest edge	On ground or in low deciduous or coniferous trees
American Robin	Earthworms, snails	Habitat generalist	
Solitary Vireo		Decid-coniferous woodland	Primarily DeTr
Warbling Vireo		Open deciduous and decid-coniferous woodland, riparian forest and thicket habitat	
Red-eyed Vireo		Deciduous forest and woodland habitat	
Orange-crowned Warbler		Deciduous and decid-coniferous woodland, chaparral, and riparian woodland	
Yellow-rumped Warbler	Insects	Coniferous-deciduous forest	
Black-throated Gray Warbler	Insects	Coniferous-deciduous forest, chaparral, scrub, and oak (<i>Quercus</i> spp.) and pinon montane woodland	
American Redstart		Forest edge	
MacGillivray's Warbler	Dense thickets (esp. riparian willow and alder (<i>Alnus</i> spp.)), edge of coniferous or mixed wood		
Wilson's Warbler		Thickets and brush in well-watered location (esp. willow and alder bogs and riparian woodland habitat)	

Table 3. Continued. AqIn = aquatic invertebrates, AqVeg = aquatic vegetation, DecShr = deciduous shrubs, DeTr = deciduous trees, SmVert = small vertebrates, EmVeg = emergent vegetation, WillTh = willow thickets.

Species	Food	Breeding Habitat	Nest site
Black-headed Grosbeak		Riparian woodland and thickets, edge of pond, and open woodland habitat	
Lazuli Bunting	Arid brushy canyons, riparian thickets, chaparral, open woodland		
Rufous-sided Towhee		Forest edge, chaparral, thickets, woodland habitat	
Chipping Sparrow		Forest edge	
White-crowned Sparrow		Coastal scrub, wet meadow	
Brewer's Blackbird	Spiders, crustaceans, snails	Shrubby, brushy area esp. near water, riparian woodland	occ. DeTr and EmVeg
Brown-headed Cowbird	Spiders, snails	Forest edge	
Purple Finch		Forest edge	
Pine Siskin	Seeds of deciduous trees		
American Goldfinch		Open deciduous and riparian woodland	
Evening Grosbeak	Insects, seeds, berries		

SMALL MAMMALS

In this review the term "small mammals" denotes non-carnivorous, non-volant mammals up to the size of the beaver. It includes insectivores, rodents, and lagomorphs.

Small mammals are important in the food chain as part of the prey base for carnivorous mammals and raptors (Soutiere 1979). In addition, many small mammals consume fungi and disperse their spores (Maser et al. 1978, McIntyre 1984, Rhoades 1986, Maser and Maser 1987); this is crucial for trees that depend upon symbiotic mycorrhizae (Harris 1984). A few members of this group, such as the muskrat, nutria, and beaver are valued as furbearers.

Much of the information on the life histories and habitat requirements of small mammals has grown out of studies concerned with economic damage caused by rodents. Although ponds created by beaver dams are beneficial to a variety of species, including fish, amphibians, reptiles, waterfowl, shorebirds, small mammals, and furbearers, beaver do damage by causing local flooding, burrowing into banks, and cutting trees for use in construction or as food (Miller 1983a, Medin and Clary 1991). Mountain beaver, muskrat, pocket gophers, nutria, and voles damage fields, orchards, forests, and levees by burrowing, girdling trees, and feeding on vegetation (Neal and Borrecco 1981, Case 1983, Evans 1983, Miller 1983b, O'Brien 1983, Teipner et al. 1983). Shrews, deer mice, chipmunks, and tree squirrels can hinder reforestation efforts by consuming seeds (Jackson 1983, Timm and Howard 1983, West 1992). Studies of the relationship of these seed predators to logging practices have provided a great deal of information on their habitat preferences and population dynamics in managed forests (Tevis 1956a,b, Gashwiler 1965, 1967, Ahlgren 1966, Harris 1968, Sullivan 1979b, West 1992).

Because small mammals are often abundant and have small home ranges and high reproductive rates, this group has been used in many ecological studies. This fact, coupled with the economic importance of small mammals, has resulted in the accumulation of a large amount of data on small mammal communities. Thus, when we assess the use of riparian zones by small mammals, we have available data on parameters such as survival, dispersal, competition, abundance, diversity, and biomass that are seldom available for other groups.

Use of riparian habitats

Relative dependency

Obligate inhabitants of riparian zones

Several small mammals of the Pacific Northwest are obligate inhabitants of streamside zones. The water shrew, *Sorex palustris* (Bailey 1936, Conaway 1952, Anthony et al. 1987), is semi-aquatic, and the marsh shrew, *S. bendirii* (Pattie 1973, Hooven and Black 1976, Anthony et al. 1987), is generally captured adjacent to running water. McComb et al. (1993) reported that captures of marsh shrews dropped sharply 50-100 m from a stream. The exotic nutria (*Myocastor coypus*) (Maser et al. 1981), as well as the muskrat (*Ondatra zibethica*) (Willner et al. 1980), beaver (*Castor canadensis*) (Hill 1982), and water vole, *Microtus richardsoni* (Bailey 1936, Hooven and Black 1976, Ludwig 1984, Doyle 1985, Anthony et al. 1987) are also restricted to sites near water.

Habitat generalists that use riparian zones

Many small mammals typical of northwestern forests occur in both upland and riparian habitats but are more abundant at riparian sites in some areas or seasons. This is the case for the following insectivores and rodents: masked shrew, *S. cinereus* (Larrison 1976), Trowbridge's shrew, *S. trowbridgii* (Anthony et al. 1987, Doyle 1990, McComb et al. 1993), montane shrew, *S. monticolus* (Doyle 1990), pygmy shrew, *Microsorex hoyi* (Long 1974, Stinson and Gilbert 1985), coast mole, *Scapanus orarius* (Hartman and Yates 1985), and shrew-mole, *Neurotrichus gibbsii* (Dalquest 1948, Terry 1981, Cross 1985, Anthony et al. 1987, Doyle 1990, McComb et al. 1993), southern red-backed vole, *Clethrionomys gapperi* (Hoffman 1960, Cross 1985, McComb et al. 1993), northern flying squirrel, *Glaucomys sabrinus* (Cross 1985, Anthony et al. 1987, Doyle 1990), and Douglas' squirrel, *Tamiasciurus douglasii* (Anthony et al. 1987).

The deer mouse, *Peromyscus maniculatus*, is a species that makes use of forested riparian sites but for which a preference has not been demonstrated. The deer mouse occupies a wide variety of habitats, including forested uplands and riparian sites. Although not more abundant in riparian than in upland areas, the deer mouse is often the most commonly trapped member of small mammal communities on riparian sites (Anthony et al. 1987, Cross 1988, Doyle 1990, McComb et al. 1993). The association of the forest deer mouse, *Peromyscus oreas*, with riparian zones is unknown.

The long-tailed vole, *Microtus longicaudus*, occupies a variety of moist habitats in the Pacific northwest, including forests, shrubs, and marshes (Maser et al. 1981, Smollen and Keller 1987). On the other hand, several microtine rodents and other small mammals, including the creeping vole, *M. oregoni* (Goertz 1964, Carraway and Verts 1985, Cross 1985, Anthony et al. 1987, Doyle 1990), Townsend's vole, *M. townsendii* (Bailey 1936, Goertz 1964, Maser et al. 1981), and the meadow vole, *M. pennsylvanicus* (Getz 1970, Snyder and Best 1988) inhabit moist open areas adjacent to streams or springs within forest. Similarly, the vagrant shrew, *S. vagrans*, occurs in patches dominated by grasses or sedges (Hoffman 1960, Hooven et al 1975, Terry 1981, Whitaker et al. 1983, Morrison and Anthony 1989), and the mountain beaver, *Aplodontia rufa*, utilizes treeless openings and sapling stands (Neal and Borrecco 1981). The Pacific jumping mouse, *Zapus trinotatus*, is also associated with riparian sites having an open canopy (Hooven and Black 1976, Maser et al. 1981, Cross 1985, Anthony et al. 1987, Doyle 1990), particularly areas of high grass cover and low shrub cover near streams (Morrison and Anthony 1989, McComb et al. 1993). In eastern Washington moist meadows are thought to provide optimum habitat for the western jumping mouse, *Zapus princeps*, and western harvest mouse, *Reithrodontomys megalotis* (Stinson and Gilbert 1985).

Infrequent inhabitants of riparian zones

Many northwestern sciurids use upland forest and are rarely, if ever, encountered in riparian situations. This group includes the golden-mantled ground squirrel, *Spermophilus lateralis* (Medin 1986), yellow-pine chipmunk, *Tamias amoenus* (Hoffman 1960, Rickard 1960, Simons 1985, Medin 1986, Medin and Booth 1989), least chipmunk, *T. minimus* (Ahlgren 1966, Martell and Radvanyi 1977, Verme and Ozoga 1981, Scott et al. 1982, Martell 1984), red-tailed chipmunk, *T. ruficaudus* (Ramirez and Hornocker 1981, Scrivner and Smith 1981), and red squirrel, *Tamiasciurus hudsonicus* (Verme and Ozoga 1981, Sullivan and Moses 1986).

Composition of small mammal communities in riparian zones

Riparian habitats typically harbor all or most species of small mammals captured in adjacent uplands as well as some species confined to riparian areas (Cross 1985, Anthony et al. 1987, Doyle 1990, McComb et al. 1993). Consequently, species richness is greater for riparian communities. Evenness or equitability is likely to be low on upland sites dominated by one or a few abundant species, such as Trowbridge's shrew and the southern red-backed vole (McComb et al. 1993), but may also be low at riparian sites because of the presence of a few rare species (Doyle 1990).

Species requirements provided by riparian habitats

Riparian zones differ from uplands in hydrology, soils, and plant communities. These special features provide water, food, and cover and affect the microclimate available to small mammals. Inhabitants of riparian sites may respond to any of these characteristics or to a combination of several.

Water

Beaver, muskrat, and nutria construct dens in the banks of streams or ponds. In addition, many small mammals are adapted for locomotion in or on surface water. Water shrews, beaver, muskrat, and nutria are semi-aquatic; all are excellent swimmers and divers (Bailey 1936, Conaway 1952, Jenkins and Buscher 1979, Willner et al. 1980, Maser et al. 1981, Hill 1982, Perry 1982, Ludwig 1984, Beneski and Stinson 1987). Jumping mice, shrew-moles, Townsend's voles, and mountain beaver, though less closely tied to water, are also good swimmers (Bailey 1936, Maser et al. 1981, Feldhamer and Rochelle 1982). Water shrews and the water vole require moving water (Beneski and Stinson 1987), while muskrat use water that is lentic or slightly lotic (Perry 1982).

Some small mammals depend on plant or animal food found only in or near water. Riparian insectivores, such as the water shrew and marsh shrew, forage on aquatic animals. Water voles, nutria, muskrat, and beaver feed partly on aquatic or semi-aquatic vegetation.

Soils

Because many small mammals spend much of their life underground or on the soil surface, soil characteristics have a profound impact on small mammal distributions. As discussed in the background section, riparian zones are characterized by higher soil moisture, higher levels of organic matter, and larger areas of exposed soil relative to uplands. All of these features affect the abundance of small mammals.

Some small mammals of the riparian zone require wet soils. High soil moisture or a mixture of wet and dry soils appears to be important for vagrant shrews (Terry 1981), pygmy shrews (Long 1974), coast moles (Hartman and Yates 1985), southern red-backed voles (Miller and Getz 1972, 1973), and Townsend's voles (Bailey 1936). The vagrant shrew is common in areas with a high water table; its distribution is also strongly positively correlated with the depth of organic matter in the soil (Terry 1981).

On the other hand, burrowing mammals are likely to be excluded from areas where soil is usually saturated. For instance, Trowbridge's shrew is rare at sites with a high water table (Terry 1981).

The high percent of exposed soil in riparian zones results from episodes of flooding and deposition. Doyle (1987) reported a correlation between the occurrence of water voles and percentage of exposed soil.

Microclimate

In some cases terrestrial inhabitants of riparian sites require high moisture because of poorly developed physiological mechanisms of water conservation. For instance, the southern red-backed vole must drink twice the amount of water predicted for a small mammal of its weight; hence, its high moisture requirement ties it to mesic environments where succulent herbaceous vegetation is available (Miller and Getz 1977, Merritt 1981). Similarly, mountain beaver have an inefficient kidney and therefore require succulent vegetation and humid burrows (Feldhamer and Rochelle 1982).

Plant species composition

Many small mammals feed on the distinctive plants and associated fauna of riparian zones, taking advantage of the high primary productivity of riparian communities. Food resources available to small mammals in the riparian zone include aquatic vegetation, aquatic invertebrates and vertebrates, streamside vegetation, and terrestrial invertebrates.

Insectivorous habitat generalists, such as masked, Trowbridge's, montane and pygmy shrews, and coast and shrew-moles, probably benefit from the abundance of streamside insects as well as invertebrates in the moist soils characteristic of riparian zones. Similarly, the dense vegetation adjacent to surface water provides food for many herbivorous generalists. Grasses and forbs available in moist meadows are fed upon by voles, beaver, and muskrat. McComb et al. (1993) suggested that the association of the Pacific jumping mouse with streamside habitats may reflect the availability of grasses and fruits.

Tree squirrels and chipmunks are primarily granivorous and mycophagous. These guilds, while not dependent upon the riparian zone for feeding, may nevertheless feed in the dense shrub thickets and tree stands characteristic of riparian forests.

Riparian zones typically contain vegetation adapted to the high disturbance regime produced by frequent episodes of flooding, scouring, and deposition. In many cases small mammals are closely tied to these patches of early successional vegetation. For instance, grassy areas are especially important for the vagrant shrew, mountain beaver, jumping mice, and several voles. The soil beneath thickets of red alder (*Alnus rubra*), an invader of flooded sites (Agee 1988), typically has a thicker layer of organic matter than uplands stands dominated by Douglas-fir (*Pseudotsuga menziesii*); as noted above, this is a crucial element of habitat quality for vagrant shrews.

Vegetation density and quality

As noted above, taxa with high moisture requirements benefit from the succulent vegetation available in riparian zones. In addition, the high productivity of riparian sites results in dense cover, an important aspect of habitat quality for small mammals active on the forest floor (e.g., insectivores [Bailey 1936, Conaway 1952, Terry 1981, Beneski and Stinson 1987], southern red-backed voles [Miller and Getz 1972, 1973, Bondrup-Nielsen 1987], and creeping voles [Maser et al. 1981]). Vulnerability to predators has been shown to increase for meadow voles (Getz 1970) and southern red-backed voles (Wywiałowski 1987) following a decrease in cover.

Structural diversity of vegetation

Riparian zones typically exhibit greater structural diversity in vegetation than upland sites. This is likely to benefit small mammals; however, some structural features of vegetation that are important to small mammals may be less available in riparian zones than in uplands. McComb et al. (1993) reported that streamside transects had shallower litter; lower basal area of stumps, snags, and live conifers; and fewer stumps than upland sites. Litter appears to be an important component of habitat quality for Trowbridge's shrews, marsh shrews, shrew-moles, red-backed voles, creeping voles, and meadow voles (Goertz 1964, Getz 1970, Hooven and Black 1976, Terry 1981, Martell 1983a). Snags are important for Douglas squirrels, northern flying squirrels, and Townsend's chipmunks (*Tamias townsendii*) (Doyle 1990, Gilbert and Allwine 1991a).

Plant diversity

Riparian zones are typified by high species diversity of plants relative to uplands. Doyle (1990) reported that the abundance of deer mice and Pacific jumping mice in riparian and upland habitats of the Oregon Cascades was strongly correlated with plant species richness. Southern red-backed vole abundance is associated with shrub diversity (Bondrup-Nielsen 1987).

Edge

Riparian zones are typified by extensive edges with an admixing of stream and riparian or riparian and upland characteristics. This may be significant for small mammals because they are relatively poor dispersers and must meet all their habitat requirements within a small area.

Effects of timber harvest

The effects of timber harvest on small mammal communities depend on a variety of factors including original plant community; type, size, and timing of harvest; and on site treatment of slash and snags (West 1992). Nevertheless, it is possible to make some generalizations about the effects of logging on small mammals in coniferous forests of the Pacific northwest and to predict some effects of riparian buffer strips in logged areas.

Clear-cutting

A number of species are likely to benefit from clear-cutting or forest management practices, such as burning and herbicide application, that set back succession. These include the vagrant shrew; mountain beaver (Feldhamer and Rochelle 1982); California ground squirrel, *Spermophilus beecheyi* (Tevis 1956b, Gashwiler 1970); least chipmunk (Scott et al. 1982, Ahlgren 1966, Martell and Radvanyi 1977, Verme and Ozoga 1981, Martell 1984); Townsend's chipmunk (Tevis 1956b, Gashwiler 1970, Hooven and Black 1976, Gunther et al. 1983, Corn et al. 1988); and yellow-pine chipmunk (Rickard 1960, Medin and Booth 1989); red squirrel (Verme and Ozoga 1891); northern pocket gopher, *Thomomys talpoides* (Scrivner and Smith 1981); beaver (Jenkins and Buscher 1979); deer mouse (Tevis 1956b, Gashwiler 1959, 1970, Borrecco et al. 1979, Sims and Buckner 1973, Hooven and Black 1976, Martell and Radvanyi 1977, Campbell and Clark 1980, Ramirez and Hornocker 1981, Van Horne 1981, Gunther et al. 1983, Martell 1983a,b, Cross 1985, Corn et al. 1988), heather vole (*Phenacomys intermedius*) (Martell and Radvanyi 1977); meadow (Martell and Radvanyi 1977), Townsend's (Gunther et al. 1983), long-tailed (Harris 1968, Halvorson 1982), and creeping voles (Goertz 1964, Gashwiler 1970, 1972, Hooven and Black 1976, Cross 1985, Corn et al. 1988); Pacific jumping mouse (Gashwiler 1970,

Hooven and Black 1976, Borrecco et al. 1979, Gunther et al. 1983); bushy-tailed woodrat, *Neotoma cinerea*; pika, *Ochotona princeps*; and snowshoe hare, *Lepus americanus* (Gashwiler 1970).

For some small mammals that benefit from timber harvest, abundance does not increase until several years after logging, especially if clear-cutting is followed by burning. For instance, Townsend's chipmunks were captured on clear-cuts 3-10 and 8-10 yr after cutting, presumably taking advantage food and cover provided by herbs and shrubs that proliferate several years after harvest (Tevis 1956b, Gashwiler 1970).

Inhabitants of mature and old-growth forests

Similarly, some small mammals associated with old-growth forest also use cutover areas if sufficient ground cover is available. Southern red-backed voles usually decline following logging (Tevis 1956b, Gashwiler 1967, 1970, Krefting and Ahlgren 1974, Campbell and Clark 1980, Ramirez and Hornocker 1981, Corn et al. 1988), fire (Gashwiler 1959, Martell 1984), or herbicide application (D'Anieri et al. 1987). Under some circumstances, however, abundance of southern red-backed voles on clear-cuts equals or exceeds that in mature or old-growth forests (Ahlgren 1966, Lovejoy 1975, Kirkland 1977, Martell and Radvanyi 1977, Soutiere 1979, Scott et al. 1982, Gunther et al. 1983, Monthey and Soutiere 1985). Use of logged areas by southern red-backed voles is likely related to the development of thick ground cover (Gunther et al. 1983). Martell (1983a) suggested that red-backed voles use unscarified clear-cuts because of the persistence of a layer of mostly dead mosses and shrubs. High quality habitat for this genus is characterized by extensive debris and high shrub diversity (Miller and Getz 1972, 1973, Bondrup-Nielsen 1987). Lovejoy (1975) reported that 80% of red-backed vole captures on recently logged areas were in or adjacent to slash piles. Wywiałowski (1987) demonstrated a preference for high densities of vertical and horizontal cover in red-backed voles.

Forest-dwelling shrews, especially Trowbridge's shrew, are also generally not favored by management practices that lead to early seral stages in coniferous forest (Tevis 1956b, Hooven and Black 1976, Kirkland 1977, Martell 1984, Cross 1985, Corn et al. 1988) but may become abundant several years after cutting (Harris 1968, Simons 1985). This pattern contrasts with the vagrant shrew, which inhabits sites in early successional stages. A litter layer may not develop until several years after cutting; consequently, the moss and shrub layer on unscarified clear-cuts may be critical for shrews (Martell 1983a). In addition to providing litter, after several years clear-cuts provide woody debris and thick herbs and shrubs for cover, as well as dense populations of insects associated with slash (Lovejoy 1975), an important resource for shrews and moles (Gunther et al. 1983).

Northern flying squirrels (Tevis 1956b, Gashwiler 1970, Hooven and Black 1976, Gunther et al. 1983, Verme and Ozoga 1981, Cross 1985) and Douglas' squirrels (Tevis 1956b, Gashwiler 1970, Hooven and Black 1976) are unlikely to use clear-cuts, although both inhabit young stands of conifers (Anthony et al. 1987).

Although timber harvest and natural disturbances causing forest regeneration profoundly affect the composition of small mammal communities, once canopy closure is reached within unmanaged forests of Washington and Oregon few small mammals appear to be strongly influenced by stand age. Most differences in species composition in naturally regenerating forests are attributable to zoogeographic barriers rather to consistent differences between forest age classes. This may be because critical values for habitat parameters are exceeded in naturally

regenerated forests soon after the canopy closes (Corn et al. 1988, Aubry et al. 1991, Corn and Bury 1991, Gilbert and Allwine 1991a, West 1991).

Use of riparian buffer strips

To be useful management tools for small mammals, riparian buffers need to be large enough and retain sufficient habitat value to allow taxa that depend on riparian habitat as well as those that are characteristic of late successional stages to persist until tree canopy is reestablished on adjacent uplands.

Cross (1985) trapped Trowbridge's shrews, Pacific shrews, *Sorex vagrans pacificus*, deer mice, bushy-tailed woodrats, creeping voles, jumping mice (*Zapus* sp.), and one shrew-mole in riparian leave strips 9-67 m wide. Northern flying squirrels were not trapped in leave-strips; it was not known whether this was due to inadequate sampling or to lack of minimum area. McComb et al. (1993) found that capture rates of Pacific shrews, marsh shrews, and jumping mice decreased curvilinearly with stream distance. Rector (1990) found no difference between the small mammal communities of riparian and adjacent areas in old-growth Douglas fir forests.

There is some evidence that riparian habitats act as sources of individuals dispersing into uplands. Doyle (1990) found that among deer mice, Pacific jumping mice, northern flying squirrels, and Townsend's chipmunks, upland areas were characterized by more juveniles, smaller adults (except Pacific jumping mice), and reduced reproductive activity in comparison to riparian sites. She concluded that upland areas functioned as dispersal sinks for juveniles dispersing from riparian habitats. Recently logged or burned areas may be dispersal sinks for deer mice (Sullivan 1979a, Martell 1983b, 1984) or provide suitable sites for reproduction depending upon the structure of the habitat. Similarly, young stands of lodgepole pine appear to be dispersal sinks for red squirrels from mature forest (Sullivan and Moses 1986). It is not known whether riparian buffer strips can provide sufficient habitat to maintain sources to populate logged uplands.

Buffer strips are likely to be especially critical for species with low vagility. Taxa adapted to early successional stages or other disturbed habitats are good colonizers, either moving to such areas or surviving *in situ* at low density and increasing populations when conditions become favorable after disturbance. For instance, California ground squirrels do not occur in virgin forests, yet they rapidly locate new clear-cuts surrounded by forested areas and connected only by roads (Tevis 1956b, Gashwiler 1970). Meadow voles, another species of open areas, also have excellent colonization abilities (Reich 1981, Lomolino 1984). Large-bodied aquatic rodents tend to be good dispersers; muskrat and nutria are capable of dispersing dozens of kilometers (Willner et al. 1980, Maser et al. 1981, Perry 1982). Beaver are able to locate and colonize temporary patches of early successional deciduous trees (Slough and Sadlier 1977, Hill 1982). Beaver movements up to 328 stream kilometers have been recorded (Hibbard 1958).

On the other hand, for inhabitants of mature forest with limited vagility, maintenance of source populations in streamside refugia is likely to be important to long-term persistence at a site. This is likely to be the case for southern red-backed voles, which must periodically reinvade cleared sites (West et al. 1980).

It is not known whether competition between small mammal species within RMZ's has the potential to exclude some taxa. Interspecific microhabitat segregation has been demonstrated for some forest small mammals (Dueser and Shugart 1978, Terry 1981, Doyle 1985, Millar et al. 1985); however, results obtained by Morris (1983) and Morrison and Anthony (1989) do not support the hypothesis of competitive interference for space. Other workers have inferred

competitive interactions from reciprocal patterns of abundance for species pairs. For instance, Gunther et al. (1983) and Halvorson (1982) noted that numbers of deer mice and southern red-backed voles were inversely related. Direct evidence for competitive interactions among forest small mammals was provided by removal experiments conducted by Doyle (1985). Captures of all species of Insectivora present on the study area (Trowbridge's shrews, montane shrews, marsh shrews, and coast moles) increased significantly following removal of deer mice. Pacific jumping mice and northern flying squirrels also increased after removal.

To summarize, because most or all small mammals of upland forests in the Pacific Northwest are capable of inhabiting riparian zones, the species richness of riparian buffers is not likely to be enhanced after timber harvest; probably no new species will invade riparian areas from uplands. On the other hand, some species with large home range requirements, such as the northern flying squirrel, might be lost. Taxa that are poor dispersers may depend on riparian buffers as refugia because they are unable to invade uplands from more distant sites. Poor dispersers are likely to be inhabitants of mature or old-growth stands rather than early successional stages. Species normally present in low densities in riparian habitats and affected by competition with more abundant deer mice or other taxa may not be able to maintain sufficient populations to persist in riparian management zones.

Insectivores are likely to be especially vulnerable. Several are dependent on riparian habitat; they are often present at low densities (e.g., water shrews, [Beneski and Stinson 1987]), are poor colonizers (e.g., short-tailed shrew, *Blarina brevicauda* [Lomolino 1984]), and are adversely affected by competition from deer mice (Doyle 1985). If species that are poor colonizers disappear from riparian buffers, they will be unlikely to recolonize from more distant sources, and local extinctions may result.

BATS

Fourteen species of bats are found in Washington, 11 of which use forested land as either primary or secondary habitat (Dalquest 1948). Because of their nocturnal habits, they are difficult to study and until recently, information concerning specific habitat associations has been difficult to obtain. Recent advances in the miniaturization of radiotransmitters and the development of ultrasonic detectors promise to yield valuable information about habitat use patterns, roost site selection, and response to habitat alteration of bats. Much of the available information on habitat preferences comes from studies performed in areas other than the Pacific Northwest and, where appropriate, this information has been incorporated in this review (Christy and West in press).

Evidence suggests that Pacific Northwest bats are generally opportunistic in both foraging and roosting behavior and are not restricted to any given habitat, although *Lasionycteris noctivagans* and *Lasiurus cinereus* appear to be highly associated with forested areas in the Pacific Northwest (Barclay 1985, Perkins and Cross 1988). Most species forage in many different habitats, from city streets to forested areas, and prey on a wide variety of insects. Virtually any structure which provides protection and the proper conditions of temperature and humidity may be used as a roost and thirteen of the fourteen species in Washington have been found roosting in manmade structures (see Cross 1976, Maser et al. 1981, Perkins 1983, van Zyll de Jong 1985). However, in spite of the lack of information about habitat associations, riparian areas within forests appear to be of primary importance, providing more suitable feeding and roosting sites than the adjacent upland for many species (see Cross 1988).

Use of riparian habitats

Relative Dependency

Obligate inhabitants of riparian zones

There are no Pacific Northwest bat species which are known to be restricted to riparian areas.

Habitat generalists that use riparian zones

As previously discussed, bats are generalists in most respects, feeding and roosting in many different habitats. Riparian areas, however, are an important habitat element for bats, primarily as foraging and drinking habitat. Some species are apparently more reliant on water for foraging than others: *Myotis yumanensis* often forages primarily over water (Herd and Fenton 1983, Barbour and Davis 1969) while *M. ciliolabrum*, *M. thysanodes*, *L. cinereus* and *P. townsendii* commonly feed along roads or open areas within forest stands rather than over water (Black 1974, Whitaker et al. 1977, Kunz and Martin 1982, Barclay 1985, van Zyll de Jong 1985). In natural settings, riparian areas are used by all species to some degree for feeding, drinking or roosting and all Pacific Northwest species have been caught or observed while drinking and/or foraging over streams or ponds.

Infrequent inhabitants of riparian zones

Although Pacific Northwest bat species are not restricted to riparian habitats, all species frequently use lakes, streams and ponds as foraging and drinking habitat.

Species requirements provided by riparian habitats

Food

All bats of the Pacific Northwest are insectivorous. They feed primarily on flying insects although some species also glean, taking non-flying insects from foliage or the ground. Although prey selection appears to be largely opportunistic, aquatic insects are frequently a major component of the diet (Whitaker 1972, Belwood and Fenton 1976, Whitaker et al. 1977, Fenton and Bell 1979, Herd and Fenton 1983,) and many bats, particularly *Myotis* species, have been found to feed primarily over water rather than in forests, fields, or clearings. Feeding rates of eight *Myotis* species, measured with ultrasonic detectors, in the Washington Cascade and Oregon Coast Ranges were 10 times higher over water than in forest stands (Thomas and West 1991). Two of these species, *Myotis lucifugus* and *Myotis yumanensis*, usually roost near water and frequently fly directly to lakes or rivers for part of foraging (Barbour and Davis 1969). These two species are also apparently restricted to foraging over water in some areas (Davis and Hitchcock 1965, Herd and Fenton 1983), although they feed in forests and urban areas (i.e., streets and parks) in other parts of their range (Barbour and Davis 1969). In Canada, *Myotis lucifugus* preferred lakes to open fields for foraging (Fenton 1970); activity rates over lakes were 75 times greater than rates over forest (Lunde and Harestad, 1986). In the Okanagon Valley of British Columbia, Fenton et al. (1980) found that *Myotis lucifugus* foraged over fast and slow flowing water whereas *Myotis yumanensis* and *Myotis californicus* fed over slow moving water (Fenton et al. 1980). Both species also foraged along stream banks and in upland areas. However, a subsequent study in the

same area revealed a different situation: *Myotis yumanensis* foraged almost exclusively over water, preferring moving water to still water, while *Myotis lucifugus* foraged in a variety of habitats, both forested and riverine (Herd and Fenton 1983).

In more arid areas of the United States, bat activity is also frequently concentrated in riparian areas. Activity levels of *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Myotis thysanodes*, *Plecotus townsendii*, *Myotis californicus*, *Pipistrellus hesperus*, *Tadarida brasiliensis* were significantly higher in riparian forests of Arizona than in desert or scrub (Bell 1980).

Water

Riparian areas provide critical drinking habitat for bats, particularly the larger species. They drink on the wing, flying close to the water with their mouths open and skimming the surface with the lower jaw. Small, agile species may be able to drink from a pool only a few centimeters in diameter but larger, less maneuverable species require large areas of open water for drinking (Cross 1986).

Roosts

There is little direct evidence regarding the importance of riparian zones as habitat for roosting bats. However, foliage roosting bats, such as *Lasiurus cinereus*, roost preferentially in deciduous tree foliage, commonly at the edge of clearings, in the eastern United States and may prefer the same type of roost on the west coast, where deciduous trees are more abundant in riparian zones than interior forest (McClure 1942, Constantine 1958, 1966, Barbour and Davis 1969, Shump and Shump 1982, Barclay 1985).

Riparian areas may also be important roosting habitat for cavity- and crevice- roosting species, such as the *Myotis* species, *Eptesicus fuscus* and *Lasionycteris noctivagans*. Evidence suggests that proximity to open water for foraging and drinking may be an important consideration in roost site selection. In Australia, Tidemann and Flavel (1987) reported that all roost sites of several small, insectivorous bat species (*Eptesicus vulturinus*, *Chalinolobus morio*, *Nyctophilus gouldi*, *Nyctophilus geoffroyi*) were within 700 m of permanent or semi-permanent water. In a radiotelemetry study in Illinois, roosts of *Myotis sodalis* were also generally located close to water (mean = 141 m from intermittent streams, and (mean = 1097 m from perennial streams) (Gardner et al. 1991). Although riparian habitats were important to this species, selection of maternity roosts was not limited to riparian habitats. Reproductive females traveled up to 2.5 km from their roosts to foraging areas near perennial streams.

Although maternity roosts may be located far from foraging sites, distance between foraging habitat and roosting sites may be an important factor in determining juvenile growth and survival for some species. In the southeastern United States, juvenile growth rates of *Myotis grisescens* were found to be inversely proportional to distance traveled between maternity roosts and foraging habitat (rivers and lakes). Summer colonies of this species prefer caves within 1 km of a major river or lake and are rarely found in caves located >4 km from such places (caves ranged from 0-6.6 km from water) (Tuttle 1976). Although *Myotis grisescens* appears to be more dependent on water for foraging habitat than most species in the Pacific Northwest, it is likely that the distance between roosts and foraging sites (which are often associated with water) may also affect juvenile growth and survival in Pacific Northwest species.

Effects of timber harvest

Forest management

Very few studies have been performed regarding the response of bats to forest management practices worldwide and none of this research has taken place in the Pacific Northwest. However, forest age associations have been studied and most species of bats in Pacific Northwest forests have shown a preference for old stands over younger stands. In studies of eight species of *Myotis*, *Eptesicus fuscus*, and *Lasionycteris noctivagans* in western Washington and Oregon, bat activity was 2-10 times greater in old growth forests than in younger stands (Thomas and West 1991). Activity periods were highest in early evening with a 15-30 min peak in activity and few feeding buzzes, suggesting that old growth is used for roosting rather than feeding. Thomas and West (1991) found no significant difference between bat activity levels in young and mature forests, indicating that bats discern only two age classes, old growth and younger.

An affinity for old-growth Douglas-fir forests has also been shown by *Lasiurus cinereus* and *Lasionycteris noctivagans* throughout Oregon. *Lasiurus cinereus* prefers Douglas fir/western hemlock forest >200 years old, and 94% of captures of *Lasionycteris noctivagans* occurred in conifer stands >101 years old. Both species used Douglas-fir stands more frequently than stands of Ponderosa pine (*Pinus ponderosa*) or true fir (*Abies grandis* and *Abies concolor*) (Perkins and Cross 1988). Although no roost sites were found in this study, other studies have found that *Lasionycteris noctivagans* roosts in cracks and crevices in large, old trees which are more likely to be found in old-growth forests than in younger seral stages (Barclay et al. 1988). It has also been suggested that when *L. cinereus* roost in conifers they choose the largest, oldest trees, which provide more roost sites than smaller, younger trees (Verner and Boss 1980, Perkins and Cross 1988).

Structural features associated with old-growth forests, such as snags and large trees with thick, exfoliating bark, provide potential roost sites for bats. In forested habitat, colonial species use large cavities and exfoliating bark as maternity roosts while solitary species use bark crevices or foliage clumps for roosting (Barbour and Davis 1969). Higher capture frequencies in areas with snags than in areas without snags have been reported for *Eptesicus fuscus* and *Lasionycteris noctivagans* (Cross 1976), suggesting that these structures may be used for roosting.

Clear-cuts

Although data are limited, the effects of timber harvest on bats apparently depend upon the intensity of harvest, clear-cut versus selective cut. Activity is apparently reduced after clear-cutting, probably as a result of loss of potential roost sites. In northwestern coastal forests, *Myotis lucifugus* activity, measured by ultrasonic detection, was 10 times greater in 50-year-old stands than in 2-year-old clear-cuts (Lunde and Harestad 1986). A radiotelemetry study in Australia revealed similar habitat use patterns: radio-tagged chocolate wattled bats (*Chalinolobus morio* - a cavity roosting, colonial species similar to the *Myotis* bats of North America) flew 5 km from logged forest to roost in exceptionally large trees in unlogged forest (Lunney et al. 1985). Through examination of roost site characteristics it was also determined that in a managed forest, only unlogged gullies provided trees of the size and species required by another Australian species, *Nyctophilus gouldi*, for roosting (Lunney et al. 1988).

Partial cuts

The impact of selective cutting on bats will depend, in part, upon the size of trees that remain after harvest. The removal of large, old trees may render forests unusable to bats as roosting habitat but if some large trees remain after harvest, they may continue to provide suitable roosts. *Myotis sodalis* continued to roost and forage in upland and floodplain forests in Illinois in spite of selective cutting, although the number of bats roosting in the area was substantially reduced. Eight roosts were located within the harvest area before cutting and individuals returned to two of these roosts after harvest (Gardner et al. 1991).

CARNIVORES

Use of riparian habitats

Relative dependency

Many species of carnivores are associated with riparian habitats and none of the species in the PNW appears to actively avoid riparian habitats. The relative use of riparian habitats does vary between species.

Obligate inhabitants of riparian zones

River otters (*Lutra canadensis*) and mink (*Mustela vison*) are the carnivore species most closely associated with the open water in riparian areas. Both food and shelter influence otter's use of riparian areas and they are known to prefer stream-associated habitats to lakes, reservoirs, and ponds. Lakes, reservoirs and ponds are used primarily in winter while mud flats and associated open marshes, swamps, and backwater sloughs are used in summer months (Melquist and Hornocker 1983). Otters can also be found in estuaries, and they frequently visit nearshore islands off the Washington coast (Kenyon and Scheffer 1961, Aubry and West 1987). Mink inhabit all types of wetlands such as river banks, streams, lakes, ditches, swamps, marshes, and backwater areas (Chapman and Feldhamer 1982). In Michigan, 50% of all mink tracks were found in areas closely associated with water (Marshall 1936). In the Yukon, the highest density of mink occurred in swampy habitats surrounding large bodies of water which supported large numbers of fish (Burns 1964). In Louisiana, the highest density of mink occurred in coastal marshes, cypress-tupelo swamps and backwater hardwood areas (Arthur 1931). Erlinge (1972) found minks to be common along streams surrounded by marshes where fish and small mammals were abundant. Males occasionally travel far from water to feed but this is probably due to a temporary shortage of food in the aquatic part of the home range (Gerell 1970).

Habitat generalists that use riparian zones

Raccoons (*Procyon lotor*) are also aquatically oriented, although less so than otters and minks. They are strong swimmers and spend most of their life near streams, lakes, or marshes although they may move far from water while hunting (Ingles 1965, Kaufmann 1982). Raccoons are found where water is available in their range, but are scarce in dry, upland areas (Kaufmann 1982). Radio-tracked raccoons in Ohio spent long periods of time in areas with shallow water and 87% of their home range was situated in marshland (Urban 1970). In the Appalachian region,

raccoons used forested regions along streams and hillsides more than expected by availability. In land along the Potomac river, both male and female raccoons used wetlands more than expected (Ingles 1965).

The association of red foxes (*Vulpes vulpes*) with riparian areas is primarily due to the abundance of food sources in wetland habitats. Voles and rabbits constitute a large part of the diet although red foxes are opportunistic and will feed on many other items such as fruits, earthworms, insects, and other rodents (Lloyd 1980, von Schantz 1980). Red foxes and coyotes will not coexist in a given area and coyotes seem to drive foxes out of preferred habitat, such as riparian zones. Major and Sherburne (1987) reported that coyotes selected wetland bogs in eastern Maine during all seasons with the strongest selection observed in spring and fall. This may limit available habitat for red foxes (Harrison et al. 1989) as fox home ranges do not overlap coyote home ranges (Major and Sherburne 1987). Red foxes are associated with lake shores or riparian zones when outside of coyote territory (Harrison et al. 1989). Areas adjacent to streams and lake shores are used intensively by the red fox and may act as natural boundaries between coyote and fox territories (Harrison et al. 1989). However, foxes were found to be negatively associated with bog habitat in Maine (Major and Sherburne 1987).

Black (*Ursus americanus*) and grizzly (*Ursus arctos*) bear use of riparian areas varies seasonally. Black bear generally remain in close proximity to water, feeding and resting in areas less than 100 m from water during spring, summer, and fall (Unsworth et al. 1989). Grizzlies will use riparian areas for foraging when a run of salmon is active and in the summer and fall when plants are fruiting but they are not dependent on these zones for feeding (Craighead et al. 1982, LeFranc et al. 1987). Both black and grizzly bear are found to be seasonally more abundant in riparian than in upland areas during salmon runs and fruiting periods (Raedeke et al. 1988, LeFranc et al. 1987).

There are conflicting reports about the affinity of bobcats (*Felis rufus*) for water. Chapman and Feldhamer (1982) found that bobcats avoid water whenever possible whereas Yoakum (1964) observed that they swam readily in captivity. Bobcats are attracted to riparian zones because their preferred prey and carrion are generally more abundant in riparian habitats than in the adjacent upland (Sweeney 1978, Raedeke et al. 1988). For example, Koehler and Hornocker (1989) found, through radio tracking and scat analysis, that bobcat numbers increased around mesic environments during the summer due to the increased number of voles in these areas as opposed to the adjacent xeric environments. Voles made up 40% of the bobcat diet. During winter, however, the uplands were used more extensively.

Throughout its range, the marten (*Martes americana*) is associated with riparian habitats. In the northern Sierra Nevada, marten strongly prefer riparian lodgepole associations over upland forest for feeding (Spencer et al. 1983). They occupied riparian areas far more than expected based on availability in the home range. Marten are attracted to riparian areas in the Tahoe area as well (Simon 1980, Zielinski 1981). Marten in Ontario utilized riparian habitats more than upland areas (Francis and Stephenson 1972).

The distribution of ermine (*Mustela erminea*) is related to the distribution of small rodents and lagomorphs. Ermine avoid dense forests but are abundant in early successional or edge habitats, scrub, alpine meadows, marshes, riparian woodlands, and riverbanks which support large populations of small mammals (Erlinge 1977a, 1977b, 1981, Fitzgerald 1977, Simms 1979). In a mark-recapture study in the Cascade Range of Oregon ermine were captured more frequently in riparian areas than upland areas (Doyle 1990).

Long-tailed weasels (*Mustela frenata*) appear to favor areas in the vicinity of free standing water (Hall 1951, Gamble 1980). They are more generalized than ermine in feeding habits (Hamilton 1933, Polderboer et al. 1941, Quick 1951, Wobeser 1966), and this may allow the long-tailed weasel to exploit a wider range of habitat types than the ermine.

Species requirements provided by riparian habitats

Food

The association of many carnivore species with riparian habitats appears to be largely due to the abundance of animal prey, both aquatic and terrestrial. Most carnivores are omnivorous during certain times of the year, feeding on berries and other fruits in addition to animals. These plant foods are also more abundant in riparian areas than in adjacent uplands. The availability of food during the breeding season will have a direct effect on the reproductive success of any animal. Because food supplies for many carnivores are more abundant in riparian areas, breeding success will be higher for animals with access to riparian areas.

Riparian areas are very important to foraging otters because aquatic animals are their favored prey (Melquist and Hornocker 1983). They prefer more motile species (i.e., fish) over less motile species (i.e., crustaceans and amphibians) (Toweill 1974) and they prefer larger fishes (15-17 cm) over smaller ones (<15 cm) (Erlinge 1968). Otters hunt near undercut banks and logs or other debris in small streams and among log jams in deep, slow-moving pools (Melquist and Hornocker 1983). Mink generally feed on animals associated with aquatic habitats, such as muskrats, frogs, ducks and other birds, mice, insects, and fish (Gerell 1970, Errington 1943 1954, Sealander 1943, Wilson 1954, Korschgen 1958, Waller 1962, Erlinge 1969, Eberhardt 1973).

Raccoons are opportunistic and omnivorous, eating fruits, nuts, grains, insects, frogs, crayfish, bird eggs, fish, turtles, small mammals (Burt and Grossenheider 1976, Sherfy and Chapman 1980) and waterfowl crippled during hunting season (Stains 1956, Llewellyn and Webster 1960). They feed mainly along lakes and streams, often dunking their food in water before eating (Burt and Grossenheider 1976). Plants are generally more important in the diet than animals, except in the spring when animals peak in abundance (Kaufmann 1982). Most animal prey comes from shallow water or along the shore (Raedeke et al. 1988).

Riparian areas are used by black bears for foraging in both California and Idaho (Kellyhouse 1980, Young and Beecham 1986). They feed on grasses and forbs in spring, soft mast (shrub and tree borne fruit) in summer, and hard (nuts) and soft mast in fall (Chapman and Feldhamer 1982). In Idaho, the primary sources of food for black bear in the summer and fall are huckleberries (*Vaccinium* spp.), bitter cherry (*Prunus emarginata*), and chokecherry (*P. virginiana*). These fruits are abundant in riparian zones and mesic aspen stands in the summer and fall (Unsworth et al. 1989). Black bear also eat insects, fish, small rodents, and an occasional large mammal (Chapman and Feldhamer 1982). Grizzlies are common in riparian habitats that support salmon populations (Craighead et al. 1982, Raedeke et al. 1988). They are not, however, dependent solely on riparian areas for feeding. LaFranc et al. (1987) found grizzlies to be more abundant in riparian areas in the summer (due to the fruiting plants) than in the spring.

Bobcat numbers increased around riparian sites due to the increased number of voles in these areas as opposed to the adjacent upland (Koehler and Hornocker 1989). Bobcat in western Washington also eat spawned out salmon and steelhead from river bars or shallow pools, but the most abundant component of their diet in the region is mountain beaver (Sweeney 1978). In

general, bobcats are attracted to riparian zones because their preferred prey (mountain beaver, snowshoe hare, and cottontails) and carrion are generally more abundant in riparian habitats than in the adjacent upland (Raedeke et al. 1988).

Marten prey is not only more abundant in riparian zones but it is more available as the abundance of coarse woody debris in riparian habitats makes prey more accessible to the predator, especially in winter when stumps and large logs provide access to prey living under the snow (Buskirk et al. 1989). The common prey species of the marten in Ontario are the meadow vole (*Microtus pennsylvanicus*) and the southern red-backed vole (*Clethrionomys gapperi*), both of which inhabit wet coniferous areas near creek edges (Francis and Stephenson 1972). In the Sierra Nevada Mountains voles are preferred food and these are more abundant in the lush, herbaceous vegetation characteristic of riparian zones (Zielinski 1981). Microtine rodents are similarly important for marten in interior Alaska (Magoun and Johnson 1991).

The population density of prey has been shown to be the most important factor regulating ermine numbers (Aspisov and Popov 1940). Ermine populations will decline when prey density declines (Lavrov 1941). Ermine feed on small mammals, especially voles (Hall 1951, Teplov 1952, Day 1968, Erlinge 1975, Fitzgerald 1977, Simms 1979), which are more abundant in riparian areas than in the adjacent upland (Tevis 1956b, King 1983, Doyle 1990). Reproductive success in ermine is strongly influenced by food supplies prior to parturition and is a function of the availability of microtines (Vershinin 1972, Andersson and Erlinge 1977, Erlinge 1981, King 1981). In response to the diversity and abundance of small mammals in riparian habitats, the relative number of breeding female ermine was higher in riparian than upland areas (Doyle 1990).

Resting, roosting, and denning sites

Coarse woody debris, both within the aquatic and terrestrial components of the riparian zone, and hollow trees and snags provide denning sites for many species of carnivores. Otters and minks den in or directly adjacent to the water's edge. Otters often use log jams as resting sites (Melquist and Hornocker 1983). Winter dens of otters are also frequently located on shorelines, generally within 10 m of the water's edge (Reid et al. 1987). The most common type of mink den found in Sweden was located in cavities under trees at the edge of the water surface (Gerell 1970).

Flood-killed and short-lived deciduous trees, which provide tree hollows and snags, are more abundant in riparian areas than adjacent upland (Kaufmann 1982). Aggregates of coarse woody debris, in which marten and other mustelids often rest, are commonly found in steep-sloped, upper level riparian areas, made more attractive by woody debris that moves down slopes due to windthrow and earthflow (Harmon et al. 1986). Raccoons frequently use hollow trees, snags, and downed logs for breeding, resting and hiding cover (Kaufmann 1982, Raedeke et al. 1988). In Tennessee, raccoons showed a preference for tree cavities over ground burrows as den sites, and 74.4% of the den sites located during a radio tracking study were in tree cavities (Allsbrooks and Kennedy 1987). Raccoon dens are rarely far from water, averaging 67 to 140 m away with maximum distances of 180 to 800 m (Giles 1942, Stuewer 1943, Calbalka et al. 1953, Schneider et al. 1971, Hardy 1979, Taylor 1979, Allsbrooks and Kennedy 1987). Distance from water is also an important factor influencing den selection among red foxes and marten (Pils and Martin 1978, Buskirk et al. 1989). In New York, dens were most commonly located in dense cover less than .4 km from water (Layne and McKeon 1956). In a study in the northern Sierra Nevada, 58% of marten rest site observations were in live trees in riparian lodgepole associations

(Spencer 1987). In Wyoming, rest sites were significantly closer to streams or lakes (mean = 173 m) than expected from the distances between streams and lakes and 150 randomly chosen points within the study area (Buskirk et al. 1989). Skunks (*Spilogale putorius* and *Mephitis mephitis*), on the other hand, seem to avoid water and den in nearly any dry place, such as under buildings and in burrows (Bailey 1971).

Living vegetation rather than coarse woody debris or dead trees influences grizzly use of riparian areas. Grizzlies prefer alder and lodgepole "downfalls" and other dense, riparian vegetation for bedding down (Craighead et al. 1982).

Movement corridors

Carnivores will often follow streams for traveling, taking advantage of the water, vegetative cover, and food provided by the riparian area. Travel routes of otters generally follow streams and waterways. They will take overland routes across peninsulas formed by stream meanders but will generally follow stream routes (Melquist and Hornocker 1983). Raccoons use streams and greenbelts as corridors and travel routes in both urban and rural areas (Riley 1989, Sherfy and Chapman 1980). Black bears in California use riparian areas as traveling corridors (Kellyhouse 1980). Bobcats use thickets of river bottoms, swamps, dry washes, and brushy draws as travel corridors (Young 1958). Long-tailed weasels use waterways in daily activity, perhaps as dispersal and travel routes. In a study in Manitoba, trapping records of weasels showed that they were common in areas with waterways but absent in dry areas (Gamble 1981).

Effects of timber harvest

Impacts from habitat alteration due to clear-cut timber harvesting on Washington state carnivores fall into three groups:

- 1) adverse impacts usually resulting in a decrease in abundance and density, (black bear, grizzly bear, fisher, pine marten);
- 2) advantageous impacts usually resulting in an increase in abundance and density, (red fox, gray fox, bobcat);
- 3) unknown impacts, (raccoon, ermine, mink, long-tailed weasel, western spotted skunk, striped skunk, river otter).

These groups are based on results of studies performed in different regions of North America. Each study may or may not be directly applicable to animals in Washington state due to varying environmental conditions.

Clear-cutting

Clear-cut logging results in direct habitat loss for pine marten (Campbell 1979, Simon 1980, Spencer 1981). Campbell (1979) stated that marten in Montana did not use clear-cuts in the first year after cutting. Koehler and Hornocker (1977) and Soutiere (1979) found marten avoided large forest openings and clear-cuts in Montana and Maine, respectively. They reported avoidance of cut or severely burned areas for up to 15 years after the disturbance. Thompson (1982), working in Ontario, described marten abundance 2-3 times greater in undisturbed forests than in harvested areas. His capture rates in uncut forest were twice those in clear-cuts. Thompson et al. (1989) found marten tracks more abundant in uncut forest than in sites logged 5, 10, 20, or 30 years previous and use of stands logged up to 38 years earlier remained significantly lower than in uncut forest. In Maine, avoidance of clear-cuts was particularly pronounced during winter.

Marten used uncut softwood or partially cut mixed-wood stands more heavily than regenerating clear-cuts (Steventon and Major 1982). A Newfoundland study of marten by Snyder and Bissonette (1987) revealed tree DBH (diameter breast height) and stand size as the most significant variables in determining trapping success. Marten capture rates were greater in residual stands with an average tree DBH greater than 15 cm and 5-24.9 ha in size. The authors suggest that the apparent avoidance of large residual stands by marten was probably due to difficulty in sampling the larger stands. Overhead cover averaged 50-100% at successful trapping sites. Only 10.5% of the overall captures occurred in clear-cuts. These individuals may have been taking advantage of temporary increases in prey abundance. As plant growth in clear-cuts becomes more dense, it becomes more difficult for marten to capture prey. This may partially explain their avoidance of clear-cuts. Snyder and Bissonette (1987) also reported that marten tracks in snow on clear-cuts followed straight lines from one adjacent residual stand to another. In forested habitats, trails zig-zagged. Eighty-seven percent of open crossings were less than 250 meters long. During winter, 74% of all travel was in forested habitats. The authors conclude that larger residual stands and undisturbed stands, both greater than 15 ha, are important habitat components for marten in extensively clear-cut areas. Soutiere (1979) observed fewer tracks in winter, summer trapping success reduced by half, and lower marten densities in clear-cuts compared to undisturbed forests. Marten with significant amounts of clear-cut forests in their home ranges had significantly larger home ranges than those in uncut or partially cut forests (Soutiere 1979). In the taiga of interior Alaska, however, marten may not be as closely associated with older forest, and there is evidence that they respond positively to increased populations of microtine rodents which develop on areas following wildfires (Magoun and Johnson 1991). The possibility of higher marten populations on recently burned areas is currently under investigation (Johnson and Paragi 1992).

Speculation on factors resulting in reduced use of clear-cut areas by marten includes an open canopy (Koehler and Hornocker 1977), lower number of deadfalls (Steventon and Major 1982), and lower hunting success in regenerating forests (Thompson 1986).

Pine marten prefer old-growth habitat. Optimum habitat elements appear to be well established understory of trees, snags, stumps and fallen logs, and lush shrub and forb vegetation. These support squirrels and other small mammal rodent prey in mature old-growth spruce-fir communities with less than 30% canopy cover (Burnett 1981). They preferred stands with 40-60% canopy closure for both resting and foraging sites, and avoided stands with less than 30% closure (Taylor and Abrey 1982, Spencer et al. 1983). They also prefer mature coniferous or mixed forests with at least a 30-50% crown density (Clark et al. 1987).

Trees, snags, stumps, and logs provided 86% of the non-subnivean resting sites of the marten (Spencer 1987). Snags were used more, relative to availability, than any of the other three types of resting sites (Burnett 1981). Snags used as resting sites were almost exclusively large-diameter fir snags (mean = 102 cm DBH, range = 58-147). Observations in Wyoming showed a similar pattern. Fifty-six percent of rest-sites were in large Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) snags (Campbell 1979). Snags used by marten also retained most of their bark and had soft bases which provided cavities near or beneath the ground yielding ideal winter resting sites (Spencer 1987). Highly decayed logs, stumps, and snags were also used subniveanly (Spencer 1987).

Fishers (*Martes pennanti*) prefer habitat with extensive, continuous canopy and dense, lowland forests and spruce-fir forests with high canopy closure (deVos 1952, Coulter 1966, Clem

1977, Kelly 1977, Powell 1977, 1978). Fishers also avoid forests with little overhead cover and open areas (Coulter 1966, Clem 1977, Kelly 1977, Powell 1977, 1978). Fishers avoid non-forested areas (Coulter 1966, Kelly 1977, Powell 1977, 1978) but use clear-cut areas in the summer only when dense ground cover is available (Kelly 1977).

The effect of clear-cutting on black bear habitat use depends on a variety of factors including size of the clear-cut and post harvest treatment. On the one hand, black bear habitats are typically early successional areas with relatively inaccessible terrain, thick (dense) understory vegetation, and abundant sources of food in the form of shrub and treeborne soft or hard mast (Chapman and Feldhamer 1982). Most food items of the black bear are shade-intolerant, therefore, a large proportion of foraging occurs in openings (Rogers et al. 1988). Significant understory species include blueberry and huckleberry (*Vaccinium* spp.) and raspberry and blackberry (*Rubus* spp.). Considerable damage to young trees by black bears in western Washington indicates use of young second forests (Poelker and Hartwell 1973).

In western Washington, 9-14-year old clear-cuts were used more by bears than 27-year-old clear-cuts. Bears avoided 45-year old clear-cut areas. Berry-producing shrubs were 7-8 times more abundant in the 9-14-year old clear-cuts (Lindzey and Meslow 1977). However, elsewhere black bears avoid clear-cuts. Young and Beecham (1986) in North Central Idaho and Jonkel and Cowen (1971) in spruce-fir forests found that black bears generally avoided clear-cuts. Unsworth et al. (1989) reported that foods most frequently found in black bear scat were less common in clear-cuts (< 8 years old) than in mature forest stands. In part, observed black bear avoidance of clear-cuts might be a function of the size of the clear-cut. For example, Maine black bear were rarely found in clear-cuts beyond 135 yards from forest cover. They avoid large, unshaded openings because they are easily heat stressed (Hugie 1982). In addition, post harvest treatment of clear-cuts might create adverse habitat conditions for black bears. Black bear abundance is closely associated with availability of food sources, primarily berries. Silvicultural techniques which disturb vegetation preferred by black bears indirectly impact this species. The use of bulldozers and burning on harvested lands causes soil scarification and severe root damage to berry-producing shrubs. Unsworth et al. (1989) suggest that these practices may have a detrimental effect on black bear populations. Lindzey and Meslow (1977) suggest that broadcast burns or no burning be done to allow vegetation to shift from early to mid-seral stages, producing higher quantities of mast. Spraying to kill brush will also detract from the value of clear-cuts to black bears (Lindzey and Meslow 1977). Unsworth et al. (1989) suggest that the negative effects of clear-cuts could be minimized by harvesting small, irregularly shaped areas in a rotation requiring a 20-year green-up period before harvesting adjacent forests. Dense timber stands on north aspects and strips along streams and roads should be maintained for bedding and cover.

Grizzly bears (*Ursus arctos*) prefer open, early-seral vegetation (i.e., dry grass meadows, dry shrubland, and mesic shrubfields) to mature forest due to greater food abundance. Early-seral vegetation includes graminoids, yellow hedsarum (*Hedysarum sulphurescens*), buffaloberry (*Sheperdia canadensis*), and huckleberry (*Vaccinium* spp.) (Hamer and Herrero 1986). Grizzly bears inhabit forests open or immature forests with canopy cover less than 25%. Hamer and Herrero (1986) concluded that wildfires were essential to the maintenance of early successional stages for grizzlies.

Insofar as clear-cuts create early successional habitat conditions, grizzlies will use clear-cuts. However, Zager et al. (1977) reported 82% of established grizzly bear locations in clear-cuts to be less than 165 feet from cover. Grizzlies frequently used forested corridors when moving

between adjacent harvest areas. However, as habitat becomes more forested grizzlies are replaced by black bears (Hamer and Herrero 1986).

Red foxes utilized woods more in winter in Illinois, but dense forests are undesirable (Follman 1973, Samuel and Nelson 1982).

Partial cuts

Soutiere (1979) reported little difference in marten density between partially harvested and undisturbed forests. Partial harvesting involved removal of balsam fir (*Abies balsamea*) greater than 15 cm DBH and spruce (*Picea rubens*) greater than 40 cm DBH.

Selective cutting offers another alternative for black bears. In west-central Idaho selective cutting of 10-35 year old stands allowed the growth of a wide variety of black bear foods (Unsworth et al. 1989). In northern Idaho, black bear preferred 20-40-year old selective cuts during all seasons, possibly due to abundant food species and escape trees (Young and Beecham 1986).

Harvesting disturbance

Actual harvesting activity did not seem to cause any shifts in marten home ranges (Soutiere 1979), and individuals remained in the area despite ongoing timber harvest in close proximity (Steventon and Major 1982).

Grizzly bears require habitat that receives only light recreational, logging, or livestock use (Craighead et al. 1982). Consequently, extensive timber harvest activities will drive grizzly bears from an area.

Timber harvest activities provide suitable habitat for bobcat, red fox, and gray fox. Miller and Speake (1978) found bobcats intensively using recently logged areas because of increased prey species (*Sylvilagus* spp., *Peromyscus* spp., *Sorex* spp., *Thomomys* spp.) found in these areas. Sweeney (1978) reported mountain beaver (*Aplodontia rufa*) to be the primary component of western Washington bobcat diets. Bobcat ranges extended into clear-cut areas with lush, understory vegetation that supported mountain beaver. If ledges are present within a logged area and urban development does not surround it, bobcat can use the remaining natural habitat (Chapman and Feldhamer 1982).

The Wildlife Habitat Management Handbook (1971) states that most types of tree harvest benefit red foxes. Regeneration should maximize edge effects and conversion of pine forest to mast and fruit producing hardwoods to enhance red fox habitat. The handbook describes red fox as a forest edge and open land animal that avoids virgin forests and treeless prairies. During the eighteenth and nineteenth centuries as northeastern U.S. forests were cut, the red fox increased its range, moving on to new farmlands. The gray fox also benefits from edge effects (Trapp and Hallberg 1975). Wood et al. (1958) suggested that a trend in Georgia to decrease cultivated land and increase timber and pasture land would reduce the state's gray fox population.

Use of riparian buffers

Stands need not be large to be used by marten. Riparian areas are used for foraging. Small, scattered old-growth stands may be sufficient for marten if located adjacent to riparian areas (Spencer 1981). The impact of clear-cutting may be reduced by leaving clusters of trees no further than 50 m apart and leaving logs and slash for foraging, winter dens, and subnivean travel (Campbell 1979, Simon 1980, Spencer 1981).

UNGULATES

Six wild ungulate species are found in the Pacific Northwest (PNW). Five of these occupy riparian zones. Their dependence on riparian zones varies over time and with other available habitat on a landscape level. The sixth species, the mountain goat, *Oreamnos americanus*, is generally not associated with riparian habitats in forests of commercial value (Rideout 1978). In the past two decades it has become evident that riparian zones play a major role in ungulate ecology in forested as well as unforested habitats. Consequently, timber management practices that impact riparian zones may affect ungulates negatively or positively. Ungulates can be divided into three groups in relation to their need for riparian habitat types.

Use of riparian habitats

Relative dependency on riparian zones

Obligate inhabitants of riparian zones

The Columbian white-tailed deer, *Odocoileus virginianus leucurus*, is found in southern Washington and northern Oregon along the Columbia River. It is well isolated from other white-tailed deer populations (Halls 1984). Gavin (1984) describes sightings until the 1940's of the Columbian white-tailed deer; they all appear to be within riparian zones of the Columbia River system. Today, the Columbian white-tailed deer is restricted to the lower Columbia River bottomlands, which have little elevational relief. The native vegetation at these sites consists of a dense shrub and tree community containing Sitka spruce (*Picea sitchensis*), red-osier dogwood (*Cornus canadensis*), black cottonwood (*Populus nigra*), red alder (*Alnus rubra*), and willow (*Salix* sp.) (Franklin and Dyrness 1984). Small, isolated populations of the Columbian white-tailed deer are also found along a few large rivers in Oregon (Gavin 1984). This subspecies might be restricted to riparian zones. Because its present range is limited to habitat along large rivers, its conservation might be more related to agriculture than forestry. Riparian zones along the larger rivers have been converted to fields or urban areas (Raedeke et al. 1988).

The Columbian white-tailed deer has the smallest rumen volume:body weight ratio of any white-tailed deer subspecies (Dublin 1980). This implies a high quality diet consisting of large amounts of browse and herbs and low amounts of grasses (Hanley 1982, Hofmann 1988). In the PNW, this combination of foods is found year around only in riparian habitats. Dublin (1980) found that Columbian white-tailed deer relied heavily on high quality food throughout the year. This suggests that the Columbian white-tailed deer might require riparian habitats. If this is the case, we would expect to find it only along large rivers, because they provide riparian zones large enough to sustain populations throughout the year.

Habitat generalists that use riparian zones

Habitat generalists that use riparian zones in the PNW include Rocky Mountain white-tailed deer, *O. v. ochronra*; Columbian black-tailed deer, *O. hemionus columbianus*; sitka black-tailed deer, *O. h. sitkensis*; mule deer, *O. h. hemionus*; Rocky Mountain elk, *Cervus elaphus nelsoni*; Roosevelt elk, *C. e. roosevelti*; 2 subspecies of moose, *Alces alces shirasi* and *A. a. andersoni*; and woodland caribou, *Rangifer tarandus caribou*. The Rocky Mountain white-tailed deer is found east of the Cascade Range (Peek 1984). The Columbian black-tailed deer is found throughout the PNW west of the Cascade Range. North of Vancouver Island, it is replaced by the

Sitka black-tailed deer, and east of the Cascades it is replaced by the mule deer (Wallmo 1981). The distributions of these 3 subspecies are almost continuous and some traits intergrade, forming a cline (Covan 1956).

The Rocky Mountain elk occurs in the Cascade Range and eastern Washington. These populations are the result of several transplants in the beginning of the century (Thomas and Toweill 1982). From the Olympic Peninsula to northern California along the Pacific coast, the Roosevelt elk occupies coastal forests such as the Sitka, western hemlock (*Tsuga heterophylla*) and redwood (*Sequoia*) temperate coniferous zones. Both subspecies are common throughout their range (Thomas and Toweill 1982).

Alces alces shirasi ranges from eastern Washington into Idaho and Montana. It is replaced by *A. a. andersoni* in the extreme northeast of Washington and southeastern British Columbia (Franzmann 1978, Hall 1981). Washington is the southernmost extension of this subspecies.

The woodland caribou occurs in the northeast corner of Washington (Bergerud 1978, Williams and Heard 1986). The majority of its range is boreal forest and taiga biome (Franzmann 1978, Williams and Head 1986). The woodland caribou found in Washington constitutes the southern Selkirk herd of approximately 30 individuals, which also ranges into adjacent Idaho and southern British Columbia. The recovery plan for the herd has the objective of having a self-sustaining caribou herd in this region (Danielle 1983). Because this herd is very isolated from the nearest herds of other woodland caribou in southern British Columbia (Stevenson and Hutler 1985), establishment of satellite herds has been recommended (Danielle 1983, Stevenson and Hutler 1985). Thus this subspecies must be considered closely in relation to forest practices in Washington in the future.

Historical records of caribou show that large population fluctuations occur. These fluctuations display no predictable period or amplitude, therefore, they should not be termed cycles. The causes and long-term dynamics of caribou fluctuations are poorly understood (Valkenburg and Davies 1989, Alaska Dept. of Fish and Game 1990); however, hunting, predation, and changes in range conditions are known to influence population size (Bergerud 1978). Therefore, it can be problematic to sort out these effects from the effects of silvicultural practices on population fluctuations.

None of these ungulates are tied exclusively to riparian zones. Rather they utilize riparian areas for food, cover, or water to varying degrees depending on season, local temperature and moisture regimes, and the habitat types available on a landscape level.

In addition to wild ungulates, forested riparian areas east of the Cascade range are often used for cattle grazing. In many places this has caused vegetational changes (Hall 1988). This is very important to keep in mind, if riparian buffer zones are to be managed for wildlife. For example, Loft et al. (1991) found that female mule deer showed habitat shifts in response to cattle grazing.

Infrequent inhabitants of riparian areas

The mountain goat is not considered dependent on riparian habitat types as it requires vegetation types above and around timberline (Rideout 1978). These areas are generally not of significant value for commercial timber harvest (Franklin and Dyrness 1984); however, information on habitat preference in the Cascade Range is relatively limited compared to other ungulates in Washington State.

Species requirements provided by riparian habitats

The most important characteristics of riparian areas for ungulates are the presence of free water, high quality foods, and cover. The dependence of ungulates on these habitat factors often varies seasonally.

Food and water

All wild ungulate species in the PNW have been reported to utilize riparian zones to obtain drinking water, and strong relationships between habitat use and the availability of water have been established (e.g., Thomas et al. 1979, Carson and Peek 1987).

Black-tailed and mule deer: In north-central Washington conifer and riparian habitat provided high forage availability and quality for mule deer (Carson and Peek 1987). The quality and quantity of forage in riparian areas were also important to mule deer in southeastern Oregon (Dealy et al. 1981, Leckenby et al. 1982). The availability of free water seemed to be important during summer in these studies.

White-tailed deer: Columbian white-tailed deer utilize and seem to depend almost exclusively on the high quality forage in riparian zones. In addition, riparian agricultural fields are used as foraging areas (Dublin 1980, Gavin 1984). Rocky Mountain white-tailed deer do not seem to depend on riparian vegetation for food (Peek 1984, Halls 1984).

Elk: Marcum (1976) found that elk on their summer range in the dry forests of western Montana most frequently selected areas within 46 m of water. Areas within 320 m of free water were utilized in excess of their availability, whereas areas more than 320 m from water were not. Dependence on free water increases as the climate gets dryer. In the arid shrub-steppe of eastern Washington, natural springs were especially important to lactating females, whereas bulls were less constrained by free water (McCorquodale et al. 1986). Preliminary results from the Colockum study in central Washington indicated that half of the observed elk were within 200 m of water (Musser and Bracken 1990); however this study used radio telemetry observations obtained only during daylight hours. In the wetter forests of the western Cascades access to free water is less critical (Schoen 1977). The degree to which elk depend on free water in western Washington has not yet been determined (Lyon 1980, Raedeke et al. 1988). On the Olympic Peninsula Jenkins and Starkey (1984) showed that old-growth bottomland forests provided adequate forage for Roosevelt elk over most of the year; however, alluvial and colluvial substrates were also important seasonally. Other studies have also indicated the importance of riparian zones as foraging areas for elk (Marcum 1976, Schoen 1977, Thomas et al. 1979).

Moose: Moose are primarily browsers and require high quality regenerating forest communities, where they utilize deciduous shrubs and young trees (Coady 1982). Their use of riparian vegetation seems to depend on the availability of suitable upland vegetation. Use of aquatic areas and communities has been observed in all populations of moose, but it is difficult to determine how important these are. In Nova Scotia aquatic habitats were relatively unimportant when moose populations were high (Telfer 1967). Other studies have reported extensive use of aquatic habitats for feeding on emergent and submergent vegetation (Peek et al. 1976, Coady 1982).

Throughout Alaska, riparian willow communities provide moose with browse during winter (LeResche et al. 1974). Riparian habitats also serve as calving and summering areas for moose in interior Alaska (LeResche et al. 1974). Streamside habitat provides high quality food, adequate water, and cover for female moose with calves. Moreover, protection from predators is

an important feature of riparian areas (Franzmann 1978). During winter, riparian willow communities provide moose with high quality browse. These early- to mid-successional stage riparian zones are essential to moose, unless early successional forage is available from regenerating burns or logged areas (LeResche et al. 1974). In Idaho (Pierce and Peek 1984) winter browse in old-growth and mixed-age stands constitute a large part of the winter diet for moose.

Caribou: Woodland caribou sometimes use streamside habitat (Danielle 1983) or muskegs (Darby and Duquette 1986), perhaps because of the availability of high quality food; however, this use seems to be limited. Information on use of riparian areas is not available for the Selkirk herd, although several studies currently are underway.

Cover

Riparian zones, as discussed in the introductory section, often support dense and structurally diverse vegetation. These areas can therefore provide important thermal, escape, and hiding cover for ungulates. Hiding cover was defined by Thomas et al. (1979) as any vegetation capable of hiding 90% of a standing adult deer or elk at 61 m or less. Thermal cover is provided if the canopy is 12 m in height with at least 70% tree canopy cover (Witmer et al. 1985). Riparian zones are used for thermal cover only if timber is large and dense enough (Oakley et al. 1985). In severe winters with heavy snowfall, riparian zones may be the only habitat where snow does not render the habitat unsuitable for ungulates such as deer, elk, and moose (Oakley et al. 1985). Escape cover has not been formally defined but can be understood to mean any vegetation that can partially obscure an animal. When ungulates are disturbed they escape to the nearest cover and continue from there to more dense hiding cover (Loft et al. 1984, Jeppesen 1987).

Black-tailed and mule deer: In southeastern Alaska old-growth and large saw-timber reduce snow depth on the forest floor (Kirchhoff and Schoen 1987). Snow interception reduces locomotion costs for deer (Parker et al. 1984). Cover by large canopy trees also provides thermal cover (Thomas et al. 1979).

In northern California, Columbian black-tailed deer utilize timbered stringers within clear-cuts as escape routes to more dense cover (Loft et al. 1984). Migrating mule deer in southeastern Idaho select open nonagricultural cover types in spring and fall (Thomas and Irby 1990); however, human disturbance was minimal within the study area.

In north-central Washington, mule deer utilize riparian habitat, which provides excellent thermal and escape cover throughout the year (Carson and Peek 1987). Riparian areas comprised 1.8% of the area but received 23% utilization. Studies in southern Oregon have also indicated the importance of riparian zones in providing cover for black-tailed deer (Dealy et al. 1981, Leckenby et al. 1982).

White-tailed deer: Along the lower Yellowstone River, Compton et al. (1988) found that the most significant habitat attribute for white-tailed deer in riparian zones was shrub and forest cover. Only 30% of the available habitat was riparian forest, but it received 70-80% use. Portions with high deer densities also had greater river sinuosity and larger tracts of riparian cover. Channel sinuosity may be an important factor determining relative abundance of riparian cover (Compton et al. 1988). As sinuosity increases, the area of alluvial flats increases, thereby creating larger patches of riparian vegetation. Compton et al. (1988) concluded that the amount of riparian cover probably determined the number of white-tailed deer that bottomland habitat can support. Any substantial decrease in cover through interruption in succession in riparian communities, as

may occur with alterations of streamflow and dynamics or logging of riparian timber, may reduce the potential for sustaining deer. The relative density of white-tailed deer in the lower Yellowstone River drainage varied directly with availability of riparian forest and shrub cover (Dusek et al. 1989).

Elk: The importance of riparian zones in providing escape and hiding cover for elk has been demonstrated in many projects (e.g., Taber 1976, Thomas et al. 1979, Oakley et al. 1985). Studies on the Olympic Peninsula have shown the importance of cover for Roosevelt elk (Witmer 1982). Old-growth bottomland forests provide adequate cover for Roosevelt and Rocky Mountain elk during most of the year (Hanley 1983, Jenkins and Starkey 1984).

Moose: In north-central Idaho a radio telemetry study by Pierce and Peek (1984) indicated the importance of old-growth and mature mixed-age stands as cover for moose. Mature conifers are important because they intercept snow; snow depths of 60-70 cm impede moose movement, and snow depths greater than 90 cm severely restrict their movement (Coady 1974). Mature stands are also used by moose for escape from predators. At Isle Royale cover seems to be more important than food availability, especially during calving (Edwards 1983).

Caribou: Escape cover for woodland caribou differs from that of other ungulates. Woodland caribou do not aggregate into large herds like the barren ground Rangifer. Rather, they stay in small groups scattered throughout suitable habitat, like forest reindeer in Fennoscandia and European Soviet Union (Eriksson 1975, Baskin 1986). Though woodland caribou are forest animals, they prefer semi-open habitat and require good visibility to avoid predators (Klein 1986). This is important when managing riparian zones for caribou and is in strong contrast to other ungulate species, which require closed stands for cover.

Seasonal use of riparian zones

Use of riparian zones by PNW ungulate species varies from year-round to highly seasonal, depending upon the species and location. Many seasonal shifts in use of riparian zones, as outlined below, are associated with annual breeding and movement patterns.

White-tailed deer: Along the lower Yellowstone River white-tailed deer strongly prefer riparian forest throughout the year; no major seasonal differences have been observed (Dusek et al. 1989). Similarly, year-round use of riparian zones has been reported for white-tailed deer at the George Reserve from a habitat use study using radio collared animals (Beier and McCullough 1990). In contrast white-tailed deer in northeastern North America likewise utilize forest stands along lakes and rivers primarily during winter. These provide cover and forage. During summer they consistently select habitats that contains mixed stands, openings, and clear-cuts (Halls 1984).

Moose: In Alaska riparian willow communities are the year-round habitats of moose at the edges of their geographical range (Svendsen 1987). In the boreal forest zone, riparian zones become important winter habitats wherever they occur (LeResche et al. 1974). As forest habitats become more diverse (i.e., at lower latitudes) the dependence on riparian habitat tends to diminish (LeResche et al. 1974). Shrub communities are important winter forage habitat for moose in the western North America (LeResche et al. 1974, Peek et al. 1976); however, when deep snow accumulates at higher elevations, shrub communities are abandoned in favor of lowland riparian areas (Coady 1982).

Riparian habitats serve as calving and summering areas for moose in interior Alaska (LeResche et al. 1974). The streamside habitat provides high quality food, adequate water, and cover for females with calves as well as protection from predators (Franzmann 1978).

Black-tailed and mule deer: Most seasonal variation in habitat use by black-tailed deer has been associated with seasonal changes in the availability of food and protective cover (Dasmann and Taber 1956, Mackie 1970, Loft et al. 1984, Murphy et al. 1985). Food availability depends on phenological changes in the landscapes, which in turn vary with elevation. During winter, only forested areas provide cover, whereas grasslands and cut-over areas provide some cover during summer. On the west side of the Cascades, black-tailed deer utilize riparian areas during fawning.

Mule deer fawns in the Missouri Breaks of north-central Montana select habitat types with dense vegetative cover and typically use the mid- and lower portions of slopes. Seasonal shifts in habitat use are correlated with desiccation of herbaceous cover and associated changes in the diet of does (Riley and Dood 1984). Coniferous and riparian habitat types are important mule deer fawning areas in north-central Washington (Carson and Peek 1987), in the Great Basin of southeast Oregon (Leckenby et al. 1982), in wooded riparian areas of the northern Great Plains (Uresk 1983), and along the mid-Columbia River (Fielder and McKay 1984). Both cover and plant phenology influence selection of riparian zones during fawning.

In the Blue Mountains of Oregon and Washington riparian zones provide migration routes for seasonal movements between winter and summer range (Thomas et al. 1979). Similarly, in northern California Columbian black-tailed deer utilize riparian areas as seasonal migratory routes between summer and winter ranges (Loft et al. 1984). In contrast, mule deer in southeastern Idaho do not preferentially use riparian areas during migration (Thomas and Irby 1990); however, hunting season in this region did not coincide with fall migration during this study, and the deer might have been more likely to use open slopes.

Elk: In western Washington the mountain hemlock (*Tsuga mertensiana*) zone is little used by elk at any season. The true fir (*Abies*) zone is favored only during summer and rut; clear-cut areas and second-growth in this zone are favored over old-growth and are most heavily used in fall and winter. Riparian zones and wetlands are used during all seasons, especially in winter, spring, and during the rut (Taber 1976).

Like black-tailed deer, Roosevelt elk on the west side of the Cascades elk utilize riparian areas during calving, presumably because of the proximity of open water or other habitat attributes found in the riparian area. The width and type of vegetation needed to maintain the integrity and value of riparian habitat for deer and elk have not been thoroughly investigated (Witmer et al. 1985, Harper 1987, Raedeke et al. 1988).

Caribou: Woodland caribou exhibit seasonal differences in habitat use. During summer, alpine areas are used for foraging. Seasonal changes in habitat use by the Selkirk herd cover a wide range of elevations within the range of commercial timber harvest. During the rut in the early fall, considerable movement takes place, but data on habitat selection are not yet available. In fall and winter caribou are reported to use low elevation forests, where they forage on arboreal lichens. Old-growth stands are important throughout winter whenever severe storms increase the availability of arboreal lichens by blowing down limbs and branches (Rominger and Oldemeyer 1989). During spring low elevation valley bottoms with Engelmann spruce/subalpine fir (*Picea engelmannii/Abies lasiocarpa*) forests interspersed with wet meadows are used as foraging sites (Danielle 1983, Stevenson and Hatler 1985). During spring the Selkirk herd uses cutover areas for forage, because of accelerated snowmelt, which allows early green-up (Servheen and Lyon 1989). Spring habitat appears to be the only seasonal habitat that can be created or improved through clear-cutting or selective harvest (Servheen and Lyon 1989).

Calving areas of the Selkirk herd of woodland caribou are poorly documented. It is thought that calving occurs in snow-free areas at high elevations, but cows with newborn calves have also been observed in timbered areas (Danielle 1983, Stevenson and Hatler 1985). In the central Arctic, Jakimchuk et al. (1987) observed that female caribou avoided riparian areas during the spring calving period whereas males preferentially used these areas. They attributed this to females avoiding increased predation pressure in riparian areas (Jakimchuk et al. 1987).

Effect of timber harvest

Clear-cutting

Complete removal of the overstory promotes growth of many herbaceous forage species, resulting in excellent forage opportunities for deer (Nyberg 1987) and elk (Brunt 1987); however, it is important to keep in mind that these areas can only be utilized if all other requirements are within close proximity (Brunt 1987, Thomas et al. 1979). Seeding of grasses and legumes does not appear to enhance elk use of clear-cuts (Skovlin et al. 1989).

Disturbance by clear-cutting or fire has three major effects on deer forage plants in forests of the PNW: a change in plant species composition, an increase in forage production, and changes in nutrient quality (Taber and Hanley 1979). Although the composition of the plant community growing within a clear-cut area depends upon the composition of the understory before disturbance, it is also affected by soil disturbance during logging, methods of slash disposal, fire, and herbicide treatment (Taber and Hanley 1979). Removal of trees, whether by thinning or clear-cutting, encourages understory plants that constitute potential deer forage. The degree of use that a foraging area will receive is dependent upon deer density, home range size, and quality of the habitat in terms of degree of interspersion, species composition, and adequacy of escape and thermal cover.

Deer density, home range size, and clearing size interact in determining the potential use of a given clear-cut (Taber and Hanley 1979). For an animal to be attracted to a clear-cut, it must be aware of the cut area. In this respect home range size is important. Black-tailed deer generally have relatively small home ranges. Assuming an average seasonal home range of about 80 ha, a black-tailed deer would be expected to be aware of a new clear-cut at a distance of about 1 km, and a 10-ha clear-cut in a mature forest with 4 deer per km² will attract about 4 deer. However, larger clear-cuts would still only attract about 4 deer.

Some plants respond to herbivory by changing their chemical composition to render their tissues less suitable to herbivores (Crawley 1983, Rhoades 1985). This response to herbivory depends on the carbon/nutrient balance within the plant and the carbon/nutrient balance within the ecosystem; these vary with successional stage (Bryant 1985). In southeast Alaska, it has been shown that timber harvest influences the yield and protein content of *Vaccinium* browse.

In the rainforests of the PNW early stages of succession following logging or fire provide favorable habitat for deer unless snow accumulations restrict foraging during winter (Wallmo 1981). Old-growth timber or thinned mature stands with understory vegetation and the ability to intercept snow are critical for deer if permanent snow accumulates during winter (Jones 1974).

Bitterbrush and snowberry are important for mule deer in the sagebrush steppe and ponderosa pine zones of eastern Washington (Wallmo 1981). Mule deer in eastern Washington summer in the mountains and winter at lower elevations where forage is more accessible (Wallmo and Regelin 1981).

White-tailed deer utilize early successional stages after fire or logging for forage, as long as cover is not far away (Peek 1984). During winters with light snow open areas are utilized for forage, while during winters with heavy snowfall open areas are abandoned and white-tailed deer are restricted to forest stands that intercept snow; these are usually closed-canopy mature forests (Peek 1984).

Early successional stages are highly preferred by moose for foraging because of their shrub/young tree component (LeResche et al. 1974). Early successional plant communities associated with riparian zones are especially important as feeding areas for moose (LeResche et al. 1974, Coady 1982). In a long-term study in Minnesota, clear-cutting was beneficial in providing abundant deciduous browse for moose, if adequate cover for winter was provided (Peek et al. 1976). Lowland mid-successional stage plant communities were utilized throughout the year.

In northwestern Ontario moose preferred mixed hardwood and conifer stands during winter because these offered less snowpack than clear-cuts but still provided critical browse (Mastenbrook and Cummings 1989).

Woodland caribou are displaced by logging operations (Darby and Duquette 1986). In Alberta, caribou did not feed in clear-cuts larger than 2 ha, and only very occasionally crossed any larger clear-cuts (Edmonds and Bloomfield 1984). Bergerud et al. (1984) argued that increased hunting and predation are the main causes of caribou declines rather than habitat disturbance per se. They found evidence that increased road access resulted in greater hunting mortality among caribou, and increased moose density resulted in greater wolf predation on caribou (Edmonds and Bloomfield 1984). Nevertheless, forage and range conditions can limit *Rangifer* population size and affect distribution (Klein 1968). Caribou have low reproductive potential (Bergerud 1978), and occupy habitats in which deep snow can limit food availability (Darby and Pruitt 1984). The low density of woodland caribou in boreal forest (Fuller and Keith 1981, Darby and Duquette 1986) is a reflection of low productivity in this environment. As a consequence of their low density, populations of 50 caribou are very sensitive to slight changes in productivity or mortality (Bergerud 1978). Displacement to less suitable habitat may result in the carrying capacity being exceeded; this has been shown for Norwegian reindeer (Reimers et al. 1983).

Selective cutting

Jenkins and Starkey (1990) concluded that thinning practices produced only negligible forage benefits for elk in regenerating Douglas-fir stands in western Washington. It appeared that herbaceous forages important to elk had already declined by the time stands were thinned at approximately 20 years of age. In the Blue Mountains of Oregon, Skovlin et al. (1989) came to similar conclusions; elk use had already returned to prelogging levels after 5 yrs. Partial cuts were used the least because they neither afforded good cover nor increased the available forage (Skovlin et al. 1989). The same was concluded for small-stem lodgepole pine (*Pinus contorta*) stands in the Rocky Mountains (Lyon and Barger 1987).

Forest practices that produce large amounts of browse while maintaining winter cover appear to enhance moose habitats (Monthey 1984). Where a variety of forest practices such as clear-cutting, selective cutting, and buffer stands were used within a predominantly clear-cut forest in northern Maine, a mosaic of forage and winter cover areas favorable to moose was created (Monthey 1984). In contrast, partial stand harvesting resulted in a more homogeneous habitat with less browse available for moose.

Integrated management can be beneficial to both timber and ungulates (Brunt 1987, Nyberg 1987). Commercial thinning has been of special concern since it reduces a stand's ability to provide adequate cover for elk at certain times; however, thinning eventually enhances a stand's ability to intercept snow because it stimulates growth of wider crowns and stronger branches (Brunt 1987). On the other hand, removing understory species which compete with crop trees not only reduces forage availability in the short term but also encourages tree growth, which reduces the time during which the stand provides forage (Brunt 1987).

Interspersion of different aged stands

The use of different habitat types by ungulates varies spatially and temporally. Ungulates utilize habitat types on a landscape level. Different habitat types are needed simultaneously to maintain viable ungulate populations. The spacing, size, and juxtaposition of different habitat units can be critical (Thomas et al. 1979, Wisdom et al. 1986, Raedeke et al. 1988).

Moose require an interspersion of early and late successional stages (Welsh et al. 1980). Old-growth grand fir/Pacific yew (*Abies grandis/Taxus brevifolia*) stands in Idaho provide critical winter habitat for moose; even-aged pole timber stands and open areas, including clear-cuts and lakes, are only used during summer (Pierce and Peek 1984). Optimum moose habitat contains both disturbed areas providing food and mature conifers for cover (Hamilton and Drysdale 1975). Large areas disturbed by logging retain little cover and hence are not as useful for moose as small ones (Telfer 1978, Hamilton et al. 1980). In Ontario moose cows with calves utilized 18-yr-old cutovers if at least three residual stands of timber were present and the cutovers did not exceed 64 ha in early winter and 16 ha in late winter. In addition, at least one of the residual stands needed to be a mesic upland habitat of at least 107 ha (Thompson and Vukelich 1981).

In the coastal forests of Washington, Roosevelt elk are most abundant in floodplains, deltas, beaver meadows, and other areas associated with fluvial activities. These areas provide continuous forest cover interspersed with moist, productive forage areas throughout the year (Raedeke and Taber 1982, Jenkins and Starkey 1984).

Young stands are used for escape cover by elk and deer (Thomas et al., 1979, Brunt 1987, Wisdom et al. 1985). Forested areas are utilized by mule and black-tailed deer for cover during winter, and for water, cover, and food during summer and winter (Wallmo and Regelin 1981). Most deer and elk winter ranges in coastal areas include old-growth forests, which possess excellent winter forage availability and snow interception characteristics (Carpenter and Wallmo 1981, Brunt 1987).

The size of a clear-cut unit affects its use by both deer and elk. Foraging areas should be near escape cover and, in winter, to thermal cover (Brunt 1987, Nyberg 1987). Forest edges between early and late seral stage forest communities are extremely important for deer and elk (Hanley 1983, Brunt 1987, Nyberg 1987). In northern Maine white-tailed deer were adversely affected by extensive clear-cutting. Softwood stands of at least 2 ha separated by narrow clear-cut strips were recommended to promote white-tailed deer (Monthey 1984). The dependence of deer on mature softwood stands is related to their greater snow interception ability (Keraney and Gilbert 1976, Wallmo and Schoen 1980, Monthey 1984, Kirchhoff and Schoen 1987).

Response to harvest disturbance

If disturbance by logging results in increased activity budgets, the health of the animals might be impacted. Consequently, Darby and Duquette (1986) recommended that logging be

restricted to summer. In Montana the fidelity of elk to their home ranges decreased only slightly in response to logging activities (Edge et al. 1985); however, all elk had extensive areas of cover available within their traditional home ranges. A buffer zone of 500-1,000 m separated areas of high elk use from areas of disturbance (Edge and Marcum 1985). Hershey and Leege (1982) reported that cow elk demonstrated home range fidelity regardless of disturbance, phenological conditions, and changing weather.

Slash treatment

The effects of broadcast burning on ungulates are not well understood. It has been suggested that broadcast burning enhances forage quality for deer and elk (Wisdom et al. 1988). However, an analysis of forage quality in response to burning after logging indicated that burning did not promote a detectable increase in quality in shrubs commonly utilized by elk and deer; rather, quality decreased in species sensitive to site conditions (Friesen 1991).

Large slash left in piles after logging operations can provide cover for deer (Bartels et al. 1985), but often slash has a negative impact on movements of ungulates (Thomas et al. 1979, Witmer et al. 1985).

Burning following clear-cutting reduces slash, thereby enhancing access for elk, and provides space for growth of preferred species. The release of soil nutrients also increases soil productivity (Brunt 1987). A comparison of elk use in Oregon on burned and unburned logging units after harvest showed that burning was followed by decreased use for 2 yrs, but use increased during the following 2 yrs (Harper 1987).

Use of riparian buffer strips

As noted in the background section, riparian areas serve as natural travel corridors because of their shape, extension from high to low elevations, and habitat characteristics. This is especially true of riparian buffer strips remaining in a logged landscape. One reason ungulates travel along timber strips is the snow interception provided by mature conifers. In the Cedar River drainage, Washington, riparian areas were used as travel corridors by elk (Taber 1976). Mastenbrook and Cummings (1989) showed that timber corridors or scattered coniferous stands may be used as escape cover, thermal cover, or travel zones by moose. These results suggest that riparian buffers remaining after timber harvest may be beneficial to moose. Similarly, Darby and Duquette (1986) recommended leaving buffer zones of standing timber 1-2 km wide around the majority of the winter range for woodland caribou and restricting cutting to summer.

Riparian zones provide more edge than the surrounding upland forests because of their linear shape and the high disturbance regime experienced in and around streams (Thomas 1979, Harper 1987). This increases the habitat for black-tailed deer and elk, which benefit from edge (Taber and Raedeke 1980, Hanley 1984). Aerial surveys in Ontario showed that corridor edges within a clear-cut were either preferred by moose or used in proportion to their availability. Thus timber strips are an effective management option for increasing the amount of cutover area available for use by moose because they increase the amount of edge in relation to cutover areas (Mastenbrook and Cummings 1989).

Riparian buffer zones may also be a useful tool to provide escape and thermal cover for ungulates along clear-cuts (Taber and Hanley (1979). Furthermore, unharvested riparian buffers will eventually provide mature trees that intercept snow. This is important in eastern Washington and at elevations in western Washington above 610 m, where snow may be permanent for several

months in some years. If riparian buffer zones along streamsides are provided in western Washington, they will likely serve as hiding and thermal cover for black-tailed deer.

Timber corridors are generally not used as feeding areas (Mastenbrook and Cummings 1989); however, buffer zones adjacent to clear-cuts and young regenerating stands might be used by high numbers of deer since the juxtaposition of these habitats would provide both cover and forage. Columbian black-tailed deer in northern California utilized timbered strips within clear-cuts as escape routes to more dense cover (Loft et al. 1984). In southwestern Montana mule deer on exposed winter ranges selected feeding sites where forage availability, security, and thermal cover were optimized (Wamboldt and McNeal 1987).

The narrow riparian buffer strips provided by the current regulations in Washington may provide only escape cover and not hiding or thermal cover. If buffer zones along streams were wide enough, they could also provide hiding cover for elk, deer, and moose (Oakley et al 1985) but the required width may differ east and west of the Cascade Range.

Many ungulate species are dependent on riparian zones for critical stages of their life cycle (Oakley et al. 1985) or for high quality forage or cover (Raedeke et al. 1988). As a consequence, biotic disturbance from ungulates can be extensive. Herbivores may alter structure and function of riparian zones (Hanley and Taber 1980, Pastor and Naiman 1992). Selective feeding by herbivores may alter species composition and/or plant diversity. This is important to keep in mind if riparian buffers are provided as a substitute for rather than in addition to existing forage and cover areas. The greatest use of streamsides occurs in late successional patches of riparian communities (Kauffman 1988). However this does not infer that early- to mid- successional stages are unimportant. They receive great herbivore impact as well.

Ungulates are not confined to a single habitat type (Thomas et al. 1979, Raedeke et al. 1988). They utilize entire landscapes consisting of several different habitat types, daily as well as seasonally. This is in sharp contrast to small mammals and amphibians, which are characterized by availability of most requirements for a particular species within a given habitat type and by low mobility. The amount and juxtaposition of habitat types required to maintain an ungulate population are usually found in a landscape matrix or patchwork (Thomas et al. 1979). In particular, forest edge is important for elk and deer. Habitat selection studies of Rocky Mountain elk (Hanley 1983, Musser and Bracken 1990) and Columbian black-tailed deer (Hanley 1983) have indicated that these species prefer ecotones. The areas immediately inside stands of timber adjacent to clear-cuts are most heavily utilized, probably because these areas provide cover as well as adequate forage as a result of increased light. Thus management of riparian buffer zones must be viewed in the context of entire landscapes and how these are utilized by ungulates rather than as isolated entities.

In Florida riparian corridors are viewed as an integral part of applied landscape ecology in terms of both content and context (Noss and Harris 1989). Riparian corridors are considered to be landscape linkages as well as systems of their own. Noss and Harris (1989) describe 163 m buffers on either side of rivers used by river otters, bobcats, and black bears; however, no data are available yet on the width of buffers used by deer.

Current knowledge of wildlife use of riparian zones along large streams and rivers suggests that riparian buffer zones along streams with early- to mid- successional stage plant communities should be delineated along the border between riparian and upland areas, rather than along a predetermined width. This procedure provides ungulates with riparian forests of a variety of patch sizes. Sinuous streams, because they provide larger patches of riparian habitat, will be

most beneficial to ungulate populations in Washington. For buffer zones along streams and creeks with very narrow or non-distinct riparian vegetation, a predetermined width would probably be advantageous, since the vegetation along narrow streams is very similar to that of the nearby upland. The denser the vegetation the thinner the buffer can be and still to provide adequate hiding cover for ungulates.

Potential interspecific interactions

If ungulates are to be managed on a landscape level, possible ecological interactions between sympatric species should be considered. A given management scheme may prove positive to one species but detrimental to another. Accordingly, such interactions need to be considered in designing riparian management zones.

Bergerud et al. (1984) showed that increases in moose were accompanied by adverse effects on woodland caribou. Darby and Duquette (1986) suggested that in areas managed for woodland caribou moose and deer densities should not be allowed to rise as a consequence of large scale logging. They recommended prohibitions on burning, to stimulate growth of lichens, and application of herbicides, to reduce browse for deer and moose and stimulate conifer regeneration beneficial to caribou.

In the last decade the beavers have increased dramatically in numbers and distribution in Washington (Naiman et al. 1988). As a consequence, many streamside riparian areas are rapidly being converted from forest to meadow. This dramatic change may influence elk and deer in both eastern and western Washington. Presently, little data are available on the consequences of this habitat conversion for elk and deer; however, some possible interactions between beaver and cervids can be suggested. Loss of thermal and hiding cover may be detrimental. On the other hand, wet meadows will provide elk with an increase in high quality forage. Both beaver and deer are browsers, but in spite of dietary overlap between the two species, they may not impact each other negatively. Furthermore, beaver logging activity may provide deer with additional winter browse. On the other hand, beaver may speed up succession by removing deciduous early successional species, allowing species of later stages to prevail. In western Alaska, moose provide snowshoe hares with high quality browse from tree tops left after moose break down mid-size trees (Svendsen 1987).

In Olympic National Park elk appear to have a competitive advantage over deer, perhaps because of their larger size and greater reach, mobility, and group size (Jenkins and Starkey 1984). This study indicated a population ratio of 3 elk:1 deer in the Hoh Valley. The small deer populations in this habitat may be able to persist because large numbers of downed trees provide forage accessible only to deer (Leslie and Starkey 1982, 1984). This study was done in an ancient old-growth forest; competitive interactions between elk and deer may differ after logging and in remnant buffer zones around streams. In western Washington elk preferred mesic habitat patches dominated by graminoids and forbs, while black-tailed deer preferred xeric patches where browse and forbs dominated (Hanley 1984). These different habitat preferences may minimize interspecific competition between elk and deer.

Mule deer and white-tailed deer in Montana show considerable habitat and forage overlap; however, mule deer utilize intermediate to high elevations within pine-bunchgrass/shrub/coniferous plant communities, while white-tailed deer utilize mid-elevation bunchgrass/shrub/aspen communities and willow/meadow communities at low elevations (Martinka 1968). In southern Texas, Kraussman (1978) also found that sympatric white-tailed

deer and mule deer chose somewhat different habitats and preferred different forage types. Analysis of niche overlap patterns between white-tailed deer, elk, and moose in the northern Rocky Mountains provided little evidence that interspecific competition was important in shaping niche relationships. There was no evidence of competitive exclusion, despite considerable overlap in habitat, space, and diet between seasons and years (Jenkins and Wright 1988). Thus, although there is some evidence for competitive interactions between elk and deer in old-growth forest, studies of elk, white-tailed deer, mule deer, black-tailed deer, and moose provide little evidence of competition pairs of cervid species in other habitats.

Beier and McCullough (1990) suggested that spatial and habitat segregation between sexes may minimize intersexual competition between white-tailed deer. Such differences in habitat preferences between the sexes can complicate management of riparian zones.

Conclusion

Our knowledge of ungulate use of riparian zones is incomplete. In eastern Washington riparian zones clearly comprise critical habitat for ungulates, because they provide dense vegetation, abundant of forage, and accessible water within a relatively arid landscape mosaic. In western Washington little information is available on use of riparian zones by ungulates. It is therefore important to obtain information on ungulate use of riparian zones as well as information on ecological interactions between herbivores.

METHODOLOGIES

FIELD SAMPLING OF VERTEBRATE TAXA

Amphibians and reptiles

Sampling methods for amphibians and reptiles are described in great detail by Corn and Bury (1990), Bury and Corn (1991), and Jones (1986). Following is a summary of the most common methods and their advantages and disadvantages.

Aquatic survey techniques

Stream surveys are most commonly used to sample stream amphibians. In smaller streams a three person team is needed to do an effective and thorough hand search. While one person stays on land to record data, the other two methodically work their way upstream turning over rocks, searching gravel bottoms and under overhanging vegetation. Hand-held nets are placed downstream to catch amphibians dislodged during the search process. The minimum length for a single survey of a headwater stream is 10 m (Bury and Corn 1991). Some species present in the stream are missed if a shorter sampling length is used. This method provides information on species density, diversity, and relative abundance. Measurements may include physical and biological stream parameters as well as information on individuals caught. Information on habitat characteristics and microhabitat use is obtainable. Hand searching is limited to smaller order streams; larger streams are difficult to search effectively by hand. Habitat disruption is limited if the surveyors replace rocks and gravel as they were found.

In larger streams electroshocking techniques have been used to sample amphibians as well as fishes (Hawkins et al. 1983, Murphy and Hall 1981, Murphy et al. 1981). This technique requires at least two people. One operates the electroshocking equipment while the other holds a net to capture shocked animals. This method appears to be biased toward capturing large giant salamander larvae and may miss the smaller torrent salamanders. Studies in streams greater than 2 m wide may need to employ both techniques to obtain adequate data. Like hand searching, electroshocking provides data on density, diversity, relative abundance, and microhabitat use. This technique is more expensive than hand searching.

Terrestrial survey techniques

Terrestrial survey techniques include time or area constrained searches, surveys of downed wood, and pitfall trapping. Time or area constrained searches require a team of samplers to thoroughly search for a specified length of time or a predetermined area within the sampling unit. The search can provide data on species presence and microhabitat use. To thoroughly look for amphibians, rotten logs must be turned over and torn apart, all rocks must be turned over, and ground litter must be moved to search underneath. This method is destructive and can lead to biases in subsequent years due to loss of habitat. It is labor intensive and provides insufficient data for reliable estimates of population parameters.

Surveys of coarse woody debris use techniques similar to time-constrained searches. However, the quantity of wood to be searched is predetermined. This allows the calculation of

minimum density estimates relative to the amount of downed wood and the quantification of microhabitat use. From this information, meaningful comparisons among species can be made. A limitation of this method is that density estimates apply to only one feature of the habitat.

The use of pitfall traps circumvents most of the problems and biases associated with time-constrained searches and coarse woody debris surveys. Pitfall traps are usually constructed from two #10 tin cans taped together and buried in the ground. Environmental damage from this method is minimal. If checked frequently, the traps can function as live traps. They are arranged in transects, grids, arrays, or used to encircle specialized habitats. Drift fences are used to increase the capture probability of pitfall traps. An aluminum sheet approximately one meter high is placed between traps. The lower edge is buried several inches into the ground. An animal running into the aluminum fence is forced to run along its edge until it falls into one of the pitfall traps. Data are used to estimate species diversity, relative abundance, and microhabitat use. Mark-recapture techniques may be used to provide population and home range estimates. Trapability differs among species. Amphibians and reptiles which move vertically in the forest are unlikely to be caught. Snakes are rarely caught in pitfall traps and have been observed feeding from them. Small mammals and amphibians are caught most frequently. Mortality is high among small mammals; populations may be depleted if traps are checked infrequently. Water may be put into the traps to drown the small mammals immediately. This can affect the condition of amphibians depending on the frequency with which traps are checked. Despite the disadvantages, these traps offer flexibility and can be left intact and covered when not in use.

Birds

Some of the most common bird sampling techniques are described below. The most appropriate method depends on the objectives of the study. For a more detailed description of each technique refer to Verner (1985) and Manuwal and Carey (1991).

Variable circular plot technique

Reynolds et al. (1980) proposed a variable circular-plot (VCP) method for determining absolute abundance. The method makes use of timed counts of species numbers and distance estimations from observer to bird at a number of stations located along a transect. The VCP method is reported to offer distinct advantages for surveying large geographical areas, for comparing different habitats, and for working in rugged and remote terrain (Scott and Ramsey 1981). It was found to be more effective within a study on riparian areas in the Western Cascades of Oregon than the line transect method (Anthony 1984). Reynolds et al. (1980) found that a stationary observer spent more time searching for birds and less time watching the path of travel than one walking along a transect. They reasoned that stationary observers have less effect on bird activity and provide better density estimates. Edwards et al. (1981) found that significantly more species were detected by the VCP plot technique than by the fixed radius plot (Bond 1957) or the line transect method (Emlen 1971). Some of the major drawbacks of the VCP method have to do with biases with respect to distance estimation and inter-observer differences (D. Manuwal, UW, personal communication).

Point count methods

There are three types of point count methods: simple point count, fixed radius point count, and variable radius point count (Verner 1985). The simple point count is employed when

information is needed on species richness, presence, and abundance (Manuwal and Carey 1991). The fixed radius point count is used to compare differences in community composition and relative abundance between sites. Its advantages are that it has fewer assumptions than variable distance transects and point counts, it is easy to conduct in the field, and the data are easy to analyze. A 50-m radius is adequate for most species in typical Douglas-fir forests west of the Cascade mountains. However, rare species with long detection distance, such as the pileated woodpecker, will be under-represented (Manuwal and Carey 1991).

Point counting is superior to transects for studying annual trends, primarily because the time spent counting can be controlled, and more sites can be sampled, permitting more representative sampling (Verner 1985). Point counts are also preferable to transects in areas of rugged, densely vegetated terrain, where movement along the transect could interfere with bird sampling (Manuwal and Carey 1991). By not recording distances, the point count method eliminates the distance estimation bias associated with the similar VCP technique.

Transects

Variable width transects are used when the objective is to estimate densities and when it is necessary to account for variance in detectability due to differences among species, observers, or habitats (Emlen 1977). Transects and point counts are more efficient for abundance measures than mapping (Verner 1985). The area sampled increases linearly with distance from the observer with transects but geometrically with point counts. If certain assumptions are violated, point counts result in much larger errors in density estimations than do transects (Verner 1985).

Anderson and Ohmart (1981) found that the time spent in the field was shorter for the variable strip transect method of Emlen (1971) than with the VCP technique. However, the total area censused was significantly greater with the transect method because of the 100-m interval between plots that was not censused in the variable circular plot technique. Total detections were always significantly greater with the transect technique.

Mapping

Mapping involves plotting the locations of singing males on gridded maps during each of several visits to a plot. Information from the maps is then transferred to composite maps for each species. The maps provide information on species abundance, composition, density, and territoriality. Studies of energy consumption by birds as a part of a study of trophic dynamics should not be attempted with any method other than total mapping (Verner 1985). For most bird species, mapping provides a better estimate of density than the VCP. The advantage to using the mapping technique is that it produces the most reliable estimates of absolute density (Franzreb 1981). The disadvantages to this method are that it requires a great deal of time and effort, its use is restricted to the breeding season, for large species such as raptors it is difficult to determine what portion of a territory is on the plot, observer bias increases with variability in territory delineation, and counting singing males may not give a reliable estimate of breeding males. Kendeigh (1944) noted that 9% of singing house wrens were unmated.

Small mammals

The estimation of population structure and the population density or number of animals per unit area is an important consideration in many ecological studies concerned with interactions between animals and their habitats. For most wild mammals accurate estimation of density and

population structure is difficult to obtain because of their generally secretive and inconspicuous natures. Small mammals are additionally difficult to census because of their size and general lack of signs to indicate their presence. These difficulties are overlaid with biases introduced by the choice of sampling method (Williams and Braun 1983). There apparently is no single type of trap or combination of traps that will capture individuals of all species, sexes, and age-classes with equal probability. Thus, the selection of a method depends on the objectives of the study or the questions being asked. The techniques can be considered broadly in three categories: capture-mark-recapture methods, intensive removal methods, and indirect methods.

Capture-mark-recapture methods

The technique of capture, marking, release, and recapture is one of the most frequently used sampling techniques for small mammals. The proportion of marked individuals recaptured in the second sample, along with the known number of marked individuals released, permits an estimate of the total population size. Two situations each of which has different approaches for estimating population parameters must be considered (Otis et al. 1978, McCullagh and Nelder 1983). A population is defined as *closed* if it is not changing in size during the period of capture, marking, and recapturing. A population is defined as *open* if it is changing in size during the study period. Open populations experience recruitment through immigration (or birth) and emigration (or death). Real populations are clearly open, unless they are sampled for a very brief period.

This approach can estimate population abundance, population structure, survival rate, growth rates, and emigration and immigration rates. It requires intensive sampling effort. Consequently, the number of sites that can be analyzed is relatively small. Live traps and pitfall traps are the most commonly used traps for capture-mark-recapture methods.

Live traps

There are several designs for livetraps, some for catching multiple individuals and others for single captures. Most of the commercially available traps are single-capture traps, either consisting of a spring-driven door triggered by a treadle on the floor of the trap (Sherman, Havahart, and Tomahawk traps) or a door released by a wire treadle placed in the trap entryway (Longworth) (DeBlase and Martin 1981, Taber and Cowan 1969). Traps usually are baited, but type of bait varies widely in accordance with food preferences of the species in question. Some of the advantages of live traps are that they are easy to set, can be used in large arrays for estimating population density, and they are non-destructive (Otis et al. 1978). Some of the disadvantages are the large effort/time commitment needed to conduct livetrapping and the expense involved in surveying a large area (or several areas).

Typical marking techniques for small mammals involve ear tagging or toe clipping. Other methods such as hair clipping, hair dyeing, freeze-branding, and numbered collars also have been used (DeBlase and Martin 1981, Taber and Cowan 1969).

Pitfall traps

Pitfall trapping is a technique that is increasingly used to sample amphibian and reptile populations (Corn and Bury 1990) as well as certain small mammal species. Pitfall traps are very efficient at capturing species of low agility or species that use tactile and olfactory rather than visual cues (West in press). This technique is mostly effective for capturing insectivores and non-jumping rodents, but is less effective at capturing species such as deermice, chipmunks, and

jumping mice (Briese and Smith 1974, Bury and Corn 1987, Williams and Braun 1983). Substantial effort is required to place pitfalls in the ground, especially in rocky soil and gravel. Because the technique primarily is effective in capturing insectivores, which must feed every 2-4 hours, traps must be provisioned with sufficient food and checked frequently (7 hours or less). Because pitfall traps catch relatively few agile rodents when used as live traps, other methods should be employed at the same time to assess the small mammal community fully (Bury and Corn 1988).

Intensive removal methods

When many kill traps are set in a small area, the total number of individuals removed can provide an estimate of density. Hayne (1949) and DeLury (1947) first proposed an estimation procedure for such intensively trapped areas in which they plotted a regression line for the number of animals caught each day against the cumulative number previously caught. This technique provides an estimate of density at the point where the regression line intersects the abscissa. The statistical basis for this technique was discussed in Zippin (1958). Currently the computer program CAPTURE developed by White et al. (1982) is the best treatment on removal estimates for small mammal population size and density.

Although removal methods change the population under study, this method has its own advantages. It provides information on questions of age, sex, reproductive condition, and diet. These kinds of data are very useful for assessing population performance and habitat suitability. In some cases, notably diet and reproductive condition, removal methods and subsequent necropsy are necessary. Snap traps and pitfall traps are the two most common techniques for the removal methods.

Snap traps

Snap trapping is the one of the most common methods for censusing small mammals. The frequently used Museum Special snap trap is larger than household-variety mousetraps and has a longer bail wire which is designed to strike the back rather than the head of animals (West 1985). In a study by Wiener and Smith (1972) Museum Special snap traps proved to be more effective due to a more sensitive trigger mechanism than conventional snap traps during periods of strong winds or rain. Although many different baits have been used, a common bait is a mixture of rolled oats and peanut butter.

Snap traps are easily set, inexpensive, and have a rapid rate of return for effort. They are useful for collecting information in a short time period, and in sampling extensive areas. They are more efficient at capturing species that orient visually, but they are less efficient at capturing species that orient by tactile or olfactory cues. Snap traps are disadvantageous in that they are single capture traps and must be checked rather frequently and reset.

Pitfall traps

This technique can be used for live or removal trapping, although it is most commonly used for the latter. In the Pacific Northwest many animals drown due to the accumulation of water in the traps. Drowning is recommended as a humane technique by the American Society of Mammalogists (1987) when pitfall traps are used as removal traps. Pitfall traps permit both simultaneous and sequential multiple captures without the need for constant or frequent trap attendance (Williams and Braun 1983).

Indirect methods

The characteristic feature of all methods for measuring relative density is that they depend on the observation of sign that represents some relatively constant but unknown relationship to the total population size. They provide no estimate of density but rather an index of abundance (Krebs 1985). Most methods are useful as supplements to more direct census techniques and for picking up large changes in population density.

For small mammals in this region, the most common techniques involve counts of runways (species of voles and moles) (Sarrazin and Bider 1973), counts of burrow systems (moles, gophers and ground squirrels) (Scrivner and Smith 1981), counts of vocalization (tree squirrels) (Davis and Winstead 1980), and counts of nests and middens (nests of woodrats, flying squirrels, and tree squirrels, middens of red squirrels) (Wolff and Zasada 1975).

Bats

The following discussion is based primarily on material presented in Kunz and Kurta (1988) and Thomas and West (1989).

Methods of capturing bats

There are two widely used methods of capturing bats in the field: mist nets and Tuttle traps. Mist nets are portable and can be set up to cover a large area; however, nets must be watched constantly and entangled bats removed promptly to avoid mortality. In contrast, Tuttle traps (Tuttle 1974) do not have to be monitored constantly and several traps can therefore be run simultaneously. In addition, Tuttle traps protect captured bats from weather, and are 10 times more efficient than mist nets. Several disadvantages. Bats in traps may bite or prey on one another and are vulnerable to predators such as snakes. If large numbers of bats are caught at one time bats may suffocate.

Capture methods are subject to several sources of bias. Wind and rain can affect success by making nets or traps more visible. When Tuttle traps are used, variations in line tension can also introduce bias because different species may be caught with different line tension. When lines are too loose, large bats pass through; if too tight, small bats bounce off. It is desirable to find a moderate tension to catch as many species as possible, but some may still be missed.

Capture rates vary with species, behavior, and age of individuals. Some bats (both species and individuals) avoid capture. High flying and maneuverable bats are not easily captured, and gleaning and hovering bats, such as the long-eared bat (*Myotis evotis*) and the pallid bat (*Antrozous pallidus*), are especially good at avoiding traps. Adults are better at avoiding nets than juveniles, and near-term pregnant individuals are caught more often than male, non-parous, or lactating individuals.

Although biased, trapping provides information on reproduction, sex, and age that cannot be obtained by methods in which bats are not handled, such as visual counts and ultrasonic detection.

Visual counts

In visual counts bats are counted as they emerge from a roost. This is a precise but labor-intensive method of monitoring bats, with as little as 0.5% variation between counts (Swift 1980). The utility of visual counts is limited to estimating numbers of individuals using a given roost

because in order to use this method to estimate population size, the number of roosts in an area, individual foraging ranges, and immigration rates must be known.

Visual counts have also been used to monitor habitat use of several species in urban areas. Using visual strip counts in which bats were counted along a transect, Gaisler (1979) was able to identify three species on the basis of size seen against an open sky in a city. This technique has several drawbacks. It cannot be used in forested areas because the bats must be silhouetted against a light background to be identified; detection distance varies depending on bat size, flight levels, and light intensity; and the species of interest must be of substantially different sizes for positive identification.

Ultrasonic detection

Ultrasonic detection systems have been developed that allow remote sensing and recording of calls for later playback and recognition. These techniques offer the ability to census bat activity over many areas simultaneously without some of the biases of capture techniques. Bats need not be trapped or handled and the detector microphones cover a larger area than traps or nets, allowing the collection of larger samples.

However, ultrasonic detection also has shortcomings. Many species cannot be distinguished from one another based on echolocation call characteristics (Thomas and West 1991, Fenton et al. 1973) and species with similar calls must, therefore, be grouped in analysis. This limits the effectiveness of this method for monitoring habitat use by individual species (Thomas and West 1991). In addition, detectors cannot yield absolute measures of abundance. They are only useful for measuring relative levels of activity among different areas because there is no one-to-one correspondence between the number of calls recorded and the number of bats present; a single individual emitting several calls cannot be distinguished from several individuals emitting single calls. Finally, detectors cannot be used to compare activity among species. Calls of different species vary in intensity and detection distance such that lower frequency calls are detected at greater distances than high frequency calls (Griffin 1971, Fenton and Fullard 1981).

Carnivores

Many of the methods for the studying carnivores are designed to determine population size, densities, physical characteristics, and home range. Some of the more common methods for censusing carnivores are described below. The advantages and disadvantages of each technique depend on the objectives of the study being designed.

Census techniques

Capture-mark-recapture

Capture-mark-recapture (CMR) methods have been used for many years and incorporate a variety of techniques to provide information for population estimates, densities, movements, weight variation, home range, and external characteristics (King and Edgar 1977). In general, traps are set at regular intervals over a plot of land, animals are marked and released, and recaptured a number of times (Stickel 1954). The grid size, configuration and number of traps established is specific to the animal population being studied (White et al. 1982). Four critical assumptions of the CMR methods are:

1. Marked and unmarked animals are captured randomly (Krebs 1972).

2. Marked animals are subject to the same mortality rate as unmarked animals (Krebs 1972).

3. Marks are not lost or overlooked (Krebs 1972).

4. The size of the population is constant over the period of census. This means that no recruitment (birth or immigration) or losses (death or emigration) occur (White et al. 1982).

CMR methods are most appropriate for animals with high densities and small movement patterns (Montgomery 1987). Some advantages to using the CMR methods are that they allow the observer to estimate the population size of elusive, mobile organisms that are seldom amenable to direct counts, and that the animal populations being studied remain alive and intact. One major disadvantage is the difficulty in incorporating heterogeneity in catchability, behavior, and age structure into the design (Montgomery 1987, White et al. 1982). Consequently, catches could misrepresent the population in various ways (King 1983).

Removal

Removal techniques involve trapping the animals along a grid system similar to the CMR methods and removing the animal from the population, either by marking unmarked animals or kill trapping. An estimation of population size can be determined by analyzing the decreasing proportion of captures in successive trapping efforts (West in press). Data necessary for determination of age, breeding condition, and digestive tract analysis can be obtained by kill trapping (King and Edgar 1977).

One advantage to the removal method is that it is a quick and efficient way to estimate population numbers. Daily inspections of traps may not be necessary (King and Edgar 1977). One of the major disadvantages to the removal method is that it may change the population structure and additionally may alter the responses of surviving individuals (King and Edgar 1977).

Camera traps

Camera traps involve the connection of a detector or baited trigger mechanism to a battery operated camera with flash. Upon detection of the animal or upon release of the bait from the trigger, the camera will photograph the animals (Joslin 1988). Care must be taken to strategically place the camera in a position where it will receive the best full body shot of the animal.

Some advantages to this method are that it requires little time commitment and is sufficient for determining presence or absence. Presence information can be a useful and efficient way to describe large scale ecological patterns (West in press). Some of the disadvantages to camera traps are that visitation rates may be low, they can be expensive, and they provide only presence data.

Aerial surveys

Aerial surveys involve photographing mammals from aircraft fitted with aerial survey cameras (Ward et al. 1987). The photos are then examined to provide an indication of population size, habitat use and location, and migration patterns. An advantage to this method is that it provides information on more elusive animals that are difficult to track by other methods. One disadvantage to aerial surveys is that they are expensive in terms of flight costs, camera equipment, and time spent searching for animals. Also, the sightings from aerial surveys are a function of habitat "transparency." For example, one would inevitably count more numbers of individuals in an open meadow than in a closed canopy forest.

Tracking

The use of tracks as a population estimation technique has been offered as an inexpensive technique (Reid et al. 1987). It involves tracking animals by their prints in the snow, on track plates, or other appropriate medium to provide information on distribution, dispersion, activity (time or space), habitat preference, and species interaction (King and Edgar 1977). Some of the advantages to tracking are that there is little interference with the animals' activities and a larger area can be censused than with a trapping method (King and Edgar 1977). One disadvantage to tracking is that it provides no physical information about the animals (i.e., sex, size, reproductive condition) (Teplov 1952). An obvious disadvantage specific to snow tracking is that its use is temperature dependent. Snow tracks may indicate winter habitat use but the habitat requirements of a species may change seasonally, particularly during the breeding season (Van Horne 1983).

Sign analysis

The analysis of sign to index abundance may be used when the actual capture of animals is not necessary and when the animal species is very difficult to capture. Some examples of sign analyses include: counts of vocalizations, dens, scat, prey kills, marked trees, trails and sign posts (West in press). The type of sign chosen for analysis is a function of natural history and varies greatly with respect to different species. For presence-absence techniques any sign of presence will do, while for indices of abundance the signs must have some consistent relationship to abundance (West in press).

In summary, the technique used to determine and describe a population of carnivores depends on the species being studied and the questions being asked. In general, CMR, removal techniques, aerial surveys, and sign analysis can be used to obtain population estimates for carnivores. Camera traps are most frequently used to determine the presence or absence of a species. The most effective method to obtain information regarding reproductive success of carnivore populations is CMR. The determination of carnivore-habitat relationships is dependent on the distribution or territory of the species being studied. For wide-ranging carnivores (i.e., bear, opossum, and raccoon), carnivore-habitat relationships are determined by tracking, aerial surveys, sign analysis, and radio telemetry (explained below). For narrow ranging carnivores CMR may also be employed.

Auxiliary methods

Radio telemetry

Radio telemetry is used primarily for the study of movement patterns, but can also be very useful in augmenting census data. Radio telemetry, in conjunction with trapping methods for population estimates, provides information on the animals that were not in the population during a particular trapping period (Hallett et al. 1991) In radio telemetry, an animal is equipped (by collar, harness, or surgical implant) with a miniature signal-emitting radio transmitter which does not affect its capture probability or survival. The animal carrying the transmitter is then located by receivers fitted with directional antennae. The directional antenna indicates the direction from which the transmitter signals are coming by emitting louder signals when the antenna is pointed in the right direction (Riney 1982). Locations of the animals can be marked on maps to provide information regarding the movement patterns.

Some advantages to using this method to study carnivores include:

1. It, like CMR, is an effective way to monitor shy animals in good cover.
2. It has the advantage of getting the observer quickly to a position where he can observe a particular instrumented animal. (Craighead and Craighead 1965).

Some of the main disadvantages to radio-telemetry are the initial cost of equipment and the expertise and time required to develop a workable system for relocating the animals (Riney 1982).

Ungulates

Two general approaches can be taken to gather information about ungulates. First, the animals themselves can be surveyed and sampled using visual observations, radio telemetry, and vocalization. Second, indirect methods using tracks and traces can be surveyed and sampled, including pellets, browse, and rutting pits.

Direct visual observation of ungulates is a useful method for obtaining information on habitat selection, activity patterns, and to some degree food selection, and it has been widely used throughout the world. However, the method is only useful if the animals are visible the majority of the time. This is not the case in the PNW, where ungulates utilize forested areas. Therefore, radio telemetry might prove to be a more useful method. If animals are equipped with motion sensitive transmitters, both habitat selection and activity patterns can be obtained. Aerial surveys are also useful to obtain locations of ungulates, marked as well as unmarked individuals (Kenward 1987).

Spotlight techniques have been used with a variety of animals. The method is easy in the field and relatively inexpensive. From spotlight counts population estimates can be calculated (Harestad and Jones 1980).

Browse inventories have been used frequently to get information on plant species preference by an ungulate species and carrying capacity evaluation (Telfer [1980] for a review). The method is fairly robust, since it gives a good estimate of browse pressure. On the other hand, if two or more ungulate species are involved, only the accumulated browse effect (result) can be measured. There is no way to tell what kind of ungulate browsed a particular twig. Browse inventories cannot be used to distinguish browse of different ungulate herbivores.

In ungulate ecology, animal abundance in relation to their food resource is important. For browsing ungulates the estimation of browse biomass is important. Marshall et al. (1990) developed a method to estimate browse biomass using multiple regression and plotless density estimates. The technique is inexpensive since it requires relatively small sample sizes.

In the evaluation of ungulate habitat, measuring availability of key forages is important (Wallmo et al. 1977, Hanley and McKendrick 1985). The availability of browse changes when snow accumulates. A commonly accepted alternative to direct measurement involves estimating proportions of browse present before snowfall that exceeds heights of various snowpacks (Telfer 1980). In Montana it was found that there is a nonlinear relationship between available browse and increasing snowpack (Jenkins et al. 1990). If a simple linear relationship is used it leads to overestimation of browse (Schwab and Pitt 1987).

Strip and line transects have traditionally been used to estimate populations, and browse pressure. (Eberhardt 1980). Burnham et al. (1985) compared the two types and found that in general the line transect method should be preferred over strip transects on the basis of human bias and efficiency.

Line transect surveys of pellet groups provide a very useful method to get a population estimate or an index of use of a habitat type compared to others (Eberhardt 1980). When the

population of interest consists of groups or clusters of individuals such as elk rather than single individuals, group size may influence the probability of detecting a group. Drummer et al. (1990) incorporated group size as a covariate in their line transect method to eliminate overestimation of density of individuals. One of the problems using pellet transect surveys is variation in the persistence of fecal pellets from deer and elk. Loft and Kie (1988) compared radio-triangulation methods for assessing deer habitat use and came to the conclusion that pellet group counts are useful in ranking relative use of habitats, but may not be reliable for ranking habitats that receive similar levels of use. One of the weaknesses is that the pellet group counts does not indicate the kind of use a given habitat receives. Additional data are needed to supplement the information from the pellet group counts. Harestad and Bunnell (1987) showed for black-tailed deer in British Columbia that twice as many pellets remain in a dry site compared to a moist site after one year. Furthermore, defecation rate of an ungulate depends on forage quality (Robbins 1983). As food quality decreases (i.e., as the fiber content increases) ungulates pass more indigestible material. This is most strongly pronounced between seasons. Winter pellets are more persistent than spring and early summer pellets where ungulates forage on early phenological plant material, which is low in fiber.

Estimates of home-range size are very sensitive to the length of sampling intervals. Moreover, if large sample sizes are acquired over a short period of time, the samples may not be independent (Swihart and Slade 1985).

Especially during winter ungulates may suffer nutritional constraints (Hanley and Rose 1987). Hanley and McKendrick (1985) showed for Sitka black-tailed deer in Southeast Alaska that the winter energy limiting hypothesis may be true, when deep-snow winters or when herb-layer evergreen forages are not available. In addition, the role of protein digestion-inhibitors play an important role.

Tracks left in the snow by wild ungulates have been used to estimate relative abundance of species between years (Fedyk et al. 1984). It is a very inexpensive method and not very labor intensive. It could also be used to indicate differential use between habitat types. On the other hand, if it is not combined with other field data, the habitat use may be meaningless because tracking data does not indicate the animals activity patterns.

Modeling of ungulates

Over the years several ungulate models have been developed. The advantage of models is that they can provide a quick and fairly inexpensive idea of what might be accomplished under different management manipulations in a given habitat or in particular at a landscape level. Within their limited scope, models can be used as a predictive framework of a given ungulate population.

A resource limitation model for black-tailed deer was developed by Garcia et al. (1976) based on the Leslie matrix. The model will generate a possible carrying capacity for a given area but is probably too simple to give valid population numbers. Raedeke and Lehmkuhl (1986) constructed the HABSIM-model. It predicts population sizes of elk on a landscape level, and is useful for making predictions due to large scale logging or habitat alterations.

For the commercial timberlands north of Mt. Rainier National Park along the White River in western Washington a model was constructed for assessing influences of forest harvesting activities on elk forage conditions (Jenkins and Starkey 1990). The model is used to assess influences of several possible forest harvesting rates, rotation lengths, thinning rates, hardwood cutting rates, and winter snowfall on forage conditions in the White River drainage (Jenkins and

Starkey 1990). This model may be a useful tool in predicting the outcome of riparian management zones under different management schemes.

Hanley and Rogers (1989) developed a general ungulate model based on nutritional requirements and their availability. The advantages are that it can be used in a variety of habitats and it is not restricted to one species.

Wisdom et al. (1989) refined the model developed by Thomas et al. (1979) for elk to be useful in western Oregon. The original model by Thomas et al. (1979) was created for the Blue Mountains of Oregon and Washington. Several improvements have been made since then (Musser and Bracken 1990).

POPULATION AND COMMUNITY PARAMETERS

Population ecology

A primary concern of population ecology is how population parameters are related to the environment where animals live (Caughley 1977). Parameters of interest include abundance, density, survivorship, fecundity, age-structure, sex ratio, immigration, emigration, rates of change and the variance of these estimators (Caughley 1977, Newton 1989). These estimates can be age-specific, although this generally requires intensive, long-duration study and the ability to accurately age and identify individuals (Caughley 1977). Long-term, age-specific data would permit partitioning of estimator variance between habitat types, social factors (e.g., density dependence), environmental stochasticity, and individual life-time reproductive success (Clutton-Brock 1988, Newton 1989). Long-term study is not only difficult in terms of funding and current research institutions (e.g., Verner 1992), but decisions about landscape level management may be needed before long-term research can be completed (Soulé 1986). Fortunately, it is possible to learn a great deal about relationships through experimental manipulation and short-term correlations observed in different environments. In the remainder of this section we briefly review a number of considerations about population level parameter estimation.

Relative abundance.

This is a measure of abundance based on an index which is not a direct estimate of population numbers (Caughley 1977). It is the simplest type of abundance measure both in terms of estimation and because limited information is gathered. Indices include direct counts from animal signs such as the number of fecal deposits, nests, burrows, scratching posts, and predated plants. These types of indices may require an estimate of the expected number of signs per animal and require a minimum time lag between the animal's presence and observation of signs (Caughley 1977). Another class of measures relates abundance to catch per unit effort such as with pitfall traps, track plates, and call counts. Relative abundance can be a very cost-effective and useful way to index population responses to habitat perturbations.

Density

Crude density is the estimated number of animals in a given area (Caughley 1977). This measure is most useful for comparing temporal variation within study areas. Comparisons between areas is more problematic because definitions of study area boundaries can be arbitrary relative to the sampled organisms. Measures of absolute density (i.e., total number of animals in a

given area) will require more intensive sampling methods than required for relative abundance measures (Caughley 1977). Field methods include quadrat counts (Clarke 1986), mark-recapture studies (Jolly 1965, Seber 1965, Otis et al. 1978) and transect samples (Burnham et al. 1980). Important considerations for these methods include standardization of methods, observer bias, independence of observations, and behavioral, temporal, and social dynamic effects on capture probabilities.

Ecological density is the estimated number of animals relative to the availability of specific habitats. This measure may have an *a priori* assumption of what constitutes a habitat type relative to the organism being sampled, but if this condition can be satisfied the measure provides more specific information than crude density. Both crude and ecological density estimates may be biased by study area size (Franklin et al. 1990), but this is less problematic if the numbers are used to assess temporal variation within study areas or if inter-study comparisons involve areas that are approximately equal in size. Rarefaction is a tool that can be used to standardize density estimates for study sites of various size (Tipper 1979). Interpretation of density measures should recognize that density is not always a good indicator of habitat quality (Van Horne 1983, Pulliam 1988) and a more complete assessment will require demographic estimates.

Demographic measures

These parameters, described above, provide the most complete information needed to relate how animals respond to different environmental conditions. However, sampling can be very expensive in terms of time, money and effort (Caughley 1977). It is possible to estimate a number of parameters such as reproductive condition, age-structure, and sex ratio during the course of presence/absence sampling such as with pitfall traps. Survivorship, fecundity, immigration and emigration require more intensive sampling such as mark-recapture studies with large sample sizes and involving several generations and years to accurately estimate the variance for these parameters (Caughley 1977, Newton 1989). Life stage projection parameter estimates are a useful approach to examining rates of population change where age-specific data is unavailable (Caswell 1989).

Community Ecology

Communities have been defined in a myriad of ways but a common operational theme is that a community is an assemblage of several species occupying the same area (Wiens 1989). Community ecologists are concerned with factors that influence community composition and this has been accompanied by considerable debate (e.g., Diamond 1975, Connor and Simberloff 1984, Gilpin and Diamond 1984). A number of community level relationships have been explored which we briefly review below.

Species diversity

Diversity measures combine both the variety of organisms in a community (i.e., species richness) and their relative abundance (Magurran 1988). A large number of indices of species diversity have been proposed to enumerate differences between communities. For a review of concepts and methodologies see Ludwig and Reynolds (1988), Magurran (1988), Wiens (1989), and Krebs (1989). Diversity measures are commonly a function of sampling methodology and thus standardization is needed to make comparisons between study areas (e.g., rarefaction, Tipper

1979). Diversity is a function of habitat structure, succession, seasonal changes, interspecific relationships, and other factors described below (Wiens 1989).

Species area relationship

MacArthur and Wilson (1967) examined the relationship between species richness and area for several taxa occurring on islands. They found that species richness generally increases with area when plotted on a log-log scale. In island situations and isolated mountain ranges, factors other than area may be important. Distance from sources of colonists, and habitat features have been shown to alter species-area relationships (Johnson 1975, Gilpin and Diamond 1976). Considerable debate continues as to the usefulness of species-area relationships in conservation biology (e.g., Simberloff and Abele 1982, 1984, Wilcox and Murphy 1985, Simberloff and Cox 1987).

Species abundance models

These models fit various mathematical distributions to observed abundances of species. For instance, Preston (1948) observed that the relative density of bird species commonly fits a log normal distribution. This fit was used to explain the observation that communities usually have few very common species and more species with lower abundances. However, there is considerable debate regarding the biological meaning of this relationship (May 1975, 1984, Sugihara 1981). Ugland and Gray (1982) noted that an implicit assumption in Preston's model is that the communities are in equilibrium. They found that communities in nonequilibrium (such as those undergoing habitat modification) do not fit a log normal distribution. Considerable debate exists about the equilibrium state of communities (Wiens 1989). Other distributions have been proposed such as a niche preemption model using a geometric series (Røv 1975). See Ludwig and Reynolds (1988) for a review of methodologies.

Niche

One definition of a niche focuses on single species abundance and distribution as a function of many environmental factors (Grinnell 1917, 1924, 1928). Another more community based definition describes a niche as a species' functional role in the community with interspecific competition as the primary determining factor (Elton 1927, Hutchinson (1957). Both definitions can complement one another (Wiens 1989). Niche overlap is the degree of similarity between the ecological niches of various species (Wiens 1989). Groups of species having a high degree of overlap are commonly classified as guilds (Root 1967) and are the focus of research testing ideas about competitive exclusion and niche complementarity (MacArthur 1970, Wiens 1989). Groups of species having a high degree of ecological overlap are clustered into guilds for analytical purposes. Guilds have been defined a priori (Cody 1983, Diamond 1975) using a mixture of taxonomy and behavioral differences between species. Others have defined species guilds using a posteriori methods such as cluster analysis, principal components analysis and discriminant function analysis (Holmes et al. 1979, Capen 1981). There can be considerable difficulty in measuring niche overlap because of regional differences, temporal variation in species abundance and resource availability and in defining and quantifying resource use and availability (Wiens 1989).

USE OF RIPARIAN ECOSYSTEMS BY TERRESTRIAL VERTEBRATES IN WASHINGTON: ASSESSING DEPENDENCE ON RIPARIAN HABITATS

In this section we summarize information on terrestrial vertebrates of Washington that use riparian habitats and use this information to develop a ranking system to assess their sensitivity and significance. Table 4 presents information on 1) **descriptive variables**: life forms; use of riparian habitats (rivers, streams, and creeks) 2) **variables used in assessing sensitivity**: habitat specificity, population trend, geographic range, population concentration, and reproductive potential, 3) **variables used in assessing significance**: systematic significance, biogeographic significance, and 4) **sensitivity and significance scores**. The definitions of variables and procedures for scoring used in this section were adapted from Millsap et al. 1990. Scores were determined using information from Brown (1985), Burt and Grossenheider (1976), Ehrlich et al. (1988), Hall (1981), Nussbaum et al. (1983), Stebbins (1985), and Thomas (1979). Each variable used in assessing sensitivity or significance was assigned a value from 0-6. The higher a variable's score, the greater the vulnerability or significance of that taxon: a score of 6 indicates high risk, 3 indicates moderate risk, and 0 indicates low risk. The sensitivity and significance scores represent a synthesis of these variables.

EXPLANATION OF TABLE 4

Taxa

The taxa included were designated as inhabitants of riparian ecosystems on the basis of one or more of the following: 1) lists of riparian species compiled by the Washington Department of Wildlife; 2) taxon chapters by Cross (1988), Knight (1988), Knopf and Samson (1988), and Raedeke et al. (1988) in Raedeke (1988); 3) review by regional authorities. Some species identified as riparian species by 1 or 2, above, were excluded from the ranking because they are uncommon or do not breed in the region (i.e., fall and spring migratory birds, overwintering birds).

Nomenclature for common and scientific names follows the following sources: amphibians and reptiles - Collins (1990) and Good and Wake (1992), birds - American Ornithologists' Union (1983), mammals - Jones et al. (1991).

Descriptive variables

Life form descriptions for western Washington are from Brown (1985) and those for eastern Washington are from Thomas (1979).

Life form	Reproduces	Feeds
1	in water	in water
2	in water or in trees	on the ground, in bushes
3	on the ground around water	on the ground and in bushes, trees, and water
4	in cliffs, caves, rimrock, or talus	on the ground or in air
5	on the ground without specific water, cliff, rimrock, or talus	on the ground
7	in bushes	on the ground, in water, or in air
8	in bushes	in trees, bushes, or air
9	primarily in deciduous trees	in trees, bushes, or air
10	primarily in conifers	in trees, bushes, or air
11	in conifers or deciduous trees	in trees, in bushes, on the ground, or in air
12	on very thick branches	on the ground or in water
13	in own hole excavated in tree	in trees, in bushes, on the ground, or in air
14	in a hole made by another species or in a natural hole	on the ground, in water, or in air
15	in a burrow underground	on the ground or under it
16	in a burrow underground	in the air or in the water

Primary habitat is designated by a "1"; secondary, or marginal, habitat is designated by a "2". Information on use of habitats is from Brown (1985) and Thomas (1979).

Variables used in assessing sensitivity (SW & SE)

Habitat specificity

Habitat specificity scores are derived from versatility scores in Brown (1985) for forests of western Washington (SW) and from Thomas (1979) for forests of the Blue Mountains (SE).

Versatility = Number of plant communities used for reproduction + Number of successional stages used for reproduction + Number of plant communities used for feeding + Number of successional stages used for feeding.

Numbers in left column represent scores.

- 3 High habitat specificity (versatility score 1-16).
- 2 Medium habitat specificity (versatility score 17-29).
- 0 Low habitat specificity (versatility score > 30).

If information was available for a taxon on only one side of the state, the versatility score for that taxon on the side of the state where it occurred was doubled, to give a maximum of 6 possible points.

Population trend throughout range of taxon (PT)

- 6 Populations known to be or suspected of decreasing throughout all or most of range of taxon.
- 3 Populations formerly experienced serious declines throughout range of taxon but presently thought to be stable or increasing, or population decreasing in part of its range.
- 0 Populations stable or population trend unknown.

Geographic range (GR)

Geographic range refers to the area in the U.S. and Canada over which the taxon is distributed during the season when distribution is most restricted.

- 6 (< 130,000 km², i.e., < approximately 1/3 the area of California).
- 3 (130,000 1/3 km² - 400,000 km², i.e., > 1/3 the area of California-the area of California).
- 0 (> 400,000 km²)

If a taxon has no wintering range in North America (e.g., black tern, solitary sandpiper), it scored 6, even if it has a large breeding range in Central or South America. The justification for this is that species wintering in Central or South America are likely vulnerable on their wintering grounds because of habitat loss or exposure to pesticides.

Reproductive potential for recovery - clutch size (CS)

The only risk factor affecting reproductive potential for recovery included in this analysis was the number of young produced per year, computed as litter size × number of clutches (litters) produced per year. As more information is obtained, information on survival and age at sexual maturity will be added to the matrix, so that reproductive potential will reflect these additional components as well as clutch size. A high risk factor for each component is worth 2 points; moderate risk factors score one point. In computing sensitivity scores using only clutch (litter) size, we multiplied scores by 3, so that reproductive potential had the same weight (6 possible

points) as each of the other risk factors.

- 2 For amphibians: 1-25 eggs/clutch.
- 2 For reptiles, birds, and mammals: clutch or litter size \times number of clutches (litters) produced per year <3 .
- 1 For amphibians: clutch size >25 and <76 .
- 1 For reptiles, birds, and mammals: clutch or litter size \times number of clutches (litters) produced per year >2 and <6 .
- 0 For amphibians: >76 or clutch size unknown.
- 0 For reptiles, birds, and mammals: clutch or litter size \times number of clutches (litters) produced per year >6 or unknown.

Population concentration (CO)

Population concentration reflects the degree to which individuals congregate or aggregate seasonally at specific locations (e.g., hibernacula, breeding sites, migration focal points) or daily at specific locations (e.g., communal roosts).

- 6 Majority of the Washington population concentrates at 1-5 locations within the state.
- 3 Individuals sometimes concentrate in colonies, communal roosts, or large flocks.
- 0 Individuals rarely congregate or aggregation behavior unknown.

Variables used in assessing significance

Systematic significance (SS)

This score includes total of all categories that apply:

- 3 Monotypic family.
- 2 Monotypic genus.
- 1 Monotypic species (i.e., no subspecies).
- 0 Species includes >1 subspecies.

Systematic scores are based on Collins (1990) and Good and Wake (1992) for amphibians, Collins (1990) for reptiles, Howard and Moore (1980) for birds, and Hall (1981), for mammals.

Biogeographic significance (BS)

- 6 75-100% of total range occurs in Washington.
- 4 50-74% of total range occurs in Washington.
- 2 25-49% of total range occurs in Washington.
- 0 $<25\%$ of total range occurs in Washington.

Scores

Sensitivity score (SEN)

The sensitivity score assesses the sensitivity to disturbance, especially loss of riparian habitat. This score is calculated as:

Sensitivity score = habitat specificity score for western Washington + habitat specificity score for eastern Washington [or 2(habitat specificity score for western or eastern Washington)] + population trend score + geographic range score + population concentration score + (clutch size)³.

Significance score (SIG)

The significance score assesses contribution of taxon in Washington to biological diversity. This score is calculated as:

Significance score = systematic significance score + biogeographic significance score.

Status

Identifies taxa listed or proposed for listing as threatened, endangered, or sensitive, or species of special concern.

FE: Federally-listed; Endangered.

SE: State-listed; Endangered.

FT: Federally-listed; Threatened

ST: State-listed; Threatened

SC: Species of Concern; State-listed proposed Threatened or Endangered, Sensitive, and proposed Sensitive.

SUMMARY OF RANKING

As stressed previously, we consider this ranking system to be an initial exercise that will be refined as more information is obtained on these species. Nonetheless, certain trends are apparent. First, almost all of the species listed or proposed for listing by the state or federal government receive high sensitivity scores in our ranking system. Indeed, the Columbian white-tailed deer, a federally listed endangered species received the highest score of 22. The only listed species that did not receive a high sensitivity score is the water vole. However, the low score of 5 most likely reflects our lack of information on this species. Second, certain taxonomic groups are characterized by high sensitivity scores as a result of their high degree of habitat specificity. This is the case for groups such as salamanders and the herons and bitterns. Other species receive high scores because a combination of factors including population trends, habitat specificity, and restricted geographic range.

Table 4. A ranking system to assess the relative vulnerability of Washington's terrestrial riparian vertebrates to disturbance. Variables and calculation of scores are described in the text.

Taxon	Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
	West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Amphibians													
Caudata: Salamanders													
Ambystomatidae: Mole salamanders													
Northwestern salamander	<i>Ambystoma gracile</i>	2		2		0	3	0	3	1	0	10	1
Long-toed salamander	<i>Ambystoma macrodactylum</i>	2	2	2	2	0	0	0	3	0	0	7	0
Tiger salamander	<i>Ambystoma tigrinum</i>		2		3	0	0	1	3	0	0	12	0
Dicamptodontidae: Giant salamanders													
Cope's giant salamander	<i>Dicamptodon copei</i>	1			3	0	6	1	0	1	6	15	7
Pacific giant salamander	<i>Dicamptodon tenebrosus</i>	2			2	0	6	0	0	1	2	10	3
Rhyacotritonidae: Torrent salamanders													
Cascade torrent salamander	<i>Rhyacotriton cascadae</i>	2			3	0	6	2	0	1	4	18	5
Olympic torrent salamander	<i>Rhyacotriton olympicus</i>	2			3	0	6	2	0	1	6	18	7
Columbia torrent salamander	<i>Rhyacotriton kerzeri</i>	2			3	0	6	2	0	1	4	18	5
Salamandridae: Newts													
Roughskin newt	<i>Taricha granulosa</i>	2			2	0	3	1	3	0	0	13	0
Plethodontidae: Lungless salamanders													
Ensatina	<i>Ensatina eschscholtzii</i>	5			0	0	3	2	0	2	0	9	2
Dunn's salamander	<i>Plethodon dunni</i>	5			3	0	6	2	0	1	0	18	1
Larch Mountain salamander	<i>Plethodon larselli</i>					0	6	2	0	1	2		3
Van Dyke's salamander	<i>Plethodon vandykei</i>	3			2	0	6	2	0	0	2	16	2
Western redback salamander	<i>Plethodon vehiculum</i>	5			2	0	6	2	0	1	2	16	3

Table 4. Continued.

Taxon	Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
	West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Anura: Frogs and toads													
Leiopelmatidae: Bell frogs													
Tailed frog			<i>Ascaphus truei</i>										
	2	2	3	2	0	3	1	0	3	2	11	5	
Pelobatidae: Spadefoot toads													
Great Basin spadefoot			<i>Scaphiopus intermontanus</i>										
		2		2	0	0	0	0	1	0	4	1	
Bufoidea: Toads													
Western toad			<i>Bufo boreas</i>										
	2	2	2	0	0	0	0	3	0	0	5	0	
Woodhouse's toad			<i>Bufo woodhousei</i>										
		2		2	0	0	0	0	0	0	4	0	
Hylidae: Treefrogs													
Pacific chorus frog			<i>Pseudachris regilla</i>										
	2	2	2	0	0	0	0	0	0	0	2	0	
Ranidae: True frogs													
Red-legged frog			<i>Rana aurora</i>										
	2		2		3	3	0	0	0	2	10	2	
Cascades frog			<i>Rana cascadae</i>										
	2		3		3	6	0	0	1	2	15	3	
Bullfrog			<i>Rana catesbeiana</i>										
	1	1	2	2	0	0	0	0	1	0	4	1	
Green frog			<i>Rana clamitans</i>										
					0	6	0	0	0	2	6	2	
Northern leopard frog			<i>Rana pipiens</i>										
		2		3	3	0	0	0	0	0	9	0	
Spotted frog			<i>Rana pretiosa</i>										
	2	2	3	2	3	0	0	0	1	0	8	1	
Wood frog			<i>Rana sylvatica</i>										
		2		2	0	0	0	3	1	0	7	1	
Reptiles													
Testudines: Turtles													
Emydidae: Water and box turtles													
Painted turtle			<i>Chrysemys picta</i>										
	3	3	3	3	0	0	0	0	2	0	6	2	
Western pond turtle			<i>Clemmys marmorata</i>										
	3		3		6	3	0	0	0	0	15	0	ST

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Squamata: Lizards and snakes														
Iguanidae: Iguanids														
Sagebrush lizard (Mt fence lizard)	<i>Sceloporus graciosus</i>	5	5	2	2	0	0	1	0	0	0	7	0	
Western fence lizard	<i>Sceloporus occidentalis</i>	5	5	2	2	0	0	0	0	0	0	4	0	
Scincidae: Skinks														
Western skink	<i>Eumeces skiltonianus</i>	3	3	2	2	0	0	1	0	0	0	7	0	
Anguidae: Anguils														
Northern alligator lizard	<i>Elgaria coerulea</i>	5		0		0	0	0	0	0	2	0	2	
Southern alligator lizard	<i>Elgaria multicarinata</i>	5		2		0	3	0	0	0	0	7	0	
Boidae: Boas														
Rubber boa	<i>Charina bottae</i>	5	15	0	2	0	0	1	0	2	0	5	2	
Colubridae: Colubrids														
Western yellowbelly racer	<i>Coluber constrictor mormon</i>	5	5	2	2	0	0	1	0	0	0	7	0	
Sharptail snake	<i>Contia tenuis</i>	5		0		0	6	0	0	1	0	6	1	
Ringneck snake	<i>Diadophis punctatus</i>	5	3	0	0	0	0	2	0	2	0	6	2	
California mountain kingsnake	<i>Lampropeltis zonata</i>	5		2		0	6	0	0	0	0	10	0	
Pine (gopher) snake	<i>Pituophis melanoleucus</i>	5	5	0	0	0	0	0	0	0	0	0	0	
Western terrestrial garter snake	<i>Thamnophis elegans</i>	5	5	0	2	0	0	0	0	0	0	2	0	
Northwestern garter snake	<i>Thamnophis ordinoides</i>	5		2		0	3	0	0	1	2	7	3	
Common garter snake	<i>Thamnophis sirtalis</i>	3	3	0	0	0	0	0	0	0	0	0	0	
Viperidae: Pit vipers														
Western rattlesnake	<i>Crotalus viridis</i>	5	5	2	2	0	0	2	0	0	0	10	0	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Birds														
Ciconiiformes: Herons, bitterns, and their allies														
Ardeidae: Herons and bitterns														
Great blue heron	<i>Ardea herodias</i>	12	12	3	3	0	0	1	3	0	0	12	0	
American bittern	<i>Botaurus lentiginosus</i>	3	3	3	3	6	0	1	0	1	0	15	1	
Green-backed heron	<i>Butorides virescens</i>	7	7	3		0	0	1	0	0	0	9	0	
Great egret	<i>Casmerodius albus</i>	7	7	3		3	0	1	3	0	0	15	0	SC
Snowy egret	<i>Egretta thula</i>					3	0	1	3	0	0	9	0	
Black-crowned night heron	<i>Nycticorax nycticorax</i>	7	7		3	0	0	1	3	0	0	12	0	
Anseriformes: Waterfowl														
Anatidae: Swans, geese, and ducks														
Wood duck	<i>Aix sponsa</i>	14	14	2	3	3	0	0	0	1	0	8	1	
Northern pintail	<i>Anas acuta</i>	3	3	3	3	0	0	0	0	0	0	6	0	
American wigeon	<i>Anas americana</i>	3	3	3	3	0	0	0	0	1	0	6	1	
Northern shoveler	<i>Anas clypeata</i>	3	3	3	3	0	0	0	0	1	0	6	1	
Amer. green-winged teal	<i>Anas crecca</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Cinnamon teal	<i>Anas cyanoptera</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Blue-winged teal	<i>Anas discors</i>	3	3	3	3	0	0	0	0	1	0	6	1	
Mallard	<i>Anas platyrhynchos</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Gadwall	<i>Anas strepera</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Bufflehead	<i>Bucephala albeola</i>	14	14	3	2	0	0	0	0	1	0	5	1	
Common goldeneye	<i>Bucephala clangula</i>	14	14	2	2	0	0	0	0	0	0	4	0	
Barrow's goldeneye	<i>Bucephala islandica</i>	14	14	3	2	0	0	0	0	1	0	5	1	
Harlequin duck	<i>Histrionicus histrionicus</i>	3	3	3	3	0	0	0	0	3	0	6	3	
Hooded merganser	<i>Lophodytes cucullatus</i>	14	14	3	2	0	0	0	3	3	0	8	3	
Common merganser	<i>Mergus merganser</i>	14	14	3	2	0	0	0	0	0	0	5	0	

Table 4. Continued.

Taxon	Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status			
	West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG				
Falconiformes: Birds of prey																
Cathartidae: American vultures																
Turkey vulture			<i>Cathartes aura</i>	4	4	0	2	3	0	2	3	0	0	14	0	
Accipitridae: Kites, hawks, eagles, osprey																
Cooper's hawk			<i>Accipiter cooperii</i>	11	11	0	2	3	0	1	3	1	0	11	1	
Northern goshawk			<i>Accipiter gentilis</i>	11	11	2	3	3	0	1	3	0	0	14	0	SC
Sharp-shinned hawk			<i>Accipiter striatus</i>	11	11	0	2	3	0	1	3	0	0	11	0	
Red-tailed hawk			<i>Buteo jamaicensis</i>	12	12	2	2	0	0	1	0	0	0	7	0	
Northern harrier			<i>Circus cyaneus</i>	5	5	3	3	6	0	1	3	0	0	18	0	
Bald eagle			<i>Haliaeetus leucocephalus</i>	12	12	2	2	3	0	1	3	0	0	13	0	FT ST
Osprey			<i>Pandion haliaetus</i>	12	12	3	2	3	0	1	0	2	0	11	2	
Falconidae: Falcons and caracaras																
Merlin			<i>Falco columbarius</i>	11	11	2	2	3	0	1	0	0	0	10	0	
American kestrel			<i>Falco sparverius</i>	14	14	0	2	0	0	1	0	0	0	5	0	
Prairie falcon			<i>Falco mexicanus</i>	4	4	3	3	3	0	1	0	1	0	12	1	
Peregrine falcon			<i>Falco peregrinus</i>	4	4	2	0	6	0	1	0	0	0	13	0	FE SE
Galliformes: Fowl-like birds																
Phasianidae: Pheasants, grouse, partridges, and quail																
Ruffed grouse			<i>Bonasa umbellus</i>	5	5	2	2	0	0	0	0	0	0	4	0	
California quail			<i>Callipepla californica</i>	5	5	2	3	0	0	0	3	0	0	8	0	
Mountain quail			<i>Oreortyx pictus</i>	5	5	0	3	0	0	0	0	2	0	6	2	

Table 4. Continued.

Taxon	Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status			
	West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG				
Gruiformes: Cranes and their allies																
Rallidae: Rails, gallinules, and coots																
Sora			<i>Porzana carolina</i>	3	3	3	3	0	0	0	0	1	0	6	1	
Virginia rail			<i>Rallus limicola</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Gruidae: Cranes																
Sandhill crane			<i>Grus canadensis</i>	3	3	3	3	6	0	2	0	0	0	18	0	SE
Charadriiformes: Shore birds																
Charadriidae: Plovers																
Killdeer			<i>Charadrius vociferous</i>	3	3	3	3	0	0	0	0	1	0	6	1	
Recurvirostridae: Avocets and stilts																
American avocet			<i>Recurvirostra americana</i>		3		3	0	0	1	3	1	0	12	1	
Scolopacidae: Woodcock, snipe, and sandpipers																
Spotted sandpiper			<i>Actitis macularia</i>	3	3	3	3	0	0	0	3	1	0	9	1	
Western sandpiper			<i>Calidris mauri</i>	3	3	3		0	3	1	3	1	0	15	1	
Least sandpiper			<i>Calidris minutilla</i>	3	3	3		0	0	1	3	0	0	12	0	
Willet			<i>Catoptrophorus semipalmatus</i>	3	3		3	3	0	1	3	2	0	15	2	
Common snipe			<i>Gallinago gallinago</i>	3	3	3	3	0	0	1	0	0	0	9	0	
Long-billed dowitcher			<i>Limnodromus scolopaceus</i>	3	3	3		0	3	1	3	1	0	15	1	
Lesser yellowlegs			<i>Tringa flavipes</i>	3	3	3		0	0	1	3	1	0	12	1	
Greater yellowlegs			<i>Tringa melanoleucus</i>	3	3	3		0	0	1	0	1	0	9	1	
Solitary sandpiper			<i>Tringa solitaria</i>	7	7	3	3	0	6	1	0	0	0	15	0	
Laridae: Gulls and terns																
Black tern			<i>Chlidonius niger</i>	3	3	3	3	6	0	1	3	0	0	18	0	

Table 4. Continued.

Taxon	Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status			
	West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG				
Columbiformes; Pigeons and doves																
Columbidae: Pigeons and doves																
Band-tailed pigeon			<i>Columba fasciata</i>	11	11	0		3	3	0	0	0	0	6	0	
Cuculiformes: Cuckoos and their allies																
Cuculidae: Cuckoos, roadrunners, and anis																
Yellow-billed cuckoo			<i>Coccyzus americanus</i>		8		3	6	3	1	0	0	0	18	0	
Strigiformes: Owls																
Strigidae: Typical owls																
Northern saw-whet owl			<i>Aegolius acadicus</i>	14	14	0	3	0	0	0	0	0	0	3	0	
Short-eared owl			<i>Asio flammeus</i>	5	5	3	3	6	0	0	3	0	0	15	0	
Long-eared owl			<i>Asio otus</i>	11	11	2	2	0	0	1	3	0	0	10	0	
Great horned owl			<i>Bubo virginianus</i>	12	12	0	2	0	0	1	0	0	0	5	0	
Northern pygmy owl			<i>Glaucidium gnoma</i>	14	14	0	2	0	0	1	0	0	0	5	0	
Western screech owl			<i>Otus kennicottii</i>	14	14	0	3	0	0	1	0	0	0	6	0	
Barred owl			<i>Strix varia</i>	14	14	2	3	3	0	1	0	0	0	11	0	
Apodiformes: Swifts and hummingbirds																
Apodidae: Swifts																
White-throated swift			<i>Aeronautes saxatalis</i>		4		3	0	0	1	3	2	0	12	2	
Vaux's swift			<i>Chaetura vauxi</i>	14	14	0	3	0	6	1	3	0	0	19	0	SC
Trochilidae: Hummingbirds																
Black-chinned hummingbird			<i>Archilochus alexandri</i>	8	7		2	0	6	1	0	1	0	13	1	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Coraciiformes: Kingfishers														
Alcedinidae: Kingfishers														
Belted kingfisher	<i>Ceryle alcyon</i>	16	16	2	2	0	0	0	0	0	0	4	0	
Piciformes: Woodpeckers														
Picidae: Woodpeckers														
Pileated woodpecker	<i>Dryocopus pileatus</i>	13	13	2	3	0	0	1	0	0	0	8	0	
Lewis' woodpecker	<i>Melanerpes lewis</i>		13		3	0	0	1	0	0	0	9	0	
White-headed woodpecker	<i>Picoides albolarvatus</i>		13		3	0	0	1	0	0	0	9	0	
Downy woodpecker	<i>Picoides pubescens</i>	13	13	2	3	0	0	1	0	0	0	8	0	
Hairy woodpecker	<i>Picoides villosus</i>	13	13	2	3	0	0	1	0	0	0	8	0	
Three-toed woodpecker	<i>Picoides tricdactylus</i>	13	13	3	3	0	0	1	0	0	0	9	0	
Black-backed woodpecker	<i>Picoides arcticus</i>	13	13	3	3	0	0	1	0	0	0	9	0	
Northern flicker	<i>Colaptes auratus</i>	13	13	0	2	0	0	1	0	0	0	7	0	
Williamson's sapsucker	<i>Sphyrapicus throidens</i>	13	13	3	3	0	0	1	0	0	0	9	0	
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>		13		3	6	0	0	0	0	0	12	0	
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>	13		2		0	0	0	0	0	0	4	0	
Passeriformes: Perching birds														
Tyrannidae: Tyrant flycatchers														
Western flycatcher	<i>Empidonax difficilis</i>	11	10	2	2	0	6	1	0	0	0	13	0	
Dusky flycatcher	<i>Empidonax oberholseri</i>	8	8	3	2	0	6	1	0	1	0	14	1	
Willow flycatcher	<i>Empidonax trailii</i>	7	7	2	3	3	6	1	0	1	0	17	1	
Eastern kingbird	<i>Tyrannus tyrannus</i>	7	7	2	2	0	6	1	0	1	0	13	1	
Western kingbird	<i>Tyrannus verticalis</i>	11	11	3	3	0	6	1	0	1	0	15	1	
Western wood-pewee	<i>Contopus sordidulus</i>	11	11	2	2	0	0	1	0	1	0	7	1	
Olive-sided flycatcher	<i>Contopus borealis</i>	10	10	3	3	0	0	1	0	1	0	9	1	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Hirundinidae: Swallows														
Cliff swallow	<i>Hirundo pyrrhonota</i>	4	4	3	3	0	6	1	3	0	0	18	0	SC
Barn swallow	<i>Hirundo rustica</i>	4	4	2	3	0	6	0	3	0	0	14	0	
Purple martin	<i>Progne subis</i>	14		2		3	6	0	3	0	0	16	0	
Bank swallow	<i>Riparia riparia</i>	16	16	3	3	0	6	1	3	0	0	18	0	
Northern rough-winged swallow	<i>Stelgidopteryx serripennis</i>	16	16	3	3	0	3	0	0	0	0	9	0	
Tree swallow	<i>Tachycineta bicolor</i>	14	14	2	3	0	0	1	3	1	0	11	1	
Violet-green swallow	<i>Tachycineta thalassina</i>	14	14	0	3	0	3	1	3	0	0	15	0	
Paridae: Chickadees and titmice														
Black-capped chickadee	<i>Parus atricapillus</i>	14	14	2	3	0	0	0	3	0	0	8	0	
Chestnut-backed chickadee	<i>Parus rufescens</i>	14	14	2	3	0	0	1	3	0	0	11	0	
Troglodytidae: Wrens														
House wren	<i>Troglodytes aedon</i>	14	14	2	3	0	0	0	0	0	0	5	0	
Marsh wren	<i>Cistothorus palustris</i>	3	3	3	3	0	0	0	0	0	0	6	0	
Bewick's wren	<i>Thryomanes bewickii</i>	3		3		0	0	0	0	0	0	6	0	
Cinclidae: Dippers														
American dipper	<i>Cinclus mexicanus</i>	3	3	2	2	0	0	0	0	3	0	4	3	
Muscicapidae: Thrushes, gnatcatchers, and kinglets														
Veery	<i>Catharus fuscescens</i>		5		3	0	6	1	0	0	0	15	0	
Gray catbird	<i>Dumetella carolinensis</i>		7		3	0	0	0	0	3	0	6	3	
Swainson's thrush	<i>Catharus ustulatus</i>	8	8	0	0	0	0	0	0	0	0	0	0	
Hermit thrush	<i>Catharus guttatus</i>	8	8	0	0	0	0	0	0	0	0	0	0	

Table 4. Continued.

Taxon	Life Forms	Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status	
		West	East	West	East	PT	GR	CS	CO	SS	BS		SEN
Vireonidae: Vireos													
Warbling vireo	<i>Vireo gilvus</i>	11	11	2	3	3	6	1	0	0	0	17	0
Red-eyed vireo	<i>Vireo olivaceus</i>	11	11	3	3	3	6	1	0	0	0	18	0
Hutton's vireo	<i>Vireo huttoni</i>	11		3		0	0	0	0	0	0	6	0
Emberizidae: Wood warblers, blackbirds, tanagers, sparrows, grosbeaks, and buntings													
Red-winged blackbird	<i>Agelaius phoeniceus</i>	7	7	3	3	0	0	0	3	0	0	9	0
Yellow-rumped warbler	<i>Dendroica coronata</i>	10	10	0	2	0	0	0	3	0	0	5	0
Yellow warbler	<i>Dendroica petechia</i>	8	8	2	3	3	6	1	0	0	0	17	0
Black-throated gray warbler	<i>Dendroica nigrescens</i>	10		2		0	0	1	0	0	2	7	2
Orange-crowned warbler	<i>Dendroica celata</i>	6	6	0	3	0	0	1	0	0	0	6	0
Townsend's warbler	<i>Dendroica townsendi</i>	10	10	2	3	0	0	1	0	0	0	8	0
Hermit warbler	<i>Dendroica occidentalis</i>	10		2		0	0	1	0	0	0	7	0
Common yellowthroat	<i>Geothlypis trichas</i>	3	3	3	3	0	0	0	0	0	0	6	0
Yellow-breasted chat	<i>Icteria virens</i>		8		3	6	0	1	0	2	0	15	2
Wilson's warbler	<i>Wilsonia pusilla</i>	6	5	0	3	0	0	0	0	0	0	6	0
Northern oriole	<i>Icterus galbula</i>	9	9	2	3	0	6	1	0	0	0	14	0
Nashville warbler	<i>Vermivora ruficapilla</i>		9		3	0	0	1	0	0	0	9	0
MacGillivray's warbler	<i>Oporornis tolmiei</i>	8	7	2	2	0	6	1	0	0	0	13	0
Lincoln's sparrow	<i>Melospiza lincolni</i>	6	6	2	3	0	0	1	0	0	0	8	0
Song sparrow	<i>Melospiza melodia</i>	7	7	2	3	0	0	0	0	0	0	5	0
Lazuli bunting	<i>Passerina amoena</i>	7	7	2	2	3	3	0	0	1	0	10	1
Fox sparrow	<i>Passerella iliaca</i>	7	7	0	3	0	0	0	0	2	0	3	2
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	9	11	2	2	0	6	1	0	0	0	13	0
Rufous-sided towhee	<i>Pipilo erythrophthalmus</i>	7	7	0	3	0	0	0	0	0	0	3	0
Western tanager	<i>Piranga ludoviciana</i>	10	10	0	2	0	6	1	0	1	0	11	1
Northern waterthrush	<i>Seiurus novaboracensis</i>		3		3	0	6	1	0	1	0	15	1
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	7	7	0	2	0	0	1	0	0	0	7	0
American tree sparrow	<i>Spizella arborea</i>		7		2	0	0	1	0	0	0	7	0
Chipping sparrow	<i>Spizella passerina</i>	11	7	0	2	3	0	1	0	0	0	10	0
Yellow-headed blackbird	<i>Xanthocephalus xanthocephalus</i>	7	7	3	3	0	0	1	3	3	0	12	3
Dark-eyed junco	<i>Junco hyemalis</i>	5	5	0	2	0	0	1	0	0	0	5	0

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores	Status
		West	East	West	East	PT	GR	CS	CO	SS	BS		
Fringillidae: Finches and grosbeaks													
House finch	<i>Carpodacus mexicanus</i>	9	9	2	2	0	0	1	0	0	0	7	0
Purple finch	<i>Carpodacus purpureus</i>	11	11	2	2	0	0	1	0	0	0	7	0
Cassin's finch	<i>Carpodacus cassinii</i>	11	11	2	2	0	0	1	0	0	0	7	0
American goldfinch	<i>Carduelis tristis</i>	8	8	2	2	0	0	1	3	0	0	10	0
Mammals													
Marsupialia: Marsupials													
Didelphidae: New world opossums													
Virginia opossum	<i>Didelphis virginiana</i>	5	5	2	3	0	0	0	0	0	0	5	0
Insectivora: Insectivores													
Soricidae: Shrews													
Marsh shrew	<i>Sorex bendirii</i>	16		2		0	3	0	0	0	2	7	2
Masked shrew	<i>Sorex cinereus</i>	15		2		0	0	0	0	0	0	4	0
Montane shrew	<i>Sorex monticolus</i>	15	15	0	3	0	0	0	0	0	0	3	0
Water shrew	<i>Sorex palustris</i>	16	16	3	2	0	0	0	0	0	0	5	0
Preble's shrew	<i>Sorex preblei</i>		15		3	0	3	0		1	2	9	3
Trowbridge's shrew	<i>Sorex trowbridgii</i>	15		0		0	3	0	0	0	2	3	2
Vagrant shrew	<i>Sorex vagrans</i>	15	15	0	2	0	0	0	0	0	0	2	0
Talpidae: Moles													
Shrew-mole	<i>Neurotrichus gibbsii</i>	15		0		0	3	0	0	2	2	3	4
Coast mole	<i>Scapanus orarius</i>	15	15	0	0	0	3	1	0	0	2	6	2
Townsend's mole	<i>Scapanus townsendii</i>	15		2		0	3	1	0	1	4	10	5

Table 4. Continued.

Taxon	Life Forms	Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status		
		West	East	West	East	PT	GR	CS	CO	SS	BS		SEN	SIG
Chiroptera: Bats														
Vespertilionidae: Plainnose bats														
Pallid bat	<i>Antrozous pallidus</i>	4	4	2	3	3	0	2	3	0	0	17	0	SC
Big brown bat	<i>Eptesicus fuscus</i>	14	14	0	2	0	0	2	0	0	0	8	0	
Silver-haired bat	<i>Lasionycteris noctivagans</i>	14	14	2	2	0	0	2	0	3	0	10	3	
Hoary bat	<i>Lasiurus cinerea</i>	11	11	2	3	0	0	2	0	1	0	11	1	
California myotis	<i>Myotis californicus</i>	14	14	2	2	0	0	2	3	0	0	13	0	
Western small-footed myotis	<i>Myotis ciliolabrum</i>		4		3	0	0	2	3	0	0	15	0	
Long-eared myotis	<i>Myotis evotis</i>	14	14	0	2	0	0	2	0	0	0	8	0	
Keen's myotis	<i>Myotis keenii</i>	14		2		0	0	2	3	0	0	13	0	
Little brown myotis	<i>Myotis lucifugus</i>	14	14	0	2	0	0	2	3	0	0	11	0	
Fringed myotis	<i>Myotis thysanodes</i>	14		0		0	0	2	3	0	0	9	0	
Long-legged myotis	<i>Myotis volans</i>	14	14	0	2	3	0	2	3	0	0	14	0	SC
Yuma myotis	<i>Myotis yumanensis</i>	14	14	0	3	0	0	2	3	0	0	12	0	
Western pipistrelle	<i>Pipistrellus hesperus</i>		4		3	0	0	2	0	0	0	12	0	
Townsend's big-eared bat	<i>Plecotus townsendii</i>	4	4	3	2	3	0	2	3	0	0	17	0	SC
Lagomorpha: Pika, hares, and rabbits														
Leporidae: Hares and Rabbits														
Snowshoe hare	<i>Lepus americanus</i>	5	5	0	3	0	0	0	0	0	0	3	0	
Eastern cottontail	<i>Sylvilagus floridanus</i>	15		3		0	0	0	0	0	0	6	0	
Nuttall's cottontail	<i>Sylvilagus nuttallii</i>	15	15	3	2	0	0	0	0	0	0	5	0	
Rodentia: Rodents														
Aplodontidae: Mountain beaver														
Mountain beaver	<i>Aplodontia rufa</i>	15		2		0	3	1	0	5	2	10	7	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Sciuridae: Squirrels														
Northern flying squirrel	<i>Glaucomys sabrinus</i>	14	14	2	2	0	0	1	0	0	0	7	0	
Western gray squirrel	<i>Sciurus griseus</i>	10	10	2	3	0	3	1	0	0	0	11	0	
Golden-mantled ground squirrel	<i>Spermophilus lateralis</i>	15	15	2	0	0	0	1	0	0	0	5	0	
Cascade golden-mantled g. s.	<i>Spermophilus saturatus</i>	15		2		0	6	1	0	0	6	13	6	
Yellow-pine chipmunk	<i>Tamias amoenus</i>	15	15	0	0	0	0	0	0	0	0	0	0	
Least chipmunk	<i>Tamias minimus</i>		15		3	0	0	0	0	0	0	6	0	
Townsend's chipmunk	<i>Tamias townsendii</i>	15		0		0	3	1	0	0	2	6	2	
Douglas squirrel	<i>Tamiasciurus douglasii</i>	10	10	2	2	0	3	0	0	0	0	7	0	
Geomyidae: Pocket gophers														
Western pocket gopher	<i>Thomomys mazama</i>	15		2		0	6	1	0	0	0	13	0	
Castoridae: Beaver														
Beaver	<i>Castor canadensis</i>	16	16	2	2	3	0	1	0	3	0	10	3	
Muridae: Mice and rats														
Muskrat	<i>Ondatra zibethicus</i>	16	16	3	2	0	0	0	0	2	0	5	2	
Deer mouse	<i>Peromyscus maniculatus</i>	15	15	0	0	0	0	0	0	0	0	0	0	
Forest deer mouse	<i>Peromyscus oreas</i>	15		2		0	6	0	0	0	4	10	4	
Southern red-backed vole	<i>Clethrionomys gapperi</i>	15	5	2	3	0	0	0	0	0	0	5	0	
Long-tailed vole	<i>Microtus longicaudus</i>	15	15	2	0	0	0	0	0	0	0	2	0	
Creeping vole	<i>Microtus oregoni</i>	15		0		0	3	0	0	0	0	3	0	
Meadow vole	<i>Microtus pennsylvanicus</i>					0	0	0	0	0	0	0	0	
Water vole	<i>Mictotus richardsoni</i>	15	16	3	2	0	0	0	0	0	0	5	0	SC
Townsend's vole	<i>Microtus townsendii</i>	15		2		0	3	0	0	0	0	7	0	
Heather vole	<i>Phencomys intermedius</i>	15	15	3	3	0	0	0	0	0	0	6	0	
Northern bog lemming	<i>Synaptomys borealis</i>	15		3		3	0	1	0	0	0	12	0	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores		Status
		West	East	West	East	PT	GR	CS	CO	SS	BS	SEN	SIG	
Zapodidae: Jumping mice														
Western jumping mouse	<i>Zapus princeps</i>	3	3	2	2	0	0	1	0	0	0	7	0	
Pacific jumping mouse	<i>Zapus trinotatus</i>	3		0		0	6	1	0	0	2	9	2	
Myocastoridae: Nutria														
Nutria	<i>Myocastor coypus</i>	16	16	3	3	0	0	0	0	3	0	6	3	
Carnivora: Carnivores														
Ursidae: Bears														
Black bear	<i>Ursus americanus</i>	15	15	0	2	0	0	2	0	0	0	8	0	
Grizzly bear	<i>Ursus arctos</i>	15		2		6	0	2	0	0	0	16	0	FE SE
Procyonidae: Raccoons and coatis														
Raccoon	<i>Procyon lotor</i>	14	14	0	3	0	0	1	0	0	0	6	0	
Mustelidae: Weasels, skunks, and their allies														
River otter	<i>Lutra canadensis</i>	16	16	0	2	0	0	1	0	0	0	5	0	
Marten	<i>Martes americana</i>		14		3	0	0	1	0	0	0			
Fisher	<i>Martes pennanti</i>	14	14	2	3	3	0	1	0	0	0	11	0	SC
Striped skunk	<i>Mephitis mephitis</i>	15	15	2	3	0	0	0	0	0	0	5	0	
Ermine	<i>Mustela erminea</i>	15	15	0	2	0	0	0	0	0	0	2	0	
Long-tailed weasel	<i>Mustela frenata</i>	15	15	0	0	0	0	0	0	0	0	0	0	
Mink	<i>Mustela vison</i>	14	16	0	0	0	0	1	0	0	0	3	0	
Western spotted skunk	<i>Spilogale putorius</i>	15	15	2	3	0	0	0	0	0	0	5	0	
Canidae: Dogs														
Red fox	<i>Vulpes vulpes</i>	15		0		0	0	0	0	0	0	0	0	

Table 4. Continued.

Taxon		Life Forms		Habitat Specificity		Sensitivity Variables				Significance Variables		Scores	Status	
		West	East	West	East	PT	GR	CS	CO	SS	BS			SEN
Felidae: Cats														
Bobcat	<i>Felis rufus</i>	4	4	0	0	0	0	1	0	0	0	3	0	
Artiodactyla: Even-toed ungulates														
Cervidae: Deer														
Moose	<i>Alces alces</i>					0	0	2	0	0	0	6	0	
Rocky mountain elk	<i>Cervus elaphus nelsoni</i>		5		2	0	0	2	0	0	0	10	0	
Roosevelt elk	<i>Cervus elaphus roosevelti</i>	5		0		0	6	2	0	0	2	12	2	
Mule deer	<i>Odocoileus hemionus</i>	5	5	0	2	0	0	2	0	0	0	8	0	
	<i>hemionus</i>													
Black-tailed deer	<i>Odocoileus hemionus columbiana</i>	5		0		0	3	2	0	0	0	9	0	
Columbian white-tailed deer	<i>Odocoileus virginianus leucurus</i>	5		2		6	6	2	0	0	2	22	2	FE
White-tailed deer	<i>Odocoileus virginianus ochoura</i>		5		3	0	0	2	0	0	0	12	0	

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