

An Ecosystem Context for Bat Management: A Case Study of the Interior Columbia River Basin, USA

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ABSTRACT

The ecological role and environmental requirements of 15 species of bats were analyzed in an ecosystem assessment of the interior Columbia River Basin, USA. Ecological roles of bats potentially contribute to nutrient cycling, insect population control, transmission of disease, hosting obligate ectoparasites, and accumulation of pesticides. Such roles can influence ecological processes in forest canopies, soils, and water bodies, and population levels of arthropods and their predators, and of other species of bats. Specific studies are needed on rates of effects. The macroecology and collective environmental requirements of all 15 bat species also provide for a wide range of other species in forest, wetland, riparian, and other settings. Such a systems- and biodiversity-wide approach helps put bat management into an ecosystem context and helps focus needs for further inventory, monitoring, and research.

INTRODUCTION

Federal, state, and provincial land management agencies in Canada and the USA are moving towards ecosystem management of forests and grasslands (Bormann et al. 1994; Pojar et al. 1994). This entails crafting land management activities to better tier the ecological requirements and roles of plant, invertebrate, and vertebrate species, including bats (Kaufman et al. 1994). In such an approach, the collective macroecology, ecological roles, and environmental requirements of bats can be incorporated into an ecosystem management context. This paper illustrates one such approach from an ongoing study of species, biodiversity, and ecosystems in the interior Columbia River Basin. The study is part of a scientific assessment and land-use planning project called the Interior Columbia River Basin Ecosystem Management Project, conducted jointly by USDI Bureau of Land Management (BLM) and USDA Forest Service (FS).

The interior Columbia River Basin (CRB) includes portions of seven western states and covers about 60.9 million ha (Figures 1 and 2). (This area also contains parts of the Klamath Basin and northern Great Basin in southern Oregon, included in the land-use planning area for this project.) BLM and FS lands comprise 52 percent of this area, with the remainder in private, state and local government, tribal, and federal lands.

The CRB area contains nine major landforms ranging from arid grasslands and lowland plains and valleys, to intermontane basins and breaks, to steep mountains and glaciated ranges (Figure 3a). Precipitation, relief, and elevation vary widely throughout the study area (Figures 3b, c, and d).

The CRB area is sparsely inhabited by people as compared with other parts of the USA. However, 63 percent of the area, originally native grasslands, especially *Fescue*/bunchgrass and *Agropyron*, 24 percent of the native shrublands, such as mountain sage and big sage, and 44 percent of old-growth forests, have been greatly altered or eliminated due to agriculture, urbanization, livestock grazing, and timber harvesting.

METHODS

Information on distribution, ecology, and ecological roles of bats and other species was gathered from existing literature (e.g., Christy and West 1993; Nagorsen and Brigham 1993; Thomas 1988), and from conducting modified Delphi surveys of knowledge from panels of species experts (Marcot et al., unpub.; see Acknowledgements). This information, and vegetation cover types and structural stages used by each bat species, were described and coded into a relational database. Such information should be considered a first approximation, and may be useful in building tentative working hypotheses for management. Much further empirical work is needed to validate these hypotheses.

Range distribution maps of each bat species were drawn (scale 1:1,000,000) and digitized in a geographic information system (ArcInfo). Total area of the CRB and each species' range within it were calculated from the maps. Trends of habitat for each species were analyzed by comparing historic (early 1800s) to current area of vegetation cover types and structural stages associated with each species, using vegetation maps from W. Hann et al. (unpub., CRB Ecosystem Management Project, Walla Walla, Washington).

The CRB study area was partitioned into 7,733 sub-watersheds or sixth-level hydrologic units (see Jensen and Bourgeron 1993 for explanation of hydrologic unit coding system). Within the CRB, these sub-watersheds averaged 7,880 ha and ranged from 96 to 86,500 ha. Each was characterized according to total area; percentage of overlap of each bat species' distributional range; historic and current dominant vegetation cover type and structural stage; dominant landform category; highest and lowest annual precipitation (available data from 1989); highest and lowest elevation; and topographic relief (biophysical data from Fire Lab, FS, Missoula, Montana).

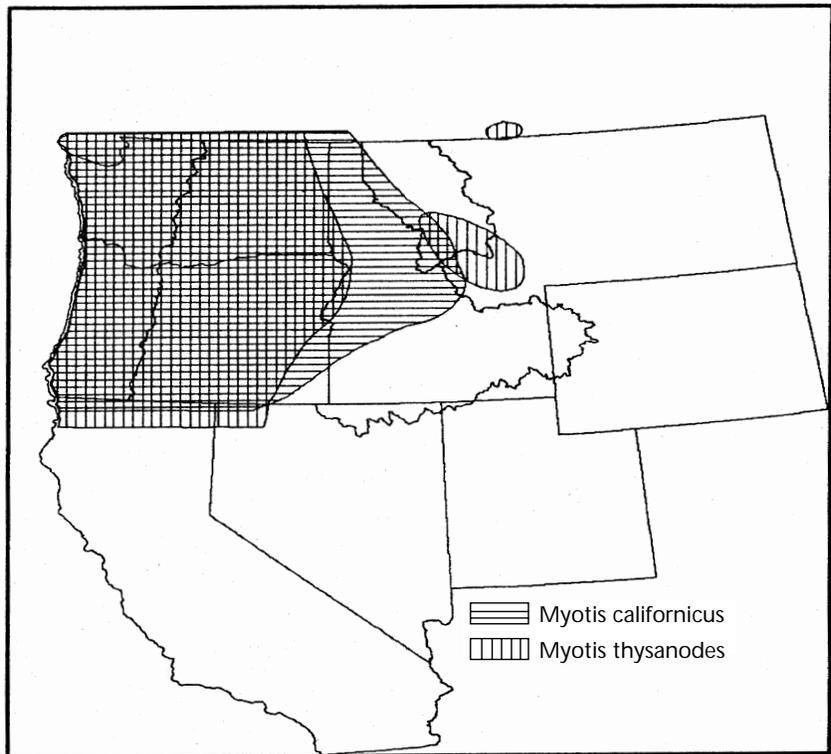
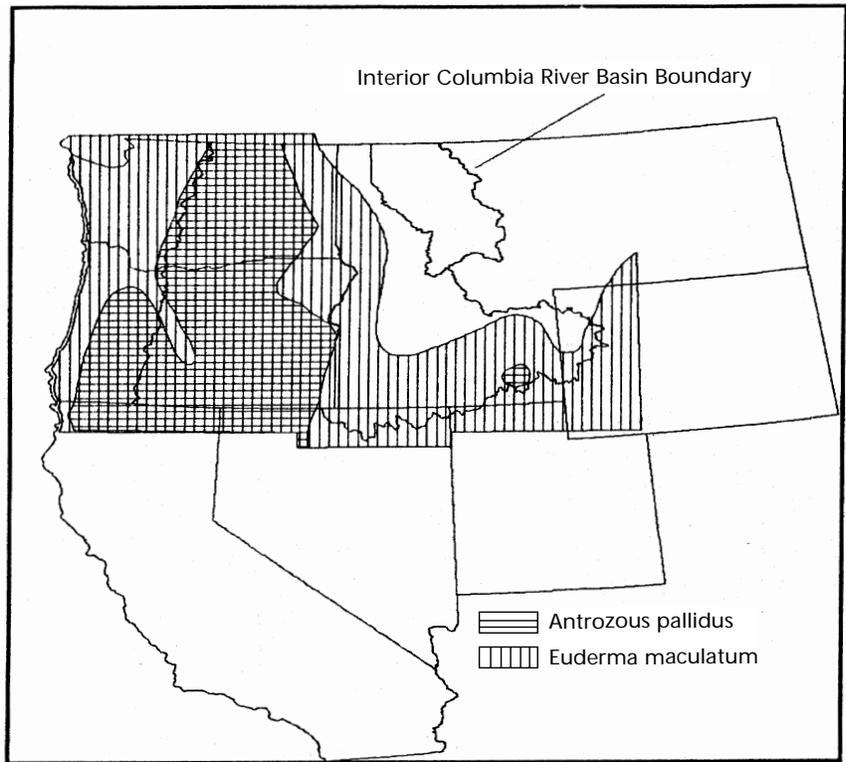


FIGURE 1 Ranges of eight bat species in the Interior Columbia River Basin. Distributions beyond the general area of the Basin are not shown. An additional seven bat species are ubiquitous throughout the Basin (see text).

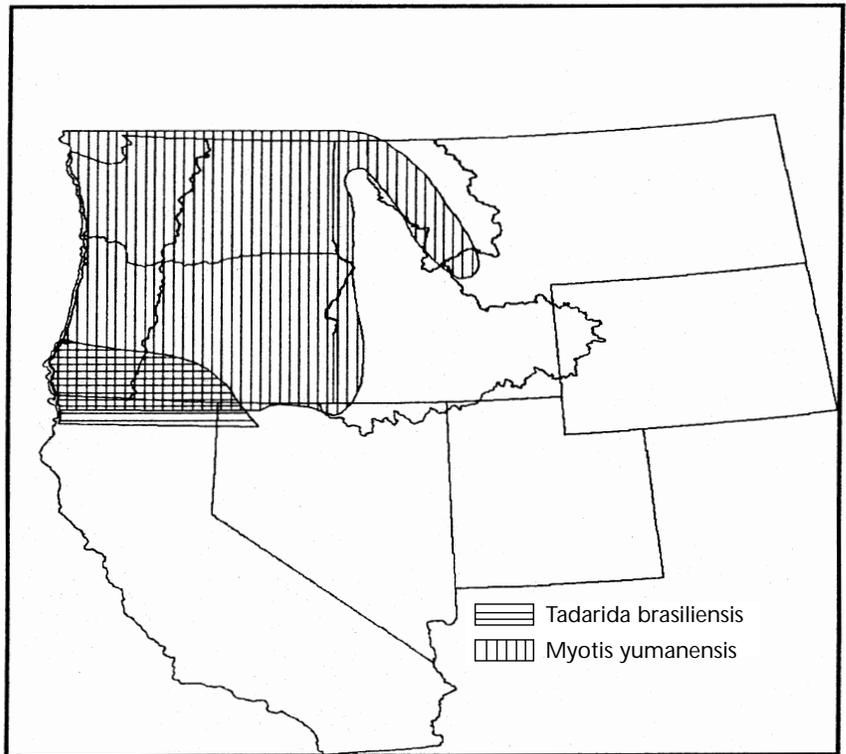
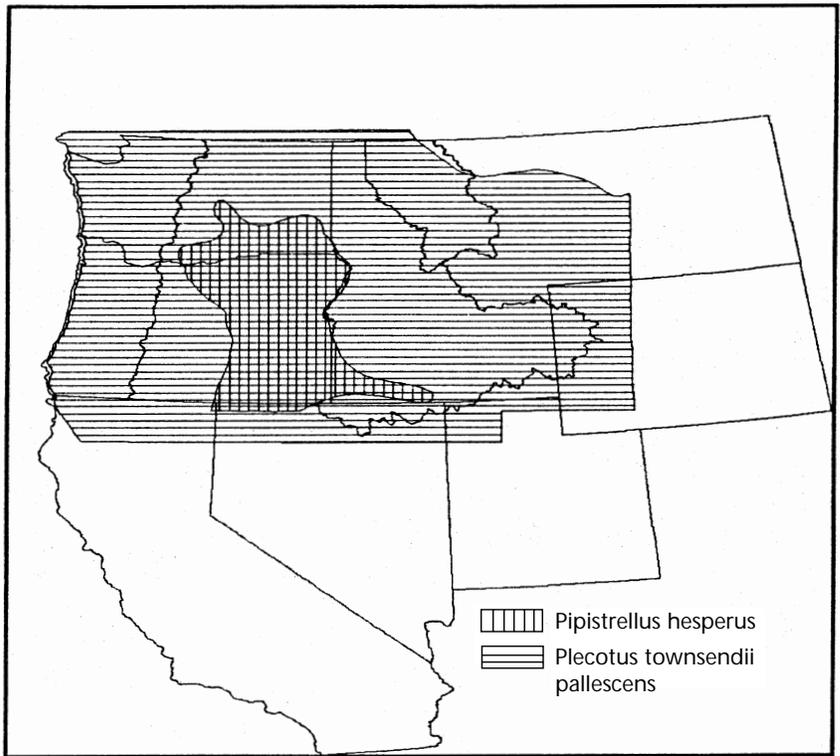


FIGURE 1 *Continued*

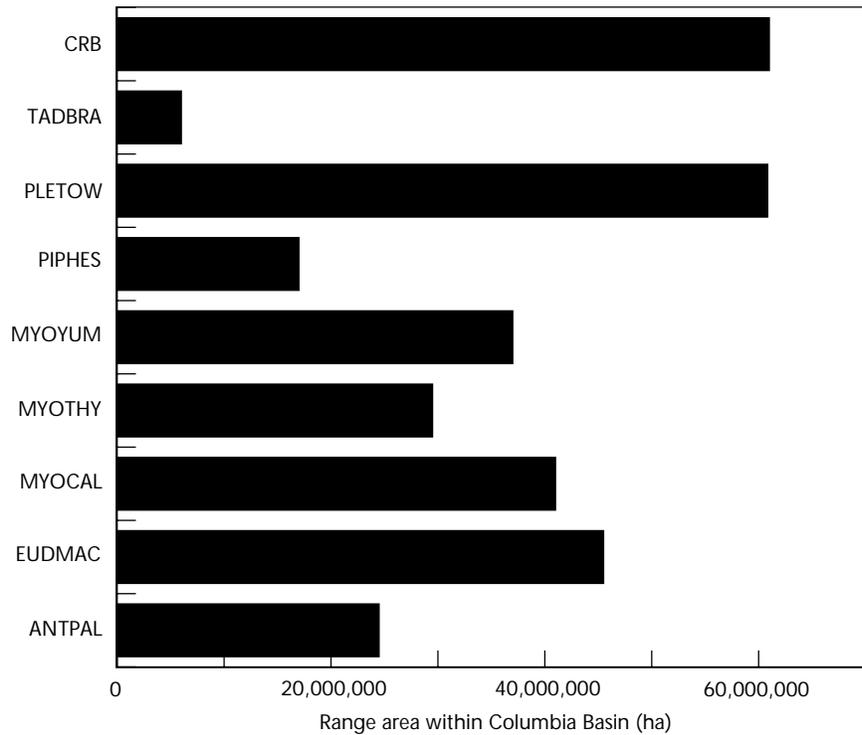


FIGURE 2 Total range of eight species of bats within the Interior Columbia River Basin, based on the distributional maps in Figure 1. See Table 1 for species codes. CRB = total area of the Basin and ranges of the additional seven ubiquitous species.

Highest and lowest annual precipitation levels within sub-watersheds were significantly positively correlated ($p < 0.01$, Pearson correlation coefficient $r = 0.677$, $n = 7739$ sub-watersheds), as were highest and lowest elevation levels ($p < 0.01$, $r = 0.700$, $n = 7739$). Thus, for further analyses only one of each variable pair, highest levels, was used. Also, slope and relief were significantly positively correlated ($p < 0.02$, $r = 0.410$, $n = 7739$), so only one of the pair, relief, was carried into further analyses.

The CRB area, and macroecology properties within each bat species' range, then were characterized by tallying the total area within each sub-watershed in each biophysical category of landform, precipitation, elevation, and relief. Data were summarized as percentage of total area, rather than as absolute area, within each bat species' range, because total macrohabitat area likely overestimated true habitat available to each species.

Each bat species was characterized according to its key environmental correlates; that set of microhabitat, substrate, and other environmental factors thought to most influence population fitness and viability. Also listed for each bat species were key ecological functions, the known or hypothesized primary set of activities performed by organisms that affect the ecological function of their ecosystem. Key environmental correlates and key ecological functions of bats were compared with those of all vertebrates in the CRB to determine the degree of similarity.

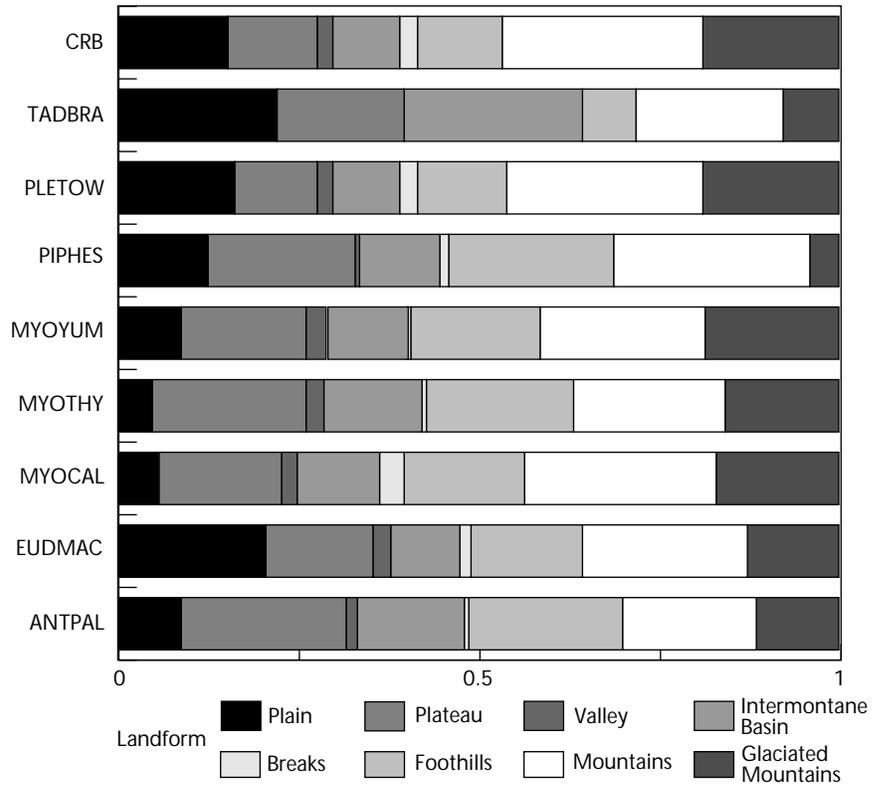


FIGURE 3A Landforms.

FIGURE 3 Proportions of each bat species' range among biophysical attributes within the 6th level hydrologic unit codes of the interior Columbia River Basin, based on habitat attributes listed in the appendices applied to the entire Basin. (See Table 1 for species codes.) CRB = overall distribution within the Basin and for the additional seven ubiquitous bat species.

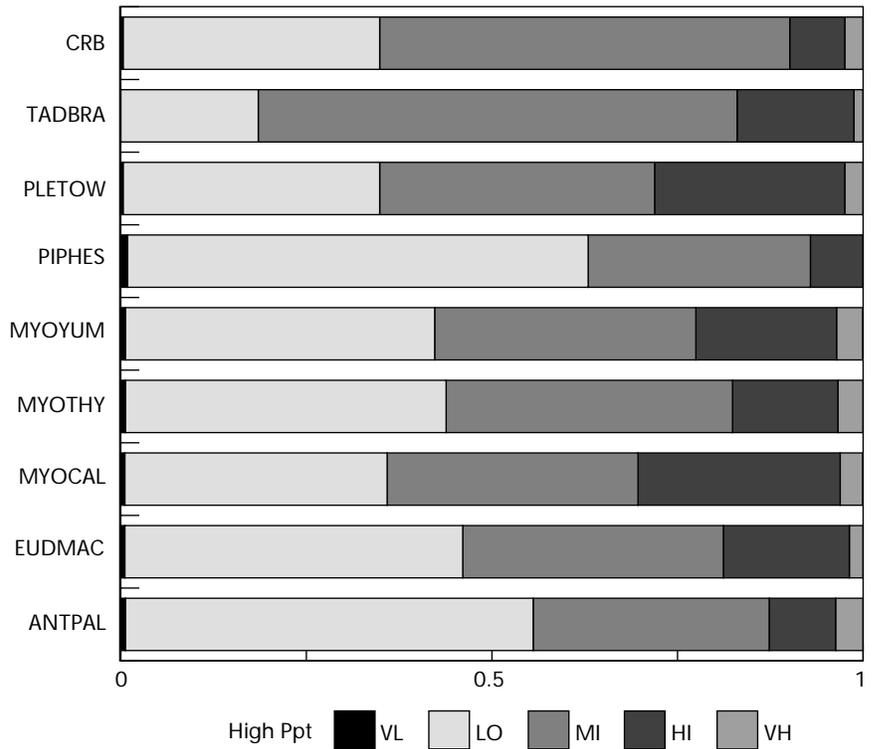


FIGURE 3B Highest mean annual precipitation. Very low = 0–203 mm, low = 204–508, mid = 509–1016, high = 1017–2032, very high = 2033+m.

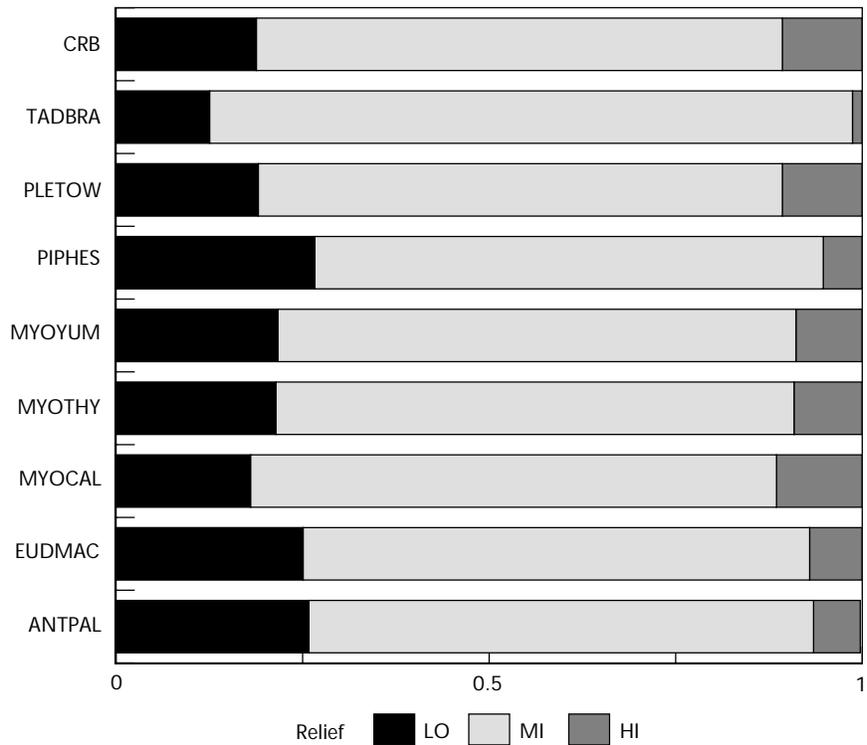


FIGURE 3C *Topographic relief. Low = 0–305 m, mid = 306–1219 m, high = 1220–2438 m.*

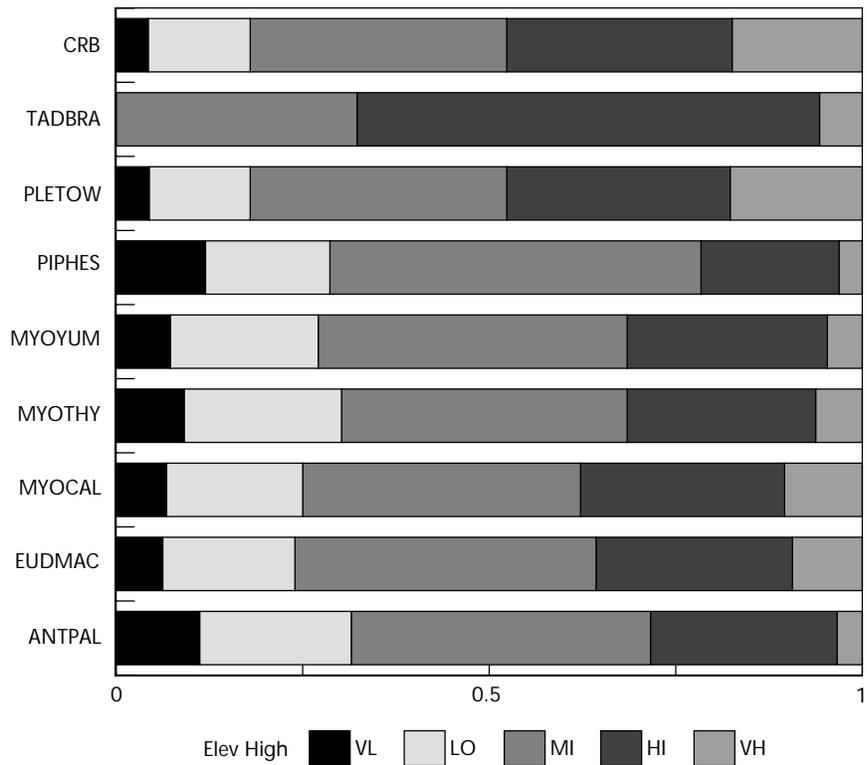


FIGURE 3D *Highest elevation. Very low = 0–610 m, low = 611–1219 m, mid = 1220–1829 m, high = 1830–2348 m, very high = 2349+ m.*

RESULTS

Distribution of Bat Species

Fifteen species of bats among nine genera regularly occur within the CRB (Table 1). Seven species are ubiquitous in the CRB, although some of these are sparsely distributed. Another eight species occupy less than the full CRB area (Figure 1), in coverage ranging from *Tadarida brasiliensis*, which occurs only in southwestern Oregon, to the nearly ubiquitous *Myotis californicus* (Figure 2). By state within the CRB, bat species' richness decreases north and east, with 15 species in Oregon, 14 in Washington, 13 in Idaho, and 11 in Montana. This trend is likely due to area and heterogeneity of habitats of each state within the CRB.

Vegetation Cover Types and Structural Stages Used

No bat species is requisitely associated with a single vegetation cover type or structural stage (Appendix 1). Of all 36 vegetation cover types within the CRB, those used by most bats (> nine species) are two woodland and five forest types, including interior Douglas-fir forest and interior ponderosa pine forest (12 bat species). Those least used (< three bat species) include three oak and conifer forest cover types peripheral to the CRB area, and two native shrub cover types (Mountain Big Sage and Chokecherry/Serviceberry/Rose) that have suffered substantial historic declines (used by *Lasionycteris noctivagans* and *Corynorhinus townsendii*).

Among the vegetation structural stages, Closed Tall Shrub and Open Tall Shrub stages are the least used (< six bat species), whereas various woodland and forest stages are most used (>11 bat species) (Appendix 2). Old Single-stratum Forests and Old Multi-strata Forests—the old-growth forests of the CRB, which have suffered historic declines—are among the stages most used, each with an associated 13 bat species. Individual species probably vary in their response. *C. noctivagans* is closely associated with old forest stages in general. *C. townsendii* is likely affected by loss of

TABLE 1 The fifteen species of bats regularly found within the interior Columbia River Basin, U.S.A.

SPPCODE	Scientific name	Common name
ANTPAL	<i>Antrozous pallidus</i>	Pallid bat
EPTFUS	<i>Eptesicus fuscus</i> ¹	Big brown bat
EUDMAC	<i>Euderma maculatum</i>	Spotted bat
LASCIN	<i>Lasiurus cinereus</i> ¹	Hoary bat
LASNOC	<i>Lasionycteris noctivagans</i> ¹	Silver-haired bat
MYOCAL	<i>Myotis californicus</i>	California myotis
MYOCIL	<i>Myotis ciliolabrum</i> ¹	Western small-footed myotis
MYOEVO	<i>Myotis evotis</i> ¹	Long-eared myotis
MYOLUC	<i>Myotis lucifugus</i> ¹	Little brown myotis
MYOTHY	<i>Myotis thysanodes</i>	Fringed myotis
MYOVOL	<i>Myotis volans</i> ¹	Long-legged myotis
MYOYUM	<i>Myotis yumanensis</i>	Yuma myotis
PIPHES	<i>Pipistrellus hesperus</i>	Western pipistrelle
PLETOW	<i>Corynorhinus townsendii</i>	Pale western big-eared bat
TADBRA	<i>Tadarida brasiliensis</i>	Brazilian free-tailed bat

¹ Ubiquitous in the interior Columbia River Basin, U.S.A.

old-growth ponderosa pine (*Pinus ponderosa*) forests. *Myotis thysanodes* selects large (>58 cm diameter at breast height) snags in remaining old forests.

Myotis californicus and *Tadarida brasiliensis* can be thought of as the most specialized on macrohabitats, each using the fewest vegetation cover types (< six cover types, compared with a median of 14 cover types used per bat species). *M. californicus* is closely associated with forest cover types and *T. brasiliensis* with grassland cover types. *Pipistrellus hesperus* and *T. brasiliensis* are the most specialized on vegetation structural stages, each using < six stages (compared with a median of 10 structural stages used per bat species); they are closely associated with herb and shrub stages. *Eptesicus fuscus* and *Lasionycterus noctivagans* are the most generalized (each using >24 cover types and >12 structural stages) (Appendices 1 and 2).

Historic Trends of
Habitat

All but three of the bat species have suffered declines in total area of their native habitats (vegetation cover types and structural stages) in the CRB since early historic times (Figure 4). Some of these declines may have occurred outside the historic ranges of individual species within the CRB, and these estimates do not account for changes in microhabitats and specific substrates used for roosting and breeding. Habitat of *Lasionycteris noctivagans* has declined the greatest in absolute area. Habitat has increased for two habitat generalists (*Eptesicus fuscus* and *Corynorhinus townsendii*) and one specialist (*Tadarida brasiliensis*, but this species occurs only in a small corner of the CRB).

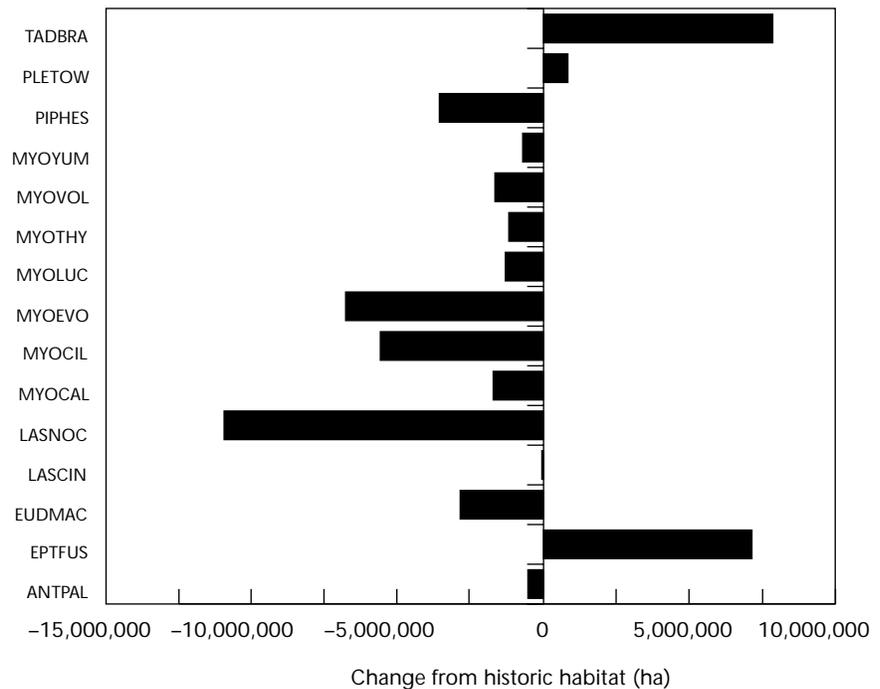


FIGURE 4 Change in the amount of habitat from early historic (early 1800s) to current times for each of the 15 bat species of the Interior Columbia River Basin. Habitat amounts were based on vegetation cover types and structural stages listed in the appendices, applied to the entire Basin. See Table 1 for species codes.

Declines in specific vegetation cover types, including native herblands, grasslands, sagebrush, and old forests, may have been accompanied by local declines in associated bat species, although data on bat population trends are lacking. Correlations are likely to be poor between some local bat populations and amount of habitat, defined here as gross vegetation cover types and structural stages. For example, although total area of habitat of *Corynorhinus townsendii* has increased, populations have declined. This is because microhabitats and specific substrates, as for roosting, and human disturbance, need to be additionally considered. However, provision of habitat is the first and most important need for conservation.

Macroecology

As a whole, bats within the CRB occur in all landforms (Figure 3a). However, *Tadarida brasiliensis* seems more associated with valleys and plains and less with mountainous landforms (Figure 3a), and with areas of somewhat higher precipitation (Figure 3b) and lower relief (Figure 3c) than generally available in the CRB. *Pipistrellus hesperus*, *Euderma maculatum*, and *Antrozous pallidus* also are somewhat less associated with mountains and are species more of drier valleys, plains, and foothills (Figures 3a and b) of moderate to low relief and elevation (Figures 3c and d). Species more associated with mountainous landforms include the seven ubiquitous species (Table 1), as well as *Myotis californicus* and *M. thysanodes* (neither associated with plains landforms), and *M. yumanensis* and *C. townsendii*.

Key Environmental Correlates

General associations with macrohabitats and biophysical characteristics, of course, are only part of the ecological story. Such associations are being used within the CRB to guide land-use planning on a broad scale. However, when broad-scale planning guidelines rank site-specific management actions, finer descriptions of habitats for conservation are needed. These are found in the listing of key environmental correlates (KECS) for each species (Table 2). KECS of the 15 bat species of the CRB were categorized into vegetation elements, biological non-vegetation elements, non-vegetation terrestrial substrates, riparian and aquatic bodies, and human disturbance elements.

The key forest vegetation elements for bats include snags (eight bat species out of 65 total vertebrate species often or primarily use snags); foliage and dead parts of live trees, as for roosting (four bat species out of 36 vertebrates); and exfoliating bark (four bat species out of six vertebrates). Also important to bat ecology are lithic substrates, used primarily by 13 bat species (out of 113 vertebrates). Specific lithic substrates used by bats are cliffs, talus, boulders, caves, outcrops/crevices, lava tubes, and canyons. Riparian and aquatic bodies used by bats include rivers, streams, ponds, and wetlands; these are used primarily by 10 bat species (out of 278 vertebrates) largely as foraging habitat.

Planning ecosystem management guidelines for bats also means addressing human disturbance elements, which can provide some (but not all) foraging and roosting requirements. These human disturbance elements used by some bats include little-used roads or trails (providing forest openings for aerial insect feeding), developments, buildings, bridges, agricultural developments, mines, and livestock guzzlers. However, it is as important to determine if such developments reduce KECS or habitats for

TABLE 2 *Key environmental correlates for bat species found in the interior Columbia River Basin, U.S.A. See Table 1 for species name codes. [] = total number of all vertebrate species within the Basin closely associated with the correlate. (Data and outline of correlates taken from a much longer classification system designed for all species [Marcot et al., in prep.])*

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1. Vegetation elements
 - a. forest or woodland vegetation substrates
 - i. snags (entire tree dead)—ANTPAL, EPTFUS, LASNOC, MYOCIL, MYOEVO, MYOLUC, MYOVOL, PLETOW [65]
 - ii. live trees (as for roosting)—ANTPAL, LASCIN, MYOEVO, PLETOW [36]
 - (1) exfoliating bark—LASNOC, MYOCAL, MYOLUC, MYOYUM [6]
 2. Biological (non-vegetation) elements
 - a. presence of nesting structures
 - i. cavities (includes in structures, rocks, tree bark)—MYOCAL, MYOYUM [39]
 3. Non-vegetation terrestrial substrates
 - a. lithic (rock) substrates
 - i. cliff—ANTPAL, EPTFUS, EUDMAC, MYOCIL, MYOEVO, PIPHES, PLETOW [55]
 - ii. talus—MYOEVO [49]
 - iii. boulder, large rocks—PLETOW [8]
 - iv. cave—ANTPAL, EPTFUS, LASNOC, MYOCIL, MYOEVO, MYOLUC, MYOVOL, MYOYUM, PLETOW, TADBRA [26]
 - v. rock outcrops/crevices—ANTPAL, EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOLUC, MYOVOL, MYOYUM, PIPHES [38]
 - vi. lava tubes—TADBRA [2]
 - vii. canyons—PIPHES [9]
 - b. forages above tree canopy—LASCIN [11]
 4. Riparian and aquatic bodies—EPTFUS, EUDMAC, LASCIN, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOYUM, PIPHES [278]
 - a. rivers—ANTPAL, EPTFUS, MYOLUC [69]
 - b. streams (permanent or seasonal)—LASCIN, MYOLUC [74]
 - c. lakes or reservoirs (lacustrine)—ANTPAL, EPTFUS, LASCIN, MYOCAL, MYOLUC, MYOYUM [134]
 - d. ponds (permanent or seasonal)—ANTPAL, EPTFUS, EUDMAC, LASCIN, MYOCAL, MYOLUC, MYOVOL, MYOYUM [96]
 - e. wetlands, marshes, or wet meadows (palustrine)—EUDMAC, LASNOC [90]
 - f. swamps—MYOCIL [7]
 5. Human disturbance elements
 - a. roads or trails (positive effect)—ANTPAL [6]
 - b. residential development (positive effect)—MYOCAL, TADBRA [15]
 - c. buildings (positive effect)—EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOVOL, MYOYUM, PLETOW, TADBRA [27]
 - d. bridges (positive effect)—ANTPAL, EPTFUS, MYOEVO, PLETOW [9]
 - e. agriculture and croplands (positive effect)—TABRA [84]
 - f. mines and mining activities (positive effect)—EPTFUS, LASNOC, MYOCAL, MYOCIL, MYOEVO, MYOLUC, MYOYUM, PLETOW [10]
 - g. guzzlers (positive effect)—ANTPAL [1]
-

other bat and non-bat species, such as reduction in old forest stages. Also, direct disturbance of bat colonies in nurseries and hibernacula, particularly in caves, is of concern and should be regulated by management (White and Seginak 1987).

Key Ecological Functions

Species, including bats, are more than just a function of their environment. Their ecological roles often affect the productivity and diversity of the ecosystems they inhabit. One key ecological function of all 15 bats of the CRB is predation of invertebrates, particularly insects. Although insectivory is shared among 225 vertebrate species of the CRB, seven of the bat species in particular might play key roles in controlling some forest and agricultural insect pests (Table 3).

Another key ecological function likely shared by all 15 bats of the CRB is that of aiding dispersal or concentration of nutrients. *Tadarida brasiliensis* produces guano so copiously that it can create and modify its own ecosystem. *Eptesicus fuscus* likely is important in aiding nutrient transport into subterranean environments; sometimes it is the only bat species occupying caves and mines in Idaho and Montana within the CRB, whereas elsewhere in the CRB *Corynorhinus townsendii* and *Myotis evotis* also play this role. *Lasionycteris noctivagans* may be an important agent for distributing riparian nutrients to upland environments as it travels from wetland foraging sites to forest roost sites. *L. noctivagans* and *L. cinereus* might aid in long-distance nutrient movement, as feeding and roosting sites can be separated by as far as 20 km.

Another key ecological function of *Eptesicus fuscus* and *L. noctivagans* is that of disease transmission, particularly rabies. *E. fuscus* is a potential threat as there are many contacts with humans and bites are known to draw blood.

In cave roosts, *Myotis evotis*, *Corynorhinus townsendii*, and possibly other species (from personal observation in northwestern California) also act as hosts in a coevolved relationship with a small group of specialized insects. These are the wingless, obligate ectoparasitic bat flies (Streblidae and Nycteribiidae: Diptera) and the bed bug *Cimex latipennis* (Cimicidae: Hemiptera).

The relation with *C. latipennis* bears further telling. In all its stages, it feeds on bats usually at roosts; it is an obligate sanguinivore, a blood-feeder. Like its Dipteran bat fly brethren, it is completely flightless and depends on bats for dispersal. It likely overwinters at roost sites whether or not bats are present, ensuring that it has ready access to the next arrivals. It is known to be associated only with *Myotis* and may control bat populations by excessive feeding on young bats, but there are no studies testing this hypothesis. It is not known to be a vector of disease as it is little studied.

Another key ecological function associated with bats is accumulation of pesticides (Clark 1981, 1988). *T. brasiliensis* may be more susceptible to pesticides than the other bat species due to its foraging in agricultural and rangeland habitats (Appendix 1). *Eptesicus fuscus* also may be susceptible. Use of selected pesticides is sometimes part of federal land management activities; for example, on federal lands of the CRB, use of any registered material to control western spruce budworm (*Choristoneura occidentalis*) is legal.

TABLE 3 Key ecological functions of bat species found in the interior Columbia River Basin, U.S.A. See Table 1 for species name codes. [] = total number of all vertebrate species within the Basin with the ecological function. (Outline of functions taken from a much longer classification system designed for all species [Marcot et al., in prep.])

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- I. Trophic relationships
 - A. heterotrophic consumer
 - 1. secondary consumer (primary predator or carnivore)
 - a. consumer or predator of invertebrates, including insects (insectivorous)—ALL 15 SPECIES [225]
 - II. Nutrient cycling relationships
 - A. aids in physical transfer of substances for nutrient cycling (C,N,P, other)—ALL 15 SPECIES [33]
 - III. Interspecies relationships
 - A. insect control¹—EPTFUS, EUDMAC, LASNOC, MYOEVO, MYOLUC, MYOVOL, PLETOW [22]
 - B. commensal or mutualist with other species²—MYOVOL [4, as affecting management]
 - C. competitor³—EPTFUS [46, as affecting management]
 - IV. Disease, pathogen, parasite, and toxins relationships
 - A. carrier, transmitter, or reservoir of vertebrate diseases (including rabies)⁴—EPTFUS, LASNOC [52]
 - B. host for invertebrate obligate ectoparasites⁵—MYOTIS? OTHERS?
 - C. accumulation of pesticides—ALL 15 SPECIES?
-

¹ Interspecies relationships—insect control:

EPTFUS—Important consumer of agricultural pests; insect/predation control (e.g., pine beetles [*Dendroctonus* spp.: Scolytidae] and cucumber beetles [*Dia-brotica* spp., *Acalymma* spp.: Chrysomelidae]).

EUDMAC—May affect community structure of noctuid moths by selective pressure.

LASNOC—Important predator of forest pests. Moth and beetle strategist.

MYOEVO—Insect predator/controller. Important due to relatively large numbers and wide distribution at higher elevations.

MYOLUC—Insect control.

MYOVOL—Important insect predator/control agent due to sheer numbers.

PLETOW—Predator/control agent of agricultural and forest pests.

² Commensal or mutualist with other species:

MYOVOL—Communal rooster. Will share roost with other species.

³ Competitor:

EPTFUS—May affect local distribution and habitat use by other bats. Known to chase off other bats.

⁴ Carrier, transmitter, or reservoir of vertebrate diseases:

EPTFUS—Potential threat of rabies to humans. Have frequent contact with humans and are known to draw blood.

LASNOC—Higher incidence of rabies than other bats.

⁵ Host for invertebrate obligate ectoparasites:

Myotis and others probably serve as host for wingless, invertebrate obligate ectoparasites (bat flies of Streblidae and Nycteribiidae, and the bed bug *Cimex latipennis* of Cimicidae).

Habitats and possibly populations of bats have mostly declined in the CRB since early historic times, the declines associated with conversion of native grasslands, shrublands, wetlands, and old forests. Current population viability of the 15 bat species in the CRB is largely unknown.

Bats of the CRB occupy a wide range of vegetation cover types and structural stages, but some species are closely associated with grassland/herbland and old forests for roosting, with riparian and aquatic bodies for foraging, and with lithic, crevice, and cave environments for roosting and nurseries. Others use a variety of human-built structures and human-altered environments.

Ecological roles of bats potentially contribute to nutrient cycling, insect population control, transmission of disease, and accumulation of pesticides. Bats also have the capacity to influence population levels of other species, including other bats and coevolved ectoparasites. They might play a key role in controlling population levels of insects, including forest and rangeland lepidoptera and agricultural and forest insect pests, although much of this needs greater study.

Such roles can influence ecological processes in a variety of ecological subsystems, including forest canopies, soils, subterranean environments, wetlands, and riparian areas. Bats might play a major but largely invisible role in enhancing productivity and trophic health, and affecting species diversity of these subsystems. Research is needed to determine specific rates to test this working hypothesis.

Integrating Bats into
Ecosystem
Management

One aim of ecosystem management is to consider the collective needs of multiple species. For bats, this means considering (1) their macrohabitat uses, depicted as vegetation cover types and structural stages; (2) their microhabitat requirements, depicted as KECS; (3) the range of ecosystems in which habitat management guidelines should be applied; and (4) how such guidelines also can serve to meet the needs of all other species (in this paper, I considered all other vertebrates; the current CRB planning project is also considering specific management needs for rare fungi, lichens, bryophytes, vascular plants, and selected invertebrates as well as all vertebrates).

Knowledge of bat ecology, such as snag and live-tree use, can help devise silvicultural activities in managed forests to meet needs of bats and other species simultaneously. Also likely important to managing population viability and long-term evolutionary potential of bats is maintaining seemingly marginal habitats (Gates et al. 1984). This would entail maintaining the full array of vegetation cover types, vegetation structural stages, and terrestrial, riparian, and aquatic substrates and environments used by the full array of bat species in the CRB.

The macroecology and collective environmental requirements of all 15 bat species also likely provides for a wide range of other species in forest, wetland, riparian, and other settings. Bats provide part, but not all, of the needs for all biota of the CRB. Of further interest in ecosystem management is knowledge of how disturbance dynamics of habitats influence suitability for bats and other species; this is little understood for bats of

the CRB. Coupled with an understanding of the key ecological functions that bats play in their sundry environments, and the fuller array of habitat conditions and disturbance conditions used by other species, a systems- and biodiversity-wide approach puts bat management into an ecosystem context.

ACKNOWLEDGEMENTS

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APPENDIX 1 Occurrence of 15 bat species of the interior Columbia River Basin, U.S.A., by vegetation cover type. See Table 1 for bat species name codes, and below for vegetation codes.

Veg. Code	ANT PAL	EPT FUS	EUD MAC	LAS CIN	LAS NOC	MYO CAL	MYO CIL	MYO EVO	MYO LUC	MYO THY	MYO VOL	MYO YUM	PIP HES	PLE TOW	TAD BRA
CRB003	×	×	×												×
CRB008		×	×	×	×			×						×	
CRBS01	×	×	×		×		×	×		×	×	×		×	
CRBS02	×	×	×		×	×	×		×	×				×	
CRBS03	×	×	×		×		×	×		×	×	×		×	
CRBS04			×		×		×	×			×		×	×	
CRBS05		×		×	×		×								
CRBS06	×		×		×		×	×							
CRBS07	×		×		×		×	×							
CRBS08	×	×	×					×						×	×
CRBS09		×		×	×			×			×				
CRBS10		×			×			×							
CRBS11		×		×	×			×							
CRBS12	×	×	×											×	×
CRBS13	×		×		×										
SAF205		×	×	×	×	×		×	×		×	×		×	
SAF206				×	×			×	×		×				
SAF208		×			×			×							
SAF210		×	×	×	×	×	×	×	×	×	×	×		×	
SAF212		×		×	×			×							
SAF215		×		×	×			×							
SAF217		×		×	×										
SAF218		×		×	×		×	×							
SAF219	×	×	×		×		×	×		×	×	×		×	
SAF227		×	×	×	×	×		×	×		×	×		×	
SAF233		×			×										
SAF235		×		×	×		×								
SAF237	×	×	×	×	×	×		×	×	×	×	×		×	
SAF243		×			×										
SAF245		×			×										
SRM104	×		×		×		×			×				×	
SRM322	×		×		×		×			×				×	
SRM402					×									×	
SRM406			×		×		×	×			×		×	×	
SRM414	×		×		×								×	×	×
SRM421					×										

Vegetation codes: CRB003 Shrub or Herb/Tree Regen, CRB008 Pacific Silver Fir/Mt Hemlock, CRBS01 Juniper Woodlands, CRBS02 Mixed Conifer Woodlands, CRBS03 Juniper/Sagebrush, CRBS04 Big Sagebrush, CRBS05 Shrub Wetlands, CRBS06 Agropyron Bunchgrass, CRBS07 Native Forbs, CRBS08 Exotic Forbs/Annual Grass, CRBS09 Grand Fir/White Fir, CRBS10 White Bark Pine/Alpine Larch, CRBS11 Red Fir, CRBS12 Cropland/Hay/Pasture, CRBS13 Fescue-Bunchgrass, SAF205 Mountain Hemlock, SAF206 Engelmann Spruce/Subalpine Fir, SAF208 Whitebark Pine, SAF210 Interior Douglas-fir, SAF212 Western Larch, SAF215 Western White Pine, SAF217 Aspen, SAF218 Lodgepole Pine, SAF219 Limber Pine, SAF227 Western Redcedar/Western Hemlock, SAF233 Oregon White Oak, SAF235 Cottonwood/Willow, SAF237 Interior Ponderosa Pine, SAF243 Sierra Nevada Mixed Conifer, SAF245 Pacific Ponderosa Pine, SRM104 Antelope Bitterbrush/Bluebunch Wheatgrass, SRM322 Mountain Mahogany, SRM402 Mountain Big Sagebrush, SRM406 Low Sage, SRM414 Salt Desert Shrub, SRM421 Chokecherry/Serviceberry/Rose.

APPENDIX 2 Occurrence (×) of 15 bat species of the interior Columbia River Basin, U.S.A., by vegetation structural stage (STR). See Table 1 for bat species name codes, and below for structure codes.

STR	ANT PAL	EPT FUS	EUD MAC	LAS CIN	LAS NOC	MYO CAL	MYO CIL	MYO EVO	MYO LUC	MYO THY	MYO VOL	MYO YUM	PIP HES	PLE TOW	TAD BRA
Ch	×	×	×		×		×	×		×			×	×	×
Clms	×	×	×	×	×		×	×		×	×		×	×	×
Ctss		×		×	×		×								
Ofm	×	×	×	×	×	×	×	×	×	×	×	×		×	
Ofs	×	×	×	×	×	×	×	×	×	×	×	×		×	
Oh	×	×	×		×		×	×		×			×	×	×
Olms	×	×	×	×	×		×	×		×	×		×	×	×
Ots	×	×	×		×										×
Sec		×	×	×	×	×	×	×	×	×	×	×		×	
Si	×	×	×	×	×	×	×	×	×	×	×	×		×	
Ur	×	×	×	×	×	×	×	×	×	×	×	×		×	
Wdl	×	×	×		×	×	×	×	×	×	×	×		×	
Yf		×	×	×	×	×	×	×	×	×	×	×		×	

Vegetation structural stages: Ch Closed Herbland, Clms Closed Low Shrub, Ctss Closed Tall Shrub, Ofm Old Multi-strata Forest, Ofs Old Single-strata Forest, Oh Open Herbland, Olms Open Low Shrub or Open Mid Shrub, Ots Open Tall Shrub, Sec Stem Exclusion Closed Canopy Forest, Si Stand Initiation Forest, Ur Understorey Reinitiation Forest, Wdl Woodland (Stand Initiation, Stem Exclusion, Understorey Reinitiation, Young Multi-strata, Old Multi-strata, or Old Single-strata), Yf Young Multi-strata Forest.