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Invertebrates of the Columbia River Basin Assessment Area

Christine G. Niwa, Roger E. Sandquist, Rod Crawford, Terrence J. Frest, Terry Griswold, Paul Hammond, Elaine Ingham, Sam James, Edward J. Johannes, James Johnson, W.P. Kemp, James LaBonte, John D. Lattin, James McIver, Joel McMillin, Andy Moldenke, John Moser, Darrell Ross, Tim Schowalter, Vince Tepedino, and Michael R. Wagner

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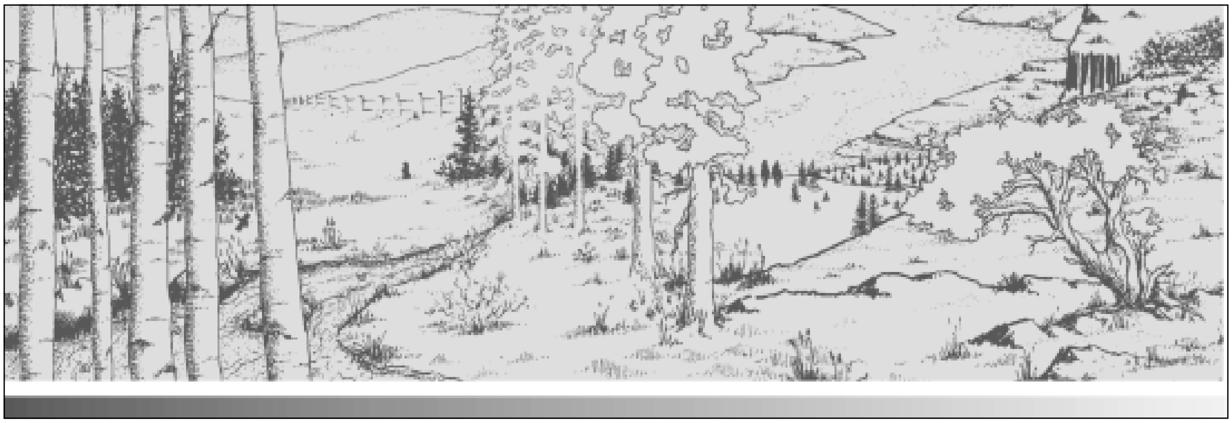

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Interior Columbia Basin Ecosystem Management Project: Scientific Assessment

Thomas M. Quigley, Editor

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Preface

The Interior Columbia Basin Ecosystem Management Project was initiated by the Forest Service and the Bureau of Land Management to respond to several critical issues including, but not limited to, forest and rangeland health, anadromous fish concerns, terrestrial species viability concerns, and the recent decline in traditional commodity flows. The charter given to the project was to develop a scientifically sound, ecosystem-based strategy for managing the lands of the interior Columbia River basin administered by the Forest Service and the Bureau of Land Management. The Science Integration Team was organized to develop a framework for ecosystem management, an assessment of the socioeconomic and biophysical systems in the basin, and an evaluation of alternative management strategies. This paper is one in a series of papers developed as background material for the framework, assessment, or evaluation of alternatives. It provides more detail than was possible to disclose directly in the primary documents.

The Science Integration Team, although organized functionally, worked hard at integrating the approaches, analyses, and conclusions. It is the collective effort of team members that provides depth and understanding to the work of the project. The Science Integration Team leadership included deputy team leaders Russel Graham and Sylvia Arbelbide; landscape ecology—Wendel Hann, Paul Hessburg, and Mark Jensen; aquatic—Jim Sedell, Kris Lee, Danny Lee, Jack Williams, Lynn Decker; economic—Richard Haynes, Amy Horne, and Nick Reyna; social science—Jim Burchfield, Steve McCool, Jon Bumstead, and Stewart Allen; terrestrial—Bruce Marcot, Kurt Nelson, John Lehmkuhl, Richard Holthausen, and Randy Hickenbottom; spatial analysis—Becky Gravenmier, John Steffenson, and Andy Wilson.

Thomas M. Quigley
Editor

United States Department of Agriculture

Forest Service

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Bureau of Land Management

Interior Columbia Basin Ecosystem Management Project

Abstract

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A general background on functional groups of invertebrates in the Columbia River basin and how they affect sustainability and productivity of their ecological communities is presented. The functional groups include detritivores, predators, pollinators, and grassland and forest herbivores. Invertebrate biodiversity and species of conservation interest are discussed. Effects of management practices on wildlands and suggestions to mitigate them are presented. Recommendations for further research and monitoring are given.

Keywords: Nutrient cycling, detritivory, predation, pollination, herbivory, bacteria, fungi, nematodes (roundworms), arachnids (spiders and scorpions), insects, gastropods (snails and slugs), oligochaetes (earthworms), invertebrate biodiversity.

Contents

Introduction

Ecological, Economic, and Scientific Importance of Invertebrates

Invertebrates other than pest insects and disease organisms have received little consideration in most planning efforts (FEMAT 1993, Gast and others 1991, Hessburg and others 1994, Samways 1994). Ginsberg (1993) lists five reasons to be interested in the status of invertebrates.

1. Invertebrates are found in most ecosystems, worldwide. Insects and other invertebrates constitute most of the biosphere faunal biomass. For example, in a hectare of tropical rain forest in Manaus in the Brazilian Amazon, there are about 1 billion invertebrates, mostly mites and springtails. This constitutes about 93 percent of the 200 kilograms of total dry weight biomass of all animals present (Wilson 1987).

2. Invertebrates drive ecosystem processes. Invertebrates are vital to energy and nutrient processing and cycling in ecosystems. All but primary producers are found at all trophic levels, and because of their abundance and diverse habitats, they play a major role in nutrient flow through ecosystems. They are important both as consumers (herbivores, detritivores, and predators) and as secondary producers (prey). The importance of herbivorous insects in forest and range systems, for example, is appreciated. Decomposers, however, often are overlooked. A square meter of North American pasture soil (to a depth of 15 centimeters), for example, yielded about 43,100 mites and 119,800 springtails (Anderson 1975, Salt and others 1948). Gastropod densities ranging between 1.5 and 4.5 million per acre have been reported for temperate habitats in the grassland to forest spectrum (Solem 1974). Pacific Northwest forest soil averages over 200 species and 250,000 individual arthropods per square meter (Moldenke 1990, 1999). Decomposers are vital to the nutrient cycling process and other ecosystem functions. Nevertheless, some of the soil and litter arthropods remain undescribed (Schaefer and Kosztarab 1991).

3. Invertebrates have unique value for scientific study, assessment, and monitoring. Invertebrates are ideal study organisms because there are many species represented by large populations and diverse habitats, with short generation times and rapid population growth, and they provide a fine-grain representation of the system. Invertebrates are amenable to experiments because of their diverse life history patterns, generation times, reproductive strategies, trophic roles, and behavior. Thus, invertebrates offer great potential for research and monitoring within an adaptive management context. Short generation times and high reproductive potential also make invertebrates excellent indicator and "early warning" organisms. A sudden reduction in population could be indicative of environmental changes such as chemical contamination, disease, drought, or overpredation. Longer lived, less diverse organisms or plants might not display obvious effects of subtle environmental perturbations for years or even decades. Much literature addresses the use of invertebrates as indicators of water quality and wetland conditions (Plafkin and others 1989).

Invertebrates are well suited for monitoring the recovery of ecosystems after large-scale perturbations such as the fires at Yellowstone National Park (Christiansen and others 1992, Pilmore 1996) and Hurricane Andrew at Everglades National Park. After a serious disturbance where a habitat has been altered (e.g., burned, covered with volcanic ash, bulldozed, or flooded), many invertebrates, because of their high dispersal rates via wind, water, and macrofauna, are generally the first animals to colonize an area. They change microhabitats, spread seeds, modify soils, and otherwise initiate processes to reestablish viable habitats for other taxa. Each stage in the development and succession of an ecosystem has its own group of invertebrates altering the habitat and paving the way for later successional stages (Brown 1982, Southwood and others 1979).

Taxonomic and faunistic data on invertebrates are also vital to long-term ecological studies, as demonstrated by the National Science Foundation's Long Term Ecological Research Program (CEQ 1985, Parsons and others 1991).

4. Invertebrates have important economic significance. Invertebrates affect human welfare in both positive and negative ways by their influence on agriculture, forestry, and industry. They are important in soil development, pollination of crops and wildland plants, and controlling important pest species. They serve as food items on a worldwide scale (for example, shrimp, lobsters, crabs, clams, scallops, and squid; in many parts of the world, various insects serve as dietary staples).

Invertebrates also can be destructive to crops and domestic animals. Great effort is devoted to minimizing pest damage and detecting nonnative pests. Effective biological control (involving introduction, release, and establishment of alien biological control agents) with minimal negative environmental effect, also requires faunal data on invertebrates in the region where pest management is conducted (Kim and Knutson 1986) to avoid greater environmental perturbances.

5. Invertebrates profoundly affect public health. Invertebrates serve as vectors and reservoirs for diseases having major effects on human populations. For example, plague (caused by a bacterium transmitted by fleas), Lyme disease and Rocky Mountain spotted fever (transmitted by ticks), and arboviral encephalitides (viral diseases transmitted by mosquitoes) pose threats to human and animal health. Invertebrate diversity data, along with geographic, geologic, biological, and social factors, are important to zoonotic research in identifying potential vectors and reservoirs and in predicting possible epidemics (Heyneman 1984).

Given the major contribution of invertebrates to global biodiversity and their importance both to natural systems and directly to humans, placing more attention in wildland management on invertebrates is critical to achieving long-term management goals. Any mandate for managing ecosystems in a sustainable manner contributes to invertebrate conservation. Management actions have important implications for invertebrate taxa to be considered when developing ecosystem management programs.

Methods

The large number of invertebrate species in some major groups precludes a species-specific treatment. Instead, in this report, invertebrates are discussed as functional groups, and individual species are addressed only as examples of a much larger biota. Not all groups are equally addressed because of the difficulty of getting all the information at a similar level of detail.

This report summarizes information derived from several sources. The primary sources were contract reports prepared by taxon or subject matter specialists and ideas and information gathered from panels of experts, some of whom are coauthors of this report. The lead authors of this report extracted and summarized information from these sources and synthesized the information into a format more accessible to wildland managers and general biologists. This report emphasizes the importance of invertebrates in the wildlands of the Columbia River basin (hereafter referred to as the basin assessment area) east of the crest of the Cascade Range including portions of the Klamath and Great Basins in Oregon.

Several science panels met to consider the effects of management practices on terrestrial invertebrates and their ecological functions. Mitigation measures were noted as well as needs for research and monitoring. Research and monitoring were discussed in the context of providing useful information on priority management issues to land managers. Appendix 1 lists participants in the panel discussions.

Each panelist was given a list (appendix 2) of potential management practices. After discussion, a shorter list of issues relating to these practices was developed. These issues were discussed for each of the taxonomic or functional groups. Effects of these issues on terrestrial invertebrates and their ecologic functions, mitigation measures, and opportunities for research and monitoring were noted.

Interior Columbia Basin Ecosystem Management Project

This report provides general background on the invertebrates of the basin assessment area and how they affect sustainability and productivity of their ecological communities. It was used by the Interior Columbia Basin Ecosystem Management Project to assess the terrestrial ecology of the basin assessment area (Marcot and others 1997). The assessment describes prehistoric, historical, and current conditions and trends in terrestrial environments, selected individual species (plants, fungi, bryophytes, lichens, invertebrates, and vertebrates), species groups, ecological communities, and terrestrial ecosystems.

Other assessments included aquatic resources, landscape ecology, economics, and social sciences. All assessments, including terrestrial ecology, were summarized in Quigley and Arbelbide (1997). Quigley and others (1996) examines the conditions of the basin assessment area by integrating the information brought forward through an examination of current conditions compared with broad societal goals.

This document provides information for public discussion about conditions, trends, and potential outcomes associated with management of the natural resources of the basin assessment area. Effects of wildland management practices by the USDA Forest Service (FS) and USDI Bureau of Land Management (BLM) are reviewed. General suggestions that may help to mitigate harmful effects are presented. Recommendations for further research and monitoring also are given.

Functional Groups of Invertebrates

What are the important roles of invertebrates in the basin assessment area? Several primary ecosystem functions were chosen to illustrate the roles of invertebrates. Not all functions are presented because resources were insufficient to cover all taxa.

In the following sections on functional groups, specific examples of management practices and their effects on biodiversity or ecological function are addressed. Information about the effects of management practices on invertebrates mostly is known but limited for specific locations. To better understand the effects of management, it is suggested that the professional judgement of specialists be considered as working hypotheses that can be tested.

Detritivores and Nutrient Cycling

In the past, soil has been perceived as inert and inanimate, and soil properties as distinctive but relatively unchanging. Faunal constituents, until recently, have been largely ignored in management activities. Soil microbes also have been ignored, except for a few high-profile organisms such as soilborne pathogens and certain mycorrhizal fungi and nitrogen (N)-fixing bacteria (Harvey and others 1994).

Studies indicate soil functions as a community of interacting organisms ranging from viruses and bacteria, fungi, nematodes, mollusks (especially slugs and microgastropods) and arthropods to mammals and other vertebrates. Microbial biomass alone can reach 10,000 kilograms per hectare in productive, inland Western forest soils (Harvey and others 1994). Combined, activities of all these organisms are responsible for developing the critical properties that underlie fundamental soil fertility, health, and productivity. Biologically driven properties resulting from such complex interactions require from only a few to several hundred years to develop (Harvey and others 1994). The greater the number of interactions of decomposers, their predators, and the predators of those predators, the fewer the losses of nutrients from that system (Harvey and others 1994).

Insects[1]—Wood-feeding insects are instrumental in the decomposition and mineralization of coarse woody debris. Secondary bark beetles (also primary, or tree-killing, bark beetles) penetrate the bark of recently dead trees and inoculate wood with, and provide access to, saprophytic

[1] This section is based primarily on Schowalter (1995).

micro-organisms. They also provide attractive volatile chemicals, habitats, and resources for other invertebrates (such as fungivores and termites), thereby accelerating decomposition (Schowalter 1995, Schowalter and others 1992, Stephen and others 1993).

Ambrosia beetles, including *Platypus wilsoni* Swaine (Platypodidae), *Trypodendron* spp., *Gnathotrichus* spp., and *Xyleborinus saxeseni* (Ratzeburg) (Scolytidae), initiate penetration of sapwood. These beetles inoculate galleries with mutualistic fungi (*Ambrosiella* spp., *Ceratocystiopsis* spp.), which the beetles cultivate (by removing other competing fungi) and eat. Studies (Moser and others 1995, Schowalter and others 1992, Zhong and Schowalter 1989) indicate these insects regulate the initial decomposer assemblage in the sapwood and thereby affect initial decomposition patterns.

Termites and other wood-boring beetles and wasps excavate large N-rich galleries in wood in concert with N-fixing and cellulytic gut symbionts. They increase wood aeration and the surface area exposed to decomposers, thereby facilitating decomposition and enriching surrounding soils that are often N-impoverished (Salick and others 1983, Slaytor and Chappell 1994, Waller and others 1989). Principal termites occurring throughout the basin assessment area include *Zootermopsis nevadensis* (Hagen) (dampwood termite) and *Reticulitermes* spp. (*tibialis* Banks and *hesperus* Banks—aridland subterranean termite). *Zootermopsis* is associated primarily with mesic forests, whereas *Reticulitermes* occupies drier habitats.

Carpenter ants (*Camponotus* spp.) and *Formica* species also excavate large galleries in wood and increase wood aeration and surface area exposed to decomposers (Harmon and others 1986, Youngs 1983). In addition, some of these ants are major regulators of canopy communities by tending aphids and preying on defoliators. They are major food resources for woodpeckers, including the pileated woodpecker (*Dryocopus pileatus*) (Torgersen and Bull 1995).

Termites and carpenter ants also provide the social structure that supports diverse assemblages of termitophilous and myrmecophilous invertebrate species. Many of these invertebrates are highly specialized to mimic their hosts and intercept food shared among colony members (tro-phallaxis). Clearly, these species are dependent on the abundance and distribution of the host termites or ants.

Other arthropods such as millipedes, sowbugs, and oribatid mites consume and shred (comminute) large quantities of dead leaves and needles in forest litter and inoculate microbes into larger detrital surface area. This fragmentation makes nutrients more readily available to microbes that continue the cycling process. Without the crushed-up plant fragments contained in arthropod frass, decomposition by bacteria and fungi would eventually occur but at a much slower rate. The decomposition process is far more efficient if leaves are shredded first.

Protozoa, rhabditid nematodes, bacterial- and fungal-feeding mites, and springtails mineralize nutrients pooled in the microbial biomass of the rhizosphere. By grazing on bacteria and fungi, N is released in the form of nitrogenous wastes, some of which are absorbed by the disturbed microbial sheaths of roots.

Earthworms[2]—Earthworms require organic matter in various stages of decay and in various locations. Three broad groups of earthworms have been described by Bouche (1977): epigeic, endogeic, and anecic. Epigeic worms are typically small, darkly pigmented, and reside in leaf litter and under the bark of decaying logs. Endogeics live in the mineral soil and consume organic matter within the soil or at the soil-litter interface. They are larger, less pigmented to unpigmented, have longer lives, and have lower reproductive rates. Anecics are those worms that inhabit a permanent or semipermanent deep vertical burrow and emerge at night to consume relatively fresh plant detritus on the surface. These are the largest and longest lived earthworms.

[2] This section is based on James (1995).

In a forested site, earthworms would be expected to have the following functional roles:

Organic matter comminution—By reducing the size of organic matter particles during passage through the worm, the organic matter is made more accessible to action by other decomposers.

Nutrient cycling—Earthworms cycle nutrients through their feces, through their urine, and in death, through their decomposing bodies. These earthworms digest organics and thus mineralize some of the nutrients bound in them. All earthworm excreta have higher levels of available macronutrients and cations than the material ingested (see Lee 1985). Urine is also a source of available N, and the soft body tissues of earthworms readily decompose at death.

Soil structural modification—Burrowing and defecation create soil structures potentially significant (though the details are unknown anywhere) to other soil biota. These soil structures promote a more stable aggregation in the presence of soil water.

Transfer of organic matter to the soil—Consumption of surface litter results in some defecation in the mineral soil, particularly if worms retreat into the mineral soil to avoid unfavorable climatic conditions in the litter.

Food for other animals—Predators of earthworms include small mammals, beetle adults and larvae, centipedes, spiders, some flies, birds, reptiles, and amphibians.

Epigeic worms are known from two sites in the basin assessment area, in an Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)-subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest type within the Grand Teton National Park, and from a riparian area within an area designated as agricultural land.

Native and exotic endogeic species occur in a wide range of habitats including forest and savannah, grassland-shrubland (including exotic grass pasture and seral stages after cessation of agriculture), and cultivated land. Piper (1982) demonstrated the importance of enchytraeid earthworms as detritivores by finding populations of up to 68,000 per square meter in a mature stand of Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) near Snoqualmie Pass. Endogeic species, though they are the majority, are the least known of all earthworms because their lifestyles are not easily observed. The fraction of the soil organic matter on which a given species feeds is known only for a few species, and for none of those present in the basin assessment area. Factors influencing populations of native species are completely unknown. If they are comparable to other earthworms, soil moisture, soil temperature, organic matter quantity and quality, and soil pH are probably the most important factors (Lee 1985).

Anecic earthworms are not known to be associated with the natural vegetation in the basin assessment area. If present, their unique contributions would be the transfer of relatively fresh plant litter from the surface to deep levels of the soil and the creation of deep vertical burrows, which assist water infiltration. Other earthworms can contribute to these processes but not directly or effectively. Anecics also provide food resources accessible to endogeic worms by the deposition of fecal organic matter in the soil.

Mollusks[3]—Over 150 described species of land snails and slugs are found in the basin assessment area. Most are found in moist forest environments and in areas around springs, bogs, and marshes. Basalt and limestone talus slopes are also important habitats for some species. The land snails and slugs are mostly herbivores. All are also detritivores, and many also consume animal (including mammal-insect) fecal matter. Some prey on other land snails. Primary food for the herbivores, in addition to soil and fecal matter, includes green and fallen deciduous tree leaves, understory vegetation, large fungi, and inner bark. Many mammals, reptiles, amphibians, and some birds prey on land snails and slugs. Various insects prey on snails or parasitize them. Some land snails are intermediate hosts for parasites of vertebrates. Snail shells are used as domiciles, shelters, or egg laying sites by various arthropod taxa.

[3] This section is based on Frest and Johannes (1995).

Soil micro-organisms[4]—Other organisms in the soil, such as bacteria, fungi, protozoa, nematodes, and microarthropods, play critical roles in maintaining soil health and fertility (Coleman and others 1992). Their roles include (1) decomposing plant material by bacteria and fungi; (2) immobilizing nutrients in soil by bacteria and fungi in the form of their biomass and secondary metabolites such as waste or defensive products; (3) improving soil aggregate structure, which increases waterholding capacity, clay surface interactions with nutrients, and plant root architecture; (4) altering the soil pH; (5) mineralizing nutrients by protozoan, nematode, and microarthropod predation of bacteria and fungi; and (6) controlling disease-causing organisms by competition for resources and space, control of soil micronutrient status, and alteration of root growth.

Productive ecosystems tend to retain nutrients. Over time, nutrients are metabolized to forms less available for plants and animals, such as phytates, lignins, tannins, and humic and fulvic acids. For nutrients to once again become available to plants and animals, they must be mineralized by the interaction of decomposers and their predators. These populations and their interactions are important to ecosystem stability, including predator and prey interactions, mutualisms, and disease.

As total ecosystem productivity increases, biodiversity within the soil food web also increases. The greater number of interactions of decomposers, their predators, and the predators of those predators, the slower the losses of nutrients from that system. In undisturbed ecosystems, the processes of immobilization and mineralization are tightly coupled to plant growth. After disturbance, this coupling is lost or reduced. Nutrients are no longer retained within the rhizosphere, thereby reducing the productivity of the ecosystem and causing problems for systems into which nutrients move, especially aquatic portions of landscapes.

[4] This section is based primarily on Ingham (1994).

Thus, the soil food web is a prime indicator of ecosystem health. Measurement of disrupted soil processes, decreased bacterial or fungal activity, change in the ratio of fungal to bacterial biomass, decreases in number or diversity of protozoa, or change in nematode numbers, nematode community structure, or maturity index, can serve to indicate problems long before the natural vegetation is obviously affected.

One estimate of bacteria species in the basin assessment area is about 160,000 species each in forests, grasslands, and agricultural fields, totaling about 480,000 species in these three environments.[5] This estimate is approximate and will change with new field information.

No study has been conducted on the total number of bacteria species or even uniqueness of species in soils of the basin assessment area. Within the basin assessment area, one study has discovered a small set of unique mutualistic bacteria that suppress weeds in the Palouse; and another study is exploring the role of beneficial bacteria that aid crop plant growth.

In one estimate, there are from several hundred to perhaps a thousand species of protozoa in forest stands and pasture or grassland, and perhaps several hundred in agricultural fields, totaling about 1,000 to 2,000 in all three environments. One report states having found species of testate amoebae in samples from the Blue and Wallowa Mountains that have never been seen in any other soils (Ingham 1999).

Soil nematodes number perhaps 100 to 150 species in a healthy forest. Many soil nematodes agriculturally important in the basin assessment area are known, and their distributions are fairly well understood.

Extrapolating from small soil samples, there are about 100,000 soil ectomycorrhizal microfungi species each in forest and grassland ecosystems.[6]

[5] Extrapolations based on work by James Tiedje, Professor, Center for Microbial Ecology at Michigan State University, East Lansing, MI 48824.

[6] Estimates based on work by T. Bruns, Associate Professor, University of California, Berkeley, CA 94720.

There may be about equal numbers of other forms of microfungi, but they are essentially unstudied in the basin assessment area. One study has found unique mycorrhizal species in larch and mixed-conifer stands of the Blue Mountains (Ingham 1994).

Implications of management practices on detritivores and nutrient cycling[7]—Detritivores are likely to be affected by fire, soil compaction, and removal of large woody debris. The effects of fire on soils, coarse woody debris, and the organisms inhabiting these habitats are many and highly variable. They depend on the timing and intensity of the fire and the amount of surface fuels consumed. Fire can affect soils physically, chemically, and biologically; it can alter nutrient cycles, soil development, and site productivity. If litter or the critical organic horizons are not entirely destroyed by fire, then fire effects on the soil are usually minimal (Harvey and others 1994). Three areas of concern for invertebrates are direct effects of fire on these organisms, the role of fire in forest or range succession, and soil chemistry. These relate primarily to intense fires that leave little undamaged refugia. In fire-adapted systems, direct effects on invertebrates are thought to be slight. In systems where large volumes of fuel litter and coarse woody material are present, however, higher intensity fires may pose hazards to organisms such as land snails, which recolonize slowly. Direct effects on invertebrates may be minimal if refugia of litter and coarse woody material are retained. Some coarse-woody-debris feeders are attracted by smoke and colonize still-smoking trees (Furniss and Carolin 1977).

Removal of organic matter by fire has similar effects on forest and range succession. In the forest, loss of organic matter may change the ratio of fungi-bacteria to favor bacteria. This favors grasses rather than woody vegetation, which is not necessarily the desired successional course in forestry. In rangelands, the consumption of organic matter and the subsequent change to a bacteria-dominated food web is beneficial to maintenance of grasses. The effects on litter or soil invertebrates by wildfire in rangelands dominated by cheatgrass (*Bromus tectorum* L.) is unknown.

Coarse woody material serves as primary habitat for invertebrate predators, xylophages, and detritivores, habitat of prey for other organisms, and as a carbon source for the soil food web. Little is known about how much litter and coarse woody material and what sizes and species are necessary to continue ecosystem functions of associated invertebrates (Torgersen and Bull 1995). It is assumed that standards intended to provide prey for vertebrate species will suffice to continue the functions of the invertebrates (Bull and others 1997).

Compaction of soils has implications for the soil food web as well as other functional groups. Compaction occurs from use of machinery on the land and the effects of large herbivore grazing. Grazing compacts soils if these activities are concentrated in small areas with many animals, and on areas with fine-textured soil. Compaction reduces soil pore size, thereby resulting in loss of nutrient retention and an increase in the bacterial component of the soil-based food web. This may cause a reversal of succession in the forested environment, with a subsequent negative effect on cyanobacteria, lichens, and mat-forming ectomycorrhizal fungi. With loss of the ectomycorrhizal fungi, tree productivity declines. Compaction changes the community of nematodes, favoring bacteria and root-feeding species. Root-feeding nematodes can be detrimental to tree and grass seedling survival. Compaction effects are particularly undesirable for groups such as mollusks and earthworms, which may occupy specific habitats or which cannot disperse quickly.

Overgrazing can adversely affect mollusks because of trampling as well as disruption of their favored riparian habitats by the congregating of livestock near water sources.

Tilling to reduce compaction as well as other means of physically mixing the duff and soil can adversely affect many functional groups. Disruption of the duff-litter layer has immediate effects

[7] This section is based primarily on discussions during the expert panels on soil-nutrient cycling and litter and coarse wood detritivores (see appendix 1).

on water and thermal relations and disrupts habitat for many functional groups inhabiting the woody material and litter, as well as forb and flowering plant communities. Mixing affects the soil food web by breaking roots, fungal mats, and changing the water and thermal conditions that encourage bacteria populations.

Predators[8]

This section covers the macroinvertebrate terrestrial predators, which are arthropods of the classes Arachnida and Insecta. Principal among these are the spiders (Arachnida: Araneae), and the major predatory insect groups, the true bugs (Heteroptera), lacewings (Neuroptera), beetles (Coleoptera), ants (Hymenoptera: Formicidae), and social wasps (Hymenoptera: Vespidae). A basic view of the diversity of predatory arthropods is provided, including their ecological function, and factors thought to affect their abundance and distribution. For more information on predatory Heteroptera, see Lattin (1995b). For a discussion of the functionally related "insect parasitoids," see Johnson (1995). Not included in this report are the following groups of invertebrates that serve as important natural enemies of other invertebrates: (1) predatory mites, most of which are just large enough to be seen without the use of a microscope, and that function as important microarthropod predators in many habitats; (2) predatory nematodes, which occur primarily in the soil and soil interface (Ingham 1994); (3) insect parasitoids, primarily wasps and true flies, in which the larva(e) consume a single host during development (Johnson 1995); and (4) those predatory insects that spend most of their lives in the aquatic habitat (e.g., dragonflies).

Predator diversity within the basin assessment area—We estimate that between 3,544 and 6,636 species (median = 5,090 species) of terrestrial arthropod predators occur in the basin assessment area (appendix 3). This estimate was obtained by identifying those families of terrestrial arthropods that are primarily predaceous, and then summing the ranges of species number estimates within the basin assessment area for each family. The wide range of this estimate is due to inadequate information on many of the families. Despite the lack of accurate knowledge of species diversity, even the lower estimate is several times greater than the diversity of all vertebrate species within the basin assessment area.

One hundred and twelve families of predators were identified in the survey, assigned to 15 orders and 3 classes (insects, centipedes, and arachnids) within the phylum Arthropoda. Five large orders contain 88 percent of the predator species in the basin assessment area: spiders (Araneae: 1,631 species), beetles (Coleoptera: 1,308 species), wasps and ants (Hymenoptera: 700 species), true flies (Diptera: 460 species), and true bugs (Heteroptera: 367 species). Arthropod predators are found in great diversity in every habitat type throughout the assessment area and prey on virtually every type of available arthropod species, as well as some mollusks and annelids. Spiders and ants dominate the predator arthropod fauna associated with vegetation, and beetles, ants, and spiders dominate the surface and immediate subsurface of the ground. Some major taxa such as the spiders, ants, true bugs and beetles contain representative species common to habitats throughout the basin assessment area, whereas others, such as the scorpions (shrub-steppe) and centipedes (forest floor) occur predominantly in certain habitats.

As a group, arthropod predators are a fundamental part of any functioning ecosystem, with this function performed by a different species composition in each major habitat type. McIver and others (1992) found that the species composition of ground-dwelling spiders common in conifer forests of western Oregon is completely replaced by an equally diverse assemblage of different ground-dwelling species after clearcut harvesting. In general, arthropod predators respond keenly to changes in microhabitat conditions that typically occur with both natural and human-induced disturbance.

[8] This section is based primarily on McIver and others (1995).

Invertebrate predators and ecological function—The primary function of arthropod predators is the role they play within food webs. But their relatively small size makes them potential prey for vertebrate insectivores as well. In this section, we will discuss these two functional roles, focusing on predation of forest pest populations, and by describing a case study of arthropod predators serving as primary prey of critical wildlife species.

Evidence supports that arthropod predation has been a major force in ecological systems for a long time. In a long-term study of the arthropod community of a desert lupine, McIver (1987, 1989) documented various evolved defensive adaptations against predation, including mimicry, warning coloration, and crypsis. In general, defensive adaptations reflect the chronic influence of predation through evolutionary time (Edmunds 1974). Although vertebrate predators most often are implicated as responsible for the evolution of defensive adaptations, behavioral and serological studies on the lupine fauna identified arthropod predators as the primary force behind some of the defensive adaptations (McIver and Lattin 1990, McIver and Tempelis 1993), thereby suggesting that arthropod predator species play an active role in determining the species composition and relative abundance of other arthropod species.

Predators also can play a major role energetically. Using isotopic tracers in a forest floor community, Moulder and Reichle (1972) showed that spiders were the dominant predators, consuming each year 2.3 times the mean standing crop of potential prey, and 44 percent of all forest floor cryptozoans (arthropods and mollusks). The importance of spiders and predatory insects in maintaining the balance of herbivorous and detritivore arthropod species is significant.

One of the best examples of how predators operate is their role in suppressing forest insect pest populations (Morris 1963). A preliminary evaluation of the "HUSSI" database (Torgersen 1997) provides insight on the prevalence of predation on pest organisms. Over 300 entries in the database reported observed predator-pest insect links, involving at least 71 predator species, preying on pine tip moths, tussock moths, budworms, sawflies, tent caterpillars, and bark beetles. A total of 33 predator species has been observed to attack species of *Dendroctonus* alone.

Although the HUSSI database identifies a diverse complex of predator species that prey on forest insect pests, many studies in North America have documented that predators can play a significant regulatory role by suppressing pest population buildup, especially defoliator species (Mason and others 1983). Predators have been implicated as primary suppressive agents of *Dendroctonus* spp. (Furniss and Carolin 1977), *Ips* spp. (Jennings and Pase 1975), pine tip moths (Bosworth and others 1971), and the two principal defoliator species of western coniferous forests, western spruce budworm (*Choristoneura occidentalis*) (Campbell and others 1983, Mason and others 1983, Mason and Paul 1988, Mason and Torgersen 1983, Torgersen and others 1983) and Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) (Mason and others 1983, Mason and Torgersen 1987).

Studies on mortality of western spruce budworm populations have implicated bird and ant predation as primary factors (Torgersen and others 1990). In whole-tree exclosure experiments, several species of passerine birds were identified as most influential in the upper third of the canopy and ants (primarily *Camponotus modoc* W.M. Wheeler) more effective in the lower third. Pupal stocking studies also have implicated thatch ants (*Formica haemorrhoidalis* Emery) as significant mortality factors of western spruce budworm. Spiders also may aid in suppressing budworm populations, particularly when caterpillars are in the earlier stages of development. These studies clearly establish that spruce budworm are preyed on by various predators, including birds, ants, spiders, and other arthropods. Management techniques that enhance the role of these predators throughout the budworm population cycle likely will be of economic benefit because of decreased loss of green trees.

Many studies have implicated predation as a primary cause of mortality in Douglas-fir tussock moth populations, including stocking experiments

(Mason and Paul 1988, Mason and Torgersen 1983) and key-factor analysis (Mason and others 1983, Mason and Torgersen 1987). Primary predators identified as mortality factors include the jumping spider (*Metaphidippus aeneolus* Curtis), philodromid hunting spiders, web-spinning spiders, heteropteran predators, and predaceous ants and birds (Mason and Paul 1988, Mason and Torgersen 1987, Wickman 1977). Although predation may contribute to well over half the total mortality of tussock moth larvae and pupae during outbreak conditions, [however], even this level of suppression may be inadequate to deflect the outbreak population trajectory (Mason and Wickman 1988). Hence predation is typically thought to exert most of its influence during nonoutbreak (or endemic) phases of the population cycle of the moth (Mason 1987). Management activities that improve the impact of predation during these endemic conditions are therefore most likely to either defer or decrease subsequent population levels during the outbreak phase. For example, in the Northeastern United States, spider populations on spruce are significantly higher than on balsam fir, and thus altering the relative abundance of these tree species may influence the total suppressive effect of arthropod predation on populations of the spruce budworm *Choristoneura fumiferana* (Clemens) (Jennings and others 1990).

Although predation is their primary ecological role, arthropod predators also serve as prey for all classes of insectivorous vertebrates, both aquatic and terrestrial. Terrestrial arthropod predators are a common component of drift in streams, where they serve as prey for freshwater fish, including salmonoids. Because they lack defensive chemicals and are soft-bodied, larger spiders are ideal prey for nesting and overwintering birds (Wise 1993). Social insect predators are common prey of vertebrates: yellowjackets have been found in feces of pine marten (*Martes americana*) (Torgersen 1999), and carpenter ants are the primary prey of pileated woodpecker (Beckwith and Bull 1985). The carpenter ant (*Camponotus modoc*) nests in down or standing dead wood, usually greater than 38 centimeters (15 inches) in diameter and in the earlier stages of decay. This places them squarely within the foraging habitat of woodpeckers, and they have been estimated to make up more than 90 percent of the diet of pileated woodpeckers in Blue Mountains mixed-conifer forests (Beckwith and Bull 1985, Torgersen and Bull 1995). Pileated woodpeckers are one of the more important cavity builders in older forests (Bull 1987), providing [nesting] habitat for many other organisms, including some, like carpenter ants [themselves], that feed on spruce budworm. Thus, *C. modoc*, as a predator of spruce budworm, and as the primary prey of pileated woodpecker, can be regarded as a keystone species, having an ecological effect possibly greater than its relative abundance would imply. Furthermore, because *C. modoc* generally nests in large-diameter dead wood, its abundance (and its function) can be managed roughly by leaving particular levels of this structure in the forest.

Implications of management practices on predators[9]—Predation is an ecological process fundamental to healthy managed ecosystems. The challenge for managers is to preserve this process so arthropod population fluctuations are contained within some desirable range. In some cases, maintaining predatory function may be as simple as retaining landscape structures predators are known to require, such as down wood, snags, special habitat features (hydrological function of a bog or spring), forbs, shrubs, and trees of various species and sizes. These are features to which predaceous arthropods will respond in much the same manner as vertebrates (Thomas and others 1979). Unlike the vertebrates, however, little is known about how particular wildland management practices influence predatory arthropod species composition, abundance, and distribution. Several studies suggest that predators as a group are particularly vulnerable to disturbances (Kruess and Tscharntke 1994, Schowalter 1995).

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[9] This section is based on McIver and others (1995) and discussions during the expert panels on range herbivores and parasites and predators (see appendix 1).

The structure of the physical environment on which arthropod predators depend for hunting and nesting is important for almost every predator species. The natural variability in spider abundance among sites suggests spider populations can be managed (Mason 1992). Plant architecture (size, number, and arrangement of leaves, needles, and branches) influences canopy spiders (Gunnarsson 1988, Stratton and others 1979), and plant species composition influences spider abundance. Jennings and others (1990) recorded a significantly greater number of spiders in spruce as opposed to hemlock in forests of the Northeastern United States. Physical structures like down logs provide nesting, foraging, or hiding habitat for important predator species, such as ants (*Formica* spp., *Camponotus modoc*) (Harmon and others 1986, Torgersen and Bull 1995), beetles, and spiders.

Silvicultural practices can profoundly affect predator species composition. In coniferous forests of western Oregon, clearcutting causes a complete replacement of forest-dwelling litter spider species with species adapted to sunny open places (McIver and others 1992). An extensive study in Finland (Huhta and others 1967) showed severe effects on spiders and other soil invertebrates by clearcutting, devastating effects by clearcutting and burning, and substantial changes even from partial cutting, apparently caused by change in microclimate from the loss of a closed canopy. Selective cutting more typical of east-side forests is not likely to have as severe an effect, but more work needs to be done to determine the connection among silviculture, predator species composition, and the quality and quantity of ecological service that predator species provide. Structural diversity, including different ages of conifers and angiosperms and standing and down dead wood are extremely important in maintaining the microhabitats, moisture regimes, light regimes, food plants, and prey base for predators.

Any disturbance affecting habitat will affect the species dependant on that habitat. For example, the short fire-return intervals on cheatgrass-dominated rangelands may eliminate dominant predator species such as the western thatching ant, *Formica obscuripes* Forel. Although thatching ant colonies can survive fire by maintaining the queen and brood belowground, postfire survival is challenged by lack of resources because the sagebrush-feeding Homoptera the ants depend on for honeydew (carbohydrates) are typically eliminated. Hence colonies generally are reduced by fire to less than 20 percent original size, and fires returning every few years likely will extirpate these disturbed colonies. Systems with short fire-return intervals (for example, cheatgrass and planted crested wheatgrass dominated) will therefore tend to favor "weedy" ant species with different ecological functions.

Pollinators[10]

About two-thirds of all flowering plant species benefit from insects visiting their flowers (Axelrod 1960). In the absence of insect pollinators, these plants would reproduce only marginally. Bees (Hymenoptera), butterflies and moths (Lepidoptera), flies (Diptera), and some beetles (Coleoptera) are the main insect taxa that pollinate flowers. Moths are extremely important pollinators, and may be the main insect pollinators of plants that bloom mainly at night. Many deep-throated flowers require hawk-moth pollinators (Grant 1983). On the other hand, butterflies are probably less important as pollinators than generally supposed (Jennersten 1984). Although beetles, moths, and butterflies play important roles in pollination, this section will focus on bees.

Most native bees are solitary rather than social. Individual females search for sites where they construct nests, and then provision the nests with pollen and nectar as food for their progeny. Most nests are constructed in either soil or wood, with the number of ground-dwelling species predominating by about 3:1.

Most soil-nesting species are also burrowers. Only a few use burrows abandoned by other animals, notably bumblebees. Soil nest sites can range from vertical clay embankments to alkali flats and agricultural fields; they may be compacted and barren or aerated and vegetated. The preferred or even acceptable type of soil for nesting is unknown for

[10] This section is based primarily on Tepedino and Griswold (1995).

most species. This is because of the difficulty of finding the solitary, dispersed nests of many species, because existing descriptions of nesting sites may not be accurate, and because soil information is rarely recorded.

Except for carpenter bees, and perhaps a few other taxa, bees that nest in wood are nonburrowing. They depend primarily on holes, mostly in dead snags, stumps, logs, twigs, and stems that have been excavated and vacated by members of the 177 genera of boring beetles in the basin assessment area (Arnett 1960). Their natural nesting habits are poorly understood. Although woody and soft-stemmed material are a necessity for these bee species, the preferred amount, plant species, diameters, and ages are generally unknown.

Bee diversity within the basin assessment area—Based on 8,350 specimen records,[11] 647 species of bees presently are known to occur in the Columbia River basin. The actual number of bee species in the basin assessment area is believed to be substantially higher as there has not been extensive collecting in many parts of this region. Little biological or ecological information exists for most of these recorded species. Because records frequently do not include a flower association, little is known about the foraging preferences of many species. Also, in most cases where records on flowers do exist, the purpose of the visit, for example collecting nectar or resting, is not stated. Based on other areas in the West that have been sampled more extensively, Tepedino and Griswold (1995) estimated the actual number of bee species in the basin assessment area is closer to 1,000.

Functional roles of bee pollinators—Bees are the only organisms, with a few exceptions, that depend exclusively on pollen and nectar for food throughout their lives. For many plants, without bee-facilitated pollination, few, if any, seeds or fruits would be produced. An exception is at higher elevations where flies and moths assume increased importance (del Moral and Standley 1979), apparently because of their greater ability to cope with high altitudes and cold temperatures. Flies mostly visit open, shallow flowers. Bumblebees account for a large proportion of bee visits to flowers with restricted accessibility at higher elevations.

Bees can influence the genetic variability of the seeds produced by the plants they visit. They can affect the rate of inbreeding in plants with self-compatible flowers by their movement patterns within and between plants. More flower-to-flower visits on the same plant will increase the likelihood of self-pollination occurring. Bees also might influence genetic variability of plant populations by the frequency of flights among populations during foraging trips. Such trips would result in gene flow among populations and would tend to make populations more uniform genetically by counteracting genetic drift and natural selection for site-specific traits.

The products of pollination, fruits and seeds, are important not only to the plants producing them but to the many birds, mammals, and insects utilizing them as food for all or part of the year. An idea of the diversity of organisms that eat fruits and seeds and the amount eaten can be gained from Janzen's (1971) review of seed predation.

Finally, ground-nesting bees, particularly those nesting in aggregations of thousands of nests, move large amounts of soil in digging their main burrows and side branches, thereby contributing to the cycling of the soil layers and of nutrients in the soil.

Implications of management for bees[12]—Four major concerns about the effects of management practices on bees are (1) nest site habitat, (2) flowering plant resources, (3) exotic flora and fauna, and (4) pesticides.

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[11] U.S. National Pollinating Insects Collection. Published and unpublished reports. On file with: USDA Agriculture Research Service, Bee Biology and Systematics Laboratory, Utah State University, Logan, UT 84322-5310.

[12] This section is based on discussions during the expert panels on pollinators (see appendix 1).

Nest site habitat—The nest sites of ground-nesting bees may be subject to various disturbances. Management activities such as grazing, mechanized activities, off-road vehicle use, and subsoiling can damage maturing progeny in the soil and can disrupt current nesting activity. Sites in vertical or near-vertical embankments are subject to erosion, whereas sites in more level ground are vulnerable to compaction. The impacts of constant or heavy use differ greatly from site to site. Limited compaction of heavier soils may be tolerable or even beneficial to certain ground-nesting bees. Bees found in light and sandy soils, however, are extremely sensitive to disturbance because high population densities and endemic species are frequently found in these soils. Human activities also can obliterate or change the subtle landmarks adjacent to nest-holes that bees use to relocate their nests when returning from foraging trips. Thus, disturbance early or late in the year, while bees and plants are not active, will tend to cause fewer adverse effects. In addition to seasonal mitigation, any reduction in the intensity and frequency of ground disturbance will help to maintain adequate ground-nesting habitat and provide time for recovery and recolonization of sites.

Habitat availability for wood-nesting bee species is affected by any management practices such as prescribed burning and intensive tree harvesting that remove nesting resources. Removing trees from the overstory opens up forest habitat for ground-nesters by increasing light penetration and abundance of flowering plants. In rangeland, fire will kill bees directly and burn up substrates for wood-nesters. The season of removal is not critical in closed-canopy forest because there is little utilization by bees except in canopy gaps. In range and open forest, however, season of disturbance will matter because resident bees will be killed.

Flowering plant resources—All bees depend on the pollen and nectar of flowers for their sustenance throughout their life cycle. Many species are specialized and collect the pollen of a restricted group of plants. Specialization can range from fairly broad (for example, pollinating composites) to generic level restrictions. Other bees are generalists such as the Halictinae and Bombinae, which visit various flowers on individual foraging trips.

For plants having known specialist bee pollinators, grazing, burning, and other activities with similar impacts on the flora should be timed to periods when these plants are not flowering. Changes in domestic grazing activities can promote both native plant and bee diversity. Careful rotations and exclusions of selected rangelands can enhance diversity, particularly in higher elevation and forested sites. Any management to reduce cheatgrass or other annuals will favor angiosperm diversity and pollinator abundance. Grazing by sheep is particularly disruptive to flowering plant diversity because sheep are forb eaters. Herbicides are the most obvious immediate detriment to floristic diversity. Current management policies that limit broadcast applications of herbicides can help maintain plant and bee diversity. Harvesting methods that leave clusters of trees encourage floral diversity while maintaining other habitat requirements.

Effects of exotic flora and fauna—This issue addresses effects of intentional and unintentional introduction of both plants and animals including honeybees (*Apis mellifera* L.). As stated in the preceding section, management activities that prevent the introduction of or reduce the dispersal or extent of communities of exotic plants such as crested wheatgrass (*Agropyron cristatum* (L.)), Russian thistle (*Salsola kali* L.), kochia (*Kochia prostrata* and *K. scoparia* L.), and cheatgrass and that increase native floral species will promote native bee communities.

The intentional introduction of nonnative bees or native bees to nonnative areas for the pollination of agricultural crops, as well as accidental introductions, poses the threat of competitive displacement of native bee species. An example of the consequences of such an introduction is the exotic leaf-cutting bee that pollinates exotic *Centaurea* spp. in California. This bee has displaced both native bees and other exotic species, including *Apis*, throughout its distribution. Stringent screening criteria are necessary to prevent both intentional and accidental introductions from displacing native bees.

Effects of pesticides—The use of carbaryl and malathion insecticides to control grasshopper populations on rangelands adjacent to agricultural lands has significant detrimental affects on honeybee colonies. Currently, the only alternative being tested is the biological control, *Nosema locustae*. Use of chemical insecticides in forestry to suppress defoliators such as western spruce budworm and Douglas-fir tussock moth may be detrimental to honeybee colonies as well as native bees.

Although there are situations where insecticides are the best choice, judicious use of them will minimize adverse impacts on bee diversity and abundance. Alternative control methods can be developed to minimize adverse effects. When chemical spraying is the treatment selected, nonsprayed strips can be left as refugia for beneficial fauna; repeated applications on the same tract of land year after year may be detrimental. The BLM guideline is that an unsprayed buffer be left around rare plants. The width of the unsprayed buffer should be determined on a case-by-case basis taking into account the expected distance of significant insecticide drift and the specifics of the reproductive biology of the plant and the ecology of the likely pollinators.

Grassland Herbivores[13]

On grasslands, several arthropod groups function primarily as grazers and are important links in food webs. Most invertebrate grassland herbivores feed on various herbs, shrubs, and trees and are seldom considered pests. Some taxa like grasshoppers, however, are of economic importance when populations reach outbreak levels and consume significant amounts of forage. In addition to being important consumers of annual primary production, grassland herbivores are important food for various wildlife and are an especially critical resource for nesting birds and their broods in spring.

Many arthropods are grassland herbivores. Limited time and available expertise has focused this discussion on three groups: grasshoppers (Acrididae) (Kemp 1995), moths and butterflies (Lepidoptera) (Hammond 1994), and true bugs (Heteroptera) (Lattin 1995b).

Grassland herbivore diversity—Within the basin assessment area grassland types, about 100 grasshopper species exist. We know much more about how to suppress rangeland grasshopper populations than we do about their specific ecological roles. Our knowledge about rangeland grasshopper ecology originates from grasslands other than, and in many cases different from, those in the basin assessment area.

Grasshoppers are a complex group of herbivores that interact in space and time. At a specific location, it is common to find 15 or more grasshopper species throughout spring and summer. Although some species are separated to an extent by differences in phenology, considerable overlap of species occurs at a given site through summer. In spite of the number of studies conducted on individual species of Acrididae (for example, Chapman and Joern 1990, Uvarov 1966, 1977) limited work has been done on macroscale grasshopper species associations (see Joern 1982 for microhabitat selection).

Less is known about Lepidoptera diversity in Western grasslands, yet 302 species of butterflies and moths were recorded from semidesert grasslands of southeastern Oregon in Harney County (Hammond 1995b).

At least 307 species of true bugs exist in the basin assessment area (Lattin 1995b), many of which are herbivores. We have knowledge of the general biogeographical distribution of the true bug fauna of the region based on collections at Oregon State University, Washington State University, University of Idaho, University of British Columbia, and the California Academy of Sciences (Lattin 1995b).

Functional roles of invertebrate grassland herbivores—Although all the insects being considered act as primary plant consumers, their host specificity differs among groups. Most Lepidoptera larvae confine their feeding to a single family of plants. Grasshoppers display varying degrees of host plant

[13] This section is based on information from three contract reports: Hammond (1994), Kemp (1995), and Lattin (1995b).

specificity; however, the pest species are generalists that graze on various grasses and forbs. For true bugs, species feeding on grasses tend to have lower specificity than those feeding on trees.

Herbivory influences rates of nutrient cycling of elements such as nitrogen and carbon. This function is relevant in regard to species that consume large amounts of vegetation, such as generalist grasshoppers in various range habitats, and plant bugs (Miridae) such as *Labops hesperius* Uhler in crested wheatgrass and some *Lygus* on *Kochia* (Moore and others 1982).

Small vertebrates such as passerine birds, rodents, shrews, and bats are particularly dependent on insects for a dietary protein source when rearing their young in spring and early summer. Nesting success for the western sage grouse (*Centrocercus urophasianus*) is tied to their dietary needs, which are primarily succulent forbs and insects (Klebenow and Gray 1968). These first-order predators then become food themselves for [arthropods and] other second-order predators such as hawks, owls, coyotes (*Canis latrans*), and bobcats (*Lynx rufus*).

Many rangeland herbivores, particularly Lepidoptera, also function as pollinators of herbs and shrubs (see “Pollination” section).

Implications of management for invertebrate grassland herbivores[14]—There are three major issues related to management for grassland herbivores: effects of plant community composition, effects of exotic flora and fauna, and effects of insecticides.

Changes in plant community composition affect the herbivore community because of changes in the availability of their host plants and the abundance and faunal composition of predators. Management activities that change vegetation structure, vegetation biomass, and plant species composition can affect presence and densities of grassland herbivores. A diverse insect herbivore fauna is best ensured by maintaining a structurally and taxonomically diverse floral community.

[14] This section is based primarily on discussions during the expert panel on rangeland herbivores (see appendix 1).

Season-long grazing can alter plant communities to earlier seral stages with increased likelihood of weedy species. Such conditions increase the probability of a less diverse grasshopper community easily dominated by pest species such as *Melanoplus sanguinipes* (F.), *Oedaleonotus enigma* (Scudder), and *Aulocara elliotti*. Season-long grazing also could reduce Lepidoptera diversity because of the loss of larval food plants (Hammond 1995a). Hammond and McCorkle (1983) found a rich diversity of plants and butterflies on pristine bunchgrass prairie, whereas adjacent overgrazed rangeland separated by a fence had few plants or butterflies. Grassland physiognomy and species composition can be manipulated to increase species diversity of grassland herbivores and to reduce the likeli-hood of irruptive outbreaks of pest species. The intensity, duration, season, and spatial extent of grazing regimes all are factors that can be restructured to favorably alter plant communities.

Fire will have little direct effect on insect herbivore populations unless burns are timed to kill a substantial portion of individuals emerging that season or occur on habitats of limited extent. The effect of most concern is how fire alters the plant community composition. If burning results in dominance by early successional forbs, especially in association with other disturbances, these conditions could result in outbreaks of some herbivorous invertebrate species, at least in the short term. A cool fire may favor Lepidoptera by opening up the community to their preferred food plants. A hot fire could result in mortality of shallow-rooted plants, which consequently could decrease herbivore diversity.

The second issue related to management for grassland herbivores is the invasion of exotic flora and fauna. Exotic flora such as cheatgrass (*Bromus tectorum* L.), knapweeds (*Centaurea* spp.), and leafy spurge (*Euphorbia esula* L.) have invaded and replaced native bunchgrasses and herbaceous plants on many basin assessment area grasslands. In addition, large areas of degraded grasslands throughout the West have been artificially planted with monocultures of exotic crested wheatgrass (*Kochia prostrata*) to provide livestock forage and prevent soil erosion. Most native insects are unable to exploit this new resource. Thus, generally a reduction in grassland insect diversity occurs (including predatory species), leading to the specific favoring of one or a few species of the community (for example, various species of grasshoppers, the true bugs *Irbisia pacifica* Uhler and *Labops hesperius* Uhler in crested wheatgrass, and *Lygus* spp. bugs in *Kochia* (Lattin and Christie, in press; Lattin and others 1995; Moore and others 1982).

The consequences of proposed introductions of exotic natural enemies (for example, scelionid egg parasites and fungal pathogens) to control native grasshoppers are unclear. Such actions may disrupt natural interactions in unanticipated ways—the effect on native biological control agents is unknown. Also, only a small proportion of grasshopper species are pests, and poorly researched biological control programs could put other species at risk. Risks can be reduced by carefully assessing the possible side or cumulative effects for significant nontarget species.

The third issue related to management for grassland herbivores is the role of insecticides. Epidemic grasshopper populations on grasslands adjacent to agricultural areas are routinely controlled by the application of insecticides. Broad spectrum insecticides like malathion and carbaryl drastically reduce both species diversity and densities of grassland grasshoppers. Furthermore, many nontarget species including desirable Lepidoptera, bees, beetles, and aphids are destroyed. Some of the arthropods affected are predators of grasshoppers that would normally exert pressure to reduce high grasshopper populations. Insecticides also may negatively affect birds feeding their nestlings and other vertebrates (for example, amphibians, reptiles, small insectivorous mammals, etc.) if most of their prey base is killed or contaminated. Bait applications of carbaryl are less harmful to flying nontarget insects but may negatively affect ants as well as other surface-active herbivores and omnivores.

The impacts of grasshopper controls on nontarget associated fauna can be mitigated in several ways. First, use selective agents that kill only the target or closely related species (for example, *Nosema locustae*, fungal, and viral pathogens) of pest grasshoppers. *Nosema locustae* can be used in many cases to reduce densities of grasshoppers without drastically altering community composition or impacting nontarget organisms. Although *N. locustae* reduces feeding on plants by about 50 percent, there is not the immediate mortality of grasshoppers as there is with chemical insecticides. This is because grasshoppers are killed gradually and cadavers quickly eaten by other grasshoppers, which aids the horizontal transmission of *N. locustae*. Public education and explicit goals such as vegetation protection rather than insect control will be necessary to gain acceptance for alternative control methods. Changing grazing practices that predispose sites to pest species outbreaks may be the best long-term solution.

Forest Herbivores

Several groups of immature or adult invertebrates are primary consumers feeding on forest forbs, shrubs, and trees. Through this function, they influence forest ecosystem processes directly or indirectly. Many are prey of various invertebrate and vertebrate predators, and they provide copious feces and corpses for detritivores.

Forest herbivorous insects have traditionally been viewed as pests that interfere with management objectives and damage forest resources. Management concerns and research emphases have concentrated on single species (principally tree defoliators and bark beetles), and then only during outbreaks (Huffaker and others 1984). Pest-related work has been useful in providing information on how these organisms affect other parts of the forest ecosystem (including influences on forest succession) and has provided the necessary tools to help managers reach desired objectives. The greatest need is for research that examines the long-term effects or beneficial impacts of individual insect species and insect assemblages on the whole ecosystem (Huffaker and others 1984, Stark 1987).

Within this assessment, two other efforts have examined aspects of arthropod forest herbivory. Hessburg and others (1995) assessed the landscape susceptibility to major defoliator and bark beetle disturbance, and Kurtz and others (1994) modeled the role that certain bark beetle and defoliator species play in forest succession. Although these topics are addressed in this paper, we refer the reader to the above reports for more detailed assessments.

The taxonomic groups addressed in this section are moths and butterflies (Lepidoptera) (Hammond 1994, Miller 1995, Wagner and McMillin 1994), bark beetles (Coleoptera: Scolytidae) (Ross 1995) and their associated mites (Acariformes) (Moser 1994), true bugs (Hemiptera: Heteroptera) (Lattin 1995b), saw-flies (Diprionidae and Tenthredinidae) (Wagner and McMillin 1994), and aphids (Aphididae) (Ross 1995).

Functional roles of invertebrate forest herbivores[15]—Forest invertebrate herbivores affect forest ecosystem processes directly and indirectly through (1) microclimate and water relations, (2) carbon and nutrient cycling, (3) energy flow, (4) plant succession or community structure, (5) food sources for other organisms, (6) wildlife habitat, (7) pollination of plants, (8) watershed properties, and (9) fuel conditions and fire hazard, (Haack and Byler 1993, Schowalter 1981, 1994). The following discussion provides examples.

Microclimate and water relations—Reductions in percentage of canopy cover or basal area by insect-caused defoliation or mortality can influence interception of precipitation, evapotranspiration (Schowalter 1994), light penetration, and wind speed (Speight and Wainhouse 1989). In addition, defoliation or tree mortality temporarily removes actively transpiring foliage from the forest canopy (Klock and Wickman 1978, Schowalter 1994). This reduces the flow of water from the root zone to the tree canopy and can lead to reductions in soil-water depletion in the stand (Klock and McNeal 1978 unpublished from Klock and Wickman 1978). These authors suggest warmer spring and summer soil temperatures, with increased soil moisture caused by changes in canopy exposure from insect defoliation, should provide a more favorable microclimate for biological activity. Environmental conditions, therefore, seem more favorable for decomposition of organic matter in defoliated stands compared to nondefoliated stands (Klock and Wickman 1978), especially during dry periods (Schowalter and Sabin 1991). Furthermore, the improved water balance, as a result of decreased transpiration, may enhance plant survival during drought (Schowalter 1994).

These microclimatic changes from defoliator-caused reductions in the canopy are likely to be temporary effects (Speight and Wainhouse 1989, Stark 1987). In contrast, when tree mortality occurs, changes in wind speed within the stand and increases in sunlight and rainfall within the affected area may persist until the forest is reestablished (Speight and Wainhouse 1989).

Nutrient and carbon cycling—The importance of arthropods in contributing to biomass decomposition, carbon cycling, nutrient cycling, maintaining soil fertility, and energy flow in forest ecosystems, has been proposed by Carpenter and others (1988), Haack and Byler (1993), Harmon and others (1986), Mattson and Addy (1975), Schowalter (1981, 1994), Schowalter and others (1991), and Stark (1987). Schowalter and others (1986) suggest that herbivore-controlled canopy-litter nutrient fluxes in forested ecosystems depend on plant species composition, the particular herbivores involved, changes in microclimate resulting from canopy opening, and the amount, composition, and seasonal pattern of material transferred relative to normal litterfall.

Herbivory influences both short- and long-term nutrient cycling processes in forest ecosystems (Schowalter and others 1986). Modest defoliation (for example, less than 7 percent) can return as much as 30 percent of foliage standing crop of potassium and 300 percent of foliage standing crop of sodium to the litter (Schowalter and others 1981, 1986, 1991). In addition, considerable amounts of mobile elements are returned indirectly by defoliation because of increased leaching from damaged foliage during rainfall (Schowalter and

[15] This section is based primarily on Wagner and McMillin (1994).

others 1986). Insect remains and frass also contribute to litterfall and may decompose faster than do fallen leaves and needles, which can result in faster cycling of elements such as calcium, potassium, nitrogen, and phosphorus (Haack and Byler 1993, Schowalter and others 1986, Speight and Wainhouse 1989).

One consequence of this increased cycling of nutrients to the litter layer (in combination with changes in the microclimate) may be compensatory growth after defoliation. Growth rates of mature Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Alfaro and MacDonald 1988), white fir *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.) (Wickman 1980, 1986, 1988), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Miller and Wagner 1989) increased after an initial decrease in growth after heavy defoliation by canopy herbivores. This effect was suggested to be a result of changes in soil nutrient levels or a thinning effect. The magnitude of this compensatory growth seems to be inversely proportional to the severity of defoliation (Alfaro and MacDonald 1988, Schowalter 1994).

Forest insects also act as pruning or thinning agents in the forest ecosystem, which may stimulate growth and increase biomass turnover (Schowalter 1986, 1994; Velazquez-Martinez and others 1992). Pruning or thinning of plant parts can stimulate plant growth by reducing competition for limited plant resources (Velazquez-Martinez and others 1992). Although insects and pathogens typically remove less than 10 percent of foliage and shoots in nonoutbreak years, removal of these plant parts apparently reduces plant metabolic demands and facilitates reallocation of plant resources (Schowalter 1994).

Bark and ambrosia beetles begin a successional process involving many species of arthropods and micro-organisms that eventually results in the complete deterioration and recycling of the dead tree (see detritivory and nutrient cycling section). For instance, *Tarsonemus endophloeus* Lindquist, a phoretic mite associated with the western pine beetle (*Dendroctonus brevicomis* LeConte) is responsible for establishing colonies of the fungus, *Ceratocystiopsis brevicomis,* which is inoculated ahead of the growing larvae and alters the phloem so the larvae can digest it (Hsiau and Harrington 1997, Moser 1994, Moser and others 1995). In Douglas-fir, deterioration occurs at a slower rate if the Douglas-fir beetle (*D. pseudotsugae* Hopkins) and associated arthropods are excluded from dead bole sections (Edmonds and Eglitis 1989).

There are no empirical data indicating how important these herbivore-mediated effects on nutrient cycling are for the long-term productivity of forest ecosystems. Growth responses of trees to the addition of nutrients, in general, will only occur when growth at that site is nutrient limited (Speight and Wainhouse 1989). In other words, nutrient-poor sites may benefit most by high rates of nutrient cycling caused by defoliators. Likewise, in boreal forests, increased leaf-fall during outbreaks of defoliators will not provide an immediate increase of nutrients because of the slow rates of decomposition (Speight and Wainhouse 1989).

Succession relations—The effects of insects and diseases on microclimate and water relations, nutrient and carbon cycling, and the direct removal of foliage cause changes in individual tree growth and mortality. These effects are ultimately manifested at stand and ecosystem levels (Schowalter and others 1986). Selective herbivory by monophagous or oligophagous insects favors competing tree species and can result in a successional transition in stand age, composition, or density (Connell and Slatyer 1977, Haack and Byler 1993, Huffaker and others 1984, Klock and Wickman 1978, Schowalter 1981, Schowalter and others 1986). These changes, in turn, affect both productivity and succession of the plant community (Huffaker and others 1984). The rate and direction of successional change depends on the severity of infestation (for example, outbreak versus nonoutbreak populations), the type(s) of insects causing the change (for example, tree-killers versus nonkillers), single-species attack versus combined-species attack (for example, western spruce budworm, bark beetles, and pathogens), and the successional stage being infested (for example, stand regeneration versus climax) (Franklin and others 1987 from Haack and Byler 1993, Schowalter and others 1986, Wulf and Cates 1985).

Succession is typically accelerated toward the climax species when there is low to moderate herbivory on dominant and codominant seral species. This alters competitive interactions among trees, thereby resulting in a reduced overstory and allows increased growth of shade-tolerant species (Connell and Slatyer 1977). An example of how canopy herbivores can accelerate forest succession is western spruce budworm defoliation of seral hosts when nonhosts are climax (for example, low-elevation sites in the Blue Mountains) (Wulf and Cates 1985). Tree-killing bark beetles can rapidly facilitate succession to shade-tolerant species on sites where hosts are seral.

Alternatively, herbivores may delay or even reset the process of succession (Haack and Byler 1993). Western spruce budworm outbreaks tend to retard forest successional development on habitat types where host trees are climax (Wulf and Cates 1985). The loss of cone crops in combination with high mortality of young Douglas-fir and true firs encourages the regeneration of seral trees, and forest succession may be effectively stopped by budworm (Wulf and Cates 1985). Bark beetles also can facilitate a return to seral forests. Mountain pine beetle killing of seral lodgepole often is followed by wildfire, leading to reestablishment of seral lodgepole forests. In addition, secondary infestations by bark beetles may further recharge the cycling nutrient pool, relieve moisture stress, and either keep or move the system toward a younger seral state (Wulf and Cates 1985). The balsam woolly adelgid (*Adelges piceae* (Ratzeburg)), which can kill subalpine fir in 3 to 5 years, can significantly impact harsh sites such as lava beds, talus slopes, and abandoned beaver marshes where subalpine fir is a pioneer species (Franklin and Mitchell 1967). Schowalter and others (1986) suggest defoliation on stressed trees accelerates the mortality of such trees and releases competing vegetation. Stands composed largely of suitable host trees often suffer extensive mortality of dominant and codominant trees. In such cases, ecological succession is typically reset to the early successional stage (for example, grasses, forbs, and shrubs).

Defoliating insects may interact with fire as well as with secondary attack by bark beetles to synergistically alter forest succession (Gara and others 1985, Geiszler and others 1980, Hadley and Veblen 1993). For example, several studies suggest fire suppression in the Rocky Mountains since the early 1900s may have led to increasingly severe and synchronous recurrences of western spruce budworm by promoting dense, multistoried stands (Anderson and others 1987, Carlson and others 1983, McCune 1983, Swetnam and Lynch 1989). Before fire suppression, it is believed small trees, seedlings, and saplings were eliminated by frequent, low-inten-sity fires, thereby decreasing the abundance of available hosts (Hadley and Veblen 1993).

Ecosystem changes reflecting reduced canopy cover have been suggested to occur earliest in the understory (Klock and Wickman 1978) and may result in increased plant and animal diversity (Schowalter and Sabin 1991). Zamora (1978) studied 98 grand fir (*Abies grandis* (Dougl.) Lindl.) stands in the Blue Mountains of Washington and Oregon that had been defoliated 2 to 4 years previously by Douglas-fir tussock moth. He found a small but significant increase in number of mainly perennial grasses and forbs and up to a 100-percent increase in total understory cover in severely defoliated stands. Because many of the insects feeding on understory plants are highly host specific, any increase in the diversity of grasses and forbs will increase their diversity as well, at least temporarily. For a fauna of 302 species of butterflies and moths in the Blue Mountains, Grimble and others (1992) found that 44 percent feed on understory hardwood shrubs, 43 percent feed on forbs and grasses on the forest floor, and only 10 percent feed on the canopy conifers.

Food source for other organisms—Forest herbivores are preyed on by various other arthropods and vertebrates (Haack and Byler 1993, Martin and others 1951, Swan 1964). Arthropod predators of defoliators include spiders, ants, true bugs, lacewings, snakeflies, beetles, flies, and wasps (Torgersen 1994). Much of the earliest research on predators of Douglas-fir tussock moth and western spruce budworm was done in east-side ecosystems

(Torgersen 1994). For example, over a dozen species of forest-dwelling ants prey on western spruce budworm and Douglas-fir tussock moth. Many arthropod species have been used in biological control programs against tree-feeding insects (Haack and Byler 1993).

Of animals other than arthropods, birds probably consume the most tree-feeding insects (Haack and Byler 1993). Increases in woodpecker populations have been observed in areas with high bark beetle populations (Koplin 1969). Torgersen and Torgersen (1995) observed at least 35 species of birds that feed on the western spruce bud-worm and Douglas-fir tussock moth in east-side ecosystems. Two species, mountain chickadee (*Parus gambeli*) and red-breasted nuthatch (*Sitta canadensis*), however, dominated observations of actual predation on the western spruce budworm and Douglas-fir tussock moth and were the most numerous species (Langelier and Garton 1986, Torgersen and others 1984). Most mammals, both large and small, consume insects to some degree (Haack and Byler 1993), and they, in turn, may be eaten by secondary predators.

Creation of, or effect on, wildlife habitat—Trees killed by insects are used as wildlife habitat both as standing snags and when they fall as downed woody material (Maser and Trappe 1984). At least 270 species of North American reptiles and amphibians, 120 species of birds, and 140 species of mammals use deadwood to roost, nest, or forage (Ackerman 1993). Wildlife needs for plant communities, successional stages, and forest edges all are affected by the activities of insects (Thomas and others 1979). In areas where cover is plentiful and forage is limiting, the increase in forage plant biomass 2 to 4 years after severe defoliation will have a positive influence on deer and elk use (Thomas and others 1979). Down woody debris is also a critical resource for invertebrates (Harmon and others 1986).

The effects of severe defoliation and tree mortality will differ depending on the habits of wildlife species. Species that normally occupy the upper half of the tree crown will be detrimentally affected by severe defoliation for 1 or 2 years. In general, however, insect damage that causes small patches of snags or more open stands will create a more diverse habitat, benefitting the bird community (Klock and Wickman 1978).

Pollination—Moths and butterflies are among the insect herbivores that as adults are pollinators. Several hardwood tree species, as well as many of the understory herbs and shrubs rely on insects for dispersal of pollen (see "Pollinators" section for a more detailed description of this function).

Watershed properties—Alterations in vegetative cover resulting from forest herbivory can affect the quantity and timing of streamflows. Bark beetle-caused tree mortallity can significantly increase water yields, and the effects can last up to 25 years (Bethlahmy 1975, Love 1955, Mitchell and Love 1973, Potts 1984). These effects apparently are due to reduced interception and evapotranspiration. In addition, peak flows may be higher and occur earlier in the season after bark beetle infestations (Cheng 1989, Potts 1984). Forest herbivory can change the biological communities within streams and the physical structure of stream channels through effects on riparian vegetation and detrital inputs.

Fuel conditions and fire hazards—Fire hazards may increase significantly after insect infestations. In the Canadian province of Ontario, repeated defoliation by the eastern spruce budworm caused high rates of mortality to balsam fir *(Abies balsamea* (L.) Mill) (Stocks 1987). Surface fuel loads and fire hazards increased for 5 to 8 years after budworm-caused mortality as the dead trees broke apart and fell to the forest floor. Fire potentials gradually declined after 8 years as the surface fuels decomposed and vegetation became established on the sites. Twenty years after a spruce beetle outbreak on the Kenai Peninsula, there was significantly more sound, dead wood >7.5 centimeters in diameter compared to uninfested areas (Schulz 1995). In addition, there was significantly greater cover of bluejoint grass *(Calamagrostis canadensis* (Michx.) Beauv.), a fine, flashy fuel that facilitates rapid fire spread. The combination of fine fuels and sound, woody material created conditions for intense and unpredictable fire behavior.

Implications of management for invertebrate forest herbivores[16]—Forest management primarily affects forest herbivores in two ways—through overstory host plants and understory host plants.

1. Overstory host plant availability and suitability. The principal way management activities affect canopy and bole herbivores is through changes in their food source, host trees. Stand traits includ-ing species composition, tree age and size, stand structure, and stress act independently and in concert to affect the composition and relative abundance of this herbivore guild.

Species composition—Tree herbivores are largely monophagous or oligophagous (Strong and others 1984). Consequently, most herbivore populations and ranges are defined by their forest tree hosts and are relatively well known (Furniss and Carolin 1977). This ecological specialization suggests a higher probability of canopy and bole herbivores being affected by management practices (for example, prescribed burning, thinning, selective harvest, and regeneration) affecting their hosts. Because of their host specificity, insect herbivore diversity will increase with a greater diversity of canopy species of trees. The guild of predators and parasites also will increase. Changes in tree composition will cause sudden impacts on herbivores, and probably will persist for a long time. Preventing large contiguous areas of host type (tree species and size) will minimize the probability of widespread outbreak of indigenous defoliators and bark beetles as well as accidentally introduced exotic species.

Tree age and size—Age and size-class distribution of hosts also govern abundance of canopy and bole herbivores. Many herbivores have specialized to feed on trees at different stages in maturation development (Nielson and Ejlersen 1977, Schowalter 1985). For bark beetles, tree species composition is important during stand development from pole to larger tree sizes because these are the tree sizes that are suitable hosts. For example, Dunbar and Wagner (1990) and McMillin and Wagner (1993) recognized that three species of pine sawflies, *Neodiprion gillettei* (Rohwer), *N. fulviceps* (Cresson), and *N. autumnalis* Smith, feed on foliage of seedlings, young pole-sized trees, and pole-sized to mature trees of ponderosa pine, respectively, in the same geographical area. Management actions like prescribed fires, thinning, harvest, and regeneration, that change the age or size-class distribution of hosts can potentially change the populations of associated herbivores. Generally, defoliator outbreaks will have the greatest effect on stands beginning from the stem-exclusion stage. Maximum diversity of herbivores and minimum outbreaks of individual species will be obtained under those management scenarios that mix age- and size-class distributions, other stand factors being equal.

Stand structure—Many aspects of forest structure including density, vertical diversity, understory vegetation, forest successional stage, and presence of coarse woody material will influence the tree herbivore community. Variation in forest structure decreases the apparency of forest resources to forest insects (Schowalter 1986). This occurs through modification of the proximity of insects to suitable resources, cues used by insects to orient to hosts, and forest microclimate. All these factors increase the functional diversity of the forest and consequently increase diversity of the canopy and bole herbivore community but likely decrease total populations of any individual herbivore species.

Stand density becomes an important factor in bark beetle population dynamics as trees reach pole size and larger; trees growing on drier sites will become susceptible to beetle infestations at lower densities than those growing on moister sites. The longer dense pole size or larger stands persist, the greater the probability they will become infested by bark beetles. Management activities that reduce stand density such as thinning and prescribed burning can reduce the probability of bark beetle infestations. Although canopy density may influence defoliator populations less than bark beetles, stand density can affect the population dynamics of western spruce budworm (Wulf and Cates 1987) and pine sawflies (McMillin and Wagner 1993, 1998).

[16] This section is based on discussions during the expert panel on forest herbivores (see appendix 1) and Wagner and McMillin (1994).

Forest successional stage is potentially important to canopy herbivore abundance. As succession progresses, forests become more diverse (Hansen and others 1991) and create more ecological niches, which in turn support greater diversity of canopy herbivores (Warren and Key 1989). In general, mature forests tend to be dominated by defoliating canopy insects, whereas young forests are dominated by sapsucking insects (Schowalter and Crossley 1987). Schowalter (1989) examined the canopy arthropod community structure in forests in various successional stages and concluded that old-growth forests supported substantially more species and functional diversity in canopy herbivores than did young regenerating forests. The greater diversity of canopy herbivores in late-successional forests implies that these forests contribute disproportionately more to total canopy diversity than do younger forests. Hence this representation on the landscape should be disproportionately higher than the other species if the objective is to maximize species diversity of canopy herbivores. Management activities that reduce late-successional forest likely will reduce diversity of canopy herbivores.

Hypothetically, more coarse woody material could indirectly reduce the frequency of defoliator outbreaks owing to increased population densities of ant predators. A confounding factor is that if ant numbers are reduced, other predators compensate for them (Campbell and others 1983).

Coarse woody material (standing and down) is suitable as a breeding site for bark beetles for 1 to 2 years after tree death. Beetle populations can increase in woody material, disperse, and then (if abundance is sufficient) cause significant mortality of standing green trees. Trees that die in late summer through spring (after dry weather and before beetle flight) will be most suitable for bark beetle infestation in most habitats. Possible actions to mitigate bark beetle buildup in woody material are to modify time of felling (to allow slash to dry before subsequent beetle flight), remove or burn woody material infested by beetles, or use semiochemicals to prevent infestations in dead and down material.

Stress—Stress to trees usually occurs over relatively short periods, one to several years. Some causes such as overstocking, understory density, drought, or defoliation, however, can develop over periods of 5 to 10 years or longer. Likewise, mitigation of the attraction of bark beetles to stressed trees can utilize either short-term control strategies (for example, removal, burning of diseased and damaged trees, or protection by using semiochemicals) or long-term management actions (for example, regulate stand density, minimize damage to trees during intermediate stand treatments, match tree species to site conditions, and manage the density of understory competition). Although some defoliators seem to respond to short-term tree stress with population increases, stress probably does not generate large outbreaks of defoliators. Low levels of stress over short periods probably have little or no impact on canopy defoliators.

2. Understory host plant availability. Management practices affect understory herbivores in several ways: (a) indirectly through changes in the density of the overstory canopy, which influences the type and abundance of understory plants; (b) indirectly through manipulations of the understory vegetation; and (c) direct mortality caused by application of insecticides for overstory defoliators. Changes in the understory herbivore guild will affect plant community dynamics and predators and parasites that use these species as prey or hosts.

Changes in overstory canopy density—Opening up the forest canopy will promote greater forb and grass growth for understory herbivores, which in turn support predators and higher levels of the food web. Selective thinning of overstocked conifer stands would open the forest for more angiosperms and therefore promote these understory species.

Manipulation of the understory vegetation—Although a certain level of disturbance may enhance herbivore diversity in the understory, excessive use of any approach on a large spatial scale will result in a depauperate flora and fauna. Periodic ground fires keep the forest floor open with plenty of light to encourage the growth of forbs, grasses, and shrubs, which in turn support detritivores, herbivores, and their predators. In the absence of such fires, dense stands of young fir and pines become established and shade out the angiosperms and thus reduce the diversity of the associated herbivores. Controlled ground fires would mimic naturally occurring fires. Cool to moderate intensity burns likely would be best because of the role litter and soil organisms play in productivity of the site. Overgrazing, scarification, and the use of herbicides all will reduce angiosperm growth, and likewise reduce the abundance and diversity of the understory fauna.

Application of pesticides—Some research[17] shows a 66-percent loss of species, 85-percent loss of individual abundance, and a 95-percent loss in biomass of understory Lepidoptera after application of *Bacillus thuringiensis kurstaki* (*B.t.k.*) for the western spruce budworm. This is not unexpected because *B.t.k.* can kill many of the moths or butterfly species that ingest it. Impacts on nontarget herbivores are expected to last from 1 to 3 years depending on the number of applications and the size of the area sprayed. The more frequent the treatments, the greater the impact. The larger the size of the spray area, the longer it will take for recolonization from untreated areas. If a spray area includes habitats not otherwise represented in the vicinity, species specific to those habitats would be the most adversely affected.

General implications of management practices on invertebrates—In general, because current conditions in many of our ecosystems have been modified so significantly by fire suppression, grazing, and the introduction of exotic species such as widespread plantings of *Agropyron* sp., a simple reversal of fire management by using prescribed burning may not accomplish an objective of returning the land to its previous condition. Thus, prescribed burning needs to be used with extreme caution, generally with native species in mind.

[17] Unpublished data. On file with: Jeffrey Miller, Professor, Department of Entomology, Oregon State University, Corvallis, OR 97331.

Overgrazing of shrub-steppe, prairie, savannah, or mountain meadows can eliminate arthropod species by conversion of perennial grasses, native forbs, and shrubs to introduced annuals. Maintaining native plant communities would foster native arthropod species.

Recreation can damage arthropod habitat through trampling or road building. Probably the most critical habitat in this category is caves, where a few unusual arthropod species live. Excessive traffic within caves, even from directed recreational use, can cause faunal deterioration. Other vulnerable areas are bogs and hot springs.

Exotic species can profoundly affect arthropod fauna. Exotic plants, or arthropods introduced as biological controls of pest species or as pollinators may competitively displace native species that are important to beneficial predators or other functional groups.

Invertebrate Biodiversity

According to Asquith and others (1990), arthropods represent 86 percent of the biota of an old-growth forest (H.J. Andrews Experimental Forest) when all vertebrate species and all vascular plants, and the then-known number of insects and other arthropods were compared. Over 3,400 species of arthropods were known then, a number approaching 4,000 species today. According to Wilson (1988), over 950,000 species of insects have been described—the most species of any group. Ultimate numbers range from 5 to 30 million species, depending on new forecasts. Large parts of our invertebrate fauna are poorly known, particularly in the tropics, but better known in temperate regions. Some species are known chiefly from the original descriptions and perhaps other localities. Our knowledge of temperate fauna is far better, although there are some groups that are poorly known because we have fewer systematists available to work on many of these groups. A renaissance is needed in most areas of systematics if we are to be able to develop adequate databases in species recognition, distribution, and habits to provide proper information to land managers. At present, support for such individuals lags far behind other areas.

No thorough survey is available of all species in the basin assessment area; we can only infer from what is known elsewhere that the number of species here is large. Table 1 gives a perspective of how great invertebrate diversity may be worldwide and how it relates to the diversity of other taxa. A total of 14,439 species is estimated to inhabit the basin assessment area based on described species. Most of the catalogued taxa are vascular plants and allies (about 10,191 taxa or 71 percent) and arthropods (about 3,400 known taxa or 24 percent), mostly insects (table 2). Only a few (609 taxa or 3 percent) are vertebrates. The number of estimated taxa (excluding micro-scopic life forms), with extrapolations for species not yet described, totals over 35,200 species (table 2). Estimated numbers of macroinvertebrates dominate this sum (24,290 estimated taxa or 69 percent), with plants and allies second (10,340 estimated taxa or 29 percent). We assume the vertebrate species of the basin assessment area, where considerable resources have been spent, have been fully described (609 taxa or 2 percent).

Approaches to Managing Invertebrate Biodiversity

Can and should invertebrate diversity be managed by using the same tenets used for vertebrates and plants? Indeed, is this philosophy working for vertebrates and plants? Will a species-by-species approach adequately protect most rare and endemic invertebrate species? What does such an approach mean with regard to the feasibility of complying with the Endangered Species Act, and what does it mean to the implementation of ecosystem management? In our effort to gather information about the invertebrate fauna of the basin assessment area, we contracted with various experts who differed widely both in their disciplines and in their viewpoints of invertebrate diversity. In the following sections, we describe several approaches to managing invertebrate diversity. Included are possible implications of these approaches to general biodiversity conservation and to the implementation of ecosystem management.

Table 1—The diversity of organisms worldwide

	Number of species	
Taxonomic group	**Currently described**	**Number including undiscovered species**
Plants and allies:		
Algae	40,000	200,000 to 10 million
Fungi	70,000	1 to 1.5 million
Plants	250,000	300,000 to 500,000
Invertebrates:		
Protozoans	40,000	100,000 to 200,000
Viruses	5,000	perhaps 500,000
Bacteria	4,000	400,000 to 3 million
Roundworms	15,000	500,000 to 1 million
Mollusks	70,000	200,000
Insects	950,000	8 to 10 million
Spiders and mites	75,000	750,000 to 1 million
Crustaceans	40,000	150,000
Vertebrates	45,000	50,000

Source: Wilson 1988; undiscovered from various sources.

Single-species approach—This is the model currently followed with the designation of FWS threatened and endangered species and FS- and BLM-sensitive species. Designations are based on criteria such as rareness, limited distribution, and present or probable threats to a species' habitat.

Certain invertebrate groups, those that are less diverse and have a solid base of information about habitat needs, will be more amenable to a single-species approach. Major difficulties in attempting to assign threatened and endangered status to invertebrates are due to the emphasis on large charismatic organisms and the apparent lack of public interest.

Given that species are continually being added to lists of special concern, what are the implications of the vast undescribed diversity of insects? What do extensive lists of sensitive plants, snails, and fungi imply about those taxa yet to be assessed in this manner? There is little reason to doubt similar work on arthropods or microorganisms would yield long lists of similarly sensitive species. Providing preserves for every sensitive organism would soon become impossible, and we are left with the question of how to deal with the potentially conflicting requirements of different sensitive species at a single location.

Formal listing or even recommendations for additional monitoring and surveys almost always has enormous economic, political, and social implications. The promotion of threatened and endangered species by either individuals or agencies has obligations, not the least of which is maintaining the credibility of threatened and endangered listings. The designation of candidate species about which virtually nothing is known or that are based solely on single collecting events are problematic. "Rare" species have too often been found to be relatively abundant or widespread, because they were cryptic, restricted to poorly accessed or "uninteresting" habitats, required special collecting techniques, or were simply not actively sought in the past (LaBonte 1995).

Although still working within the single-species approach, a more conservative plan has been advanced by many arthropod specialists. Their concern is that given the anomalies of collecting stated above, a relatively high degree of knowledge should be required before putting species on lists. In other words, to list a species as one of special concern, we should understand its distribution and requirements. The following are only a few examples of criteria to consider in determining which invertebrate species are deserving of special status (LaBonte 1995):

- The species is known from more than one collecting event.
- Evidence exists that the species is restricted to potentially threatened or patchily distributed habitat.
- Evidence exists that the species has a restricted geographic distribution.
- Evidence exists that the species has poor dispersal capabilities.
- Habitat threats can be managed or mitigated with known technologies.

A rule set could be used to determine which combination of these criteria would be required. Evaluation of whether a species meets the criteria could be judged by an unbiased panel of experts. To ensure a qualified but unbiased examination, the panel could include at least one expert from the taxonomic group under consideration, and the remainder of the panel members would have similar expertise but with unrelated taxonomic groups.

Unique-habitats approach—Preservation of rare habitats will result in the support of many rare species. Areas such as sand dunes, lava flows, mountain meadows, bogs, hot springs, and caves likely will encompass many of the species already occurring on lists (for example, the FWS candidate species of beetles *Agonum belleri* Hatch, *Cicindela arenicola* Rumpp, *Glacicavicola bathyscioides* Westcott, and the skipper *Polites mardon* Edwards), as well as more rare species that will be recognized once these areas are adequately surveyed. Many of these unique habitats are relatively small, have low economic value, and some of them (such as those within national parks and wilderness areas) are already protected. Selection of patchy areas could be by local personnel who know the locations of such unique communities.

Table 2—Counts or estimates of total species biota of the basin assessment area[a, b]

Taxonomic group	Total in basin: Known	Total in basin: Estimated	Number considered in assessment
Plants and allies:			
Fungi	394		394
Lichens	736	736	736 (39 grp[c])
Bryophytes	811[d]	860	811 (11 grp)
Vascular plants	8,250	8,350	8,078
Total	10,191	10,340	10,019 (50 grp)
Invertebrates:			
Protozoa	?[e]	?	0 (1 grp)
Rotifers	?	?	0 (1 grp)
Nematodes	?	?	0 (3 grp)
Mollusks	380[f]	790[g]	380
Insects[h]	3,400	23,500	335
Total	3,780	24,290	715 (5 grp)
Vertebrates:			
Fish (natives)	87	87	87
Fish (exotics)	54	54	54
Amphibians	26	26	26
Reptiles	27	27	27
Birds	283	283	362
Mammals	132	132	132
Total	609	609	688
Total, all taxa	14,580	35,239 (61 grp)	11,422 (143 grp)

[a] Viruses, algae, phytoplankton, zooplankton, and most aquatic arthropods are not included in this table. Fungi numbers here represent macrofungi. See text for discussion of microfungi, bacteria, protozoa, and nematodes.

[b] Figures are number of taxa (mostly species with a few subspecies of particular conservation concern).

[c] grp = a group of similar species. The group is based on taxonomic or ecological function similarity.

[d] Christy and Harpel (1995).

[e] These groups are not well enough known to estimate their numbers.

[f] The 380 known mollusks include 200 freshwater gastropods, 30 freshwater bivalves, 25 slugs, and 125 land snails (Frest and Roth 1995).

[g] The 790 suspected mollusks include 445 freshwater gastropods, 35 freshwater bivalves, 30 slugs, and 280 land snail (Frest and Roth 1995).

[h] Insects (Lattin 1995a).

Centers-of-endemism approach—For a few taxa (butterflies, for example) areas of endemism have been identified, but no attempt has been made to define areas of coincidence for endemism. Mollusks are one exception, with some endemic centers recognized since the 1860s (Frest and Johannes 1995). At least 12 such endemic centers are recognized by Frest and Johannes (1995) within the basin assessment area. The spatial and geographic features that lead to endemism in higher plants, however, generally are known and may, as a starting point, be hypothesized to be the same as those used by herbivorous invertebrates. Examples of possible centers of endemism are the Blue Mountains, which represent a potential suture zone between the Cascade-Sierra and Rocky Mountain faunas, and the Steens Mountains, which may serve as islands fostering genetic diversification.

Representative-habitats approach—The purpose of retaining areas with representative vegetation communities and habitats is to maintain the common native fauna, which account for most of the invertebrate species. Research natural areas and similar existing special-use areas could be used in preserving representative habitats.

Centers-of-biodiversity approach—Centers of high invertebrate diversity may be caused by three distinct phenomena: (a) areas of palaeoendemism, (b) areas of rapid recent evolution, and (c) areas of high geographic microclimatic heterogeneity. On the west side of the crest of the Cascade Range, the Siskiyou Mountains are well known as centers of palaeoendemism. Our knowledge of such areas in the Columbia River basin is rudimentary. Frest and Johannes (1995), however, do recognize several such areas for mollusks and specify the geologic and historical phenomena likely responsible. The best example is the Lower Salmon River-Hells Canyon area of Idaho, Oregon, and Washington. The alpine altitudinal islands of the basin assessment area may represent such areas. Several endemic carabid beetle species are known from such altitudinal islands as the Wallowa and Steens Mountains (LaBonte 1999). Present knowledge of areas of recent speciation is incomplete. In the absence of strong examples of the first two phenomena, the most likely correlate of high localized invertebrate diversity may be heterogeneity of the geologic substrate (that is, a diversity of elevations, aspects, life zones, and plant associations). If this is true, it would be relatively easy to locate geologically or botanically heterogeneous regions. An oversight panel could select the combination of areas that best ensures all biogeographic types across the basin assessment area are represented.

Towards an Approach for Conservation of Invertebrates

One or several of the above approaches could be applied to a plan to conserve invertebrate diversity. The most fundamental decision in devising such a plan is whether a species-specific or habitat-focus approach, or some combination thereof, is warranted.

A species approach would entail the need for special management restrictions for all land where designated species of special concern occur. Here again, the question is what criteria are species lists based on, and how extensive can these lists get before such a strategy is inoperable? Another concern is that such an approach protects rare and endemic species, which can be a small proportion of total species diversity with restricted distribution and may fail to protect key contributors to important ecosystem functions such as nutrient cycling, pollination, herbivory, and predation over a broad geographic area. A possible disadvantage of a species-specific approach is that it does not emphasize habitats and may be a roadblock to the study of arthropod function.

The last four approaches are aimed at conserving discrete habitat units on which the primary management goal would be the general (not species-specific) maintenance of biological diversity. The hope is that a combination of these different types of habitat conservation areas would provide protection for most invertebrates.

Invertebrate Species of Conservation Interest

Rare or Sensitive Invertebrate Species

Federally listed endangered or threatened species—Currently no terrestrial invertebrates in the basin assessment area are federally listed as endangered or threatened.

Federally listed candidate species—There are 15 terrestrial invertebrates that, before 1996, were FWS federal candidate 2 species[18] (table 3).

Arachnida, Pseudoscorpionida:

Apochthonius malheuri Benedict and Malcolm (Chthoniidae). The only known population of this species occurs in Malheur Cave, a lava tube about 1000 meters long, in Harney County, Oregon. Many other caves have been surveyed, but this species has not been found elsewhere. Malheur Cave is unique as the terminal third of the lava tube contains a geothermal lake, which modifies the microclimate. *Apochtonius malheuri* appears to be cave adapted as it has morphological characteristics such as a thin integument and an elongated body. Adequate moisture levels are necessary for this species, thus it occurs within a band from 168 to 381 meters from the mouth of the cave, depending on the level of the lake. *Apochtonius malheuri* is a predator, preying on springtails, mites, spiders, and other terrestrial microarthropods. Habitat needs include material such as wood chips or other materials that small animals and bats may bring into the cave and the warm environment provided by this thermal cave (about 10 degrees higher than average surface annual temperature). *Apochtonius malheuri* naturally occurs at low population levels because of its limited habitat. The population is stable, with all three nymphal stages and both males and females found in a 1994 survey. Although both the cave and this species are presently stable, possible threats to the cave and to *A. malheuri* are pesticide drift from nearby agricultural fields; drought or agricultural drawdown of water, either of which could cause a reduction in the level of the lake; heavy human use of the cave; and the introduction of exotic organisms via wood chips (brought into the cave by a group that owns the outer portion of the cave and uses it regularly) that may outcompete the endemic cave species. A status report by Benedict and McEvoy (1995) is available.

Gastropoda—

Cryptomastix magnidentata (Pilsbry) (Polygridae). Scattered colonies occur along one side of a half-mile stretch of Mission Creek, Idaho. The species lives in moist, rocky, well-shaded forest with common forbs and deciduous trees, and in moist and mossy, rather open grassy limestone and mixed limestone-basalt taluses a short distance above the flood plain of Mission Creek. Much of the type area has been destroyed or greatly modified because of limestone quarrying, which has proceeded sporadically and is ongoing. Sites are along the present quarry haul road, which has substantially impacted taluses in the area. Portions of the quarry area also have been heavily grazed, and much of the upland in the immediate vicinity has been logged. The species is absent from these areas and is evidently declining in numbers and area occupied; population trends are downward. Based on recently collected information and survey work, Frest and Johannes (1995) recommend this species be listed as endangered on the federal list of endangered species and in the state of Idaho; they recommend it be considered a sensitive species by the FS, BLM, Nez Perce Tribe, and other appropriate land and wildlife management agencies.

Discus marmorensis Baker (Discidae). This species occurs as a few colonies in central portions of two creek tributaries to the lower Salmon River in Idaho. It is generally found at moderate elevations on limestone terrain in relatively intact, moist, well-shaded (closed to nearly closed-canopy) ponderosa pine forests, with diverse deciduous and

[18] On February 28, 1996, the USDI Fish and Wildlife Service published in the Federal Register a change in their species status program, essentially replacing the three candidate species categories with a single category. In this change, most of the species that were classified as category 2 or 3, and 303 taxa that were category 1 candidates, are no longer included in the list of candidate species. Our report retains the category 2 listing for two reasons: (1) the data collection preceded the ruling change, and (2) the category 2 designation denotes species of potential conservation concern deserving attention.

Table 3—The USDI Fish and Wildlife Service (FWS) former federal candidate 2 species and Bureau of Land Management (BLM) sensitive species

Class and order	Genus and species	FWS candidate 2	BLM sensitive
Arachnida, Pseudoscorpionida	*Apochtonius malheuri*	C[a]	
Gastropoda	*Cryptomastix magnidentata*	C	
	Discus marmorensis	C	
	Megomphix lutarius		C
	Monadenia fidelis minor	C	C
	Oreohelix idahoensis idahoensis	C	
	Oreohelix jugalis	C	
	Oreohelix strigosa delicata		C
	Oreohelix strigosa goniogyra	C	
	Oreohelix vortex	C	
	Oreohelix waltoni	C	
Insecta, Coleoptera	*Agonum belleri*	C	
	Cicindela arenicola	C	
	Glacicavicola bathyscioides	C	
	Nebria gebleri fragariae		C
	Nebria vandykei wyeast		C
Insecta, Lepidoptera	*Charidryas acastus dorothyea*		C
	Limenitis archippus lahontani	C	
	Polites mardon	C	
Insecta, Orthoptera	*Acrolophitus pulchellus*	C	

[a] C = candidate before 1996.

forb understory. The species occasionally occurs in moist schist talus in such forests. In both cases, snail colonies are generally near stream edges and at the base of steep slopes. Much of the original area of occurrence has been logged and is now heavily grazed; the species is absent from such areas. Limestone quarrying has eliminated much or all of one colony in the last 3 years. Roads into the area generally are situated to fragment or eliminate colonies. Population trends are downward. Based on recently collected information and survey work, Frest and Johannes (1995, 1997a) recommend this species be listed as endangered on the federal list of endangered species and by the state of Idaho; they recommend it be considered a sensitive species by the FS and BLM.

Monodenia fidelis minor Binney (Bradybaenidae). This subspecies survives in a few colonies in the mouth of and in the lower Deschutes River valley, Oregon, and near Dog Falls, Washington (Frest and Johannes 1995). Most known sites are in the Columbia River Gorge National Scenic Area. The species has been observed to occur at some sites with the Larch Mountain salamander *(Plethodon larselli* Burns). It is generally in basalt talus, often north-facing, often associated with seeps and springs. Road building and modification have destroyed or fragmented some colonies. Much of the original range is heavily grazed.

Oreohelix idahoensis idahoensis (Newcomb) (Oreohelicidae). This subspecies is restricted to a few colonies in a small area a few miles along both sides of the lower Salmon River, Idaho. It is restricted to low-middle elevation limestone and calcareous schist outcrops and talus, generally in sage scrub. Grazing, gold mining, talus and limestone quarrying, and range fires pose threats to this species. One large colony is now near extinction because of a combination of grazing and recent fires. In one area, sheep grazing has eliminated most of one colony, whereas remnants on the opposite side of the road (protected from grazing) have abundant snails. Frest and Johannes (1995, 1997a, 1997b) recommend listing as threatened on the federal list of endangered species, and by the state of Idaho; they recommend it be considered sensitive by the FS, BLM, and other land management agencies.

Oreohelix jugalis (Hemphill) (Oreohelicidae). This species survives at some sites along the lower Salmon River, Idaho. It occurs at low elevation in rock taluses and boulder piles. This is a rather tolerant species, occupying the range from slightly mesophile to moderately strongly xerophile. Nearly all known sites are impacted by grazing; sheep, horses, and cattle have considerably reduced or even extirpated colonies. Road construction and maintenance have considerably reduced or extirpated the species from much of the corridor along US Highway 95. Talus mining has affected taluses in the immediate vicinity of all sites. Gold mining and prospecting impact sites in schist lithologies. Population trends are clearly downward. With thorough survey, *O. jugalis* has been noted as more common than originally expected, even though it has suffered considerable range and site loss. Frest and Johannes (1995, 1997a) suggest placing this species on a "watch" list. If sites for other more rare species in the same corridor can be pro-tected, it is possible this species will be adequately protected. They feel it should be considered sensitive by the FS, BLM, and other land management agencies; and if other species are not protected, it should be listed as threatened on the federal list of endangered species.

Oreohelix strigosa goniogyra Pilsbry (Oreohelicidae). This subspecies may be limited to a few remnant colonies in the Race Creek drainage in Idaho. This snail is found mostly on outcrops forested with ponderosa pine. Commonly, sites have a partly to completely closed canopy and diverse forb and deciduous understory. Threats include grazing, logging, road location and modifications, and forest fires. Based on recent surveys, Frest and Johannes (1995, 1997a) recommend this taxon be listed as endangered on the federal list of endangered species and by the state of Idaho; they recommend it be considered a sensitive species by the FS and other land and wildlife agencies.

Oreohelix vortex Berry (Oreohelicidae). This species remains in a few isolated colonies in the most undisturbed parts of the northern portion of the lower Salmon River valley in Idaho. It is restricted mostly to large-scale basalt taluses. Sites are typically dry and open, the most common vegetation is grasses. The species prefers low to medium elevations in large stream valleys. Threats include heavy grazing occurring in much of its range; talus mining in the lower Salmon River valley, which recently destroyed some old sites; and highway construction and maintenance. Recent surveys of the area lead Frest and Johannes (1995, 1997a) to recommend listing as endangered on the federal list of endangered species and by the state of Idaho and sensitive status by the FS and other federal and state land and wildlife agencies.

Oreohelix waltoni Solem (Oreohelicidae). This species survives in perhaps four sites near Lucile and John Day Creek, Idaho. It is found in dry, open areas in sage scrub vegetation. All known sites are impacted by grazing. Road construction and maintenance have considerably reduced the site along US Highway 95. Talus mining, especially for basalt gravel, has affected taluses in the immediate vicinity of all sites. Gold mining and prospecting impacts sites in schist lithologies. Recent surveys lead Frest and Johannes (1995, 1997a) to strongly recommend listing as endangered on the federal list of endangered species and by the state of Idaho and sensitive species designation by the BLM, FS, and other land management agencies.

Insecta, Coleoptera—

Agonum belleri Hatch (Carabidae). This species has been recorded in southwestern British Columbia, northernmost Oregon (Mount Hood) just east of the Cascade crest, and western Washington from the eastern Puget Sound to the Cascade Range. The Oregon sites are just at the western margin of the basin assessment area. *Agonum belleri* is restricted to sphagnum bogs (*Sphagnum magellanicum* Brid. and

S. squarrosum Crome) from sea level to 1050 meters. Preferred habitat appears to be the margins of bogs with open water and floating mats of sphagnum. Bogs without open water but with mats of sphagnum resting on a solid substrate are less favored, as is sphagnum in forest-open area ecotones. Circumstantial evidence suggests that *A. belleri* may be able to survive in sphagnum seeps, but this is presumably marginal habitat. Adult *A. belleri* are short-winged and incapable of flight, so all dispersal is by adult and larval walking. Although potentially suitable habitat is widely scattered along both sides of the Cascade crest (as well as a few remaining lowland bogs), accessible habitat must presumably be essentially contiguous to existing *A. belleri* populations. Historically, the overall population has declined because of habitat degradation and destruction, particularly in the Puget Sound area. Potential threats are drainage and filling of sphagnum bogs, trampling, sphagnum bog succession, and forestry use of insecticides. LaBonte (1995) suggests that continuing habitat destruction and degradation, strong stenotopy, presumably limited dispersal capabilities, and patchy habitat distribution all point to a species at risk of extinction and that is clearly threatened or endangered.

Cicindela arenicola Rumpp (Cicindelidae). This species is presumably restricted to sand dunes or sandy areas with sparse vegetation (no more than about 30 percent cover) and ranging in elevation from about 750 to 1700 meters in southern Idaho. The larvae are found in mildly sloping or flat, stable dune or sandy areas, whereas the adults are more broadly distributed throughout dune-sandy areas. The range of effective adult dispersal (via flight) may be no more than roughly 1 kilometer; larval dispersal (via walking) is probably limited to a few tens of meters. Potentially suitable habitat is widely scattered throughout much of southern Idaho. Habitat degradation through various agents is the greatest threat to *C. arenicola*. Disruption of the dune and sand substrates by human and livestock trampling and by off-road vehicles may directly destroy young larvae and collapse tunnels of older larvae. Intentional stabilization of dunes by grass seeding would completely eliminate habitat, and there is evidence that introduced weeds are encroaching on and degrading habitat at one site. The more stable and flat larval habitat is particularly susceptible to the latter influence. Rangeland pesticide applications are obvious potential threats to this species. LaBonte (1995) suggests its narrow habitat restrictions, patchiness of suitable habitat, and apparent sensitivity to habitat disruption renders *C. arenicola* as a candidate for threatened and endangered status, although suggesting more information about its habitat restrictions and overall distribution should be obtained before making this decision.

Glacicavicola bathyscioides Westcott (Leiodidae). This species is known only from southern Idaho and westernmost Wyoming. *Glacicavicola bathyscioides* has only been found in lava tube caves near permanent ice, apparently feeding on bacterial slimes, and dead and possibly live arthropods. The caves from which it is known range in elevation from 1525 to 2891 meters. This species apparently requires the constantly cool and moist conditions provided in the caves. Its eyeless condition and pale coloration suggest it is confined to, and has evolved in, cave or subterranean habitats. Dispersal capabilities of this species are unknown. Potential suitable habitat can be found throughout much of the basin assessment area. Much of this habitat, however, is effectively inaccessible given the probably limited dispersal capabilities of the species. The remote nature of the sites from which this species is known provides considerable buffering from human habitat alteration. Direct destruction or breaching of the caves is probably the greatest human-induced hazard, but this seems unlikely given the known localities. Perhaps the greatest overall threat is of regional climate change. LaBonte (1995) suggests that the remote and relatively inaccessible habitat, in combination with the greatest foreseeable threats originating from relatively unmanageable sources, render providing this species with threatened and endangered protection questionable and recommends placing *G. bathyscioides* on a “watch” list and monitoring its status in known sites.

Insecta, Lepidoptera—

Limenitis archippus lahontani Herlan (Nymphalidae). Although a federally listed candidate species, this is not a rare or endemic subspecies (Hammond 1994). It lives in riparian habitats along rivers and streams in desert lowland areas, where the larvae feed on willows (*Salix* spp.) It is widely distributed in southern Idaho, eastern Oregon, and eastern Washington.

Polites mardon Edwards (Hesperiidae). This species lives in wet meadow habitats, and the larvae feed on grasses. It appears to be an ancient, relict species of the late Tertiary period that only survives today in four widely disjunct population centers in the Pacific Northwest. It is a rare species because of natural, prehistoric decline during the Pleistocene, rather than because of human disturbance (except in western Washington). One population center is located on the Tenino prairies near Olympia, Washington. These populations are potentially threatened by human development and ecological succession to exotic Scotch broom (*Cytisus scoparius* (L.) Link). The other three population centers are high mountain meadows along the east slope of the Cascade Range near Mount Adams, high mountain meadows along the summit of the Cascade Range in Jackson and Klamath Counties in Oregon, and mountain meadows of coastal Del Norte County, California. These three populations seem to be abundant and stable at present but could be threatened by land management practices on federal lands. Hammond (1994) suggests that *P. mardon* is one of two butterfly taxa in the basin assessment area qualifying as candidates for federal listing as endangered species.

Insecta, Orthoptera—

Acrolophitus pulchellus (Bruner) (Acrididae). Only two specimens are known of this species, both collected at Birch Creek, Idaho, in 1883, associated with the plant *Grayia polygaloides* (probably *G. spinosa* (Hook.) Moq.; the only *Grayia* found in the PLANTS database) (USDA NRCS 1997). Both *A. pulchellus* and its closely related species *A. nevadensis* (Thomas) (which is a localized and rare species) are unusual because they occur significantly north and west from other related species in this genus. Surveys in Nevada and Idaho have not collected this species, thus it is likely *A. pulchellus* is rare or extinct (Otte 1996).

Bureau of Land Management sensitive species—In the basin assessment area, BLM regional offices list six sensitive invertebrate species (table 3). The FS has not listed any terrestrial invertebrates in their regional sensitive species lists.

Gastropoda—

Megomphix lutarius Baker (Megomphicidae). This species was probably originally rather well distributed in the Blue Mountains, Oregon. Its current distribution is uncertain, as recent surveys at the type locality and adjacent areas on the Umatilla National Forest have not recovered this species. Its habitat is north-facing small basalt cliffs in Douglas-fir forest with bryophytes, ferns, and bushes. Past and continuing intense logging and grazing throughout most of the Blue Mountains threaten this species. Frest and Johannes (1995) recommend federal and state listing as endangered; and sensitive species listing by the FS and BLM, because of endemism and extensive habitat modification of its known range.

Oreohelix strigosa delicata Pilsbry (Oreohelicidae). The original distribution of this subspecies is only known with certainty from the type locality. Its current distribution is uncertain; areas on the Umatilla and possibly Wallowa-Whitman National Forests should be surveyed. The type locality is in a moderately steep basalt creek canyon in fairly open ponderosa pine and Douglas-fir forest with some deciduous understory and common grasses. Grazing, logging, and road construction threaten the type locality. Much of the Blue Mountains has been affected by logging, insect infestations, and fires, all of which threaten this subspecies throughout its range. Frest and Johannes (1995) recommend this subspecies be considered for listing on the federal and states of Oregon and Washington lists as endangered, and as sensitive by FS and other federal and state land and wildlife agencies.

Insecta, Coleoptera—

Nebria gebleri fragariae Kavanaugh (Carabidae). This subspecies is only known from northeastern Oregon near the Strawberry Mountains. It has been collected from the banks of montane perennial streams at elevations ranging from 1500 to 2300 meters. The streambanks generally consist of unconsolidated cobble-gravel, sand, or mud and are probably at least ephemerally seasonally flooded. These banks range from level to steep and often have only sparse vegetation cover. Adults are fully winged, but flight has not been observed; potential flight range is unknown. If adults are not capable of flight, active dispersal would be limited to walking by adults and larvae, with the possibility of passive dispersal via downstream drift. Although seemingly suitable habitat is prevalent throughout the region, contiguous or nearby suitable habitat may be necessary for successful dispersal. Nontarget effects from insecticides is a potential threat to this subspecies. The tolerance of this subspecies to habitat perturbation and degradation by logging, stream pollution, and livestock trampling is unknown. Much of the habitat is contained within the Strawberry Mountain Wilderness, which may provide adequate buffering from management actions. LaBonte (1995) suggests that although limited in its distribution, this subspecies does not seem to be in danger of any imminent threats, especially with so much of its known range contained within a wilderness area.

Nebria vandykei wyeast Kavanaugh (Carabidae). This subspecies is known only from the Oregon Cascade Range from Mount Hood south toward the Three Sisters. It is restricted to alpine habitats, perhaps extending down into the highest subalpine areas (1350 to 3400 meters). Primary habitat consists of alpine ice and snow fields. Alpine and upper subalpine rocky stream banks function as seasonal thermal refugia during summer and early autumn. This subspecies is a predator-gleaner, foraging at night on the ice, snow, soil, and rock surfaces for dead, old-immobilized, or active invertebrates. *Nebria vandykei wyeast* is entirely flightless. Direct contact from pesticide drift or ingestion of pesticide-contaminated arthropods are possible risks to this subspecies. Based on existing knowledge, LaBonte (1995) recommends at most this species be placed on a “watch” list.

Insecta, Lepidoptera—

Charidryas acastus dorothyea Bauer (Nymphalidae). According to Hammond (1994), this may not be a valid taxonomic entity. Because this subspecies is only found at low elevations along the Snake River, a hybrid suture zone, it may be a hybrid between *C. acastus acastus* and *C. acastus sterope*.

Identified species of special concern—Experts have identified additional unlisted species as rare or endemic in the basin assessment area (see appendix 4). Although we do not necessarily advocate listing all these taxa on agency sensitive species lists, nonetheless rare or endemic invertebrates do exist in the basin assessment area and some may bear further watching. No one set of criteria was used by all specialists to determine which species should be considered rare or endemic. Contract reports should be consulted to determine the criteria used for each taxonomic group.

Frest and Johannes (1995) identified 95 terrestrial mollusks (87 land snails and 8 slugs) as species warranting additional conservation attention. Mollusk diversity is concentrated in specific, relatively small portions of the basin assessment area. In particular, some species are confined to calcareous substrates, which make up a small part of the total basin assessment area. Even in the outcrop areas, many species, particularly those of special concern, are limited to a small portion of the total outcrop area. Certain drainages and narrowly circumscribed geographic areas are particularly significant to mollusk biodiversity (Frest and Johannes 1995). Preeminent are portions of the Columbia Gorge, Hells Canyon, the lower Salmon River, the Clearwater, the Clark Fork, and the Bitterroot drainages. In some instances, other sites are also significant, such as a few localities with schist or limestone substrate in western and southeastern Idaho and in western Montana. Similarly, springs in the Upper Klamath Lake drainage, the Columbia Gorge, southeastern Idaho, and specific portions of the Oregon interior basins, western Wyoming, and the northern quarter of the basin assessment area are significant to various mollusks.

The basin assessment area is inhabited by at least three native earthworm species, belonging to three genera (James 1995). *Driloleirus americanus* Smith was considered for inclusion in the International Union for the Conservation of Nature (IUCN) Invertebrate Red Data Book (Wells and others 1983) because its habitat was threatened and its range was not known to be large. The currently available information suggests it may be a narrow endemic utilizing a threatened habitat (grassland sites with good soil). The collection data give little detailed habitat information. The three sites (near Pullman and Ellensburg, Washington, and Moscow, Idaho, [Fender and McKey-Fender 1990]) are located in what is now agricultural land, grassland, and shrubland. The other two native species, *Drilochaera chenowithensis* McKey-Fender and *Argilophilus hammondi* McKey-Fender, may be somewhat tolerant of habitat conversion to agriculture. Learning more about their ranges and ecological flexibility would enable land managers to determine if special habitat protection measures are necessary.

Hammond (1994) cites *Parnassius clodius shepardi* Eisner (Papilionidae) as the only butterfly species in the basin assessment area that is a potential new candidate for federal listing under the Endangered Species Act. This species has a restricted habitat threatened by land management practices along the Snake River. Four other butterfly species, *Pyrgus scriptura* Boisduval (Hesperiidae), *Ochlodes yuma* Edwards (Hesperiidae), *Colias gigantean* Strecker (Pieridae), and *Mitoura johnsoni* Skinner (Lycaenidae) are rare within the basin assess-ment area but are common in other parts of North America.

Based on existing information, LaBonte (1995) determined two terrestrial predaceous beetle species, *Scaphinotus mannii* Wickham (Carabidae) and *Cicindela columbica* Hatch (Cicindelidae), are potentially threatened or endangered. *Scaphinotus mannii* has stringent habitat requirements and is confined to riparian strips in the canyons of lowland tributaries of the Snake River. Probable threats include flooding of habitat from damming, human encroachment, pesticides, and cattle grazing and trampling. *Cicindela columbica* is restricted to sandbars and sand dunes in riparian zones of large lowland rivers. This is a highly sensitive species that may be threatened by damming, trampling of habitat accessible to humans and livestock, and intensive collecting by tiger beetle enthusiasts. LaBonte (1995) suggests that three additional beetles, *Ctenicera barri* Lane (Elateridae), *Nebria vandykei wyeast*, and *N. gebleri fragariae* are species that may warrant watching. Little is known of *C. barri*, *N.v. wyeast*, and *N.g. fragariae*, which have apparently stable populations largely contained within national forests and wilderness areas.

Lattin (1995b) identified five species of Hemiptera: Heteroptera of special concern within the basin assessment area. *Micracanthia fennica* (Reuter) and *Hebrus buenoi* Drake and Harris are associated with hot springs, and *Ambrysus mormon* Montandon is found chiefly in runoff from thermal waters. *Chorosoma* sp. nov. (Rhopalidae) is found on sand, adjacent to interior sand dunes. *Boreostolus americanus* Wygodzinsky and Stys occurs along the riparian zone of streams and rivers; it is a relict species of great evolutionary and biogeographical interest.

Tepedino and Griswold (1995) cite 24 species of bees endemic to the basin assessment area. Eleven of these taxa are extremely rare (some may be extinct), having been recorded at only a single site. Some have been recorded only once, many years ago. Others seem to be specialists of uncommon or heavily utilized habitats such as sand dunes or lava beds. Although most (14 species) are, or are likely to be, somewhat specialized foragers, none is likely to be so important to its plant as to threaten that plant's existence if the bee is absent. Another 168 bee species are listed that may be rare in the basin assessment area.

Crawford (McIver and others 1994) lists 147 species of arachnids believed to be largely or entirely restricted to rare or uncommon habitats, and as such, could be adversely affected by land management practices. None of these species are currently listed, and too little is known of their status to make listing practical at this time. These species are only examples, intended as an advisory that such species and their habitats exist and need further study.

Unique Habitats for Invertebrates

Given the importance of habitat for conservation of invertebrates, habitats key to the conservation of the unique invertebrate fauna of the basin assessment area are listed below (See also special habitats sections in Frest and Johannes 1995, Lattin 1995b, McIver and others 1995, Tepedino and Griswold 1995, for more specific examples). These habitats represent a partial list biased toward those taxa that have been studied enough to merit concern about their habitats. It is suggested all floral or faunal surveys include concurrent survey for invertebrates. The more taxa covered in a survey, the more likely important associations of habitat and ecological function will be illuminated. Further work will need to address all invertebrate functional groups and species of special concern.

Arid habitats—The invertebrates of arid habitats such as deserts and sand dunes need further attention throughout the basin assessment area. These habitats are known to contain many rare and endemic species of beetles, bees, and bugs, and other taxa as well. Increasing demands for recreational use by all-terrain vehicles are a threat to species restricted to dune habitats as are invasive exotic grasses and weeds.

Riparian areas—Meadows and riparian areas are known to be rich in spiders, beetles, and other arthropod predators as well as nonpredaceous beetles, bees, butterflies, and mollusks. Some general occurrence information exists, but information on a regional basis, studying invertebrates in different plant associations, is needed. The effects of livestock trampling and other soil- and litter-disturbing activities should be included in any studies.

Calcareous substrates—Calcareous substrates provide habitat for some species of mollusks. In particular, certain species are confined to such units as the Paleozoic Madison, Lodgepole, Mission Canyon, Amsden, and Phosphoria: or the Triassic Martin Bridge.

Peatlands—Bogs and fens are known to have species of spiders and insects not recorded as occurring in other habitats. One could assume the prey species and host plants of prey species also may be unique. Calcareous fens are rich in mollusks worldwide.

Geothermal areas—Geothermal areas are known for unusual assemblages of plants, invertebrate herbivores, and arthropod predators. The heated substrate provides snow-free conditions and a longer growing season. Regionally unique bug and beetle predators, relict outliers of otherwise southerly species, are found in some of these areas.

Isolated gorges and narrow canyons—Shade, moisture, and cold air drainage all contribute to conditions reminiscent of cooler periglacial climates. Unique spiders and other invertebrates (Coleoptera, Plecoptera, etc.) found in these areas suggest the possibility of a unique prey base and host plants as well. The unusual algific talus slopes and maderate cliffs of the upper Midwest harbor a unique biota of some dozen disjunct or otherwise extinct snails and over 50 disjunct plants (Frest 1984, 1991). Such sites exist in the basin assessment area as well.

Alkaline lake shores—This habitat is comparatively independent of the surrounding vegetation. The key factors for specialized invertebrates are proximity of water whose alkalinity is relatively high, availability of stones, sand, and other natural cover (for example, Saldidae: *Ioscytus politus*).

Caves—The key factors for specialized invertebrates are total darkness, constant high humidity, relatively stable temperature, few predators, food-poor environment, and import ecosystems with food webs based on organic matter from outside. Caves are also essential to the Townsend's big-eared bats (*Plecotus townsendii* Cooper) and the Van Dyke (*Plethedon vandykeii*

Van Denburgh) and Larch Mountain (*Plethodon larselli* Burns) salamanders. Caves in the Eastern United States and Texas are known to harbor an extensive endemic land snail and water snail fauna (Hershler and Holsinger 1990); little of the assessment area has been searched for such troglodytes or phreatic endemics.

Sand dunes—Sandy environments typically have high degrees of pollinator (bee) and grasshopper endemism. Also, these unique faunas face significant threats from recreational vehicle use. Off-road vehicle activity not only reduces floral resources necessary for reproduction but destroys nests and potential nest sites. Assemblages of pollinator species differ markedly among dunes.

Managing to Retain Invertebrates and Their Ecological Functions

To retain the viability of invertebrate species over landscapes, attention must be given to the effects of management practices. Three tenets summarize desirable effects of management practices: (1) various forms of compositional and structural diversity will help maintain biodiversity and ecosystem functions; (2) maintenance of litter layer and soil structure and chemistry will sustain diversity and functions of the soil food web; and (3) preventing the introduction of or eradicating exotic organisms will help maintain biodiversity and ecosystem functions. Although not the only factors affecting invertebrate diversity and function, these three are of major importance to a broad range of taxa occurring in forested ecosystems.

Compositional and Structural Diversity

Structural diversity in this discussion includes the forest canopy, understory, coarse woody material, forest floor litter, and water features. Homologous to this in the range environment are the tree or large shrub layer, forbs and flowering plant layer, and the litter layer. The structure of the canopy layer resulting from harvest, stand-improvement activities, or wildfire affects several functional groups. The remaining stand may be more or less hospitable to various herbivores, thereby resulting in different amounts of nutrients falling to the litter or different amounts of tree mortality. The changes may result in varying quality and quantity of prey available to predators, both invertebrate and vertebrate. Changes in canopy density or composition can affect habitat for predators, which may mitigate population irruptions of pest species. Also, these canopy changes result in microclimatic differences in the understory and coarse woody material-litter environment, which may be detrimental for some species. For example, if the light and moisture regime is changed sufficiently, the understory flowering plants may change, thereby resulting in effects on pollinators, herbivores, and predators. These physical changes may be inimical to species such as land snails whose lack of mobility may prevent them from seeking conditions in a patch of better habitat. Coarse woody material may dry out more quickly under open canopies affecting the internal environment within standing and down dead trees. Water features, such as rivers, streams, lakes, ponds, wetlands, and impoundments, provide critical habitat for the great diversity of terrestrial arthropods restricted to their margins.

In the understory, management practices that disturb or disrupt the flowering plants and other ground vegetation, or compact or mix the soil may profoundly effect several functional groups of organisms. Besides the direct impacts on organisms with limited dispersal capabilities or in a non-motile stage, habitats of many functional groups will be disrupted. Plant and animal communities will change, sometimes with consequences detrimental to certain species.

On the forest floor, the major structural elements are coarse woody material, primarily down tree boles and large branches, and litter. This material serves as habitat for vertebrate and invertebrate predators and their prey, and as a carbon source for the soil food web. Various species of arthropods, nematodes, fungi, annelids, and bacteria are responsible for the comminution and conversion of the wood to elements available to the soil. Sufficient coarse woody material is necessary, through time, to maintain soil productivity. Soil productivity also relies on leaf litter, corpses, feces, and other sources of detritus.

Soil Structure and Chemistry

Maintenance of soil chemistry and structure will sustain soil health and fertility. This is vital to retain forest and range productivity and biodiversity. Chemical change owing to fire and structural change owing to compaction or mixing of soil layers are the two consequences of management practices that are of concern. Fire, whether natural or planned, can consume the litter and coarse woody material that is important structurally and is the primary source of carbon and other elements necessary for the soil food web. Erosion resulting from loss of coarse woody debris or the materials binding the system further depletes the productive capacity of the soil. Secondly, fire can volatilize nutrients found in the upper horizon of the soil as well as change its water-retention characteristics. Structural changes caused by either compaction or soil mixing can have long-lasting effects, changing successional patterns and timing. These effects are expected with management requiring multiple entries into a forested area.

Exotic Organisms

The introduction or maintenance of exotic organisms can adversely affect range and forest succession and also reduce invertebrate biodiversity. Sailer (1983) and Kim and McPheron (1993) reported that nearly 2,000 species of exotic insects and mites have become established in North America. Mattson and others (1994) listed all of the immigrant phytophagous insect species known established in North America on native and introduced woody plants (trees and shrubs). More than 368 species of exotic phytophagous insects have become established in North American (north of Mexico) forests, parks, woodlots, shelterbelts, and orchards. Of the known earthworms in the area, most are exotics (Fender 1985, Gates 1967). Currently, there are at least 145 nonindigenous mollusk species (32 bivalves, 113 gastropods) in North America north of Mexico (Turgeon and others 1998). Lattin and others (1995) reported on effect of exotic crested wheatgrass on native insects in the vast east-side region.

Without their native enemies to restrain population growth, exotic organisms can prey on native species or occupy niches of native species, particularly if they are more competitive. They may necessitate pest eradication or suppression activities with concomitant risks and expenses.

Invertebrate Research and Monitoring Priorities

Invertebrate and microbial research and monitoring activities have centered almost exclusively on the management of a handful of insect and fungal pest species. These types of studies are still necessary as our forests and grasslands are managed for various consumptive, aesthetic, wildlife, and other values. The practice of ecosystem management and increased awareness of the many essential roles of invertebrates, however, necessitates broadening the scope of invertebrate investigations.

Development of sound management practices for invertebrates begins with knowledge of the species or taxonomic groups found in an area, their specific habitat requirements, geographic distributions and ranges, and their ecological function. This information is most valuable when it is integrated with information from other taxa. The species, taxa, or functional groups chosen for research could be selected on the basis of presumed ecological importance or sensitivity to particular management activities.

Research Emphasis

Active management to achieve and maintain certain desired condition or commodity output objectives, necessitates the study of organisms that affect or are affected by these objectives. As values and circumstances change, the species of importance will change as well. For instance, the conversion of extensive mixed-conifer stands to seral ponderosa pine and western larch will cause a change in the complex of species that are important disturbance agents. Impacts caused by defoliators like the western spruce budworm and Douglas-fir tussock moth could decline, whereas pine regeneration pests such as the western pine-shoot borer (*Eucosma sonomana*) and the ponderosa pine tip moth (*Rhyacionia zozana*) likely would become of more concern to managers. Likewise, the complex of bark beetle species would shift according to host tree availability. Changes in tree characteristics, such as bark thickness, have effects on subcortical faunal composition. Land managers need tools such as stand hazard rating schemes; predictive monitoring, analysis, and feedback; and nonpesticide control methods (for example, semiochemical and biological control agents) that are the result of applied research. But the basic research for such products cannot be overlooked; without studies on basic biology and taxonomy, dispersal behavior, natural enemies, and other ecological topics, applied research would be reduced to progress achieved by trial and error.

Besides their role as herbivores impacting timber and forage resources, invertebrates perform many vital functions, most of which have not been quantified or even examined to any extent in the basin assessment area. Much of our information is from related species in other areas that often have different conditions, and as such, extrapolation is extremely limited. Because insects and other invertebrates constitute most of the faunal biomass, their function as a food source to many species of birds, reptiles, amphibians, and small mammals demands research attention. Invertebrates are found at all trophic levels (except that of primary producer), and by virtue of their extraordinary abundance, play a dominant role in most ecosystem processes. We also need to know more about how invertebrates respond to various changes in ecosystems such as nutrient cycling, soil microbial biomass, etc. Thus, an understanding of nonpest invertebrate biology and ecology in the basin assessment area is essential to understanding management effects and strategies.

Soil and litter organisms—Most basic information such as species or taxonomic groups found in an area, their specific habitat requirements, geographic distributions and ranges, and their ecological function is needed. Additionally, knowledge of the effects of management practices on the coarse woody material, litter, and soils in relation to ecological function, or individual species viability is needed to extend knowledge from the west side to the vast Columbia River basin.

Arthropod predators—Basic information on species or taxonomic groups found in an area, their specific habitat requirements, and geographic distributions and ranges are needed. Additionally, information on the effects of management practices on predation and predator-prey relations are needed.

Arthropod pollinators—Basic information on species or taxonomic groups found in an area, their specific habitat requirements, breeding biology of host plants, and their geographic distributions and ranges are needed. Sandy environments could be given priority because of species endemism and because of threat from off-road vehicles. Assemblages of pollinator species differ markedly among dunes. This information will indicate which dunes have particularly high degrees of bee diversity and endemism. The next step would be to assess bee composition and abundance under different management practices.

Grassland herbivores—Studies examining the effect of range management practices on plant successional changes will help us to more fully understand the impacts of these activities on the associated herbivores. Grazing systems can provide many permutations of rotation timing, intensity, spatial and temporal extent, and length of deferment, which can differ from site to site. The implications of prescribed burning on plant and subsequent herbivore diversity are unknown. Factors such as fire interval, intensity, duration, season, patchiness, and spatial extent need to be examined to determine their effect on plant community composition, as well as on invertebrate herbivore diversity and abundance.

Proposed introductions of exotic organisms to control native pests require research to determine the impact of the exotic on displacing other native species that perform the same function as well as other nontarget hosts or prey.

Extensive work has been done on the relation of insects and other invertebrates above and below-ground in such places as Konza, Kansas; Pawnee National Grassland, Colorado; and Tornada and Seveta, New Mexico. All are long-term ecological research sites.

Forest herbivores—The management of pest species continues to warrant research effort; there is a need to monitor and manage species that threaten our ability to reach forest resource objectives. Protecting individual or groups of trees from bark beetle attack in campgrounds, historic sites, old-growth stands, and riparian buffers is an example of the need to protect against damage by specific pest species. The development of hazard rating systems are a priority for many species, including regeneration pests and bark beetles.

Adequate silvicultural guidelines for the management of invertebrates in second-growth ponderosa pine in the basin assessment area do not exist.

Lastly, studies on gaining a better understanding of the various ecosystem functions that forest herbivores perform are necessary. For instance, although it is known that herbivores are the prey base for many arthropod and vertebrate predators, little is known about the dietary preferences of bats, birds, amphibians, and other predators on invertebrate herbivores. Likewise, the contribution of invertebrate herbivores in creating wildlife habitat is relatively unexplored. One opportunity beginning to be examined is the manipulation of bark beetles by using semiochemicals to produce snags for wildlife (Ross and Niwa 1997). This type of research both expands our basic knowledge of invertebrate functions in forest ecosystems and lays the groundwork for further development of practical management tools.

Monitoring Emphasis

Invertebrates can be used as sensitive measures of forest and grassland health, by using various taxa. The taxa to be used should be relatively easy to monitor or should represent a range of functional groups (for example, millipedes, centipedes, collembola, orabitid mites, etc.). It is also desirable to select taxa that are well understood taxonomically and that have a good foundation of ecological research. For instance, butterflies are a group that can be monitored visually by nonentomologists with relatively brief training (Hammond 1995a). Some species of harvester ants are excellent for monitoring as they have ties throughout many parts of the food web. The soil food web has been suggested as a prime indicator of ecosystem health. Measurement of disrupted soil processes, decreased bacterial or fungal activity, change in the ratio of fungal to bacterial biomass, decreases in the number of or diversity of protozoa, change in nematode numbers, and nematode community structure or maturity index, can serve to indicate problems long before the natural vegetation is obviously affected.

Indicator taxa may be useful for monitoring changes because of management activities in two fundamentally different ways: (1) Their abundance or biomass may be an index or surrogate for a critical ecosystem function. As such, they are significant at an inclusive resolution (whole group census), seldom on an individual taxon basis. For instance, the ratio of total bacterivorous nematodes to fungivorous nematodes may reveal critical dynamics of how the decomposer microbial food web functions or is changed by management. (2) The richness and diversity of invertebrates or selected functional groups may serve as an index of total ecosystem diversity, which differs under various management activities. The abundance and distribution patterns of an uncommon species may indicate subtle changes in limited microenvironments of interest. For these studies, taxa are significant at a species level of resolution, and to be useful on a general basis must be readily sampled and amenable to this degree of taxonomic precision. For instance, total ant species richness may be a useful index of community diversity, whereas the presence of a specific ant species such as *Amblypone oregonense* (Wheeler) may indicate undisturbed old-growth forest-floor conditions. Thus candidates for indicator status can include the most abundant, widespread and species-rich assemblages, or the most habitat-constrained (and thus uncommon) individual species or assemblages, depending on the monitoring objectives.

A consideration in using invertebrates as bioindicators is practicality. Candidate taxa for monitoring should, in general, be relatively well-known (in terms of the taxonomy and functional role they play in a community) and functionally important; species-rich (enough species to avoid statistical errors inherent in small numbers, but not so rich as to overwhelm sampling protocols); amenable to capture or observation with standardized low-technology techniques; common and widespread (see above for exceptions); and relatively easy to identify (to an appropriate level of resolution—not necessarily to species).

Conclusions

The abundance and diversity of invertebrates present challenges to developing land management strategies. There are some general approaches, however, to managing the biodiversity of these species groups that may be effective: (1) focus on key functional groups, (2) preserve key habitats, (3) take care in management activities, (4) broaden the scope of investigations, and (5) practice adaptive management. Using these components of management likely will benefit biodiversity of invertebrates and retention of their manifold ecosystem functions.

Focus on Key Functional Groups

Because of the enormous biodiversity represented by invertebrates, with about 24,000 macroinvertebrate species in the basin assessment area, this report focused on broad functional groups of organisms. Two functional groups have species particularly susceptible to environmental perturbations: detritivores and nutrient cyclers, and predators.

Within the detritivory and nutrient cycling functional group, there are some organisms associated with litter, coarse woody debris, and soil whose populations could be in danger of extirpation. Retention of these components in sufficient amount may preserve the functions these groups perform in the ecosystem. Determining the amount sufficient is problematical. Research must determine the effects of current and past management practices on not only the abundance and diversity of these organisms but also on rates of decomposition and mineralization.

Among detritivorous species, essentially all terrestrial mollusk species were identified as species of special concern. Portions of the Columbia Gorge, Hells Canyon, lower Salmon River, Clearwater, Clark Fork, and Bitterroot drainages are areas particularly significant to mollusk biodiversity. Springs in the Upper Klamath Lake drainage, the Columbia Gorge, southeastern Idaho, and specific portions of the Oregon interior basins, and western Wyoming are also significant habitats for various species (Frest and Johannes 1998; Hershler 1998, 1999). These species can be assisted by identifying and protecting these special areas. Three species of native earthworms inhabit the basin assessment area. Learning more about their ranges and ecological flexibility would enable land managers to determine if special habitat protection measures are necessary.

Within the predator functional group, 13 species (8 beetles and 5 bugs) were given only as examples of many for which additional information is needed to determine if habitat protection measures are necessary. There are other such species in these and other functional groups, but time, space, and knowledge are inadequate to fully document here their scarcity or sensitivity to disturbance. Developing a consistent set of criteria for determining species of concern also would be helpful.

Preserve Key Habitats

Habitat protection, rather than a species-by-species approach, may be appropriate for invertebrates. Eight unique habitats key to the conservation of invertebrate fauna of the basin assessment area are arid areas, riparian areas, calcareous substrates, peatlands, geothermal areas, isolated gorges and narrow canyons, alkaline lake shores, and caves.

Take Care in Management

The viability of invertebrate species over landscapes may be retained by giving attention to three major effects of management practices. Compositional and structural diversity will help maintain biodiversity and ecosystem functions. Forest canopy, understory, coarse woody material, and forest floor litter; rangeland trees or large shrubs, forbs, and litter; canopy density and composition; light and moisture regime; and soil disturbance and compaction all are important features. Maintenance of soil structure and chemistry will sustain diversity and functions of the soil food web.

Preventing the introduction of or eradicating exotic organisms will help maintain biodiversity and ecosystem functions provided by native species.

Broaden the Scope of Investigations

Almost exclusively, invertebrate research and monitoring have centered on the management of a handful of insect and fungal pest species. The increased awareness of the multitude of essential roles of invertebrates, however, warrants a broadening of the scope of invertebrate investigations to include soil and litter organisms, arthropod predators, arthropod pollinators, grassland herbivores, and forest herbivores.

Experts have identified 132 species as examples of rare or endemic taxa in the basin assessment area. Although we do not advocate listing these taxa on agency sensitive species lists, rare or endemic invertebrates of the basin assessment area are discussed, and some may bear further watching.

Invertebrates are unique and useful bioindicators of ecosystem change: various species can be used as sensitive measures of forest and grassland health. Surveys of invertebrates could be efficiently conducted at the same time as floral or faunal surveys.

Practice Adaptive Management

The practice of adaptive management will advance basic knowledge about invertebrates and the effects management activities have on their survival and function.

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Appendix 1

The following persons participated in the panel discussions. An asterisk (*) indicates those individuals who prepared contract reports.

Soil-nutrient cycling—Feb. 1-2, Portland

Elaine Ingham*	Oregon State University	Microbes
Sam James*	Maharishi Intl. Univ.	Annelids
Bill Fender	Private consultant	Annelids
Kermit Cromack	Oregon State University	Nutrient cycling
Andy Moldenke*	Oregon State University	Arthropods
Lloyd Elliott	USDA-ARS	Bacteria
Karen Bennett	Deschutes NF, R6	Soil

Herbivores-range—Feb. 7-8, Portland

Bill Kemp*	USDA-ARS	Grasshoppers
Jim McIver*	Blue Mountains Natural Resource Institute	Ants, predators
Tony Joern	University of Nebraska	Grasshoppers
Paul Hammond*	Private consultant	Butterflies
Larry Walker	USDI-BLM	Range management

Litter and coarse wood-detritivores—Feb. 9-10, Portland

Andy Moldenke*	Oregon State University	Litter arthropods
Tim Schowalter*	Oregon State University	Coarse wood chewers
John Moore	University of Northern Colorado	Coarse wood chewers
Terry Frest*	Deixis consultants	Mollusks
David Bridgwater	Forest Insects and Diseases, R6	Insects and diseases
Robert McNeil	Malheur NF, R6	Soil

Parasites and predators—Feb. 14-15, Portland

Ding Johnson*	University of Idaho	Lacewings, parasites
Torolf Torgersen	USDA-FS-PNW Research Station	Ants, parasites
Rod Crawford*	University of Washington	Spiders
Mike Ivie	Montana State University	Beetles
Nancy Campbell	Timber, Cooperative Forestry and Pest Management, R1	Insects and diseases

Herbivores-forest—Feb. 22-23, Corvallis

Paul Hammond*	Private consultant	Butterflies
Jeff Miller*	Oregon State University	Moths, parasites
John D. Lattin*	Oregon State University	Hemiptera
Mike Wagner*	Northern Arizona University	Canopy herbivores
Darrell Ross*	Oregon State University	Bark beetles
John Moser*	USDA-FS-SRS Station	Mites, bark beetles
Bruce Hostetler	Forest Insects and Diseases, R6	Insects and disease

Pollinators—March 1-2, Corvallis

Vince Tepideno*	USDA-ARS	Pollinators
Terry Griswold*	USDA-ARS	Pollinators
Jean Findley	USDI-BLM	Range plants
Bob Meinke	Oregon State University	Rare plants
Bill Stephen	Oregon State University	Bees
Mike Burgett	Oregon State University	Honey bees

Appendix 2

Potential forest wildland management practices
by Dr. Bill Emmingham [a]

I. Site preparation

- A. Prescribed burning
  - 1. Pile and burn
    - a. Mechanical
    - b. Hand
  - 2. Jackpot
  - 3. Broadcast
- B. Ripping
- C. Scarification
- D. Herbicides

II. Intermediate entries

- A. Fertilization
  - 1. N
  - 2. K
- B. Precommercial thinning
- C. Pruning
- D. Vegetation management
  - 1. Herbicide
  - 2. Mechanical
  - 3. Livestock grazing
- E. Commercial thinning

III. Regeneration methods

- A. Even aged
  - 1. Clearcut
  - 2. Seed tree
  - 3. Shelterwood
- B. Uneven aged
  - 1. Group

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[a] Bill Emmingham, professor, Forest Science Department, Oregon State University, Corvallis, OR 97331.

2. Individual tree

C. Ground vs. cable

IV. Other

A. Grazing

B. Harvesting of special forest products (for example, fungi and firewood)

C. Pest management

1. B.t.

2. Virus

3. Semiochemicals

D. Exotics

1. Flora

2. Fauna

E. Fire control

1. Borate

2. Backfire

3. Exclusion

F. Amelioration of pest, fire, flood, wind, and volcanic disturbance

1. Grass seeding

2. Salvage logging

V. Natural disturbances

A. Drought

B. Wildfire

1. Groundfire

2. Stand replacement

C. Insect outbreaks and disease activity

1. Bark beetles

2. Defoliators

3. Root rot

4. Mistletoe

Range
by Drs. Sherm Karl and Steve Leonard[b]

I. Grazing

A. Grazing systems

1. Seasonal
2. Deferred
3. Rest rotation

B. Juniper and sagebrush control

1. Mechanical
2. Herbicide
3. Fire
    a. Prescribed
    b. Wildfire

II. Other

A. Harvesting of special products (for example, fungi and firewood)

B. Pest management

C. Exotics

1. Flora
    a. Herbicidal control
    b. Manual (grubbing)
    c. Biological control (insects, rusts, etc.)
    d. Grass seeding to prevent reinvasion after herbicide treatment.
2. Fauna

D. Fire control

1. Borate
2. Backfire
3. Exclusion

E. Amelioration of pest, fire, flood, wind, and volcanic disturbance

III. Natural disturbances

A. Drought

B. Wildfire

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[b] Sherm Karl, range ecologist, Interior Columbia Basin Ecosystem Management Project, 112 East Poplar, Walla Walla, WA 99362. Steve Leonard, range ecologist, National Riparian Service Team, PO Box 550, Prineville, OR 97754.

1. Groundfire
2. Stand replacement

C. Insect outbreaks and disease activity

Considerations

I. Temporal scale (How long would any effects last?)
   A. Immediate less than 5 years
   B. Short term (5 to 50 years)
   C. Long term (more than 50 years)

II. Spatial scale (Over how large an area would any effects occur?)
   A. Stand
   B. Landscape

III. Forest cover (What cover types would be affected?)
   A. LPP climax
   B. PP climax
   C. Dry mixed conifer—DF, GF, PP, WL
   D. Moist mixed conifer—DF, WF, WL, WWP, LPP
   E. High-elevation mixed conifer—ES, SAF, WBP, MH
   F. Riparian/wetlands

   PP = ponderosa pine, WL = western larch, DF = Douglas fir, GF = grand fir,
   WF = White fir, LPP = lodgepole pine, WWP = western white pine,
   ES = Engleman spruce, SAF = subalpine fir, WBP = whitebark pine,
   MH = mountain hemlock

IV. Range type (Which types would be affected?)
   A. Juniper woodlands
   B. Grasslands
      1. Mountain
      2. Palouse
   C. Shrublands
      1. Salt desert shrub
      2. Xeric sagebrush
      3. Mesic sagebrush
   D. Riparian-wetlands

V. Structural stage

    A. Early

    B. Stem exclusion

    C. Reinitiation

VI. Season

VII. Intensity

    A. Severity

    B. Number of entries

VIII. What is the source of knowledge?

    A. Experimental data from the basin assessment area

    B. Extrapolated from outside the basin assessment area

    C. No experimental data

Appendix 3

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a]

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
Class Arachnida: Spiders, scorpions, pseudoscorpions, harvestman (53 families)	1,156-2,735				
Order Araneida: Spiders (32 families)	983-2,279	Immatures are small replicas of adults—prey will have same features but will be smaller	As a group, spiders prey on almost every type of terrestrial arthropod	As adults	Commonly encountered terrestrial anthropod predator. Found in every major habitat, from litter to canopy, in all ecoregions
Agelenidae: (funnel-web spinners)	75-150		Medium to large-sized hopping-running arthropods		Logs, litter, soil surface, tree trunks, caves; forest-range
Amaurobiidae: (white-eyed spiders)	20-60		Medium to large-sized arthropods		Forest floor, on logs, trunks, under bark
Antrodaetidae: (folding-door tarantulas)	8-20		Medium-sized ground surface arthropods		Forest floor; burrows in range soil
Anyphaenidae: (sac spiders)	10-20		Varied insects		Trees, shrubs, under rocks; forest-range
Araneidae: (orb-weavers)	30-60		Flying insects		On shrubs, trees, rocks; forest-range
Clubionidae: (running spiders)	30-100		Running arthropods		On ground, vegetation; forest-range
Dictynidae: (hackled-band weavers)	50-100		Flying insects, hopping arthropods, esp. Diptera, Hymenoptera		Ubiquitous; ground level to shrubs, trees; forest-range; mainly on vegetation (often dead annual plants)
Gnaphosidae: (nocturnal hunting spiders)	75-150		Medium to large-sized arthropods		On ground, under bark, tree trunks; forest-range
Hahniidae: (Hahniid spiders)	12-25		Small insects		Varied, under objects on ground, logs, litter, webs on moist soil; forest; rare range species

Table 4—sList of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
Linyphiidae: (sheet-web weavers)	350-900		Small to medium-sized arthropods, flying insects		Ubiquitous; ground level to shrubs, trees, less common in dry places; forest-range
Lycosidae: (wolf spiders)	60-120		Medium to large-sized running and hopping arthropods		Ground level; forest-range
Oxyopidae: (lynx spiders)	2-5		Medium to large-sized running and hopping arthropods, flying insects		On shrubs, trees; forest-range
Pholcidae: (cellar spiders)	5-15		Flying and hopping insects		Webs under rocks; forest-range
Salticidae: (jumping spiders)	80-160		Mostly small running, hopping, flying insects		Ubiquitous; on ground, shrubs, trees; forest-range.
Tetragnathidae: (long-bodied orb-weavers)	20-50		Weak-flying insects, terrestrial and aquatic		On shrubs, trees, esp. in riparian areas, forest-range
Theridiidae: (comb-foot weavers)	60-110		Flying, hopping insects, ants, other spiders		Ubiquitous; grass and herbs, some shrubs, trees, forest-range
Thomisidae: (crab spiders)	75-150		Running-hopping and flying arthropods		Ubiquitous; ground level to shrubs, trees, on flowers; forest-range
15 additional families of Araneae	21-84				
Order Scorpionidae: Scorpions (1 family)	6-10	Immatures small replicas of adults, with similar feeding habits	Use substrate-born signals for prey detection; feed on running or hopping insects	Same as adults	Common on ground in habitats
Vaejovidae	6-10		Crickets, nocturnal insects, arachnids		On ground, in burrows, under rocks; dry rangelands; one species in dry to mesic forests
Order Phalangida (or Opiliones): Harvestmen (10 families)	83-186	Immatures have similar feeding habitats as adults, but prey is smaller	Widespread as group; small mouthparts—small prey	Same as adults	Common on ground; primarily in forested areas

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
Ischyropsalididae	22-40		Small decomposer invertebrates		Under objects, litter, caves, on ground
Phalangiidae: (daddy-longlegs)	10-25		Small-medium sized invertebrates		Vegetation, ground level, under rocks, logs; forest-range
Nemastomatidae	22-40		Small decomposer invertebrates		Litter in forest
Triaenonychidae	9-25		Small invertebrates		Logs, under wood on ground, litter; forest
Six additional families of Opiliones	20-56				
Order Solpugida: wind scorpions (1 family)hopping	10-25	Immatures small replicas of adults	Running-hopping arthropods	Same as adults	Ground level; rangelands
Eremobatidae	10-25		Ground-dwelling arthropods		Under objects, on ground; dry rangelands
Order Chernetida Pseudoscorpions (9 families)	74-235	Immatures small replicas of adults	Small insects	Same as adults	Litter, caves, moss, mammal nests, under rocks
Cheliferidae	15-50		Small flies, psocoptera, insect larvae		Under rocks, litter, tree bark
Chernetidae	15-40		Small flies, psocoptera, insect larvae		Mammal nests, tree and log bark
Chthoniidae	15-40		Collembola, mites		Litter, soil, rotten wood, moss, caves, tree bark, mammal nests
Neobisiidae:	15-40		Collembola		Litter, moss
5 other families of Pseudoscorpions	14-65		Small flies and mites		
Class Chilopoda centipedes (12 families)	149-343	Immatures small replicas of adults	Soil invertebrates	Generally same as adults	Soil, litter, under rocks, logs; forest-range
Order Lithobiomorpha: (3 families)	50-100				
Lithobiidae	50-100		Small- to medium-sized arthropods		Litter, logs, under rocks
Order Geophilomorpha (3 families)	70-145				
Chilenophilidae	30-60		Small soil invertebrates		Litter, soil
Geophilidae	15-30		Small soil invertebrates		Litter, soil
Himantariidae	15-30		Small soil invertebrates		Litter, soil

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
Schendylidae	10-25		Small soil invertebrates		Litter, soil
2 other orders and 7 other families of centipedes	29-98				
Class insecta (47 families)	2,239-3,558				
Order Thysanoptera: Thrips (2 families)	10-40	Immatures have similar feeding habits as adults, with prey size just smaller	Most are plant feeders, a few species prey on small arthropods	Same as adults	On herbs, shrubs, trees, typically near or within flowers
Aeolothripidae: (broad-winged thrips)	5-20		Other thrips, aphids, mites, other small insects		Flowers
Thripidae: (common thrips)	5-20		Other thrips, mites		Flowers, foliage of herbs, shrubs
Order Heteroptera: True bugs (6 families)	184-550	Immatures small replicas of adults, with prey size smaller	Plant feeders, predators, scavengers, parasites	Same as adults	Ubiquitous; aside from the beetles, is the most important group of insect predators
Anthocoridae: (minute pirate bugs)	10-20		Aphids, scales, other small arthropods		On ground, forbs, shrubs, trees
Lygaeidae: (seed bugs)	10		Aphids, thrips, larval Lepidoptera (most are phytophagous)		On ground, forb layer; forest-range
Miridae: (plant bugs)	100-200		Aphids, larval Lepidoptera, other small arthropods (many more are phytophagous)		On forbs, shrubs, trees; forest-range
Nabidae: (damsel bugs)	~20		Variety of small arthropods		On ground, forbs, shrubs; forest-range
Pentatomidae: (stink bugs)	~15		A few are predataors on other insects (most are phytocoris)		On forbs, shrubs, trees; forest-range
Reduviidae: (assassin bugs)	5-20		Wide variety of small arthropods		On ground, forbs, shrubs, trees
Order Neuroptera: (lacewings, owlflies) (3 families)	17-60	Mostly predaceous	Predaceous: relatively weak prey	Arboreal, arbuscular	Aerial: weak fliers
Chrysopidae: (green lacewings)	5-20	Aphids, scales	Aphids, scales	Arboreal, arbuscular	Aerial

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey		Habitat	
		Immatures	Adults	Immatures	Adults
Hemerobiidae: (brown lacewings)	5-20	Aphids, scales		Arboreal, arbuscular	Aerial
Myrmeliontidae: (antlions)	5-10	Ground-dwelling insects		Ground surface, dry places	Aerial
Order Raphidoptera (1 family) Raphidiidae: (snakeflies)	2-10	Aphids	Aphids	Arboreal, arbuscular	Arboreal, arbuscular
Order Coleoptera (28 families)	47	Invertebrates, all stages	Small soft-bodied insects, (e.g., aphids)	Epigean, litter	Flowers and foliage
Cantharidae (soldier beetles)					
Carabidae (Carabid beetles)	420	Invertebrates, all stages. Some mono- or oligophagous (e.g., mollusks), some omnivorous	Invertebrates, all stages. Many mono- or oligophagous (e.g., collembola, millipedes, mollusks), some omnivorous	Ubiquitous (see adults). Generally endo- and epigean, litter, subcortical	Ubiquitous, especially epigean. Prominent in alpine nival, burn, endogean, forest, lacustrine, riparian, and sand dune habitats
Cicindelidae (tiger beetles)	18	Epigean invertebrates, larvae and adults	Invertebrates, larvae and adults	Generally in open areas, some in forests. Endogean, with burrows opening onto soil surface	Epigean, generally in open areas, some in forests. Prominant in lacustrine, riparian and sand dune habitats
Cleridae (checkered beetles)	21	Xylophagous insects in wood, galls, cones, esp. subcortical beetles (e.g., Buprestidae, Cerambycidae, Scolytidae). Some prey on grasshopper eggs, bee and wasp larvae.	Xylophagous insects, esp. adult Scolytidae	Subcortical or within prey galleries and tunnels	Flowers, foliage, tree limbs and trunks, subcortical
Coccinellidae (ladybird beetles)	85	Same as adults	Homoptera (e.g., aphids and coccids) and phytophagous mites. Some prey on eggs, young instars or small larvae and pupae of Coleoptera, Diptera, Hymenoptera,	Same as adults	Ubiquitous when prey present. On foliage, flowers, tree limbs, and trunks

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
			Lepidoptera, Thysanoptera		
Colydiidae (cylindrical bark beetles)	7	Predators and parasites of xylophagous beetles, especially larvae (e.g., Buprestidae, Cerambycidae, Scolytidae)	Xylophagous beetles, esp. larvae (e.g., Buprestidae, Cerambycidae, Scolytidae)	Subcortical or within prey galleries and tunnels	Subcortical or within prey tunnels
Cucujidae (flat bark beeltes)	9	Subcortical insects, esp. larval and adult beetles (e.g., Cerambycidae and Scolytidae)	Subcortical insects, esp. larval and adult beetles (e.g., Cerambycidae and Scolytidae)	Subcortical	Subcortical
Elateridae (click beetles)	140	Endogean, subcortical, and xylophagous invertebrates. Facultatively herbivorous	Herbivorous or nonfeeding.	Endogean, subcortical, decaying wood	Foliage, flowers, tree limbs and trunks, some riparian under stones
Histeridae (hister beetles)	46	Invertebrates, all stages, esp. larvae of Coleoptera, Diperta, Lepidoptera. Several ant predators	Invertebrates, all stages, esp. larvae of Coleoptera, Diptera, Lepidoptera. Several ant predators	Carrion, feces, decomposing plant material lacustrine/ riparian and sandy areas, under bark, ant nests	Carrion, feces, decomposing plant material, lacustrine/ riparian and sandy areas, under bark, ant nests
Lampyridae (firefly beetles)	9	Earthworms, mollusks, insect larvae, millipedes	Many believed herbivorous or nonfeeding Some females "cannibalistic" on males of same and other species of Lampyridae. Some females larviform, feeding on millipedes and mollusks.	Epigean, litter, under rocks in riparian areas	Vegetation, esp. near riparian areas. Also subcortical
Leptinidae (mammal nest beetles): *Platypsyllus castoris* Ritsema	1	Ectoparasitic on beaver (epidermis and epidermal exudates).	Ectoparasitic on beaver (epidermis and epiderman exudates).	On beaver	On beaver
Lycidae (lycid beetles)	8	Soft or fluid material in	Small soft-bodied insects?	Litter, subcortical,	Vegetation

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey		Habitat	
		Immatures	Adults	Immatures	Adults
		decaying wood		decaying wood	
Meloidae (blister beetles)	41	Eggs of Orthoptera; eggs, larvae, and provisions of solitary bees	Herbivorous	Endogeous as Orthopteran egg predators. First instar larvae of solitary bee brood predators on flowers, in bee nests thereafter	Flowers, foliage, epigean
Melyridae (soft-winged flower beetles)	63	Small invertebrates, all stages. Many are also scavengers	Small invertebrates, all stages. Many herbivorous	Subcortical, xylophagous insect galleries, litter, vegetation, decaying wood, fungi. endo- and epigean, esp. sandy soils.	Flowers, foliage, litter
Ostomidae (bark-gnawing beetles)	14	Subcortical/ xylophagous invertebrates (esp. Coleoptera; e.g., Scolytidae), stored grain and cereal product pests. Some are fungivorous.	Subcortical/ xylophagous invertebrates (esp. Coleoptera, e.g., Scolytidae), stored grain and cereal product pests. Some are fungivorous.	Subcortical galleries of xylophagous insects, stored grains and cereal products	Subcortical; galleries of xylophagous insects; limbs, trunks, and foliage of conifers; stored grains and cereal products
Othniidae (false tiger beetles)	1	Subcortical invertebrates, all stages	Subcortical and xylophagous invertebrates, all stages	Subcortical	Subcortical; limbs, trunks, and foliage of conifers
Pselaphidae (short-winged mold beetles)	16	Mites, all stages; eggs, larvae, and pupae of ants; small invertebrates; (e.g., collembolans, fly larvae)	Mites, all stages; eggs, larvae, and pupae of ants; small invertebrates; (e.g., collembolans, fly larvae)	Endogean, epigean, litter, subcortical, ant nests, mammal nests	Endogean, epigean, litter, litter, subcortical, ant nests, mammal nests
Pyrochroiidae (fire beetles)	2	Facultative predators of subcortical invertebrates?	Herbivorous or nonfeeding?	Subcortical	Subcortical, foliage
Rhipiphoridae (rhipiphorid beetles)	6	Ecto- and endoparasites of wasps, solitary bees	Pollen feeders	Wasp and solitary bee nests	Flowers
Rhizophagidae (root-eating beetles): species of *Rhizophagus*	3	Subcortical/ xylophagous insects (esp. Coleoptera; e.g.,	Subcortical and xylophagous insects (esp. Coleoptera; e.g.,	Subcortical	Subcortical

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey: Immatures	Principal prey: Adults	Habitat: Immatures	Habitat: Adults
		eggs and larvae of Scolytidae)	eggs and larvae of Scolytidae)		
Salpingidae (narrow-waisted bark beetles)	7	Subcortical/ xylophagous invertebrates, esp. Scolytidae	Invertebrates, esp. Scolytidae	Subcortical, galleries of xylophagous insects	Subcortical, litter, flowers, and foliage
Scydmaenidae (antlike stone beetles)	3	Mites, all stages; other small invertebrates	Mites, all stages; other small invertebrates	Litter, epi- and endogean, subcortical	Litter, epi- and endogean, subcortical
Silphidae (carrion beetles): species of *Nicrophorus, Pteroloma*	11	Larvae of Diptera, possibly larvae and adults of coprophagous Coleoptera (e.g., Scarabaeidae)—*Nicrophorus* Small invertebrates—*Pteroloma*.	Larvae of Diptera-*Nicrophorus*. Small invertebrates—*Pteroloma*	Carrion, decaying vegetation, feces—*Nicrophorus*. Litter, epigean—*Pteroloma*	Carrion, decaying vegetation, feces—*Nicrophorus*. Litter, epigean—*Pteroloma*
Staphylinidae (rove beetles)	300	Invertebrates, all stages Subcortical/ xylophagous invertebrates Many mono- or oligophagous; (e.g., preying on fly larvae, all stages of ants, parasites of fly pupae). Many presumably detrivorous or fungivorous	Invertebrates, all stages Subcortical/ xylophagous invertebrates. Many mono- or oligophagous; (e.g., preying on callembola, fly larvae, millipedes, mites, all stages of ants). Many presumably detrivorous or fungivorous	Ubiquitous; epi- and endogean, litter, lacustrine and riparian areas, subcortical, decaying wood and plant material, fungi, bird and mammal nests, carrion, feces, ant nests, etc.	Ubiquitous; epi-endogean, litter, lacustrine and riparian areas, subcortical, decaying wood and plant material, fungi, bird and mammal nests, carrion, feces, ant nests, flowers, etc.
Derodontidae[c] (tooth-necked fungus beetles): species of *Laricobius*	3	All stages of Chermidae (Homoptera); (e.g., *Adelges piceae* Ratzeburg)	All stages of Chermidae (Homoptera); (e.g., *Adelges piceae* Ratzeburg)	Trunks, branches, and twigs of conifers	Trunks, branches, and twigs of conifers
Nitidulidae[c] (sap beetles)	18	*Cybocephalus* on Coccidae (Homoptera); *Epuraea* on scolytid eggs and larvae; *Glischrochilus, Nitidula, Pityophagus* on Scolytidae	Saprophagous, mycetophagous	Subcortical	Subcortical, flowers, tree wounds, fungi
Scarabaeidae[c] (scarab beetles):	5	Ant larvae	Ant larvae	Ant nests	Ant nests; under stones in fields,

Table 4—List of selected families of terrestrial arthropod predators found in the basin assessment area, with estimate of number of species, principal prey, and typical habitats[a] (continued)

Family (common name)	No. of species[b]	Principal prey		Habitat	
		Immatures	Adults	Immatures	Adults
Cremastocheilus					meadows, and pastures.
Tenebrionidae[c] (darkling beetles): *Corticeus*	4	Larvae, pupae, and teneral adults of Scolytidae	Larvae, pupae, and teneral adults of Scolytidae?	Subcortical	Subcortical
Order Diptera: True flies (3 families)	220-700	Larvae, adults eat different food		Larvae, adults occur in different habitats.	
Asilidae: (robber flies)	50-200	Invertebrates	Flying insects	Down wood	Aerial
Chamaemyiidae: (aphid flies)	20-100	Aphids		Arboreal, arbuscular	Aerial
Syrphidae:150-400 (hover flies)	Aphids	Pollen, nectar	Arboreal,	Aerial arbuscular	Aerial
Order Hymenoptera: Bees, ants, wasps (4 families)	500-900	Larvae are helpless, fed by adults	Social (ants, vespids) or solitary (mud-daubers, spider wasps)	Larvae are found within nests constructed by adults	As a group, these insects are widespread, common, and ecologically
Formicidae: (ants)	150-200	Fed by workers	Almost entirely polyphagous		Ubiquitous
Pompilidae: (spider wasps)	100-150	Fed by adult female	Spiders		Ubiquitous
Sphecidae: (mud daubers)	200-400	Fed by adult female	Medium to large arthropods, esp. Lepidoptera		Ubiquitous
Vespidae: (paper wasps, hornets)	50-150	Fed by workers	Medium to large arthropods, esp. Lepidoptera		Ubiquitous

Totals: 3 classes, 16 orders, 112 families, between 3,544 and 6,636 species.

[a] Crawford 1995. Species number of noninsects derived from Crawford (1988), of beetles (Hatch (1953, 1957, 1961, 1965, 1971), and of other insects (Danks 1978) and the list of invertebrates of the H.J. Andrews Experimental Forest (Parsons and others 1991), assuming similar percentages of species found in each taxon.

[b] Estimates of species number represent preliminary examination of literature or expert opinion.

[c] Family is predominantly nonpredaceous. Only the predaceous species are counted.

Appendix 4

Table 5—Rare and endemic invertebrate species[a]

Class-order	Genus and species	USDA Forest Service or USDI Bureau of Land Management species
Gastropoda	Snails:	
	Allogona lombardii	L[b]
	Allogona ptychophora solida	L
	Anguispira nimapuna	L
	Cryptomastix n. sp. *1*	L
	Cryptomastix n. sp. 2	L
	Cryptomastix populi	L
	Cryptomastix harfordiana	L
	Cryptomastix hendersoni	L
	Cryptomastix magnidentata	L
	Cryptomastix mullani blandi	L
	Cryptomastix mullani clappi	L
	Cryptomastix mullani latilabris	L
	Cryptomastix mullani tuckeri	L
	Cryptomastix n. sp.1	L
	Cryptomastix n. sp. 2	L
	Cryptomastix n. sp. 3	L
	Cryptomastix n. sp. 4	L
	Cryptomastix sanburni	L
	Discus brunsoni	L
	Discus marmorensis	L
	Monadenia fidelis n. subsp. 1	L
	Monadenia n. sp. 1	L
	Ogaridiscus subrupicola	L
	Oreohelix alpina	L
	Oreohelix amariradix	L
	Oreohelix carinifera	L
	Oreohelix elrodi	L
	Oreohelix hammeri	L
	Oreohelix haydeni hesperia	L
	Oreohelix haydeni perplexa	L
	Oreohelix idahoensis baileyi	L
	Oreohelix idahoensis idahoensis	L
	Oreohelix intersum	L
	Oreohelix junii	L
	Oreohelix strigosa delicata	C[c]
	Oreohelix strigosa goniogyra	L
	Oreohelix strigosa n. subsp. 1	L
	Oreohelix tenuistriata	L
	Oreohelix variabilis	L
	Oreohelix variabilis n. subsp. 1	L
	Oreohelix vortex	L

Table 5—Rare and endemic invertebrate species[a] (continued)

Class-order	Genus and species	USDA Forest Service or USDI Bureau of Land Management species
	Oreohelix waltoni	L
	Pristiloma arcticum? *crateris*	L
	Pristiloma idahoense	L
	Pristiloma wascoense	L
	Vespericola columbiana depressa	L
	Vespericola n. sp. 1	L
	Vespericola sierranus	L
	Slugs:	
	Hemphillia camelus	L
	Hemphillia danielsi	L
	Hemphillia malonei	L
	Magnipelta mycophaga	L
	Prophysaon humile	L
	Udosarx lyrata lyrata	L
	Udosarx lyrata russelli	L
Arachnida-Araneida	Spiders:	
	Microhexura idahoana	
	Orchestina sp. 1 (undescribed)	
	Zanomys kaiba	
	Zanomys aquilonia	
	Mallos niveus	
	Dictyna piratica	
	Enoplognatha wyuta	
	Dipoena sp. 1 (undescribed)	
	Chrysso pelyx	
	Chrysso nordica	
	Theridion sp. 1 (undescribed)	
	Zygiella carpenteri	
	Frontinella communis	
	Lepthyphantes rainieri	
	Scotinotylus sp. 6 (undescribed)	
	Tachygyna exilis	
	Diplocephalus subrostratus	
	Ceratinella sp. 3 (undescribed)	
	Scotinotylus sp. 8 (undescribed)	
	Disembolus torquatus	
	Walckenaeria communis	
	Wubana utahana	
	Dolomedes triton	
	Arctosa littoralis	
	Zora hespera	

Table 5—Rare and endemic invertebrate species[a] (continued)

Class-order	Genus and species	USDA Forest Service or USDI Bureau of Land Management species
	Clubiona mimula	
	Scotinella sp. 2 (undescribed)	
	Zelotes josephine	
	Zelotes exiguoides	
	Zelotes tuobus	
	Callilepis eremella	
	Ebo iviei	
	Xysticus gosiutus	
	Ozyptila conspurcata	
	Tmarus angulatus	
	Pseudidius sp. 1 (undescribed)	
	Sitticus finschii	
	Marchena minuta	
	Metaphidippus sp. 2 (undescribed)	
	Neon ellamae	
	Euophrys monadnock	
	Habronattus kubai	
	Habronattus jucundus	
	Habronattus sansoni	
	Habronattus sp. 3 (undescribed)	
	Pellenes shoshoneus	
	Synageles occidentalis	
Arachnida-Opiliones	Harvestmen:	
	Speleonychia sengeri	
Insecta-Coleoptera	*Cicindela columbica*	
	Ctenicera barri	W[d]
	Scaphinotus mannii	L
Insecta, Hemiptera: Heteroptera	*Micracanthia fennica*	W
	Ambrysus mormon	W
	Boreostolus americanus	W
	Wygodzinsky:Stys	
	Chorosoma n. sp.	W
	Hebrus buenoi	W
Insecta, Hymenoptera	*Andrena aculeata*	
	Andrena winnemuccana	
	Ashmeadiella sculleni	
	Hesperapis (Hesperapis) n. sp.	
	Heterosarus (Pterosarus) n. sp.	
	Hoplitis producta subgracilis	

Table 5—Rare and endemic invertebrate species[a] (continued)

Class-order	Genus and species	USDA Forest Service or USDI Bureau of Land Management species
	Hylaeus lunicraterius	
	Macropis steironema opaca	
	Megachile umatillensis	
	Calliopsis barri	
	Osmia ashmeadii	
	Osmia n. sp near *laeta*	
	Perdita accepta	
	Perdita crassihirta	
	Perdita similes pascoensis	
	Perdita barri	
	Perdita salicis euxantha	
	Perdita salicis sublaeta	
	Perdita wyomingensis sculleni	
	Perdita wyomingensis wyomingensis	
	Hoplitis n. sp. near *plagiostoma*	
	Hoplitis orthognathus	
	Synhalonia douglasiana	
	Synhalonia frater lata	
Insecta-Lepidoptera	*Colias gigantean*	L
	Mitoura johnsoni	
	Ochlodes yuma	L
	Parnassius clodius shepardi	L
	Pyrgus scriptura	L
Oligochaeta	*Driloleirus americanus*	L
	Drilochaera chenowithensis	
	Argilophilus hammondi	

[a] These species are currently not listed by any public entity as needing protection. It is the judgement of species or functional group experts that these species be considered for possible measures by federal or state agencies to protect these species. Gastropoda—Frest and Johannes 1995; Arachnida—McIver, LaBonte, and Crawford 1995; Coleoptera—LaBonte 1995; Hemiptera/Heteroptera—Lattin 1995b; Hymenoptera—Tepedino and Griswold 1995; Lepidoptera—Hammond 1994; Oligochaeta—James 1995.

[b] L = recommended for listing. For reasons specified in the contract reports, these species are thought to need specific protection.

[c] C = currently listed.

[d] W = recommended to watch. These species are either rare or endemics. There is no information to indicate that special measures are needed at this time to protect them or their habitats; however, because of reasons listed in the contract reports, it is prudent to validate their status occasionally. Species with no indicators (L, C, or W) are not known to need special protection.

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