COARSE WOODY DEBRIS CHEWERS IN THE COLUMBIA RIVER BASIN

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This report addresses the functional importance of coarse woody debris chewers, factors influencing their abundances, and their responses to alternative management scenarios. -This group is poorly known in the Columbia River Basin (CRB) area of concern. In fact, most research on this group has addressed their effects on timber quality and control measures. Few species have sufficient economic importance in the forest to have warranted focused research. Factors affecting the diversity, species abundance and ecological roles of this group have been addressed only recently as the importance of woody litter management has focused attention on factors influencing woody litter persistence and decomposition. Much of the information in this report will be inferred from the limited number of studies conducted elsewhere, particularly in western Oregon and Washington.

The community of woody debris chewers is composed primarily of xylophagous insects in the orders Isoptera (termites), Coleoptera (beetles) and Hymenoptera (horntails and ants), but including some saprophagous species of coleoptera and Diptera (flies) which contribute to woody litter decomposition through feeding on fungi and bacteria. A variety of invertebrate predators also inhabit decomposing wood but will not be addressed in this report.

The diversity of species in this functional group is likely highest in late successional, mesic forests where the diversity of tree species and abundance and diversity of decomposing wood are greatest. This functional group is distributed geographically in areas where coarse woody debris is available, i.e., primarily forest and Savannah habitats.

Species associations are not documented for the CRB area, but the communities of wood chewers are likely to be locally complex. Furniss and Carolin (1977) provide a compendium of frequently observed species along with notes on biologies, host and habitat associations, regional distributions, and general abundance or rarity. However, information on fine-scale habitat and geographic distribution needed to predict occurrance at particular sites is lacking.

AS an example of the difficulty in projecting species occurrances, a concentrated one-year study of arthropods associated with coarse wood decomposition at the H.J. Andrews Experimental Forest in western Oregon (Parsons et al. 1991, Parsons and Schowalter unpubl. data, Schowalter et al. 1992) produced 154 species of wood-associated insects (including xylophages, saprophages and predators). Seventy of these were new records for this intensively studied site and some (e.g., Drosophila montana) represented new associations with decomposing wood. In other words, the number of known wood associates from this relatively well-studied site was nearly doubled by one intensive study.

'Surveys of decomposing wood in the CRB area similarly will substantially increase the numbers of species- known from this area and 'from particular habitats. Data'from such surveys Will be necessary to provide the information on species diversity, abundances and distributions necessary to accomplish the goals of the Eastside Assessment and Analysis. For the purposes of, this report, available information on woody debris chewers known to be distributed in the CRB area (Furniss and Carolin 1977), together with limited ecological data from other regions, will be used to project regional abundance, distribution, regulatory. factors, and functional':importance. The report is organized around the nine species criteria requested.

1. Species. of special concern

None of the listed species of "specialconcern'! - were members of this functional group. This does not mean that no woody debris chewers are sensitive to environmental changes or threatened by, anthropogenic activity. In fact, many species in this functional group will be threatened by silvicultural alternatives that reduce the size or availability of coarse woody debris. Current information is inadequate to assess Current population viabilities for many of these species.

Species that could be'considered bioindicators or "keystone" species include many of the "secondary" bark beetles (i.e., those that colonize only dead or dying trees); ambrosia beetles: other wood boring beetles and wasps: termites: and carpenter ants. The importance, habitat associations, distributions, functional roles, sensitivity to disturbance, and population trends for these species are discussed below.

Major species of secondary bark beetles probably occur where their hosts occur throughout the CRB area.. These beetles may be useful indicators of the rate of woody litter generation because of their restricted occurrence in'the phloem (inner bark) of freshly dead or dying trees of particular'species or related species and of-sufficient size and moisture-content for- beetle reproduction. For example, the.different Phloeosinus spp. occur in particular members of the cypress family; Dryocoetes spp. primarily colonize Abies spp. and Picea spp.; species of Pseudohylesinus and Scolytus colonize various conifer species. Trees become unsuitable for initial colonization or recolonization one year after death because of rapid phloem drying and deterioration. Hence,. these.insects are sensitive to disturbances or other processes that affect the continuous availability.of freshly dead trees of the suitable species over distances that can be reached by beetles dispersing from population sources (e.g., Raffa et al. 1993). However, population trends have not been studied for these/non-economically important bark beetles.

Secondary bark beetles (also primary, or tree-killing, bark beetles) act as keystone species by a) penetrating the bark of freshly dead trees and inoculating wood with, and providing access to, saprophytic microorganisms, and b) providing attractive aerosols, habitats and/or resources for other invertebrates (such as fungivores and termites) thereby accelerating decomposition (Schowalter et al. 1992, Stephen et al. 1993). Saprophytic microorganisms have no means other than insect tunnels of colonizing wood resources. Hence, decomposition would be substantially delayed if insects were absent.

Ambrosia beetles, including _Platypus wilsoni_ (Platypodidae), _Trypodendron_ spp., _Gnathotrichus_ spp. and _Xyleborus saxeseni_ (Scolytidae), initiate penetration of sapwood and inoculate galleries with a variety of associated fungi, most of which become important only after the beetles emerge from the log. These beetles inoculate galleries with mutualistic fungi (_Ambrosiella_ spp.) which the beetles cultivate (by removing other competing fungi) and eat. Studies of these insects in western Oregon (Schowalter et al. 1992, Zhong and Schowalter 1989) indicated that these insects regulate the initial decomposer assemblage in the sapwood and thereby affect initial decomposition patterns.

These insects are widely distributed (although _Platypus_ is rare) in the CRB area (Furniss and Carolin 1977). Various species show preferences for different tree species. For example _T. retusus_ colonizes aspen and poplars, whereas _T. lineatum_ colonizes conifers (Furniss and Carolin 1977), although Zhong and Schowalter (1989) found that this species did not colonize Pacific silver fir or western redcedar logs intermixed with Douglas-fir and western hemlock logs. As with bark beetles, woody debris typically is suitable for ambrosia beetles for only one year after tree death (unless wood remains suitably moist, Schowalter et al. unpubl. data), making these insects sensitive to the temporal availability of this restricted resource.

Various other wood boring beetles (Coleoptera: Buprestidae and Cerambycidae) and wood wasps (Hymenoptera: Siricidae) show preferences for particular tree species, for different decomposition stages, and for different woody debris substrates (phloem, sapwood or heartwood). These species also are sensitive to disturbances that create woody litter resources and are adapted to detecting these resources over long distances, e.g. several miles. In fact, some wood wasps (_Sirex_, _Urocerus_ and _Xeris_ spp.) and some buprestids (_Melanophila_ spp.) are known to orient upwind toward sources of smoke or bark beetle pheromones and lay eggs in freshly-killed, often still-smouldering, trees. (Furniss and Carolin 1977, Schowalter 1985). However, population trends for these species are unknown.

Ergates spiculatus is a particularly large member of this subgroup (one of the largest North American beetles). Large size and apparent preference for freshly dead (especially fire- or beetle-killed) standing trees make this species ('and the related

Prionus californicus) a potential bioindicator Of forest conditions, specifically the availability of this resource. Methods for assessing population trends have not been developed, but this insect frequently is attracted to lights and could be monitored using light trapping. This species also might be considered a keystone to the extent that its boring at the base of dead standing trees (primarily ponderosa pine and Douglas-fir) hastens treefall (Furniss and Carolin 1977) and wood availability to the majority of xylophagous and saprophagous organisms that require moist wood in contact with the ground. Its role in toppling standing dead trees also reduces fire hazard (Furniss and Carolin 1977).

Termites act as keystone species by excavating large nitrogen-rich (through symbiotic nitrogen fixation) galleries in wood, increasing wood aeration and surface area exposed to decomposers, thereby facilitating decomposition and enriching surrounding soils often impoverished in terms of nitrogen (Slaytor and Chappell 1994, Salick et al. 1983, Waller et al. 1989). Principal species in the CRB area 'include Zootermopsis nevadensis (dampwood termite)-and Reticulitermes tibialis (aridland subterranean termite), both distributed throughout the CRB area. Zootermoosis is associated primarily with mesic forests, whereas Reticulitermes occupies drier habitats. -Both would be sensitive indicators of the availability of coarse wood at advanced-stages of decomposition. Population trends are unknown but measureable through surveys of woody debris.

Carpenter ants (Camoonotus spp.) also excavate large galleries in wood and increase wood aeration and surface area exposed to decomposers. In addition, carpenter ants are major regulators of canopy communities (through tending of aphids and predation on defoliators) and are major resources for woodpeckers, including the pileated woodpecker (Torgersen and Bull, unpubl. data).

Various Camnonotus spp. are distributed throughout the CRB area, usually in relatively dry wood. Torgersen and Bull (unpubl. data) found that carpenter ants were associated' primarily with the largest bole diameters, with Larix (which comprised most of the larger logs), and with intermediate decomposition stages, perhaps avoiding vulnerability to woodpecker predation in smaller or more decayed wood. -Population trends are unknown but could be monitored using relatively simple survey techniques.

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

Various fungivores and predators also depend on the abundance of coarse woody litter chewers either for access to microbial-resources in wood or for their'insect hosts. The distinction between coarse woody debris chewers and fungivores is weak because-many xylophages depend on fungal preconditioning of wood for adequate nutrition, and-some fungivores consume degraded wood infused with the fungal resource.

2-5. Major cover types for this-area are:

a. Interior ponderosa pine
b. Lodgepole pine
c. Interior Douglas-fir
d. White fir
e. Grand fir
f. Western- redcedar-western hemlock
g. Englemann spruce-subalpine fir
h. Western larch
1. Aspen

Virtually nothing is known about particular associations between coarse woody debris chewers and vegetation types, successional stages, or stand structures. However, in general, these insects will be more abundant where coarse woody litter is more available. Individual insect species discriminate among pine, Douglas-fir, true fir, western redcedar, western hemlock, larch, juniper, and hardwood hosts (Furniss and Carolin 1977, Zhong and Schowalter 1989) and among size and/or decay classes of woody debris (Furniss and Carolin 1977, Torgersen and Bull unpubl. data) and would be absent where their preferred hosts were absent.

Available data are insufficient to support construction of models describing interactive effects of environmental factors on representative species and their functional roles for each habitat condition. Key environmental variables include wood abundance: temperature and moisture: species, size and decay class: proximity to insect population sources: and factors (such as wind and canopy opening) that affect chemical aerosol dispersion and insect detection of woody litter resources. However, no data are available even to indicate required amounts of woody debris per acre, although all of these insects are responsive to amounts of dead wood available (Schowalter 1985) and some have mechanisms that limit their density in available resources (Raffa et al. 1993). Therefore, a general model for the key insect groups identified above seems more appropriate, especially since the responses and roles of these insect groups (and representative species) likely are similar among habitat types.

Secondary Bark Beetles and Ambrosia Beetles

Major environmental factors affecting both groups are a) wood availability and distribution, b) temperature and moisture, c) wood age and d) chemistry. Abundance and distribution of woody debris is important to maintaining populations of these insects, but some species persist during long periods when only very scattered dying trees are available. Bark and ambrosia beetles are particularly sensitive to the time since tree death such that only the subset of woody litter that is within one year after tree death is available. These insects maximize colonization efficiency by producing pheromones that attract con-specific individuals within an attractive pheromone plume, the size of which is governed by forest canopy structure and wind speed and direction. Pheromone plumes extend farther under closed canopy conditions. Lethal temperatures for bark beetles often are reached under bark on the tops and exposed sides of woody debris under open canopies. Moisture loss results in desiccation of larvae and symbiotic microbes often necessary to enhance wood nutritional value (especially for ambrosia beetles) (Raffa et al. 1993). Moisture loss may be the critical environmental factor that restricts these insects to freshly dead woody debris. Size of wood is important in regulating internal temperature and moisture (larger size classes buffer temperature and moisture fluctuation) and the thickness of phloem and sapwood substrates (larger bark beetles require thicker phloem for development). 'Bark and wood chemistry is important in determining colonization patterns. These insects require both feeding stimulants and non-detrimental concentrations of plant defensive compounds, such as phenolics and terpenoids (Raffa et' al. 1993).

Major functional roles include a) bark penetration, permitting entry by other organisms (Stephen et al. 1993), b) direct inoculation of woody debris with saprophytic microbes, perhaps including inoculation with nitrogen-fixing bacteria by bark beetles (Bridges 1981, Schowalter et al. 1992), c) providing food for a variety of predators, especially woodpeckers (Stephen et al. 1993). Their presence indicates freshly dead woody debris.

Wood Boring Beetles and Wasps

These insects mine sapwood and heartwood of dying and dead, often fire- or beetle-killed, trees. Life cycles often require several years (usually 3-10) in this nutritionally-poor resource, even when aided by symbiotic microorganisms (Furniss and Carolin 1977, Schowalter 1985). Major environmental factors influencing these insects include a) wood availability, b) chemistry, c) moisture, and d) persistence. Not all woody litter is equally available to these insects. Some show preferences for particular tree species (Zhong and Schowalter 1989) or decay classes (Furniss and Carolin 1977), perhaps reflecting chemical conditions of wood. Wood chemistry includes concentrations of essential nutrients, often limited in woody tissues, and toxic or detrimental defensive compounds such as phenolic and terpenoid compounds, typically concentrated in heartwood (Schowalter et al. 1992). Wood moisture affects insect survival directly as well as indirectly through effects on symbiotic microorganisms that enhance wood nutritional quality. Wood persistence is necessary to ensure complete development of the insect during its multiyear life cycle. Tree size will affect persistence as well as extent of heartwood development. Predation by birds and bears or other grub-feeding vertebrates capable of excavating woody litter may be a locally important factor affecting abundance of these insects.

The major roles of these insects include a) toppling standing dead trees, b) increasing wood porosity, aeration and water-holding capacity, c) reducing fire hazard through water retention and accelerated fragmentation, and d) providing food for wildlife ranging from birds to bears.

Termites

Major factors affecting termites include a) woody litter availability;' b) prior fungal conditioning, c) wood moisture, and perhaps d) prior entry by beetles. Reproductive kings and queens typically are found initially in bark beetle galleries, gradually enlarging feeding areas and galleries as fungi pervade the wood, softening it and increasing its. nutritional value (Schowalter et al. 1992). Fungal preconditioning may be essential for nutritional enhancement and alters chemical factors that affect termite feeding preferences (Hendee 1'935, Smythe et al. 1967, Mankowski, Schowalter and Morrell unpubl. data). Termites also host gut symbionts that are responsible for cellulose digestion and nitrogen fixation (Slaytor and Chappell 1994, Walier et al. 1989). Wood moisture is critical to survival both the soft bodied termites and the saprophytic fungi that promote termite activity. 'Subterranean-termites in the more arid regions often build earthern tubes connecting woody debris to moister substrates (Furniss and Carolin 1977).

Termites perform a variety of functional roles, 'including a) providing nitrogen- and other nutrient-rich "hot spots" around colonies (Salick et al. 1983, Schaefer and Whitford 1981, Gutierrez and Whitford 1989), b) increasing wood porosity, aeration and moisture retention, c) providing nutrient-rich food for wildlife, including birds and bears, and d) providing colony conditions that support a variety of termitophilic arthropods.

Carpenter Ants

Factors affecting carpenter ant abundance include a) wood availability b) decay class, c) tree species, d) size of woody debris, and e) predation, especially by pileated woodpeckers (Torgersen and Bull unpubl. data). No data are available on the amount of wood needed to support minimal populations, but Torgersen and Bull (unpubl. data) reported that woody debris >2 m long and >15 cm in diameter amounted to 290 logs or 110 m^3/ha. Carpenter ants occurred in lo-15% of these logs, primarily in larger size classes and western larch. Carpenter ants were most abundant in intermediate decay classes, perhaps because colony development progresses with decay and is limited by predation in the most decayed wood (Torgersen and Bull unpubl. data). Tree species and size of woody debris may be correlated: Torgersen and Bull (unpubl. data) found that apparent preference for larch wood was correlated with the larger average size of larch snags and logs. Size of wood may be related to predation. Colonies in larger sized woody debris may be better protected from predators.

Carpenter ants perform several important roles, including a) nutrient enrichment of colony logs, b) tending aphids, especially <u>Cinara</u> spp., c) preying on canopy defoliators, such as western spruce budworm, d) girdling seedlings, e) providing food for pileated woodpeckers and other wildlife, and f) providing colony habitats for a variety of myrmecophilic arthropods (Furniss and Carolin 1977, Campbell and Torgersen 1982,' Torgersen and Bull unpubl. data).

6. Biogeography

Little is known about the distribution of species in this group. No surveys of diversity are available. Given the general habitat requirements of this functional group, diversity would be highest where tree species diversity and availability and decay class diversity of coarse woody debris are highest, i.e., in old-aged mixed conifer forests. Federal lands, with their relatively older forest age classes and larger trees, likely contribute significantly to abundance and diversity of this group. The major forested zones on the east side of the cascade Mountains, the Blue Mountains and the Rocky Mountains probably support the majority of species. However, coarse woody debris in the intermountain area probably supports some more specialized species, especially those adapted to the particular wood chemistry of junipers or large woody shrubs and/or to more arid conditions. Mesic forests may be too wet for some species characterizing more open pine forests.

Some species characterizing particular tree species or older decay classes are likely to be restricted to scattered landscape patches where these tree species and decay classes occur. Many species rely on chemical odors carried on the air stream to locate suitable wood resources. Species that orient toward sources of smoke may locate host resources in burned over forest but some insect species will fail to detect chemical cues carried out of the forest by convection currents in intervening cleared or disturbed patches. Current knowledge about the species in this group indicates that individual species will not be distributed evenly among available habitat units but would spread across the landscape from refuges during favorable periods, then be restricted to scattered refuges, perhaps different from the previous refuges, during unfavorable periods. This shifting distribution of population centers requires a landscape perspective and allowance for sufficient habitat availability over landscapes to provide adequate refuges for maintenance of viable populations.

7. Special Habitats

No special underrepresented or disappearing habitats are known for this group. However, habitats that support unique assemblages of other functional groups likely would support critical assemblages of coarse woody debris chewers as well.

8. Responses to Management Alternatives

NO specific alternatives were provided for assessment. However, any alternative that affects the a) abundance, b).tree species, c) size class distribution, or d) decay class representation of.woody litter will affect the abundances and diversity of woody litter chewers. Examples include removal of woody material through harvest, salvage or burning: afteration of tree species (and wood) representation through selective harvest or plantation forestry; and more frequent harvest or burning, resulting in loss of wood in the larger size classes and older decay classes.

Many woody litter chewers are associated with late successional firs that now are abundant in the understory of forests historically dominated by open pine woodland as a result of fire suppression. These insect species would not have occurred naturally in pine stands but have naturally-occurring population sources at higher elevations and in west-side forests. Reduction of these and other groups promoted by. recent changes in, forest condition may result from restoration of natural forest ecosystems. However, such restoration should promote woody litter chewer populations that have been reduced by changes from natural forest conditions.

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