

AN ABSTRACT OF THE THESIS OF

James R. LaBonte for the degree of Master of Science in Entomology presented on March 18, 2002. Title: Habitat Associations of Riparian Beetles (Coleoptera) at Big Beaver Creek Research Natural Area, North Cascades National Park, Washington.

Abstract approved:

Redacted for Privacy

John D. Lattin

Abstract approved:

Redacted for Privacy

Jeffrey C. Miller

Beetle diversity and habitat associations of five prevalent riparian plant communities were examined along the lower reaches of Big Beaver Creek Research Natural Area, North Cascades National Park, Washington. These communities were defined by dominant tree species, and included Alder Swamps, Cedar-Hemlock Forests, Douglas-fir Forests, Gravel Bars, and Willow-Sedge Swamps. Monthly samples were taken with pitfall traps from 10 randomly selected patches per habitat during the snow-free periods (mid-June through mid-October) of 1995 and 1996.

A total of 8,179 non-necrophagous beetles was collected, comprising 41 families and 290 species. Four families - Staphylinidae (43%), Carabidae (31%), Elateridae (12%), and Anthicidae (6%) - accounted for 92% of all individuals. Four families encompassed 65% of all

species - Staphylinidae (31%), Carabidae (19%), Elateridae (8%), and Leiodidae (7%).

A few species accounted for the majority of individuals. Almost 51% of individuals were found among just 20 species. The five most abundant species in each habitat accounted for 33% (Alder Swamps) to 71% (Gravel Bars) of individuals.

Beetle abundance and species composition differed among habitats. Abundance ranged from 1,530 (Cedar-Hemlock Forests) to 2,071 (Alder Swamps). Abundance per trap per month varied from 16 (Willow-sedge Swamps) to 27 (Alder Swamps). Species richness was lowest in Douglas-fir Forests (76) and highest in Alder Swamps (119). Simpson's 1-D index ranged from 0.74 (Douglas-fir Forests) to 0.96 (Alder Swamps).

Species were categorized as detritivores, fungivores, herbivores, omnivores, predators, and unknowns. Individuals and species of predators and fungivores were generally numerically dominant. Herbivores and omnivores contributed few species and individuals. Gravel Bars virtually lacked fungivores and were the only community with many (more than 30%) detritivorous individuals.

Two patterns of seasonal abundance were evident. Abundance was highest in June in the two open habitats, Gravel Bars and Willow-Sedge Swamps, thereafter sharply and continuously declining into October. Abundance peaked during September in the forested habitats.

Baseline data was acquired about the North Cascades National Park beetle faunas, furthering Park goals to perpetuate habitat and community assemblage integrity. In a larger context, this information has also enriched the understanding of the arthropod faunas of the Pacific Northwest.

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Habitat Associations of Riparian Beetles (Coleoptera) at
Big Beaver Creek Research Natural Area, North Cascades
National Park, Washington.

By

James R. LaBonte

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APPROVED:

Redacted for Privacy

~~James R. LaBonte~~

Co-Major Professor, representing Entomology

Redacted for Privacy

~~James R. LaBonte~~

Co-Major Professor, representing Entomology

Redacted for Privacy

~~James R. LaBonte~~

Chair of Department of Entomology

Redacted for Privacy

~~James R. LaBonte~~

Dean of Graduate School

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James R. LaBonte, Author

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advice and personal encouragement above and beyond the call of duty.

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**HABITAT ASSOCIATIONS OF RIPARIAN BEETLES (COLEOPTERA) AT
BIG BEAVER CREEK RESEARCH NATURAL AREA, NORTH CASCADES
NATIONAL PARK, WASHINGTON**

CHAPTER 1. INTRODUCTION

**SECTION I: INSECTS AS SUBJECTS FOR BIODIVERSITY AND
ECOLOGICAL STUDIES**

Insects are among the most abundant and diverse animals on Earth (e.g., Borror et al. 1989). Insect diversity is expressed through their incredibly varied behavior, ecology, morphology and physiology, and, of course, numbers of species. These creatures thrive in almost all non-oceanic habitats (a few species are oceanic), and can be found from sub-sea level deserts to glaciers atop alpine peaks. Aquatic or semiaquatic insects exist in or at the margins of intertidal rock crevices, the interstices of aquifers and artesian wells, ultrasaline lakes, hot springs, peat bogs, all manner of swamps and marshes, and mountain freshets and tarns. Terrestrial insects can be found at the terrestrial-aquatic interfaces of all the preceding habitats, as well as burrowing in the sand and soil, clambering over the ground, climbing vegetation, burrowing under bark or into woody shrubs and trees, or scampering over alpine ice and snow. In almost all these habitats, adult insects fly through the lower atmosphere, dispersing, foraging, and reproducing. Insect trophic roles include detritivory,

fungivory, herbivory, predation, omnivory, and parasitism. Especially with endopterygotes, different life stages may have radically different diets and feeding strategies. Furthermore, insect trophic specificity ranges from strict monophagy upon a single plant, prey, or host species (or individual) to foraging upon a vast array of species, genera, families, orders, classes, or phyla.

Such characteristics of insects have made insects integral components of virtually all aquatic (other than marine), semiaquatic, and terrestrial habitats. They generally hold intermediate positions in food webs (although they may be top consumers in some truncated food webs), supplying vertebrates and other invertebrates with prey. Insect hosts enable pathogens and parasites to find lodging within and upon their bodies and various life stages. Of course, these relationships enable insects to play critical roles as vectors of animal and plant pathogens. Their corpses and feces provide nutrients to an array of saprophages and plants. Not only do plants serve as food for a staggering diversity of herbivorous insects, but many critical and unique coevolutionary relationships have developed between these organisms, not the least of which are pollination services by insects.

Their abundance, ubiquity, diversity, ecological roles and relationships render insects extremely valuable as probes of a vast array of biological questions. Many

insect faunas include species diversity at least several orders of magnitude greater than that of vertebrates. Thus, for a given area, a relatively modest research program can yield information on more species of insects, and more trophic roles and interactions, than all the vertebrate species to be found therein. Furthermore, insects are widely regarded as "canaries in the coal mine" capable of responding more readily to environmental changes and perturbations than many other organisms (Collins and Thomas 1991, Kremen et al. 1993, New 1995). Insects are slowly, but surely, gaining recognition as subjects worthy of study in biodiversity, conservation, and ecological investigations (e.g., Price 1984, Wilson 1988, New 1995). Among such studies are those providing vital baseline data about a given locale and various habitats therein (e.g., Parsons et al. 1991). This is the nature of the following study, with reference to the terrestrial riparian habitats of the Big Beaver Creek Research Natural Area in the North Cascades National Park of Washington.

SECTION 2: INSECTS AND RIPARIAN HABITATS

Riparian habitats are currently recognized as essential to watershed integrity (Gregory et al. 1991, Malanson 1993). Wetland and riparian habitats are vital to nutrient and energy transfers between aquatic and

terrestrial systems, and are major biodiversity foci within landscapes (Thomas et al. 1979, Gregory et al. 1991, Malanson 1993, Primack 1993). The Western Forest Plan for the Northern Spotted Owl, the plight of anadromous fishes (Nehlsen et al. 1991), the apparent dire straits of amphibians (Blaustein and Wake 1990), and deteriorating water quality (Karr 1991) have done much to increase awareness of these critical habitats.

The aforementioned generalization that insects are essential to most ecosystems, based in large part upon their intermediate positions in trophic webs, is equally true of riparian and wetland systems. Aquatic habitats often lack substantial autochthonous primary production other than that provided by algae and cyanobacteria. Thus, many aquatic habitats are highly reliant upon allochthonous input, much of which consists of insects (Hynes 1970, Vannote et al. 1980, Gregory et al. 1991). Riparian insects are a vital food source for fish (Elliott 1967, Garman 1991, Gregory et al. 1991, Cloe and Garman 1996) and other aquatic consumers, other riparian insects, and those terrestrial invertebrates and vertebrates utilizing riparian habitats.

The abundance and biomass of riparian insects potentially available for input into aquatic systems, or available to consumers from adjacent habitats, can be impressive. For instance, densities of water scavenger beetles (Coleoptera: Hydrophilidae) up to 600 individuals per m² and as much as 80 individuals per m² of

a single species of carabid beetle (Coleoptera: Carabidae) were documented from the banks of a modest-sized Oregon Coast Range stream (Hering 1998).

Riparian insects and other arthropods also have important ecosystem effects by linking riparian and aquatic habitats through feeding upon aquatic insects and other aquatic invertebrates. The vast majority of aquatic insects pupate and eclose in riparian and lacustrine zones (Erman 1984, Merritt and Cummins 1984), while many also feed and oviposit in these zones (Erman 1984). These activities provide riparian arthropods access to aquatic taxa. For instance, spiders have been documented preying upon aquatic insects eclosing in riparian zones (Clark 1986). Several recent studies have found that much, perhaps most, of the food of terrestrial riparian beetles consists of aquatic insects (Hering and Plachter 1997, Hering 1998). Stranding also exposes aquatic species, including vertebrates, to riparian insect predation and scavenging.

Since each insect species has numerous interactions with other species, insect or otherwise, and presumably has a unique niche, such diversity has profound ecological effects. As is true of most other habitats, riparian, lacustrine, and wetland habitats have a diverse insect fauna. A two-and-a-half month study of the riparian beetle fauna of a coastal Oregon creek documented 41 species in just three beetle families, Carabidae, Dytiscidae, and Hydrophilidae (Hering 1998).

Even the seemingly monotonous mud flats of Harney Lake, an alkaline lake in eastern Oregon, were found to have up to 32 species of carabid beetles (Coleoptera: Carabidae) present at any one time (LaBonte 1996).

While aquatic and terrestrial insect faunas are often relatively well known (e.g., Anderson and Hansen 1987 and Parsons et al. 1991), this generalization does not hold for those insects existing at the aquatic-terrestrial interface. Surprisingly little has been published upon riparian insect faunas of the United States (the riparian insect literature will be explicitly addressed in the discussion chapters). The Pacific Northwest has fared no better in this respect than the rest of the United States. Given this paucity of information, increasing the knowledge of Pacific Northwestern riparian insects is highly desirable. This is particularly true for land management agencies responsible for maintaining the lands they oversee (see below). Insect taxa which are abundant, as well as taxonomically and ecologically diverse, would be most suitable for study. Beetles are one such group.

SECTION 3: BEETLES AS SUBJECTS FOR INVESTIGATING TERRESTRIAL RIPARIAN HABITATS

Beetles (Coleoptera) are among the most diverse groups of organisms, comprising approximately one-quarter of all known species (Elias 1994). Approximately 5,000

species are known from Oregon alone (Parsons, LaBonte, and Miller, unpublished). Of the ~3,450 arthropod species recorded from the H.J. Andrews Experimental Forest in the western Oregon Cascade Mountains (Parsons et al. 1991), 824 species (24%) were beetles. Beetles are also among the most abundant arthropods in many riparian and wetland habitats. For instance, studies of riparian arthropod communities in Germany and Oregon revealed that beetles represented 50-90% of individuals (Manderbach and Reich 1995, Hering 1998).

Furthermore, beetle taxonomic diversity is reflected in a wide array of trophic strategies and roles, ranging from detritivores to parasites. These insects utilize virtually all terrestrial (and most freshwater) habitats, from the deep soil and aquifer interstices to the canopies of the tallest trees and the glaciers atop mountain peaks. As is true of many other insects, beetles are often sensitive to small differences in temperature, humidity, and habitat structure, selecting discrete and well-defined microhabitats (Andersen 1969, 1978, 1986; Wallin 1986, Wiens and Milne 1989, Quinn et al. 1990, Landry 1994). Such taxonomically and ecologically diverse organisms are desirable when analyzing faunal differences among habitats, particularly those which are essentially contiguous.

Beetles offer several practical advantages for faunal investigations. They tend to remain identifiable in pitfall traps, even those left for long periods or in

which the preservative becomes diluted. Beetles are easy to prepare for identification. The Pacific Northwest beetle fauna is also taxonomically relatively well known, largely through Beetles of the Pacific Northwest (Hatch 1953, 1957, 1961, 1965, 1971). This is in stark contrast to many insect orders and arthropods, such as flies (Diptera). Although much can be said for utilizing "morpho-species" in lieu of available taxonomic expertise or literature (New 1996), this practice does not readily enable comparisons between studies, nor does it allow access to species-specific literature. The latter is crucial to the interpretation of biodiversity studies, particularly when working with diverse taxa such as beetles.

The combination of abundance and availability, great species and ecological diversity, practicalities of collection and preparation, and a relatively sound taxonomic foundation led to beetles being selected by the North Cascades National Park as one of the key taxa to be studied in a riparian research natural area located within a watershed of the Park.

SECTION 4: THE RATIONALE FOR A STUDY OF THE BEETLES AND OTHER INSECTS OF THE NORTH CASCADES NATIONAL PARK, WA.

Central to the mission of the National Park Service is a mandate to "maintain, restore, and perpetuate the inherent integrity of ecosystems and their component habitats and community assemblages" (Glesne et al. 2000, p. i). In order to meet this charge, basic biodiversity data must first be acquired for those taxa within national parks. Most national parks lack even an elementary understanding of the nature and composition of their insect faunas, with the possible exception of high profile groups such as butterflies (Lepidoptera) and dragonflies (Odonata). This is the case with North Cascades National Park.

Of particular concern to national parks are the effects of global warming and the incursion of exotic species (R.S. Glesne, personal comment). However, assessing the effects of such changes cannot be accomplished without first acquiring baseline data on the insect faunas. As with general insect biodiversity data, this information is, for the most part, absent for national parks. Again, North Cascades National Park is typical in this respect.

Linked to these issues is the need for national parks to understand the community ecology and ecological dynamics of the habitats within their jurisdiction. This is especially true of key habitats, such as riparian areas. Such goals cannot be achieved without good data

on the elements of these habitats and the ecological interactions of these components. Not surprisingly, such information is generally lacking for most invertebrates within the environs of national parks.

Thus, furthering the understanding of their insect faunas can provide valuable information for the management and maintenance of national parks. The current paucity of such information hampers achievement of these goals. A study of the riparian beetles of a watershed within the North Cascades National Park would help the Park attain information aiding in the management and maintenance of that resource. In a larger context, this data would be valuable to the appreciation of the critical role insects play in the landscapes and habitats throughout the Pacific Northwest.

SECTION 5: OBJECTIVES

This project was part of a larger effort to document and describe arthropod diversity and habitat associations in wetlands and adjacent habitats along the Big Beaver Creek Research Natural Area (BBCRNA), North Cascades National Park, WA. As previously mentioned, little is known about the insect fauna of the North Cascades National Park Complex (NOCA). The riparian insect fauna of the BBCRNA has never been studied.

The objectives of this study were to (1) ascertain the efficacy of the sampling methodology (using pitfall traps) in distinguishing differences in the beetle associations of the selected habitats, (2) examine patterns of beetle biodiversity at the BBCRNA, including abundance, species and family diversity, phenology patterns, and the presence of exotic species (if any), and (3) add to the general knowledge of the beetles of North Cascades National Park and the Pacific Northwest. This study, in conjunction with the extensive data available on the arthropods of the H.J. Andrews Experimental Forest (e.g., Voegtlin 1982, Moldenke and Fichter 1988, Parsons et al. 1991), will also contribute to future comparisons of Cascadian arthropod faunas of different latitudes, such as those proposed by Lattin (1997).

CHAPTER 2: METHODS

SECTION 1: CHARACTERISTICS OF THE STUDY SITE.

Abiotic Characteristics.

Big Beaver Creek Research Natural Area is located approximately 25 km south of the Canadian border and about 75 km east of Bellingham, WA (Figure 1). The creek flows to the southeast into the northwest end of Ross Lake, a power-generating impoundment occupying the northern portion of the Skagit River Valley. The Big Beaver watershed is a pristine natural area that encompasses approximately 17,000 hectares including the tributary drainages of Luna Creek and McMillan Creek. Within this watershed there are 174 km of streams and 62 lake/ponds represented on the USGS 7.5' topographical maps. The geographical coordinates of the center of this area were latitude $48^{\circ} 48' 10''$ N and longitude $121^{\circ} 07' 21''$ W. The elevation of the watershed ranges from 488 m on the east, where Big Beaver Creek flows into Ross Lake, to 2502 m at the summit of Mt. Challenger on the western boundary of the watershed. Study site elevations were modest, ranging from 494 to 579 m.

The bedrock of Big Beaver Valley is composed almost entirely of Skagit Gneiss with a few scattered outcrops of Cascade River Schist (Misch 1966). Several periods of glaciation have carved a typical U-shaped, flat-bottomed,

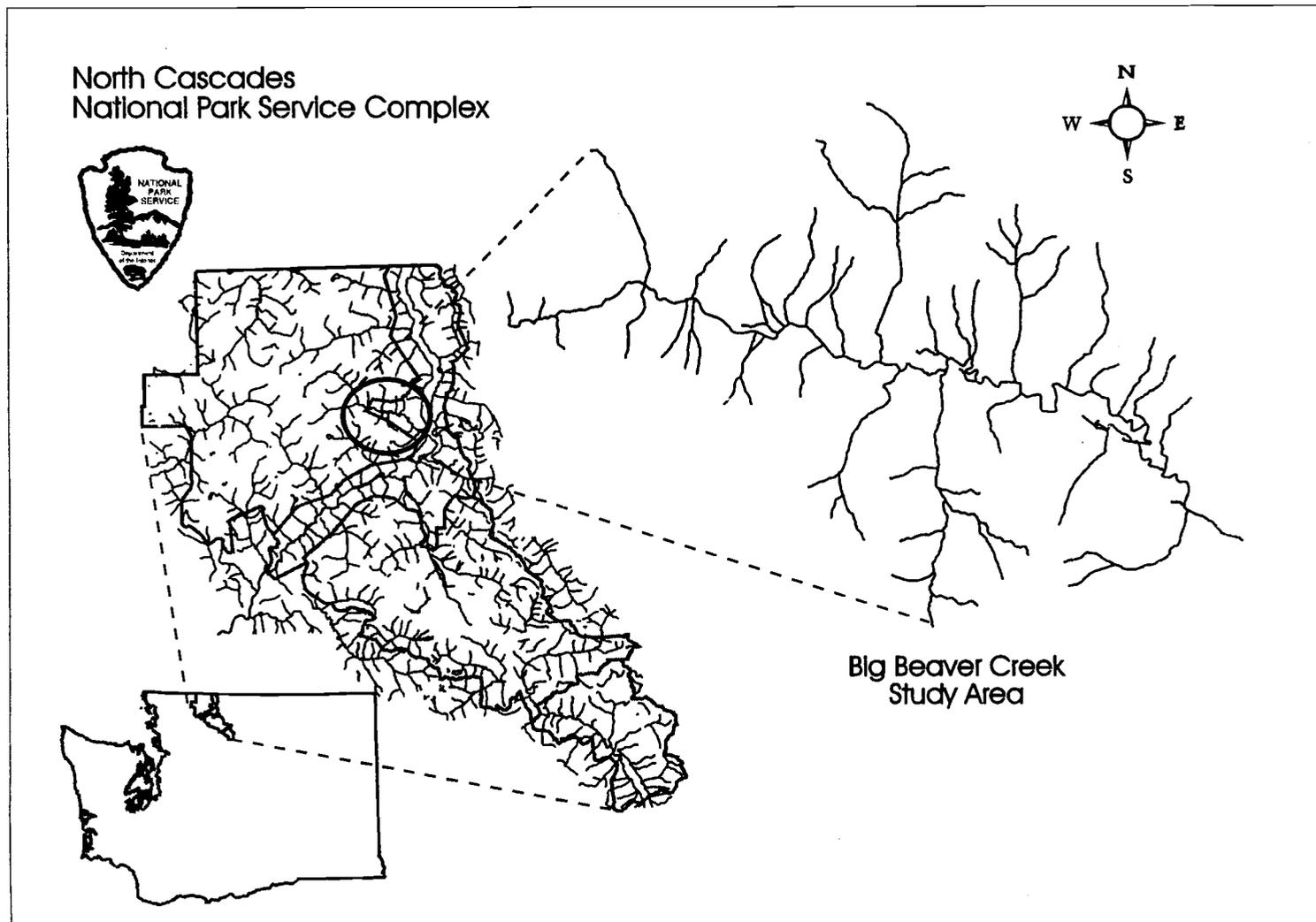


Figure 1. Location of the Big Beaver Creek Research Natural Area in North Cascades National Park, Washington.

steep-walled valley (Figure 2). There is a soil moisture gradient from the well-drained rocky soils on the upper slopes to the saturated silty-peat soils of the valley bottom. The headwaters of all streams begin in the steep upper canyon walls, often flowing down into a loose talus slope and finally entering the valley bottom. Along the portion of the reach studied, Big Beaver Creek is a fourth order, low-gradient stream with many meanders. There are substantial gravel bars along this section, while the low-gradient, relatively broad valley floors have enabled the formation of extensive swamps and marshes.

The climate in Big Beaver Valley is determined by general weather patterns of the North Cascades, which are modified by topographic features in and around the valley. Air masses originating as frontal systems over the Pacific Ocean release rain or snow as they rise over the Pickett Range to the west of the valley (Miller and Miller 1971). This results in a rainshadow effect for Big Beaver Valley, and a strong west-to-east moisture gradient. Annual precipitation is estimated to range from approximately 250 cm in the higher western end of the watershed to 150 cm in the lower eastern end of the valley (Taber and Raedeke 1976). The summer months are generally dry. Temperatures are relatively mild, with mean daily minimums for the coldest month, January, of $\sim -2^{\circ}$ C. The orientation of the valley on a northwest-southeast axis creates strong microclimatic variation.

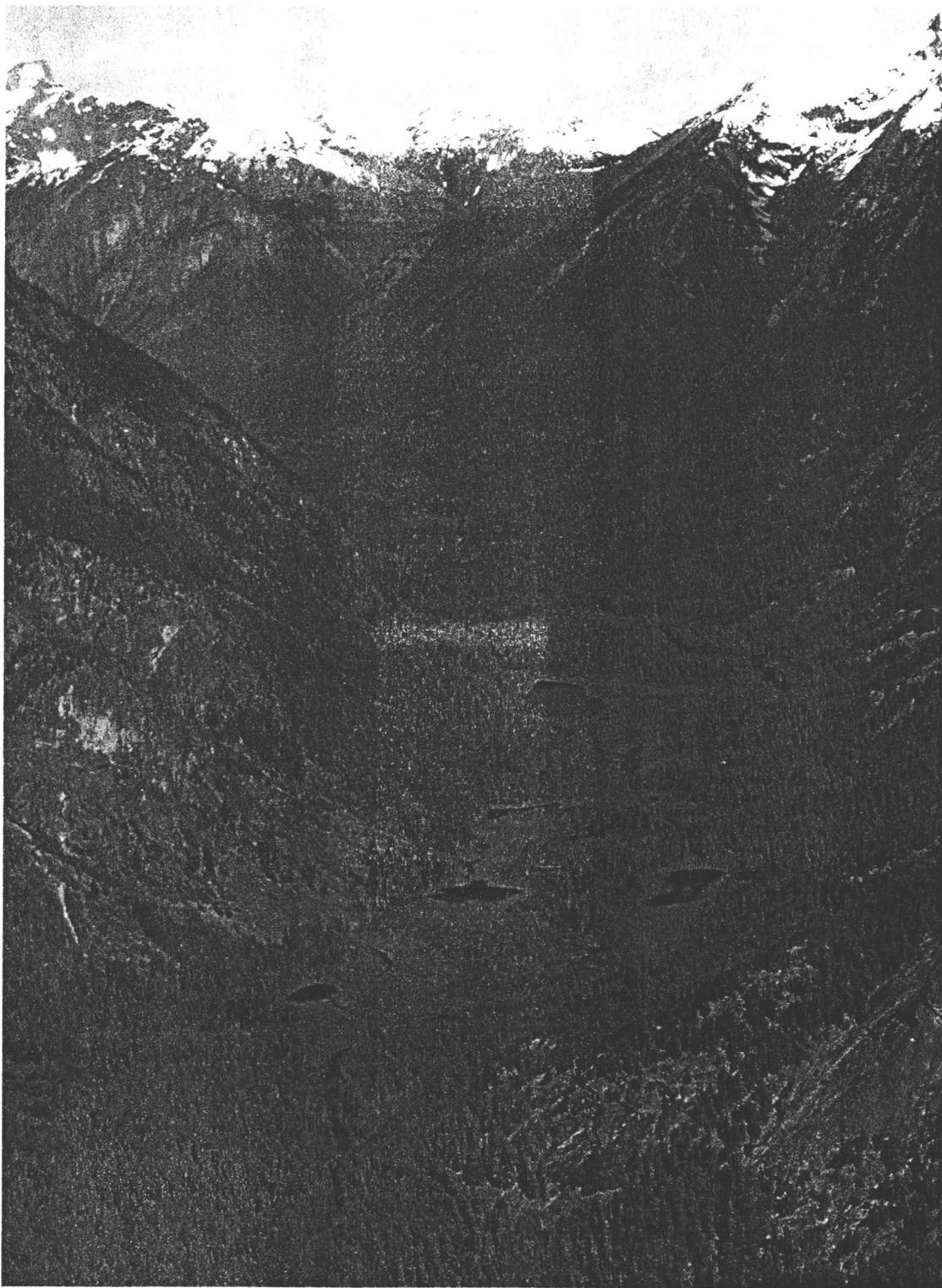


Figure 2. Oblique aerial view of Big Beaver Creek R.N.A. looking West, up the watershed, from above Ross Lake, North Cascades National Park

For example, the north facing slopes stay cool and moist through the summer months because they receive very little direct sunlight.

Biotic Characteristics.

The Ross Lake area is a transition zone between moist coastal forests west of the Cascade crest and dry interior forests (Franklin and Dyrness 1973). Big Beaver Valley reflects this pattern, sharing plant associations and floristic affinities with both regions (Vanbianchi and Wagstaff 1988).

The Big Beaver Creek watershed vegetation can be divided roughly into three communities: wetlands, shrubs, and forests. Finer resolution divisions have been made based on dominant species and age structure (Vanbianchi and Wagstaff 1988). Common wetland plant species include: aquatic species, *Potamogeton natans*, *Nuphar polysepalum*, and *Menyanthes trifoliata*; emergent species, *Carex* spp., *Potentilla palustris*, *Habernaria dilatata*, *Glyceria elata*, and *Equisetum* spp.; bog species, *Sphagnum* spp., *Drosera rotundifolia*, *Tofieldia glutinosa*; shrub species, *Salix sitchensis*, *Salix lasiandra*, *Spiraea douglasii*, *Cornus stolonifera*, *Acer circinatum*, *Alnus sinuata*, and *Sambucus racemosa*. Common trees in forest communities include deciduous trees, *Alnus rubra*, *Acer macrophyllum*, *Populus trichocarpa*, and conifers, *Thuja plicata*,

Pseudotsuga menziesii, *Tsuga heterophylla*, *Abies amabilis*, *Pinus contorta*, *Pinus monticola* and *Picea engelmanni*.

Biotic agents of disturbance.

The vegetation and hydrography in the lower gradient sections of Big Beaver Valley are, appropriately, profoundly affected by the activities of beavers. They constantly reshape their channels, alter water levels, and harvest vegetation for food and construction materials. They create and maintain wetlands and kill large areas of riparian forest by inundation (Vanbianchi and Wagstaff 1988). Beavers are responsible for the formation of most ponds in the lower valley.

Human disturbance has been surprisingly minimal. It has been limited to one homestead around the turn of the century, snow survey cabins and gauging stations, trail construction, subsequent recreational use, and the hydrological effects upon the lowest reach stemming from the creation of the impoundment (Miller and Miller 1971).

SECTION 2: SAMPLING DESIGN AND PROTOCOLS

Sampled Habitats.

Sampling was limited to the riparian zones along the lower 13 km of Big Beaver Creek. Riparian zone habitats were defined as those extending from the active channel or backwaters of the creek up to the floodplain limits (*sensu* Gregory et al. 1991), including habitats directly adjacent to the maximum flood boundaries. A vegetation map of the lower reaches of Big Beaver Creek (Vanbianchi and Wagstaff 1988) was used to select sampling sites (Figure 3). This map shows the locations and conformations of twenty-eight plant communities. Five habitat types representing dominant vegetation associations, or habitats of special interest, were selected for survey: Alder Swamps, Cedar-Hemlock Forests, Douglas-fir Forests, Gravel Bars, and Willow-Sedge Swamps.

Extensive habitat information was recorded in an 8 X 8 m grid centered upon each trap: UTM coordinates, elevation, crude soil type (e.g., clay versus loam), soil moisture during August, litter depth, per cent canopy closure, slope, aspect, per cent herb and shrub cover (by species), tree species inventory (number of individuals and diameter at breast height, DBH) and coarse woody debris inventory. The number and species of any incidental vertebrates collected by the pitfalls were



Figure 3. Plant association types of Big Beaver Creek R.N.A., North Cascades National Park, map from Vanbianchi and Wagstaff 1988.

also recorded, and all such specimens were retained. A summary description of each habitat follows, with parameters averaged over all trap sites.

Alder Swamps soils were wet, predominantly sandy or loamy, with an average litter depth of 5.7 cm. The mean coarse woody debris volume was 2.3 m³ per plot. The sites were essentially flat, with an average slope of 0.6%. Mean herb species richness was 4.4 species per plot, herb cover averaged 53%, and the dominant herbs were *Athyria filix femina* and *Lysichitum americanum*. Mean shrub species richness was 4.5 species per plot, average shrub cover was 64%, and the only common shrub was *Rubus spectabilis*. Canopy closure averaged 96%, with an mean of 8 trees per plot. The mean tree DBH was 24 cm. The only common tree was *Alnus rubra*.

Cedar-Hemlock Forests soils were dry, organic or loamy, and had an average litter depth of 5.0 cm. Average coarse woody debris volume was 3.2 m³ per plot. Mean slope per plot was 4.8%. Herb species richness averaged 6.0 species per plot, mean herb cover was 49%, and the dominant herbs were mosses. Mean shrub species richness was 2.7 species per plot, shrub cover averaged 41%, and *Acer circinatum* was the dominant shrub. Canopy closure averaged 99.4%, with 6.3 trees per plot. The mean tree DBH was 50 cm. Dominant trees included *Thuja plicata*, *Acer circinatum* and *Abies amabilis*.

Douglas-fir Forests soils were dry, organic or loamy, with an average litter depth of 7.6 cm. The mean

coarse woody debris volume was 5.3 m³ per plot. Slopes averaged 7.8%. Mean herb species richness was 3.3 species per plot, with herb cover averaging 61%, and mosses were the dominant herbs. Shrub species richness averaged 2.6 species per plot, mean shrub cover was 26%, and there were no dominant shrubs. Canopy closure averaged 99.5%, with 15 trees per plot. The mean tree DBH was 17 cm. The dominant trees included *Abies amabilis*, *Pseudotsuga menziesii* and *Tsuga heterophylla*. These forests were the steepest of all sampled habitats, had the greatest average canopy closure, the greatest mean woody debris volume, the greatest number of trees per plot and the greatest average litter depth of all sampled habitats.

Gravel Bars soils were dry, lacked litter and were composed of sand, gravel and cobbles. The average coarse woody debris volume was 1.5 m³ per plot. The mean slope was 3.2%. Average herb species richness was 2.6 species per plot, mean herb cover was 5.7%, and there were no dominant herbs. Shrub species richness averaged 1.9 species per plot, mean shrub cover was 11%, and there were no dominant shrubs. Mean canopy closure was 17%, with 0.2 trees per plot. The average tree DBH was 27 cm. No trees were dominant. Gravel Bars had the least mean herb and shrub cover of sampled habitats, as well as the least species richness of herbs and shrubs.

Willow-Sedge Swamps soils were wet and organic, with an average litter depth of 6.3 cm. There was no

discernible coarse woody debris. These swamps were essentially flat, with a mean slope of 0.3%. Average herb species richness was 6.1 species per plot, mean herb cover was 157%, and dominant herbs were *Carex* spp. and species of *Equisetum*. Shrub species richness averaged 2.2 species per plot, mean shrub cover was 40%, and the dominant shrubs were *Salix sitchensis* and *Spiraea douglasii*. Canopy closure averaged 4.5%, with no trees per plot. There were no dominant trees.

Sampling Method.

Part of the purpose of the BBCRNA Terrestrial Riparian Arthropod Project was to develop and assess a simple sampling protocol that required a minimum of resources. The basic sampling design, utilizing pitfall traps, was developed in consultation with Reed Glesne (NOCA) and Greg Brenner (Pacific Analytics, Albany, OR). Pitfall trapping is a well-established and resource-efficient method for sampling ground-active arthropods, with an extensive literature base (e.g., Southwood 1978, Quinn et al. 1990, Spence and Niemela 1994, and Digweed et al. 1995). The benefits and limitations of this method are addressed in the discussion pertaining to sampling protocols.

Trap Design and Placement.

For each habitat type, ten separate patches were randomly selected. One pitfall trap was placed in each patch (Figure 4), for a total of ten traps per habitat. Each patch functioned as a replicate within the respective habitats. Thus, 50 total traps were utilized per year. Each 1996 trap was shifted in a randomly chosen direction approximately 10 m from the 1995 position. This approach was taken to minimize individual trap location bias and population depletion effects (Digweed et al. 1995), where trap catches gradually decline as populations of susceptible taxa are reduced by the traps. The pitfall traps were based upon a design used extensively in studies conducted at the H.J. Andrews Experimental Forest in Oregon (Parsons et al. 1991). Each trap consisted of a plastic bucket 18 cm tall with a diameter of 14 cm at the top and 12 cm at the bottom. An aluminum funnel was placed inside the top to prevent arthropods from escaping. The funnel extended about 8 cm down into the bucket with a bottom opening of 3 to 4 cm and the top tightly wedged inside and near the rim of the bucket. A 16 oz plastic cup, filled with approximately 100 ml of propylene glycol (non-toxic Sierra™ brand antifreeze) preservative, was placed inside the bucket, below the bottom of the funnel. This design reduced the continual disturbance that occurs with a cup set directly in the ground, minimizing "digging-in effects" (Digweed

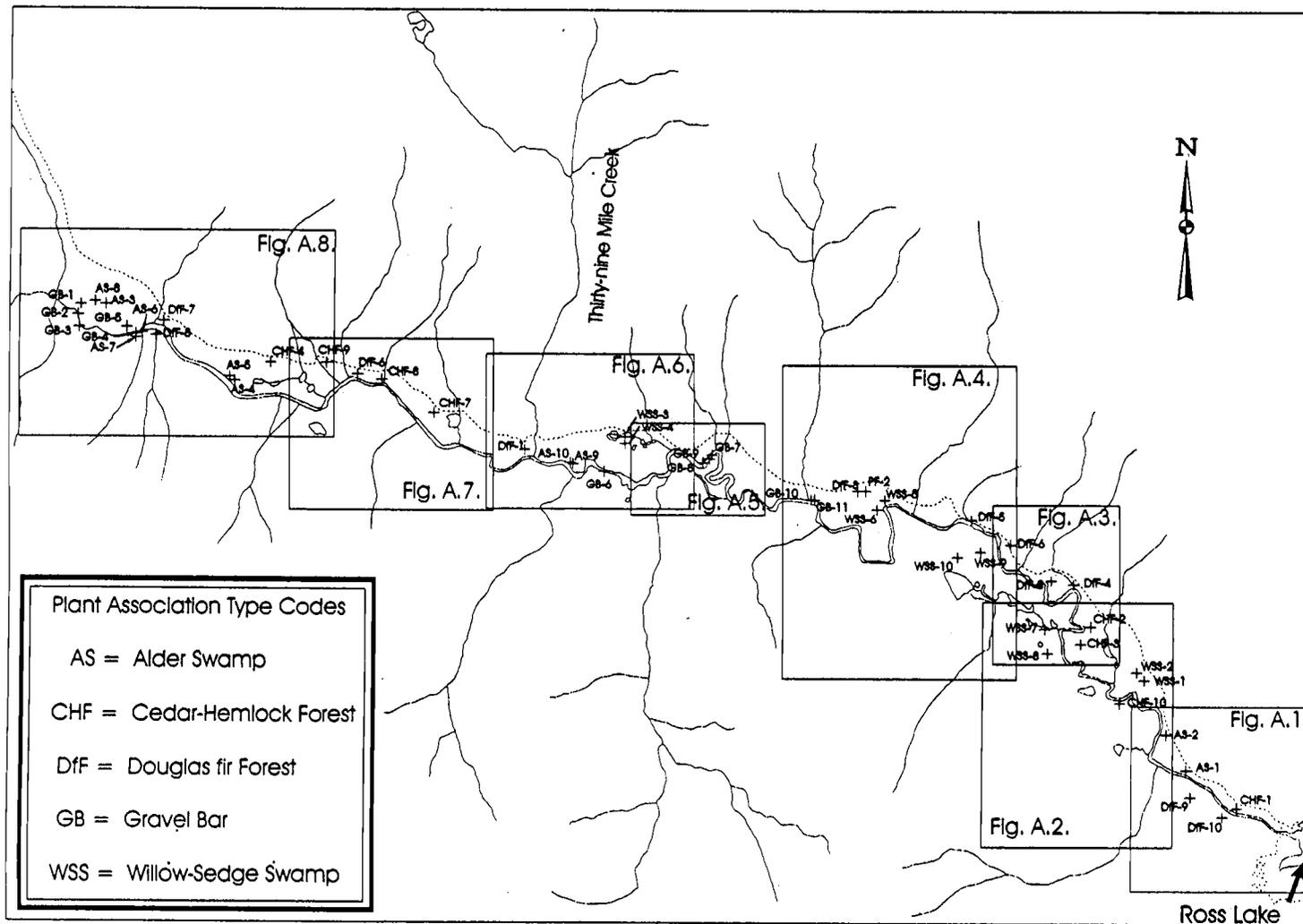


Figure 4. Beetle pitfall trap locations, Big Beaver Creek R.N.A., North Cascades National Park, Washington, 1995-1996.

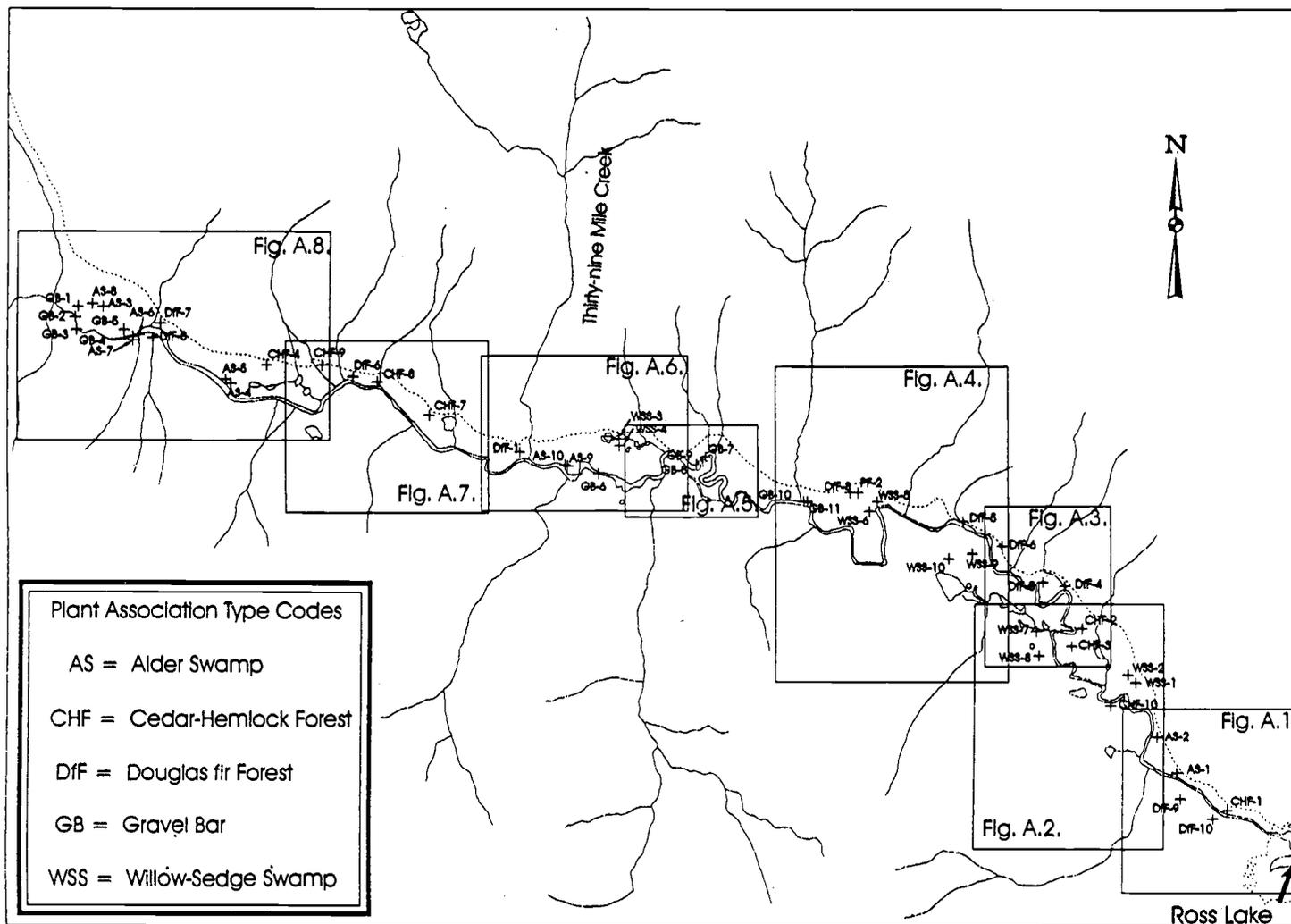


Figure 4. Beetle pitfall trap locations, Big Beaver Creek R.N.A., North Cascades National Park, Washington, 1995-1996. Figures A.1 through A.8 are not included in this document.

et al. 1995), where catches are greatest immediately after a pitfall trap has been set. This effect is distinct from depletion effects (Digweed et al. 1995).

A trap was set into the ground so that the top of the bucket was even with the level of the surrounding substrate. The bucket hole was excavated with a hand trowel, with backfill and litter repositioned to approximate the original condition of the trapsite. The cup with the antifreeze was set inside the bucket and the funnel was installed. Finally, a 2 x 25 x 25 cm wooden board supported by 2 x 2 x 5 cm legs was set over the trap to keep out debris and rain.

Sampling Protocols.

Sampling was conducted from mid-June to mid-October of 1995 and 1996, periods predominantly free of snow. Traps operated continuously throughout these sampling periods. Samples were collected monthly. Severely damaged or disturbed samples were noted and discarded. Intact samples had the liquid decanted through a fine-mesh net into a container. Cups were rinsed with 70% ethanol and decanted through the net to acquire any residual specimens. Fresh antifreeze (~100 ml) was then added to the cups and the pitfall traps were reset. Used antifreeze was poured into a container for subsequent toxic waste disposal at NOCA facilities. Large detritus

was disposed of in the field after rinsing with ethanol to remove any adhering specimens. Samples were then placed within sealed containers with sufficient 70% ethanol to cover the specimens. The net was rinsed with ethanol over a container to ensure no small specimens remained. A data label recording the date of collection, habitat, and trap number was also placed inside the container. Samples were then transported back to the NOCA facilities for processing.

Upon receipt of samples at the NOCA facilities, NOCA staff cleaned and extracted all arthropods from each sample. Larvae and soft-bodied taxa were stored in 70% alcohol. With the exception of necrophagous beetles (see below), all other arthropods were mounted and labeled. Processed and mounted sample material was then transported to OSU, where I identified the beetles.

SECTION 3: BEETLE IDENTIFICATION AND BIOLOGICAL DATA

All beetle specimens were identified, most to species, via the literature, comparison with named material in the OSU Oregon State Arthropod Collection, and consultation with other taxonomists. It was not possible to identify several species as the gender collected lacked the necessary taxonomic characters, e.g., *Lobrathium* sp. (Staphylinidae). Most Aleocharinae (Staphylinidae) could not be identified below the subfamily because there were no adequate taxonomic

treatments for most members of this taxon at the time of my study.

Family boundaries largely followed Lawrence and Newton (1995) and Arnett and Thomas (2001). Consequently, *Cicindela* species (formerly Cicindelidae) were included within the Carabidae; *Leptinus occidentamericanus* Peck (formerly Leptinidae) was included in the Leiodidae; former Pedilidae were treated as either Anthicidae (*Eurygenius campanulatus* LeConte) or Pyrochroidae (*Pedilus jonae* Young), while *Ischalia vancouverensis* Harris (formerly Pyrochroidae) was transferred to the Anthicidae; and all former Pselaphidae, *Empelus brunnipennis* Mannerheim (formerly Clambidae), *Baocera humeralis* Fall (formerly Scaphiidae), and *Micropeplus nelsoni* Campbell (formerly Micropeplidae) were included within the Staphylinidae.

Nomenclature and species level identification for a wide variety of families was acquired via Hatch (1953, 1957, 1961, 1965, 1971), Arnett (1968), Bousquet (1991), Downie and Arnett (1996a, 1996b), and Poole and Gentili (1996). Much of the ecological and trophic information was gleaned from Balduf (1935), Crowson (1981), Klausnitzer (1983), White (1983), Parsons et al. (1991), Stehr (1991), and Arnett and Thomas (2001).

Literature used to identify Carabidae included Lindroth (1961-1969), Wallis (1968), Erwin and Kavanaugh (1981), and Liebherr (1994). Several of these sources also provided ecological and trophic data. Sources of

general carabid ecological and trophic data included Erwin et al. (1979), den Boer et al. (1986), Stork (1990), Desender et al. (1994), Niemela (1996), and Brandmayr et al. (2000). Carabid nomenclature and distributions generally followed Bousquet and Laroche (1993).

Elateridae were largely identified using Hatch (1971). Several members of the Denticollinae were identified with Horn (1891), since no more recent treatment exists. Paul J. Johnson (South Dakota State University) provided much valuable information on current nomenclature and elaterid trophic roles. Becker (1991) provided a useful general discussion of elaterid biology.

Many Staphylinidae were identified to species with Hatch (1957), as no more recent treatments were available. Current revisions for several taxa included Smetana (1971) and Campbell (1973, 1978, 1979, 1982, 1988, 1989, 1991, 1993). Newton et al. (2001) provided revisions for some genera. General discussions of staphylinid biology were provided by Frank (1991) and Newton et al. (2001). Known distributions, as well as some habitat and trophic data, were found in Moore and Legner (1975) and Newton et al. (2001). Chandler (1997) was used for Pselaphinae.

The literature cited below was used to identify members of the following families: Byrrhidae (Johnson 1991), Cerambycidae (Linsley and Chemsak 1976), Coccinellidae (Gordon 1985), Hydrophilidae (Smetana

1978), and Leiodidae (Baranowski 1993, Peck and Stephan 1996). Distributional and habitat information was also available from some of these publications.

Beetle species were assigned trophic categories based upon the literature referenced above and personal observations. These categories were detritivores, fungivores, herbivores, omnivores, and predators. Those taxa for which no reliable trophic data was available were referred to the "unknown" category.

Dual reference collections of all identified beetles were developed for NOCA and OSU. Species represented only by single specimens were deposited in the NOCA reference collection. The NOCA reference collection resides at the North Cascades National Park Research Center, while the OSU reference collection is housed in the Oregon State Arthropod Collection.

SECTION 4: ANALYSIS

All known necrophagous beetles, those species feeding upon carrion, were excluded from analyses, based upon the rationale of Brenner (2000) (see the discussion on the sampling method). Unless otherwise stated, in the following text "all beetles" or "beetles" refers only to non-necrophagous beetles.

The monthly count of each species from each of the ten traps per habitat was combined to yield a total count

for each species per each habitat per month. These monthly counts were used for most analyses and were pooled as needed for monthly, annual, or biennial totals. For trophic categorization, only those species with at least six total individuals among all habitats for both years were considered. Species represented by only one individual could not occur in more than one habitat, so were useless for habitat comparisons. A species represented by five or fewer individuals could be apparently confined to a single habitat through simple probability.

Sampling effort, as measured by trap days, was calculated on a basis of 30 days per month times the number of undisturbed trap-samples per habitat. For instance, 1995 Alder Swamps effort was calculated as follows: 4 months X 10 traps X 30 days = 1200 trap days. The efficacy of the sampling in detecting the total beetle fauna was addressed via comparative species curves. These curves were smoothed by ordering the numbers of new species accumulated per sample in descending order, using the method of Brenner (2000).

Percentages, for example, of the individuals per family per habitat or species per family per habitat, were generally rounded to the nearest whole percent. Percentages originally calculated with a fraction of 1/2 percent were rounded to the next highest whole percent. Table 2 was an exception to this practice. Percentages therein were carried out to two decimals so "rare"

families were not ranked equally when their abundance values were below 1%.

Most tabulation and basic computation was performed with Microsoft Excel, as was the computation of information used in constructing the comparative species curves. The comparative species curves were made in Excel as well. Excel was also used to perform any statistical tests not associated with biodiversity indices. Diversity and evenness indices were performed using BioStat II (Sigma Soft 1993). Indices used included: the Shannon-Wiener index, H' , a Type I index sensitive to changes in rare species; the complement of Simpson's index, $1-D$, a Type II index sensitive to changes in more abundant species; and the most commonly used index of evenness, J' , derived from the Shannon-Wiener index (Ludwig and Reynolds 1988, Krebs 1989).

CHAPTER 3: RESULTS

SECTION 1: SAMPLING EFFORT

Trap days totalled 11,430, with 5,790 in 1995 and 5,640 in 1996 (Figure 5). Annual trap days per habitat ranged from 990-1,290 and total trap days per habitat from 2,100 (Douglas-fir Forests) to 2,460 (Gravel Bars).

SECTION 2: PATTERNS OF INDIVIDUALS

A grand total of 8,179 non-necrophagous beetles were trapped in 1995 and 1996. Fewer beetles were trapped in 1995 (3,813) than in 1996 (4,366) (Table 1). Alder Swamps had the greatest raw beetle abundance (2,071), followed by Gravel Bars (1,746), Douglas-fir Forests (1,571), Cedar-Hemlock Forests (1,530), and Willow-Sedge Swamps (1,261) (Figure 6).

Grand total standardized abundance averaged 21 individuals per trap per month (Figure 7). Annual standardized abundance reflected that of raw totals, with 20 for 1995 and 23 for 1996. Alder Swamps had the greatest total standardized abundance (27) and Willow-Sedge Swamps (16) the least, with Cedar-Hemlock Forests, Douglas-fir Forests, and Gravel Bars essentially equal with values in the low twenties.

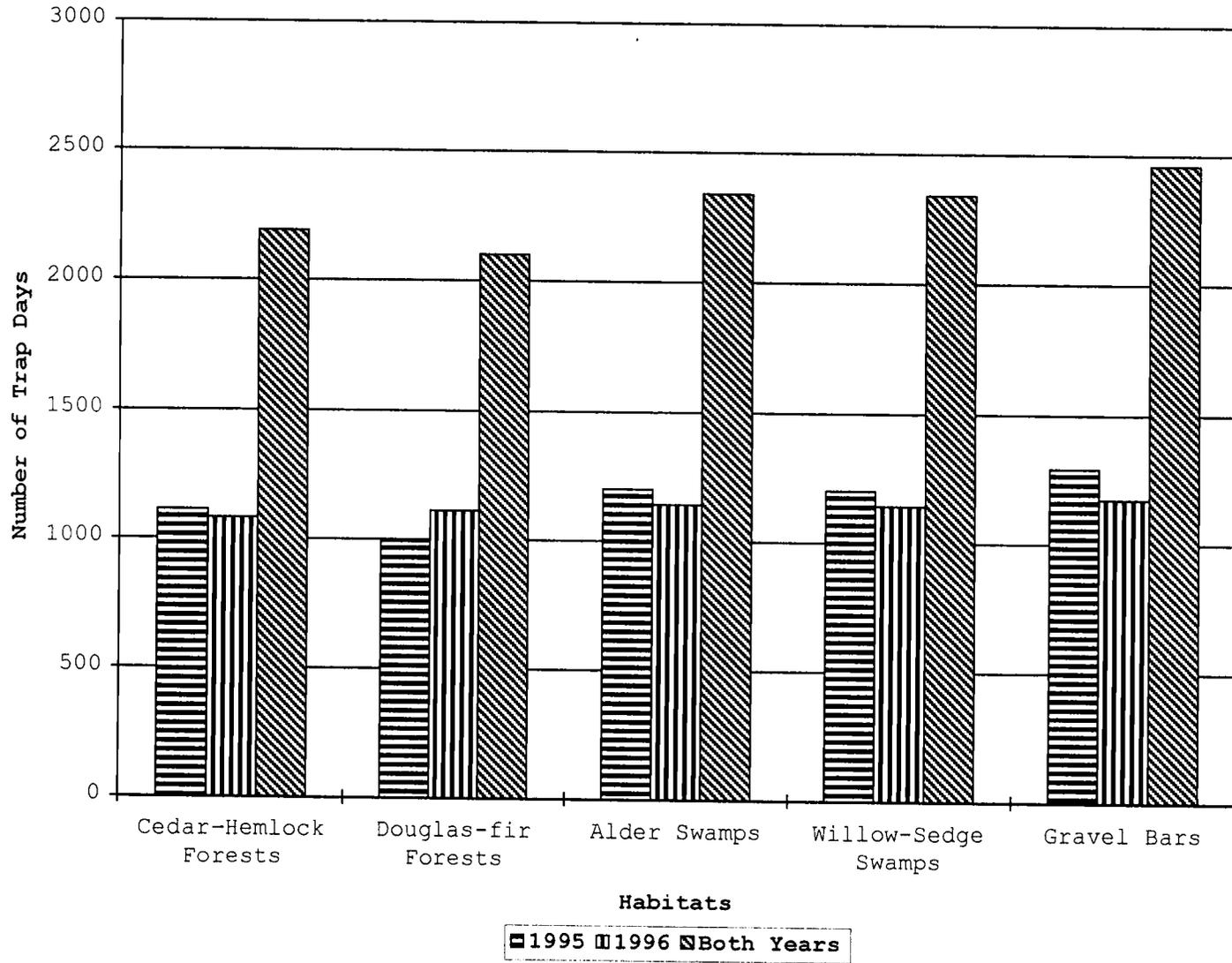


Figure 5. Trap Days Per Habitat.

Table 1. Beetle Species and Habitats.

Key to Years: 95 = 1995, 96 = 1996, Tot. = Total

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
Amphizoidae (1 species)																		
<i>Amphizoa insolens</i> LeConte														1		1	1	1
Anthicidae (3 species)																		
<i>Anthicus nanus</i> LeConte										1		1	8	5	13	9	5	14
<i>Eurygenius campanulatus</i> LeConte													363	116	479	363	116	479
<i>Ischalia vancouverensis</i> Harris	1	1	2				1	11	12							2	12	14
Byrrhidae (5 species)																		
<i>Byrrhus kirbyi</i> LeConte							1		1							1		1
<i>Curimopsis albonotata</i> (LeConte)												1		1	1	1		1
<i>Cytilus alternatus</i> (Say)										8	11	19				8	11	19
<i>Morychus aeneolus</i> (LeConte)		1	1										2		2	2	1	3
<i>Morychus oblongus</i> (LeConte)													1		1	1		1
Cantharidae (4 species)																		
<i>Malthodes alexanderi</i> Fender					1	1											1	1
<i>Malthodes</i> sp.					1	1											1	1
<i>Podabrus conspiratus</i> Fall				1		1										1		1
<i>Podabrus piniphilus</i> (Dejean)				1		1							1	1	1	1	1	2
Carabidae (55 species)																		
<i>Agonum brevicolle</i> Dejean										117	308	425				117	308	425
<i>Agonum consimile</i> (Gyllenhal)		1	1														5	5

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Agonum ferruginosum</i> (Dejean)							1	1	2	17	34	51				18	35	53
<i>Agonum piceolum</i> (LeConte)		1	1				1	3	4							1	4	5
<i>Agonum thoreyi</i> Dejean										1	3	4				1	3	4
<i>Amara littoralis</i> Mannerheim										2		2				2		2
<i>Anchomenus quadratus</i> (LeConte)										1		1				1		1
<i>Anisodactylus binotatus</i> (Fabricius)										1		1				1		1
<i>Apristus constrictus</i> Casey													1	1	2	1	1	2
<i>Bembidion breve</i> (Motschulsky)													1		1	1		1
<i>Bembidion concretum</i> Casey										1		1				1		1
<i>Bembidion convexulum</i> Hayward										3		3				3		3
<i>Bembidion erasum</i> LeConte											1	1					1	1
<i>Bembidion forttestriatum</i> (Motschulsky)										5	7	12				5	7	12
<i>Bembidion hesperum</i> Fall													1		1	1		1
<i>Bembidion incrematum</i> LeConte										3	5	8				3	5	8
<i>Bembidion kuprianovi</i> Mannerheim	3		3	1	1	20	5	25					2		2	25	6	31
<i>Bembidion planatum</i> (LeConte)													20	22	42	20	22	42
<i>Bembidion planiusculum</i> Mannerheim													2	2	4	2	2	4
<i>Bembidion quadriveolatum</i> Mannerheim											1	1					1	1
<i>Bembidion quadrimaculatum dubitans</i> (LeC.)											1	1					1	1
<i>Bembidion semipunctatum</i> (Donovan)											1	1					1	1
<i>Bembidion stillaguamish</i> Hatch														1	1		1	1
<i>Blethisa oregonensis</i> LeConte										20	3	23				20	3	23

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Bradycellus conformis</i> (Fall)										8		8				8		8
<i>Bradycellus nigrinus</i> (Dejean)										26		26				26		26
<i>Calathus fuscipes</i> (Goeze)								1	1								1	1
<i>Chlaenius interruptus</i> Horn										13	5	18				13	5	18
<i>Cicindela depressula</i> Casey													9	8	17	9	8	17
<i>Cicindela oregona oregona</i> LeConte													16	29	45	16	29	45
<i>Diplous aterrimus</i> (Dejean)													3	2	5	3	2	5
<i>Elaphrus clairvillei</i> Kirby										1		1				1		1
<i>Elaphrus purpurans</i> Hausen							1	5	6							1	5	6
<i>Harpalus cordifer</i> Notman							4	1	5							4	1	5
<i>Harpalus somnulentus</i> Dejean										1	3	4				1	3	4
<i>Leistus ferruginosus</i> Mannerheim	22	7	29	1		1	11	7	18							34	14	48
<i>Loricera decempunctata</i> Eschscholtz	1		1				2	7	9	18	25	43				21	32	53
<i>Nebria gebleri cascadenis</i> Kavanaugh														1	1		1	1
<i>Nebria mannerheimi</i> Fischer													39	2	41	39	2	41
<i>Nebria sahlbergi sahlbergi</i> Fischer													20	7	27	20	7	27
<i>Notiophilus sylvaticus</i> Eschscholtz	2		2	1		1										3		3
<i>Opisthius richardsoni</i> Kirby													10		10	10		10
<i>Patrobus fossifrons</i> (Eschscholtz)	1	1	2				2		2		1	1				3	2	5
<i>Pterostichus adstrictus</i> Eschscholtz	1	6	7				14	6	20	21	11	32				36	23	59
<i>Pterostichus castaneus</i> (Dejean)		1	1														1	1
<i>Pterostichus herculeanus</i> Mannerheim	11	15	26	20	26	46	8	6	14				2		2	41	47	88

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Pterostichus neobrunneus</i> Lindroth	37	36	73	33	33	66	1	1	2							71	70	141
<i>Pterostichus riparius</i> (Dejean)	5	1	6				21	12	33	13		13	4		4	43	13	56
<i>Scaphinotus angulatus</i> (Harris)				2	3	5										2	3	5
<i>Scaphinotus angusticollis</i> (Fischer)	207	252	459	318	200	518	28	31	59							553	483	1036
<i>Scaphinotus marginatus</i> (Fischer)	17	15	32	3	1	4	29	23	52	9	4	13	1		1	59	43	102
<i>Synuchus impunctatus</i> (Say)	2	1	3	1		1										3	1	4
<i>Trechus chalybeus</i> Dejean							4	3	7	17	13	30				21	16	37
<i>Trechus oregonensis</i> Hatch							5		5			2			2	5	2	7
<i>Trichocellus cognatus</i> (Gyllenhal)										9	2	11				9	2	11
Cerambycidae (3 species)																		
<i>Brachyleptura dehiscens</i> (LeConte)													1		1	1		1
<i>Stenocorus flavolineatus</i> (LeConte)		1	1														1	1
<i>Xestoleptura crassipes</i> (LeConte)										1		1				1		1
Chrysomelidae (8 species)																		
<i>Altica tombacina</i> (Mannerheim)										2	1	3				2	1	3
<i>Chaetocnema irregularis</i> LeConte										1	1	2				1	1	2
<i>Chrysomela mainensis</i> Bechyne							1		1							1		1
<i>Crepidodera nana</i> (Say)										1		1				1		1
<i>Hippuriphila mancula</i> (LeConte)										2		2				2		2
<i>Macrohaltica ambiens</i> (LeConte)								1	1					1	1		2	2
<i>Macrohaltica caurina</i> (Blake)													1		1	1		1
<i>Pyrrhalta punctipennis</i> (Mannerheim)											3	3					3	3

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
Clidae (3 species)																		
<i>Cis americanus</i> Mannerheim					1	1											1	1
<i>Cis maritimus</i> (Hatch)	1		1													1		1
<i>Octotemnus laevis</i> Casey								1	1								1	1
Coccinellidae (3 species)																		
<i>Hippodamia washingtoni</i> Timberlake											1	1					1	1
<i>Scymnus caurinus</i> Horn													2	1	3	2	1	3
<i>Stethorus punctum picipes</i> Casey							1		1							1		1
Colydiidae (1 species)																		
<i>Lasconotus vegrandis</i> Horn								1	1								1	1
Corylophidae (1 species)																		
<i>Orthoperus scutellaris</i> LeConte											1	1					1	1
Cryptophagidae (11 species)																		
<i>Anchicera ephippiata</i> (Zimmerman)								1	1								1	1
<i>Anchicera kamtschatica</i> (Motschulsky)							6	11	17							6	11	17
<i>Anchicera postpallens</i> (Casey)										12	2	14				12	2	14
<i>Antherophagus ochraceus</i> Melsheimer													1		1	1		1
<i>Atomaria constricta</i> (Casey)													1		1	1		1
<i>Caenoscelis ferruginea</i> (Sahlberg)		1	1														1	1
<i>Cryptophagus cellaris</i> (Scopoli)					1	1											1	1
<i>Cryptophagus confertus</i> Casey	5	7	12	1	13	14	1	4	5							7	24	31
<i>Cryptophagus lapponicus</i> Gyllenhal	2	2	4		2	2										2	4	6

Table 1 (continued).

SPECIES	HABITATS															TOTALS			
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.	
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.				
<i>Cryptophagus tuberculosus</i> Maklin							1		1							1		1	
<i>Henotiderus loma</i> (Hatch)				2	1	3										2	1	3	
Curculionidae (6 species)																			
<i>Geoderces homi</i> (Van Dyke)	1		1	1		1										2		2	
<i>Lepesoma lecontei</i> (Casey)				1	3	4										1	3	4	
<i>Lepesoma verrucifa</i> (Casey)	1		1		1	1										1	1	2	
<i>Rhyncolus brunneus</i> Mannerheim	5	10	15	3	12	15					1	1		1	1	8	24	32	
<i>Steremnius carinatus</i> (Boheman)	4	4	8	13	6	19										17	10	27	
<i>Sthereus horridus</i> (Mannerheim)	4	5	9	1	3	4	17	11	28							22	19	41	
Dytiscidae (6 species)																			
<i>Agabus anthracinus</i> Mannerheim											2	2					2	2	
<i>Agabus strigosus</i> (Crotch)										1	4	5				1	4	5	
<i>Agabus tristis</i> Aube											1	1					1	1	
<i>Agabus</i> sp. (female)							1		1							1		1	
<i>Hydroporus pacificus</i> Fall								1	1		1	1					2	2	
<i>Rhantus suturellus</i> (Harris)											2	2					2	2	
Elateridae (23 species)																			
<i>Ampedus carbonicolor</i> (Eschscholtz)					1	1		1	1									2	2
<i>Athous rufiventris</i> (Eschscholtz)													1		1	1		1	
<i>Athous vittiger</i> LeConte	1		1				1		1							2		2	
<i>Cardiophorus amplicollis</i> Motschulsky													7	3	10	7	3	10	
<i>Cardiophorus propinquus</i> Hatch													163	61	224	163	61	224	

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Ctenicera angusticollis</i> (Mannerheim)	1	1	2	1	1	2	1	1	2							3	3	6
<i>Ctenicera propola columbiana</i> Brown		1	1														1	1
<i>Ctenicera resplendens</i> (Eschscholtz)					1	1											1	1
<i>Ctenicera suckleyi</i> (LeConte)					1	1											1	1
<i>Ctenicera umbripennis</i> (LeConte)					1	1											1	1
<i>Ctenicera volitans</i> (Eschscholtz)		1	1														1	1
<i>Dalopus maritimus</i> Brown										1	1	1	2	3	1	3	4	4
<i>Hemicrepidius pallidipennis</i> (Mann.)		1	1		1	1	3	2	5						3	4	7	7
<i>Hypnoidus bicolor</i> (Eschscholtz)													5	5	5		5	5
<i>Hypolithus nocturnus</i> Eschscholtz													1	1	1	1		1
<i>Hypolithus squalidus</i> (LeConte)													3	1	4	3	1	4
<i>Ligmargus funebris</i> (Candeze)													86	12	98	86	12	98
<i>Migiwa striatulus</i> (LeConte)										1	1	9	17	26	9	18	27	27
<i>Negastrius ornatus</i> (LeConte)												20	3	23	20	3	23	23
<i>Zorochrus caurinus</i> (Horn)												8	7	15	8	7	15	15
<i>Zorochrus dispersus</i> (Horn)												61	46	107	61	46	107	107
<i>Zorochrus musculus</i> (Eschscholtz)							1	1				33	257	290	33	258	291	291
<i>Zorochrus</i> sp.										2	2	17	103	120	17	105	122	122
Endomychidae (1 species)																		
<i>Xenomycetes laversi</i> Hatch		1	1														1	1
Erotylidae (1 species)																		
<i>Triplax antica</i> LeConte							1		1							1		1

Table 1 (continued).

SPECIES	HABITATS															TOTALS			
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.	
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.				
Gyrinidae (1 species)																			
<i>Gyrinus picipes</i> Aube											2	2					2	2	
Histeridae (1 species)																			
<i>Hypocaccus bigemmus</i> (LeConte)													2		2		2	2	
Hydraenidae (2 species)																			
<i>Hydraena vandykei vandykei</i> Orchymont										2	1	3					2	1	3
<i>Ochthebius cribricollis</i> LeConte										1		1					1		1
Hydrophilidae (4 species)																			
<i>Cercyon adumbratum</i> Mannerheim							3	22	25								3	22	25
<i>Crenitis paradigma</i> (Orchymont)										1		1					1		1
<i>Helophorus auricollis</i> (Eschscholtz)										2		2					2		2
<i>Megasternum posticatum</i> (Mannerheim)					1	1		1	1									2	2
Laemophloeidae (1 species)																			
<i>Rhinomalus cygnaei</i> (Mannerheim)								1	1									1	1
Latridiidae (5 species)																			
<i>Enicmus cordatus</i> Belon	1	1	2	2	7	9											3	8	11
<i>Melanopthalma americana</i> (Mannerheim)							1	1	44	23	67						44	24	68
<i>Melanopthalma distinguenda</i> (Comolli)									1		1						1		1
<i>Melanopthalma gibbosa</i> (Herbst)									1		1						1		1
<i>Stepostethus liratus</i> (LeConte)							1	1	2		1	1					1	2	3
Leiodidae (20 species)																			
<i>Agathidium californicum</i> Horn	1		1				1	1	2								2	1	3

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
Agathidium concinnum Mannerheim	1		1				1		1							2		2
Agathidium contiguum Fall							1	2	3							1	2	3
Agathidium jasperinum Fall				1		1	2		2				1		1	4		4
Agathidium sp. (NEAR contiguum Fall)					2	2											2	2
Anisotoma confusa (Horn)		1	1														1	1
Anisotoma errans Brown		1	1														1	1
Colon asperatum Hom										4	34	38				4	34	38
Colon celatum Hom		1	1														1	1
Colon discretum Hatch											1	1					1	1
Colon inerme Mannerheim								1	1		1	1					2	2
Colon magnicolle Mannerheim		1	1					1	1	1	1	2	1		1	2	3	5
Colon sp.	2		2	2		2										4		4
Hydnobius simulator Brown		1	1														1	1
Leiodes cascadenis Baranowski	2		2				8	1	9	2		2				12	1	13
Leiodes lateritia (Mannerheim)	2	5	7		3	3	1	3	4							3	11	14
Leiodes puncticollis (Thomson)	1		1	3		3										4		4
Leptinus occidentamericanus Peck	1	1	2		2	2	4	1	5				1	2	3	6	6	12
Nemadus decipiens (Horn)		2	2		7	7											9	9
Platycholeus opacellus Fall													1		1	1		1
Lucanidae (1 species)																		
Ceruchus striatus LeConte					1	1											1	1

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
Lycidae (1 species)																		
<i>Dicyopterus simplicipes</i> Mannerheim		1	1														1	1
Melandryidae (1 species)																		
<i>Xylita laevigata</i> (Hellenius)										1		1					1	1
Melyridae (1 species)																		
<i>Hypebaeus bicolor</i> (LeConte)					1	1											1	1
Oedemeridae (3 species)																		
<i>Ditylus gracilis</i> LeConte	2	1	3	1		1	2	1	3							5	2	7
<i>Ditylus quadricollis</i> LeConte		1	1				4	6	10				10	1	11	14	8	22
<i>Xanthochroa testacea</i> Horn	1		1													1		1
Phalacridae (1 species)																		
<i>Phalacrus pencillatus</i> Say										2		2				2		2
Ptiliidae (4 species)																		
<i>Acrotrichis cognata</i> (Matthews)		27	27	1	1	2		7	7		15	15				1	50	51
<i>Acrotrichis henrici</i> (Matthews)								8	8		1	1					9	9
<i>Acrotrichis vicina</i> (Matthews)	1		1				8	9	17	4		4				13	9	22
<i>Ptenidium pusillum</i> (Gyllenhal)								3	3	1	3	4				1	6	7
Pyrochroidae (2 species)																		
<i>Dendroides ephemeroides</i> (Mannerheim)							2		2				1		1	3		3
<i>Pedilus jonae</i> Young		1	1				1		1							1	1	2
Scarabaeidae (4 species)																		
<i>Aegialia lacustris</i> LeConte													2		2	2		2

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Aegialia opaca</i> Brown													1	1	2	1	1	2
<i>Aphodius opacus</i> LeConte	1		1	1	1	2										2	1	3
<i>Onthophagus nuchicornis</i> (Linnaeus)										1		1				1		1
Scirtidae (3 species)																		
<i>Cyphon brevicollis</i> (LeConte)					1	1	1	1	2	1		1				2	2	4
<i>Cyphon padi</i> (Linnaeus)												3	3				3	3
<i>Cyphon variabilis</i> (Thunberg)										1	13	14				1	13	14
Scydmaenidae (3 species)																		
<i>Scydmaenus californicus</i> Motschulsky	1	5	6	2	2	4	2	1	3				1		1	6	8	14
<i>Scydmaenus fuchsi</i> (Brendel)	1		1													1		1
<i>Veraphis mirabilis</i> Marsh		7	7	4	2	6	2		2		1	1				6	10	16
Spaeritidae (1 species)																		
<i>Sphaerites politus</i> Mannerheim		1	1				1	1	2							1	2	3
Staphylinidae (92 species)																		
<i>Acidota crenata</i> (Fabricius)	1		1				5	3	8							6	3	9
<i>Actium barri</i> Park & Wagner	2	2	4	1		1										3	2	5
<i>Actium hatchi</i> Park & Wagner								1	1								1	1
<i>Aleochara bilineata</i> Gyllenhal										1		1	2		2	3		3
<i>Aleochara bimaculata</i> Gravenhorst													1	1	2	1	1	2
Aleocharinae	112	267	379	133	388	521	324	346	670	46	35	81	4	6	10	619	1042	1661
<i>Anthobium clarkae</i> Hatch	1	1	2	5	4	9	1		1							7	5	12
<i>Anthobium reflexicollis</i> (Casey)	11		11				13	54	67					2	2	24	56	80

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Anthobium sinuosum</i> Hatch		4	4		3	3	1	4	5					1	1	1	12	13
<i>Atrecus macrocephalus</i> (Nordmann)								1	1								1	1
<i>Atrecus punctiventris</i> (Fall)											1	1					1	1
<i>Baeocera humeralis</i> Fall							1	1	2							1	1	2
<i>Bisnius hesperidum</i> Smetana								1	1			3	3				4	4
<i>Bisnius siegwaldii</i> (Mannerheim)	5	3	8	1	1	2	14	4	18	1		1				21	8	29
<i>Bledius cedarensis</i> Hatch								1	1								1	1
<i>Bledius suturalis</i> LeConte													6	1	7	6	1	7
<i>Bolitobius kremeri</i> Malkin	1	1	2	1		1	2	3	5							4	4	8
<i>Bryophacis canadensis</i> Campbell							2		2							2		2
<i>Bryophacis punctatissimus</i> (Hatch)		1	1	1		1	2		2							3	1	4
<i>Cupila excavata</i> Park & Wagner							2		2	2		2				4		4
<i>Cypha crotchii</i> (Horn)													1		1	1		1
<i>Deinopteroloma pictum</i> (Fauvel)		1	1		4	4											5	5
<i>Deinopteroloma subcostatum</i> (Maklin)	1		1	1		1										2		2
<i>Dianous nitidulus</i> LeConte											1	1					1	1
<i>Dinothenarus pleuralis</i> (LeConte)	17	28	45	22	7	29	2	3	5							41	38	79
<i>Elonium</i> sp. (NEAR <i>barri</i> (Hatch))	7	23	30				2	11	13							9	34	43
<i>Empelus brunnipennis</i> (Mannerheim)	3	5	8	1	3	4	2	8	10				1		1	7	16	23
<i>Erichsonius cinerascens</i> (Gravenhorst)										1		1				1		1
<i>Eusphalerum fenyese</i> (Bernhauer)							2	29	31							2	29	31
<i>Eusphalerum pothos</i> (Mannerheim)								89	89					4	4		93	93

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Gabrius cushmani</i> (Hatch)	3	1	4													3	1	4
<i>Gabrius picipennis</i> (Maklin)							2	2	4	1	1	2				3	3	6
<i>Gabrius seattlensis</i> (Hatch)							37	23	60	1		1				38	23	61
<i>Gabrius shulli</i> (Hatch)							2		2							2		2
<i>Heterothops fuscus</i> LeConte													1		1	1		1
<i>Ischnosoma fimbriatum</i> Campbell		1	1				1	3	4							1	4	5
<i>Ischnosoma pictum</i> (Horn)				1		1	1	1	2							2	1	3
<i>Ischnosoma splendidum</i> (Gravenhorst)		2	2														2	2
<i>Lathrobium punctulatum?</i> LeConte										3	1	4				3	1	4
<i>Lathrobium vancouveri</i> Casey											1	1					1	1
<i>Lithocaris capitula</i> (Casey)											2	2					2	2
<i>Lordithon fungicola</i> Campbell	7	23	30	13	26	39	39	18	57				4	1	5	63	68	131
<i>Lordithon poecilus</i> (Mannerheim)	3	16	19	2	27	29	12	2	14							17	45	62
<i>Lordithon thoracicus</i> Fabricius							1		1							1		1
<i>Lucifotychus cognatus</i> (LeConte)	3	1	4		1	1	2	6	8	1	1	2	1		1	7	9	16
<i>Lucifotychus impellus</i> Park & Wagner													1		1	1		1
<i>Megarathrus arcuatus</i> Hatch		1	1								1	1					2	2
<i>Megarathrus pictus</i> Motschulsky	9		9				7	17	24							16	17	33
<i>Megarathrus sinuaticollis</i> (Boisd.&Lac.)	1	1	2	3	4	7	26	20	46							30	25	55
<i>Microedus austinianus</i> LeConte													1		1	1		1
<i>Microedus laticollis</i> (Mannerheim)														3	3		3	3
<i>Micropeplus nelsoni</i> Campbell							4	15	19							4	15	19

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	TOT.
<i>Mycetoporus americanus</i> Erichson							2		2							2		2
<i>Mycetoporus bipunctatus</i> Campbell	1	1	2					2	2							1	3	4
<i>Mycetoporus pacificus</i> Campbell	2	2	4				3		3							5	2	7
<i>Nitidotachinus tachyporoides</i> (Horn)								1	1								1	1
<i>Omalius foraminosum</i> Maklin		1	1				3	1	4				1	1		3	3	6
<i>Ontholestes cingulatus</i> (Gravenhorst)	1		1								2	2				1	2	3
<i>Oropus striatus</i> (LeConte)	3	5	8	3	1	4	2	1	3							8	7	15
<i>Oxytelus laqueatus</i> (Marshall)	1		1				37	6	43	1		1				39	6	45
<i>Philonthus crotchi</i> Horn								1	1	9	5	14				9	6	15
<i>Philonthus furvus</i> Nordmann		2	2		1	1	1	2	3	1	1	2				2	6	8
<i>Philonthus spiniformis</i> Hatch											2	2					2	2
<i>Phlaeopterus frosti</i> Hatch													1	1			1	1
<i>Proteinus basalis</i> Maklin	4	2	6	2	4	6	12		12							18	6	24
<i>Proteinus collaris</i> Hatch	26	9	35				63	91	154							89	100	189
<i>Proteinus limbatus</i> Maklin	11	4	15		2	2	7	4	11				1	1		18	11	29
<i>Pseudopsis sulcata</i> Newman							2	1	3							2	1	3
<i>Quedius breviceps?</i> (Casey)							1		1							1		1
<i>Quedius crescenti</i> Hatch	1	1	2				1		1							2	1	3
<i>Quedius fulvicollis</i> (Stephens)								2	2								2	2
<i>Quedius griffinae</i> Hatch	1		1				1		1							2		2
<i>Quedius horni</i> Hatch	7	1	8				21	23	44	2	1	3	1		1	31	25	56
<i>Quedius oculus</i> (Casey)				1		1										1		1

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-flr Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
<i>Reichenbachia albionica</i> Motschulsky	2		2		1	1	17	1	18	34	48	82	1		1	54	50	104
<i>Sonoma hespera</i> Park & Wagner				1	2	3		3	3							1	5	6
<i>Stenus junio</i> Fabricius										5		5				5		5
<i>Stenus laccophilus</i> Casey							1		1	8	5	13				9	5	14
<i>Stenus maritimus</i> Motschulsky								1	1								1	1
<i>Stenus morio</i> Gravenhorst										23	9	32				23	9	32
<i>Stenus occidentalis</i> Casey											3	3					3	3
<i>Stenus plicipennis</i> (Casey)											1	1					1	1
<i>Stenus</i> sp.													1	1			1	1
<i>Tachinus basalis</i> Erichson	3	6	9	1	16	17	3	1	4		1	1	1		1	8	24	32
<i>Tachinus crotchii</i> Horn	10	8	18	13	16	29	56	42	98	8	7	15	6	2	8	93	75	168
<i>Tachinus maculicollis</i> Maklin	7	2	9		2	2	8	7	15					2	2	15	13	28
<i>Tachinus nigricornis</i> Mannerheim	6		6	2	1	3										8	1	9
<i>Tachinus semirufus</i> Horn	7	35	42	9	69	78										16	104	120
<i>Tachyporus canadensis</i> Campbell										2		2				2		2
<i>Tachyporus maculicollis</i> LeConte										1		1				1		1
<i>Tachyporus mexicanus</i> Sharp										2	1	3				2	1	3
<i>Trichophya pilicornis</i> (Gyllenhal)													5		5	5		5
Tenebrionidae (2 species)																		
<i>Helops pemitens</i> LeConte	1		1													1		1
<i>Scaphidema pictum</i> Horn													10	5	15	10	5	15

Table 1 (continued).

SPECIES	HABITATS															TOTALS		
	Cedar-Hemlock Forests			Douglas-fir Forests			Alder Swamps			Willow-Sedge Swamps			Gravel Bars			95	96	TOT.
	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.	95	96	Tot.			
Throscidae (1 species)																		
<i>Pactopus hornii</i> LeConte													1	1	2	1	1	2
Trogositidae (1 species)																		
<i>Temnochila chlorodia</i> (Mannenheim)				1		1										1		1
Zopheridae (1 species)																		
<i>Phelopsis porcata</i> (LeConte)		3	3	1	2	3										1	5	6
TOTAL INDIVIDUALS	2059	2336	1530	2065	2371	1571	2408	2528	2071	1984	2142	1261	2422	2189	1746	5238	5806	8179
NUMBER OF SPECIES	71	76	102	49	59	76	92	92	119	68	72	105	67	45	81	220	216	290

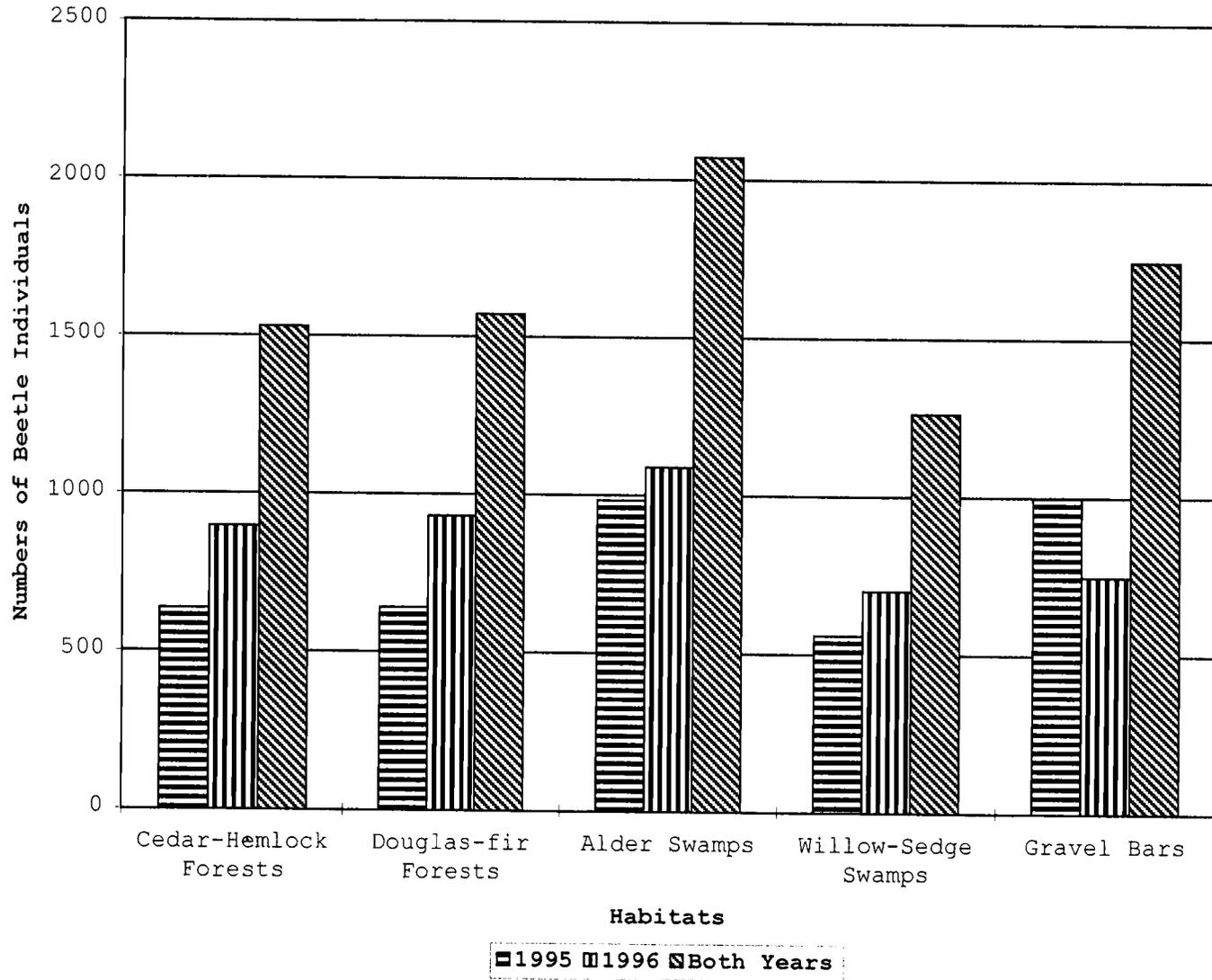


Figure 6. Individual Beetles Per Habitat.

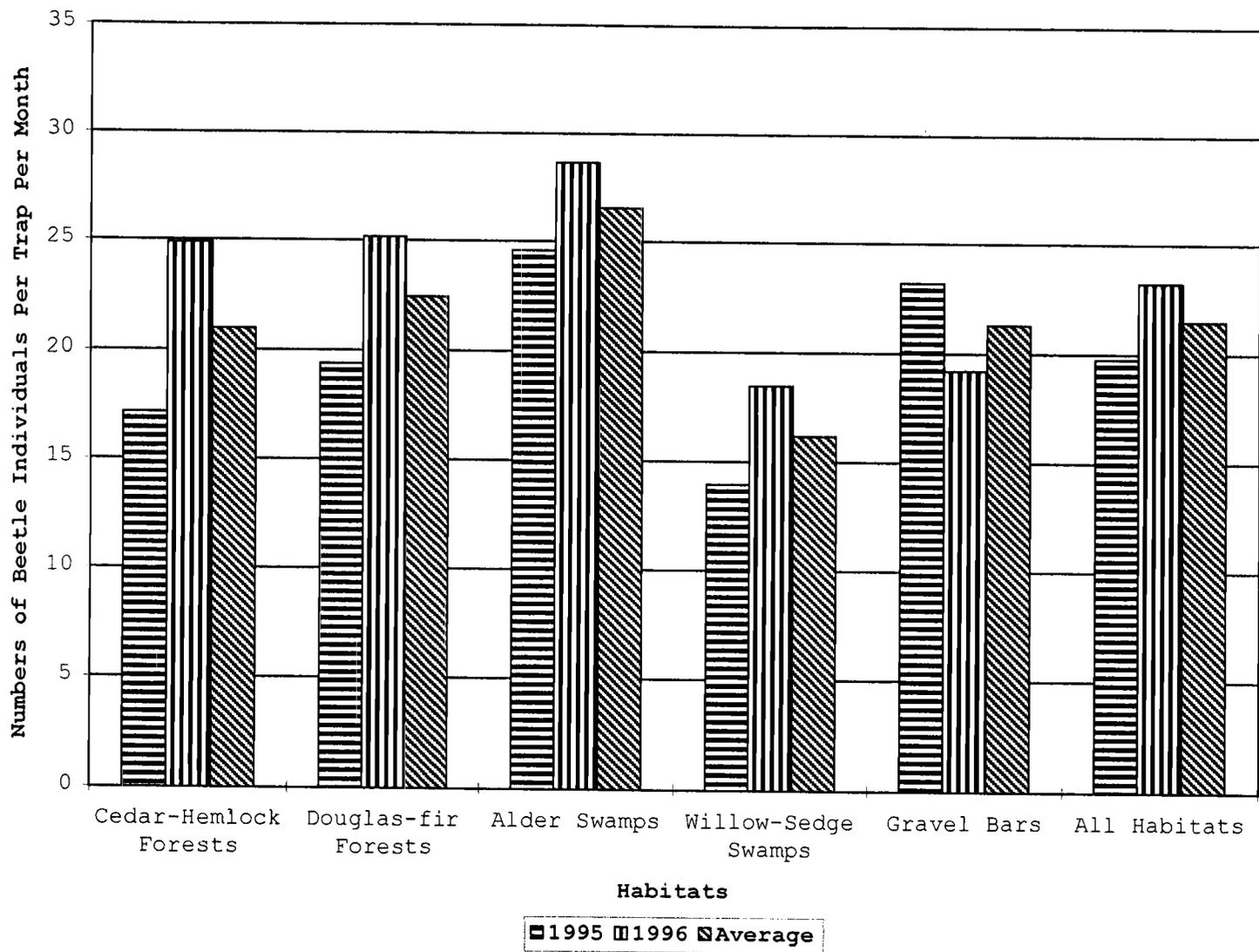


Figure 7. Phenology of Beetle Individuals.

Both the numbers of individuals per habitat and standardized abundance (Figures 6, 7) were, in general, greater in 1996 than 1995, with increases ranging from 11% (Alder Swamps) to 45% (Douglas-fir Forests). Gravel Bars were an exception to this trend, with the total number of individuals declining by 25% in 1996. The pattern for total abundance was the same for each year, except Gravel Bars had the second-to-lowest abundance in 1996.

Percentage of total beetle abundance was greatest in July (just over 30%) and lowest in October (about 15%) (Figure 8). Monthly abundance patterns varied among habitats. Alder Swamps were most similar to the overall pattern, although abundance was slightly greater in September than in July. Cedar-Hemlock and Douglas-fir Forests showed virtually identical patterns, with peak abundance (slightly more than 40%) in September. Gravel Bars and Willow-Sedge Swamps were similar, with greatest abundance in July (60% and 45%, respectively), although minimum Gravel Bar abundance was in October (5%), versus September for Willow-Sedge Swamps (near 11%).

SECTION 3: SPECIES DIVERSITY PATTERNS

A grand total of 290 species was collected (Table 1). Annual species richness was essentially invariant, with 220 species in 1995 and 216 in 1996, a difference of

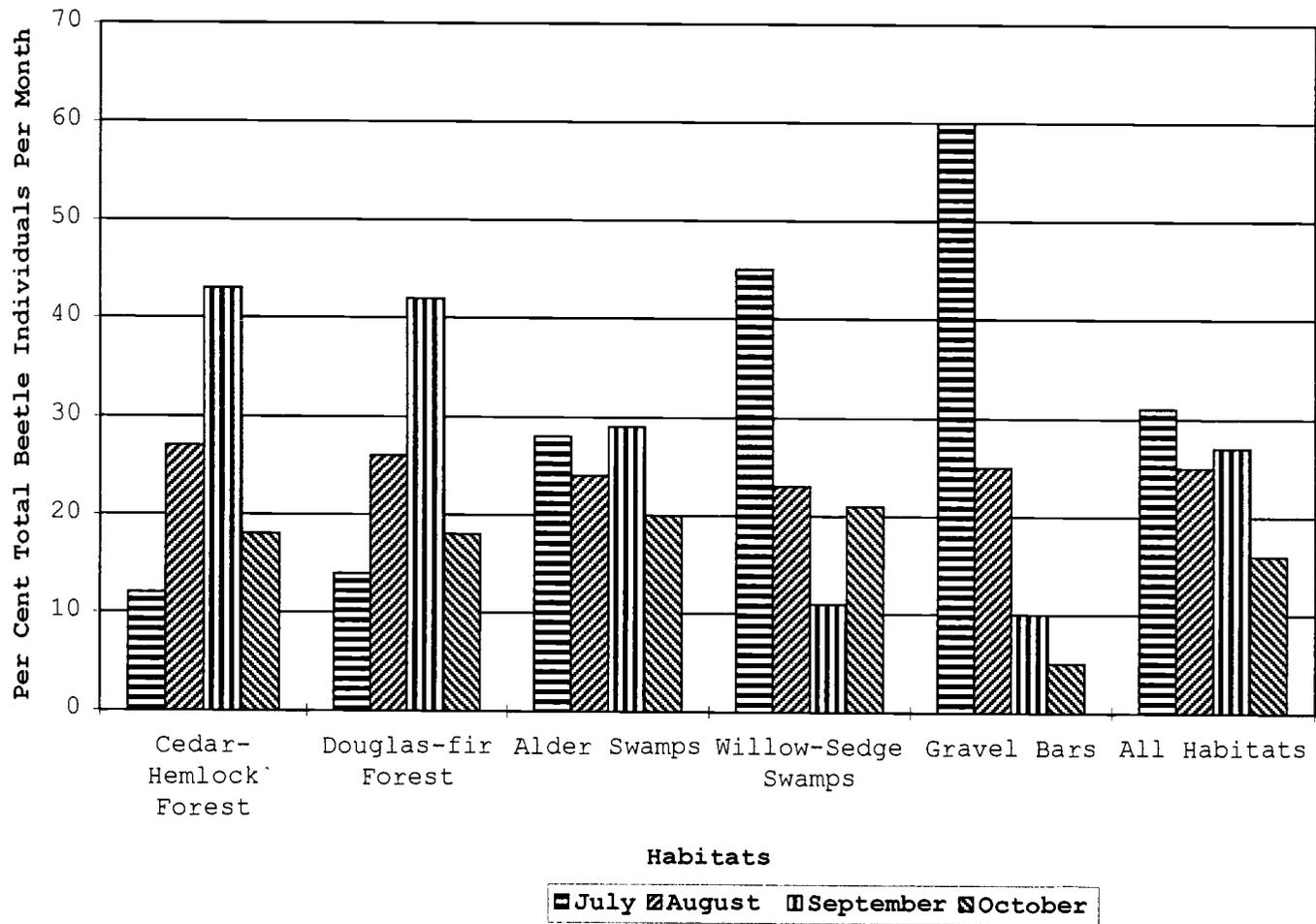


Figure 8. Per Cent Beetle Individuals Per Month Per Habitat.

less than 2%. While the annual species richness exhibited little change, the species composition varied between years (Table 1).

Total species richness varied among habitats (Figure 9). Alder Swamps had the greatest species richness (119), followed by Willow-Sedge Swamps (105), Cedar-Hemlock Forests (102), Gravel Bars (81), and Douglas-fir Forests (76). Annual habitat species richness varied little, in general, and overall reflected the grand total pattern. Douglas-fir Forests increased from 49 species in 1995 to 59 in 1996, a 20% gain. Gravel Bars declined 30% in 1996, from 67 species to 45 species. Annual species richness for all habitats was substantially less than total species richness per habitat, ranging from 56% (1996 Gravel Bars) to 77% (Alder Swamps, both years) of the totals per habitat.

The Shannon-Weiner diversity index revealed a pattern identical to that of grand total species richness (Figure 10). Alder Swamps had the highest total value, 5.5, while Douglas-fir Forests, at 3.4, had the lowest value. Willow-Sedge Swamps Cedar-Hemlock Forests had similar values, 4.3 and 4.2, respectively, and Gravel Bars, at 3.8, were slightly lower. For the most part, habitats also showed little difference in the Shannon-Weiner index between years and reflected the grand total pattern. Douglas-fir Forests increased from 2.6 in 1995

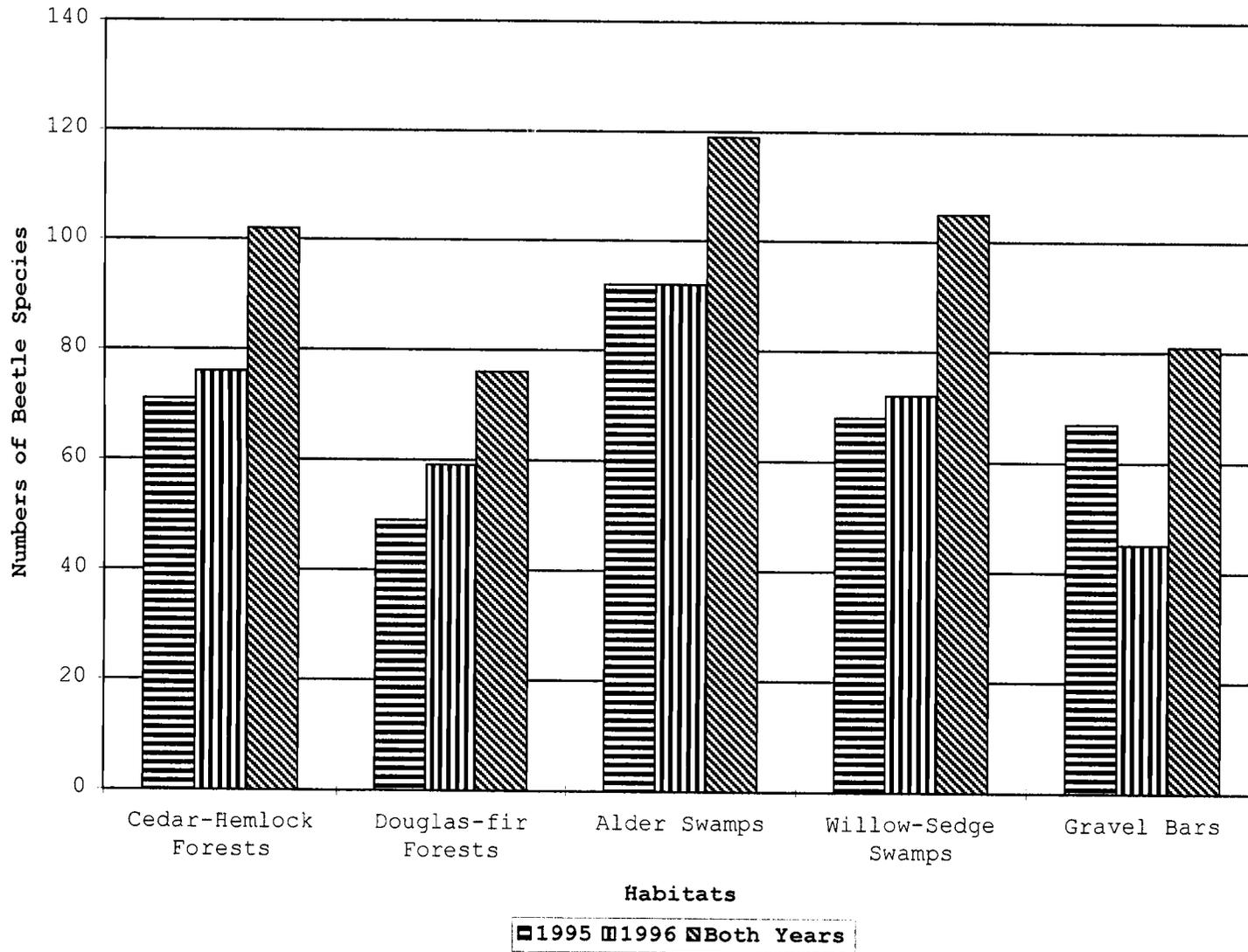


Figure 9. Beetle Species Richness Per Habitat.

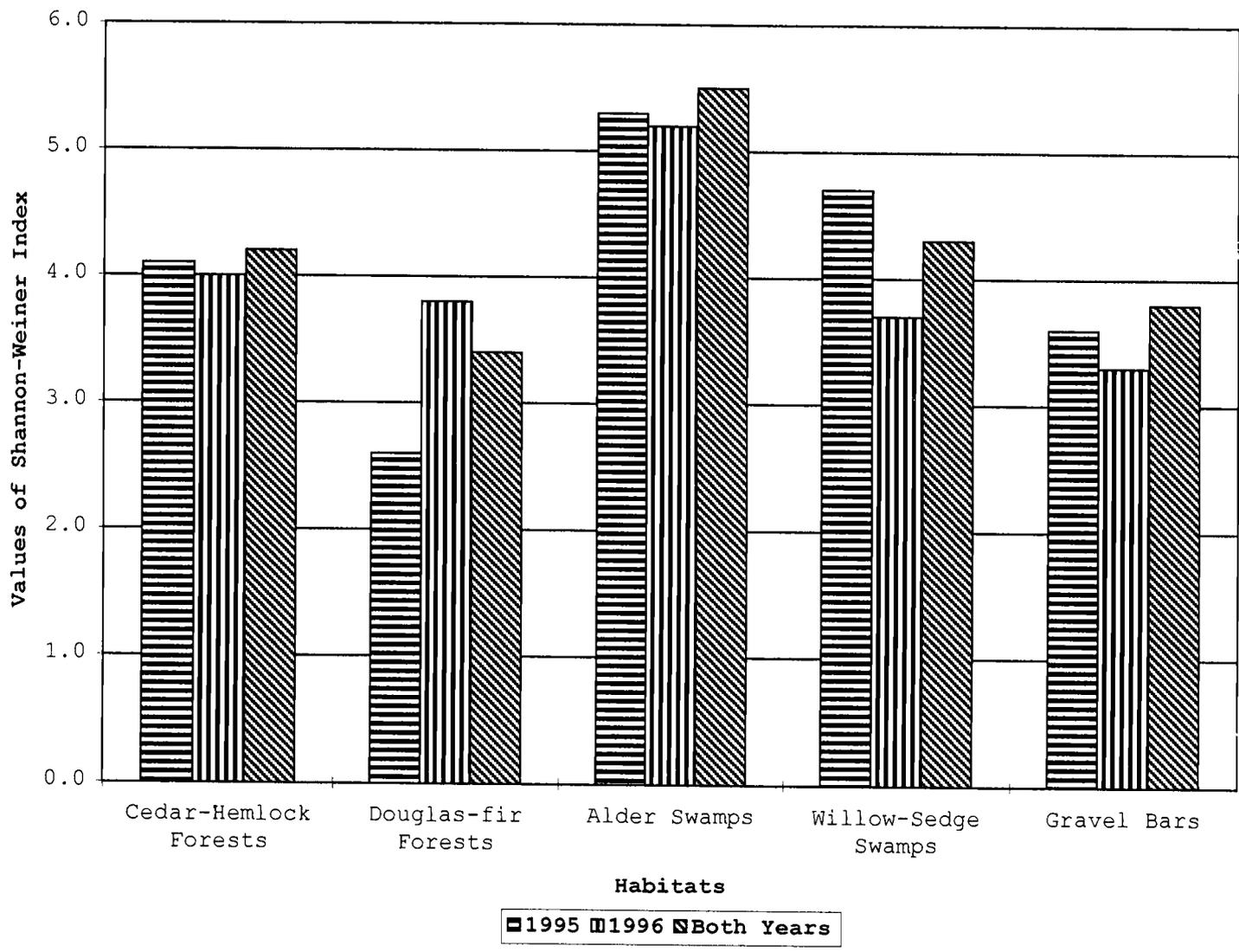


Figure 10. Values of the Shannon-Weiner Index Per Habitat.

to 3.8 in 1996, while Willow-Sedge Swamps decreased from 4.7 to 3.7. The other habitats showed small declines in 1996.

Slightly different patterns were demonstrated by Simpson's 1-D diversity index (Figure 11). While Alder Swamps (0.96) retained the highest value, Gravel Bars were second (0.87), followed by Willow Swamps (0.85), Cedar-Hemlock Forests (0.83), and Douglas-fir Forests (0.74). As with the Shannon-Weiner index, the annual Simpson 1-D values reflected those of the grand total pattern. Similar to the Shannon-Weiner pattern, Douglas-fir Forests diversity increased from 1995 (0.60) to 1996 (0.84), while Willow-Sedge Swamps diversity declined from 0.92 to 0.77. There were virtually no differences between years for the remaining habitats.

The grand total J' evenness index demonstrated little difference among habitats (Figure 12). All habitats had evenness indices ranging from 0.76-0.82, except for Gravel Bars (0.64). Annual J' evenness indices generally followed the grand total pattern. Evenness between years was either invariant or declined very slightly in almost all habitats. Gravel Bars displayed the greatest change between years, declining from 0.70 in 1995 to 0.66 in 1996.

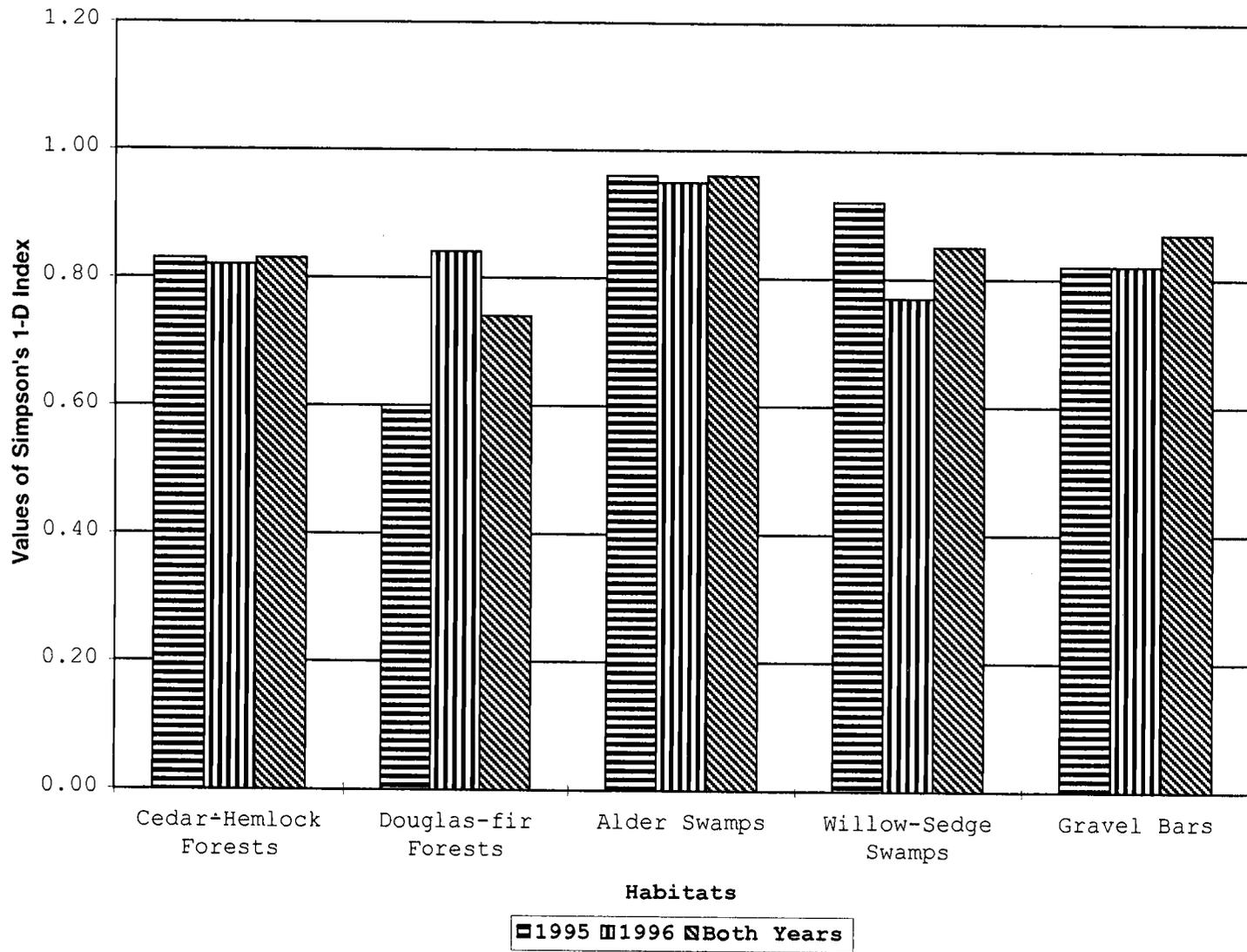


Figure 11. Values of Simpson's 1-D Index Per Habitat.

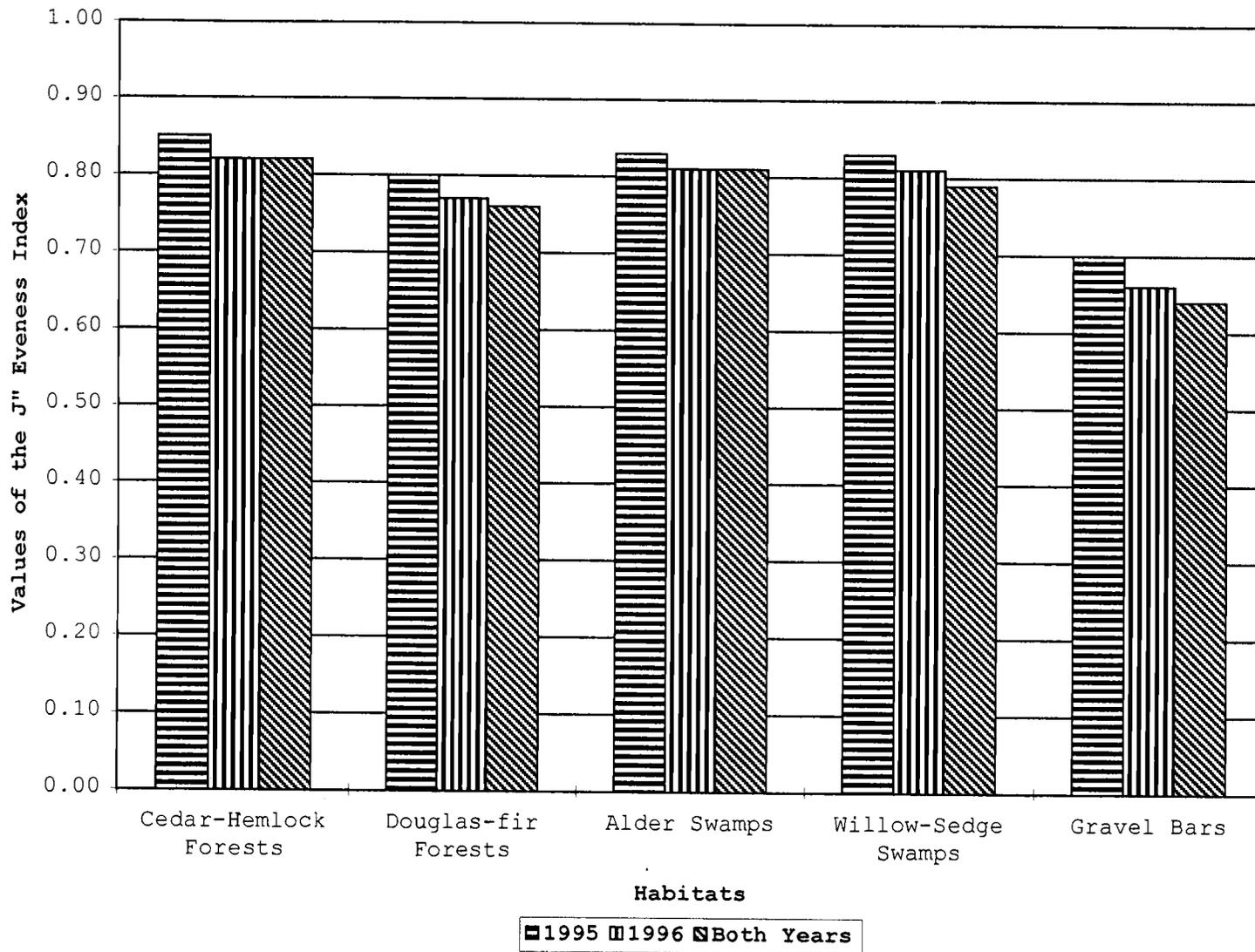


Figure 12. Values of the J' Evenness Index Per Habitat.

SECTION 4: FAMILY DIVERSITY PATTERNS

Number of Families.

A grand total of 41 beetle families were collected. In 1995, 33 families were collected, with 35 in 1996. Six families occurred only in 1995: Amphizoidae, Erotylidae, Histeridae, Melandryidae, Phalacridae, and Trogositidae. Eight families were found only in 1996: Colydiidae, Corylophidae, Endomychidae, Gyrimidae, Laemophloeidae, Lucanidae, Lycidae, and Melyridae. All of these single-year families were represented by only one or two individuals (Table 2).

The number of families differed little among habitats, ranging from 19 (Douglas-fir Forests) to 23 (Alder Swamps and Willow-Sedge Swamps) (Figure 13). The patterns between years generally resembled those for abundance. The only substantial change occurred in Gravel Bars, where numbers of families declined by 28% in 1996, from 18 to 13.

Family abundance.

Most families were represented by only a few total individuals (Table 2). The majority, 24 (59%), had fewer than ten total individuals. Four families accounted for

Table 2. Beetle Family Overall Abundance.

Superscripts designate families whose primary adult habitat is other than soil or litter: A = Aquatic, F = Fungi, especially woody fungi, V = Vegetation, including flowers and foliage, W = Wood, primarily decaying, or under bark.

FAMILY	NUMBER OF INDIVIDUALS	PERCENT TOTAL INDIVIDUALS
Staphylinidae (including Aleocharinae)	3497	42.76
Carabidae	2500	30.57
Elateridae	954	11.66
Anthicidae	507	6.20
Leiodidae	121	1.48
Curculionidae	108	1.32
Ptiliidae	89	1.09
Latridiidae	84	1.03
Cryptophagidae	77	0.94
Scydmaenidae	31	0.38
Hydrophilidae	30	0.37
Oedemeridae ^{V,W}	30	0.37
Byrrhidae	25	0.31
Scirtidae ^V	21	0.26
Tenebrionidae	16	0.20
Chrysomelidae ^V	15	0.18
Dytiscidae ^A	13	0.16
Scarabaeidae	8	0.10
Zopheridae ^F	6	0.07
Cantharidae ^V	5	0.06
Coccinellidae ^V	5	0.06
Pyrochroidae ^W	5	0.06
Hydraenidae ^A	4	0.05
Cerambycidae ^V	3	0.04
Ciidae ^F	3	0.04
Sphaeritidae	3	0.04
Gyrinidae ^A	2	0.02
Histeridae	2	0.02
Phalacridae ^V	2	0.02
Throscidae	2	0.02
Amphizoidae ^A	1	0.01
Colydiidae ^W	1	0.01
Corylophidae	1	0.01

Table 2 (continued).

FAMILY	NUMBER OF INDIVIDUALS	PERCENT TOTAL INDIVIDUALS
Endomychidae ^F	1	0.01
Erotylidae ^F	1	0.01
Laemophloeidae ^W	1	0.01
Lucanidae ^W	1	0.01
Lycidae ^W	1	0.01
Melandryidae ^W	1	0.01
Melyridae ^V	1	0.01
Trogositidae ^W	1	0.01
TOTAL	8179	

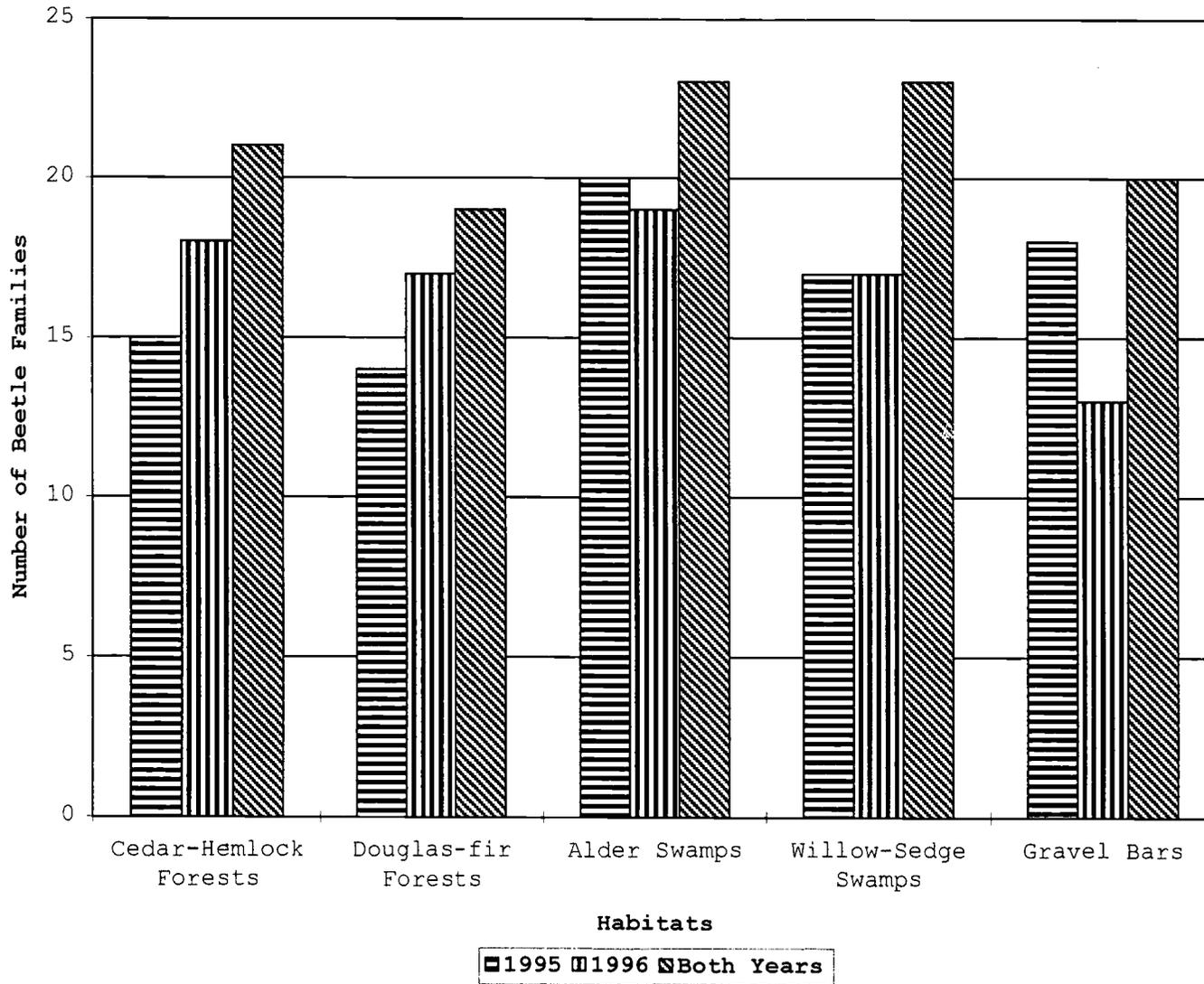


Figure 13. Beetle Family Richness Per Habitat.

92% of all beetle individuals: Staphylinidae (43%), Carabidae (31%), Elateridae (12%), and Anthicidae (6%) (Figure 14).

Two of these families, Anthicidae and Elateridae, had very similar overall phenological patterns of abundance (Figure 15). Both had their greatest relative abundance, over 65% of total individuals, in July. Thereafter, relative abundance sharply declined. October relative abundance for Anthicidae was about 3% and about 1% for Elateridae. The pattern for Carabidae most closely approximated the bimodal pattern for all beetles combined (see Figure 8), although carabid bimodality was more pronounced. July carabid relative abundance was 28%, 19% in August, 33% in September, and 21% in October. Relative abundance of Staphylinidae resembled none of the other families. This pattern was unimodal. Both July and October relative abundance was near 20%, August was ~26%, and peak staphylinid relative abundance, 35%, was in September.

One or more of the "Big Four" families was numerically dominant in all habitats, although the patterns of relative abundance of the "Big Four" varied among the habitats (Figure 16). Staphylinidae dominated all but the Gravel Bars and Willow-Sedge Swamps. This family's dominance was particularly pronounced in Alder Swamps, comprising 78% of all beetles. Carabidae were slightly less abundant than Staphylinidae in the conifer forests, but were the dominant family (59% of

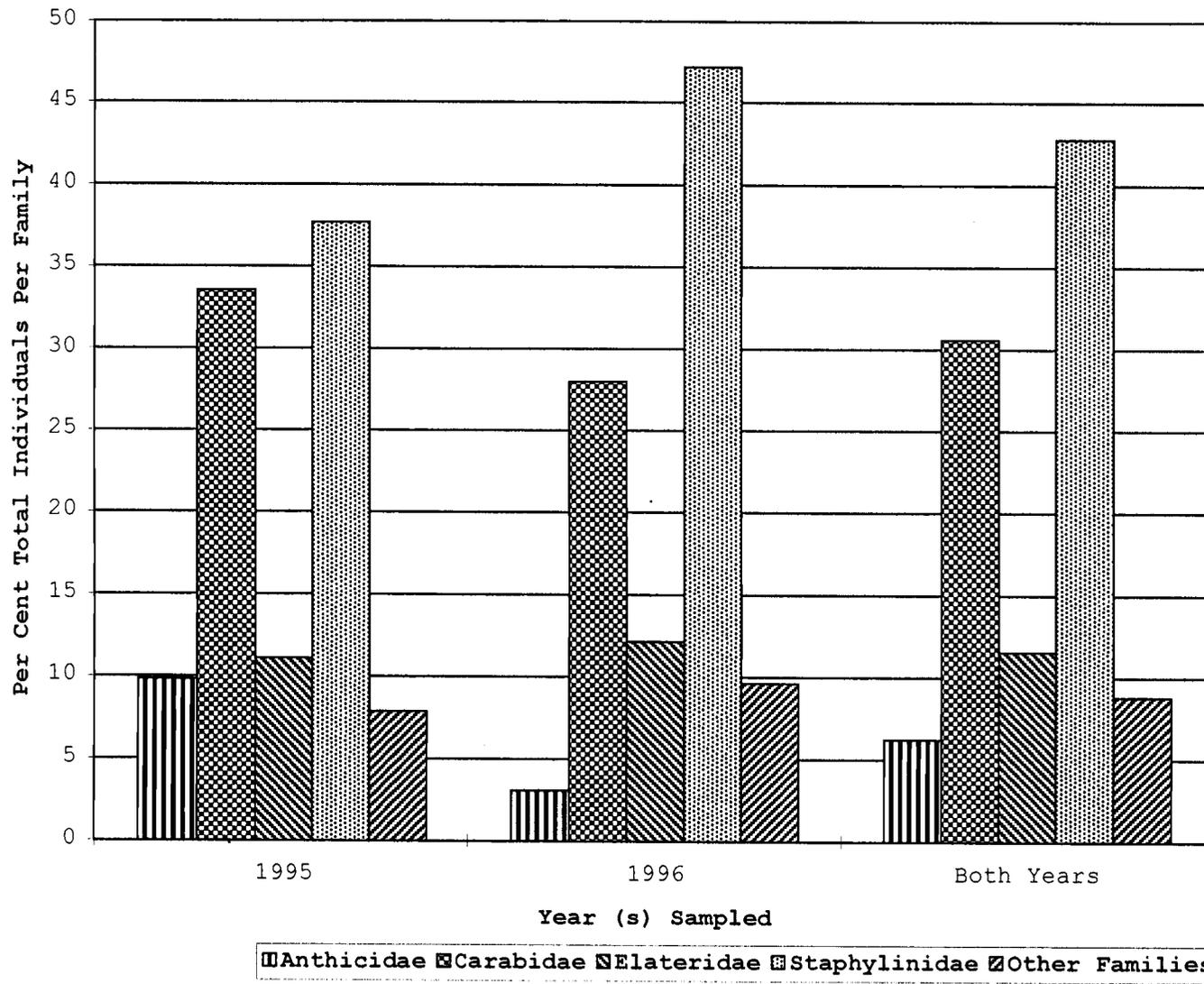


Figure 14. Overall Relative Abundance of Beetle Families.

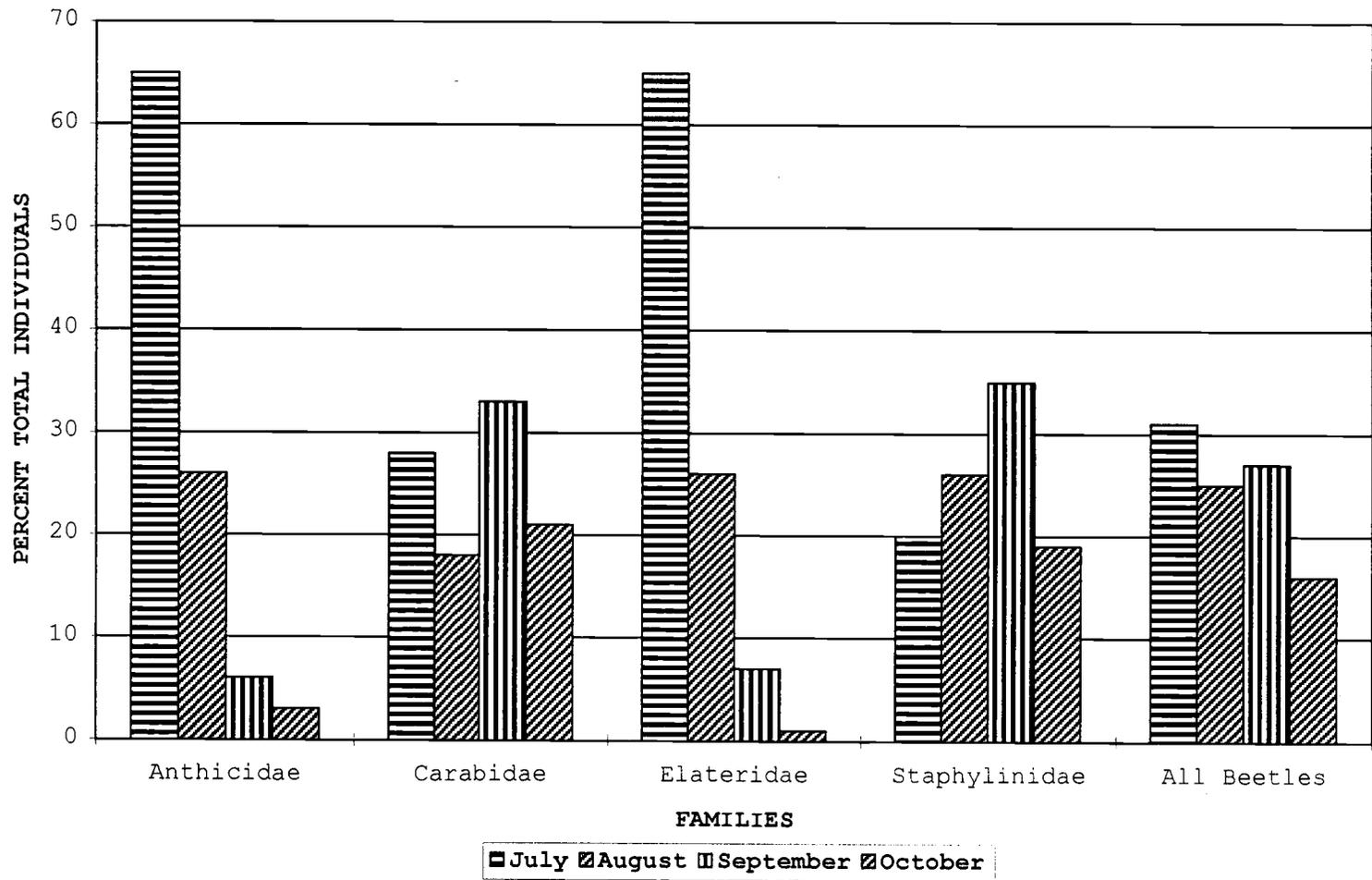


Figure 15. Beetle Family Phenology Patterns, Both Years.

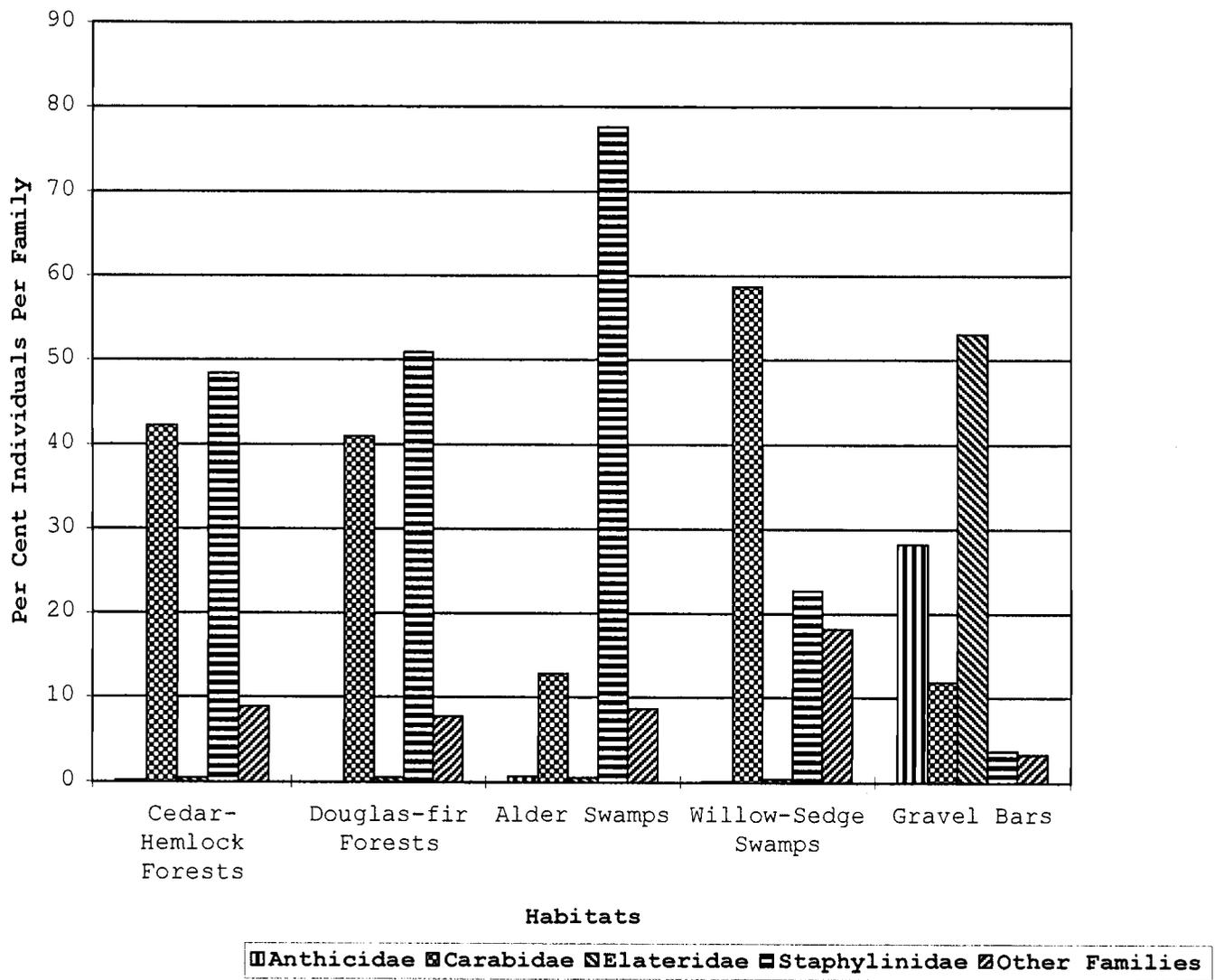


Figure 16. Relative Family Abundance Per Habitat, Both Years.

individuals) in Willow-Sedge Swamps. Anthicidae and Elateridae, minor components in the other habitats, were dominant families in Gravel Bars, with 53% and 28% of individuals, respectively. The aggregate totals of all other families contributed less than 10% in all habitats but Willow-Sedge Swamps, where they were 18% of the total individuals.

The patterns of relative abundance among the "Big Four" families varied, to differing degrees, between years for all habitats (Figures 17, 18). Carabidae declined in Alder Swamps, from 16% in 1995 to 10% in 1996. A decrease of Staphylinidae in Willow-Sedge Swamps (27% in 1995, 19% in 1996) was virtually mirrored by similar Carabidae increases (55% to 62%). Changes of similar, but opposite, magnitude occurred in Cedar-Hemlock Forests, with Staphylinidae increasing from 44% to 52% and Carabidae declining from 49% to 38%. Representation of Staphylinidae almost doubled in Douglas-Fir Forests, from 34% to 63% and Carabidae were more than halved, from 59% to 28%. Anthicidae declined from 37% to 16% in Gravel Bars, with Elateridae increasing from 42% to 68%, while there was little change in relative abundance in Carabidae.

Similar to individual abundance, just four families accounted for most, 65%, of the species (Figure 19). As with abundance, the most speciose families included the Staphylinidae (31% of all species), Carabidae (19%), and Elateridae (8%). However, Anthicidae contributed

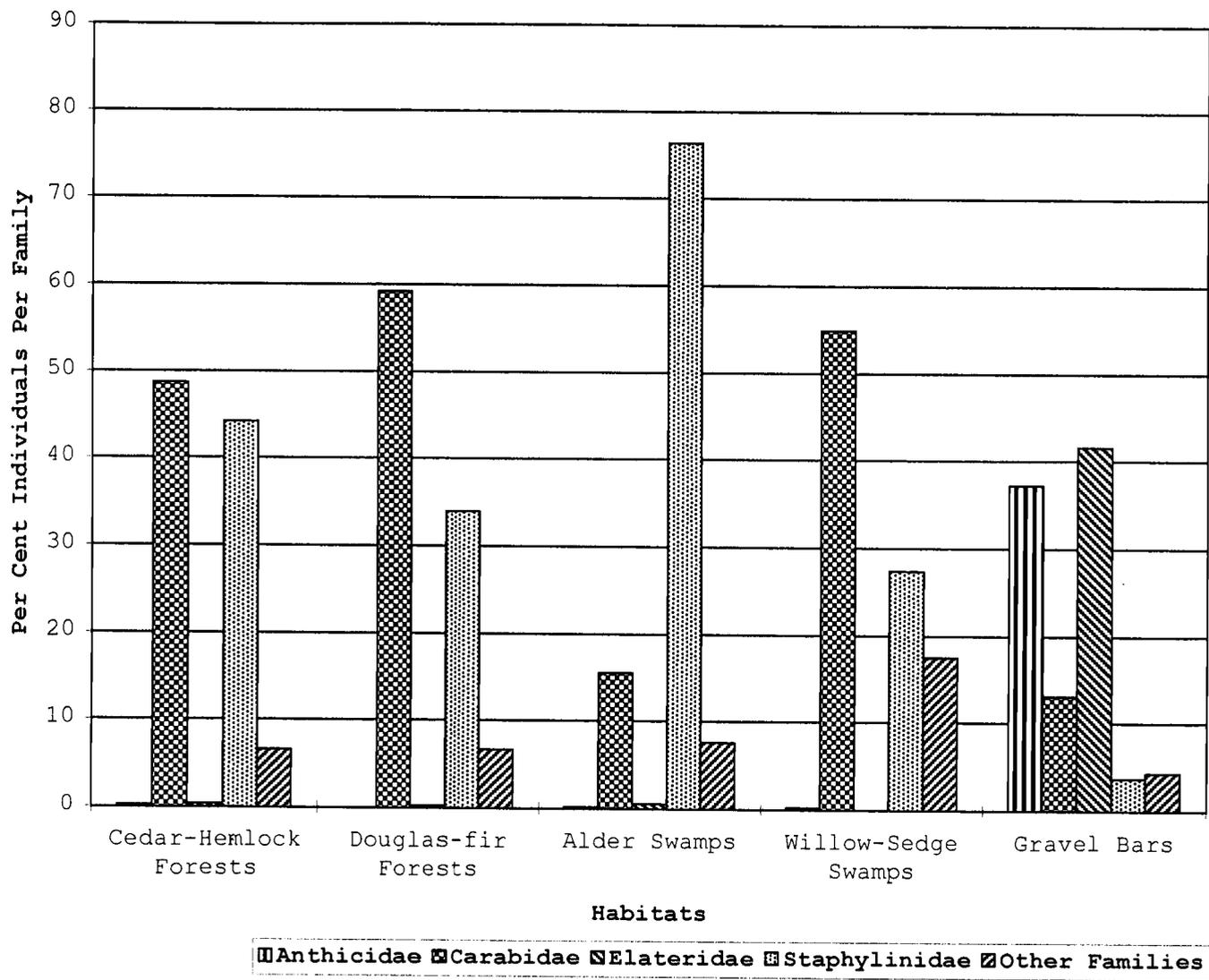


Figure 17. Beetle Family Relative Abundance Per Habitat, 1995.

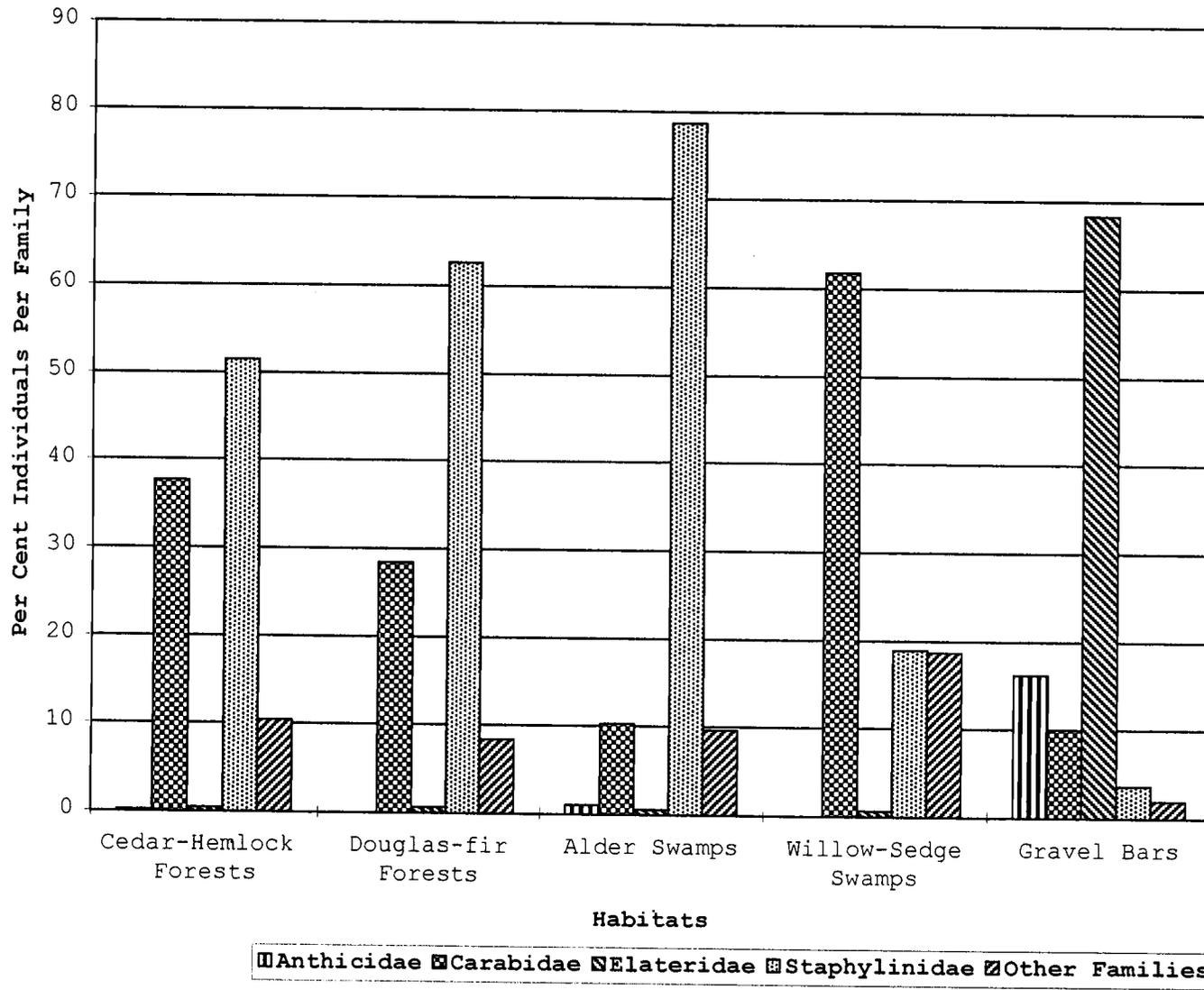


Figure 18. Beetle Family Relative Abundance Per Habitat, 1996.

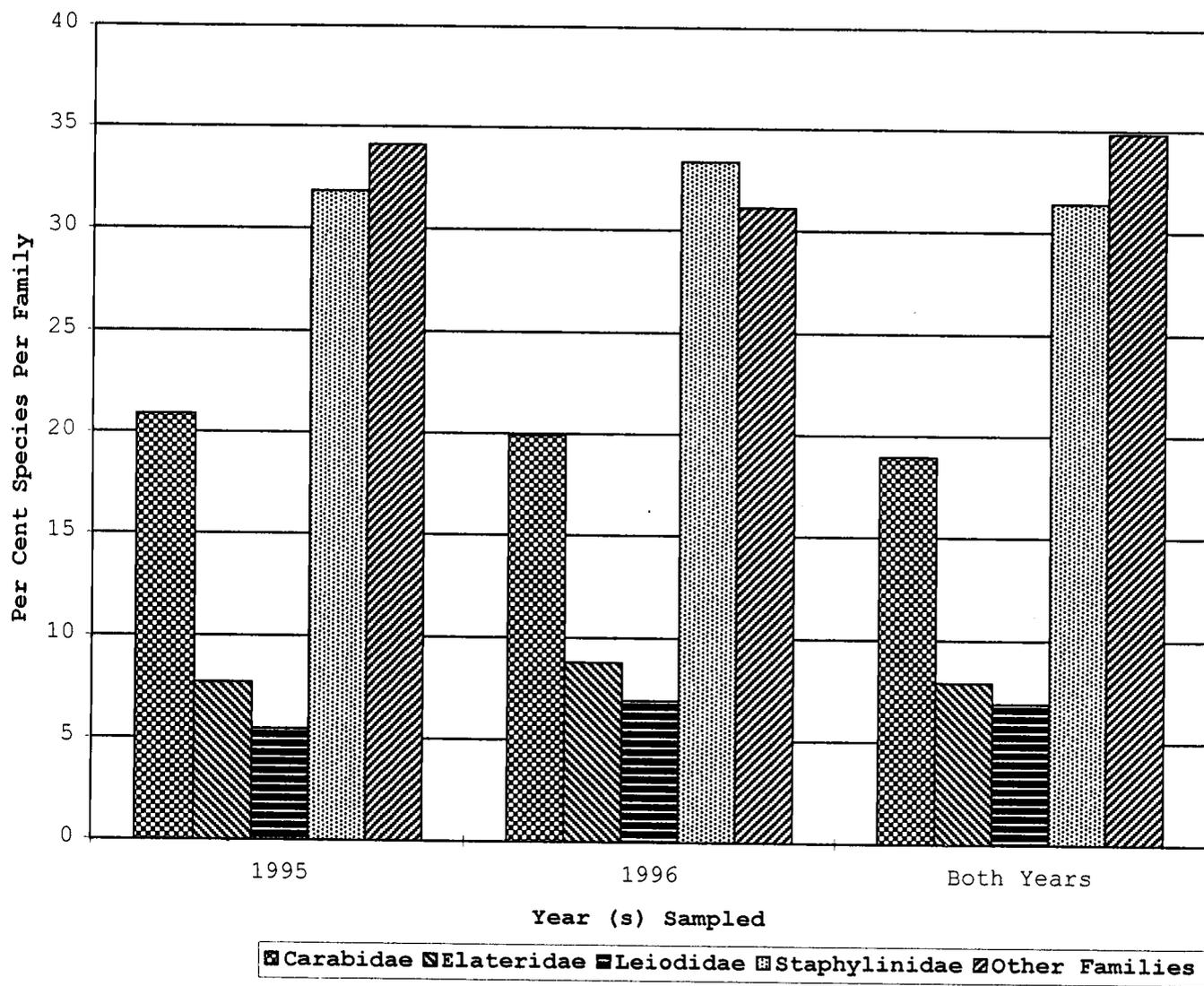


Figure 19. Overall Relative Species Richness of Beetle Families.

negligibly to species richness, less than 1%. Leiodidae replaced Anthicidae as the fourth "big" family, with 7% of the species. The relative dominance of these "Big Four" families was not as pronounced as with individuals. The other families, in aggregate, contributed approximately 35% of the species.

Family Species Richness.

As was true of individual abundance, patterns of family species richness varied among habitats (Figure 20). Staphylinidae were the most speciose family in all habitats, ranging from 31% of Gravel Bar and Willow-Sedge Swamp species to 48% of all Alder Swamp species. Carabid representation was generally modest, from 12% in Douglas-fir Forests to 21% in Gravel Bars, although this family comprised 28% of species in Willow-Sedge Swamps. Elateridae were only speciose in Gravel Bars, with 17% of the total for that habitat. Leiodidae contributed relatively few species in all but Cedar-Hemlock (13%) and Douglas-fir (9%) forests. The influence of "other families" was more pronounced than with individuals, ranging from 26% in Alder Swamps and Gravel Bars to 34% in Douglas-fir Forests and Willow-Sedge Swamps.

The general patterns of family species richness were consistent for each year (Figures 21, 22). There were few relatively great changes between years. Elateridae

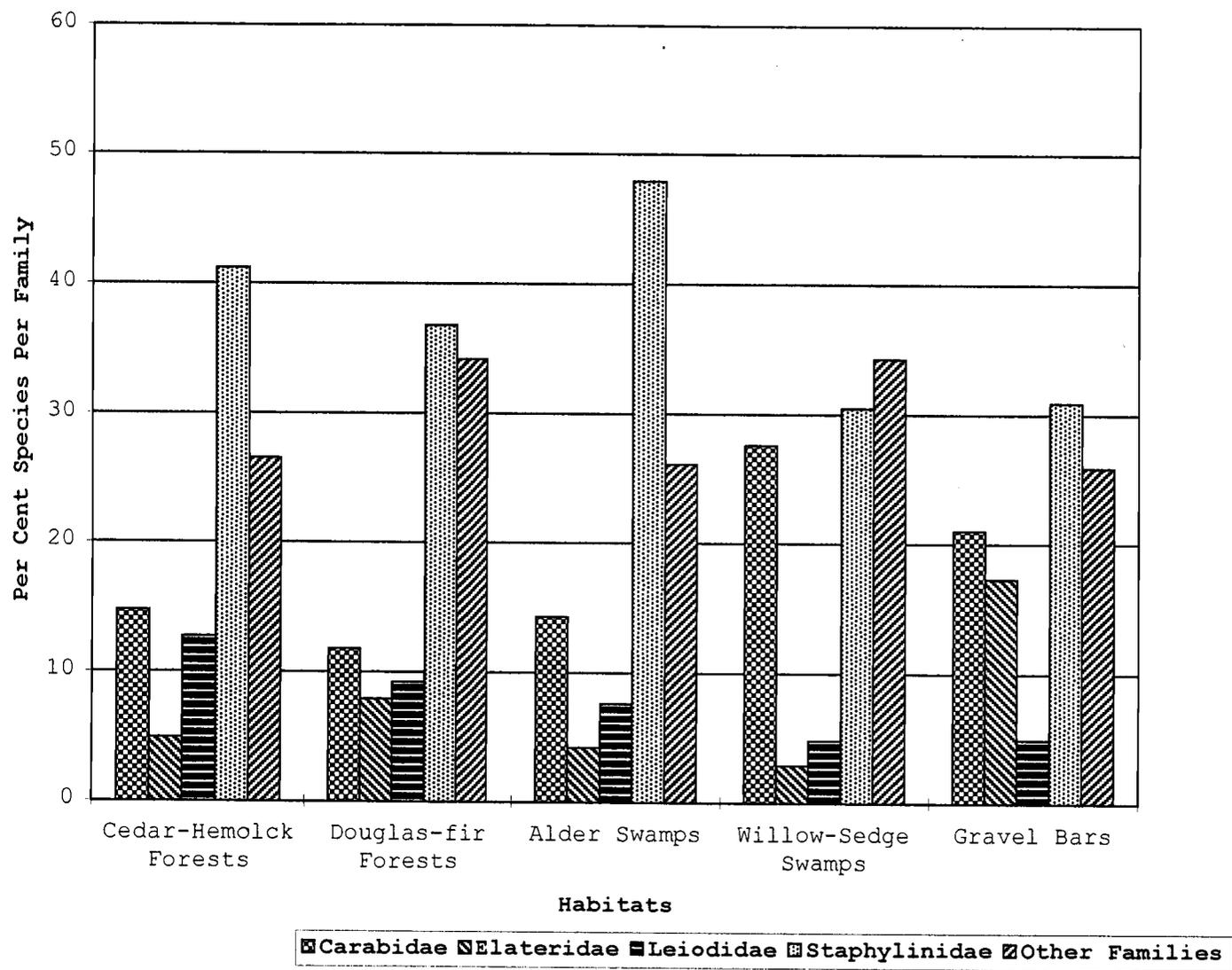


Figure 20. Overall Relative Family Species Richness Per Habitat.

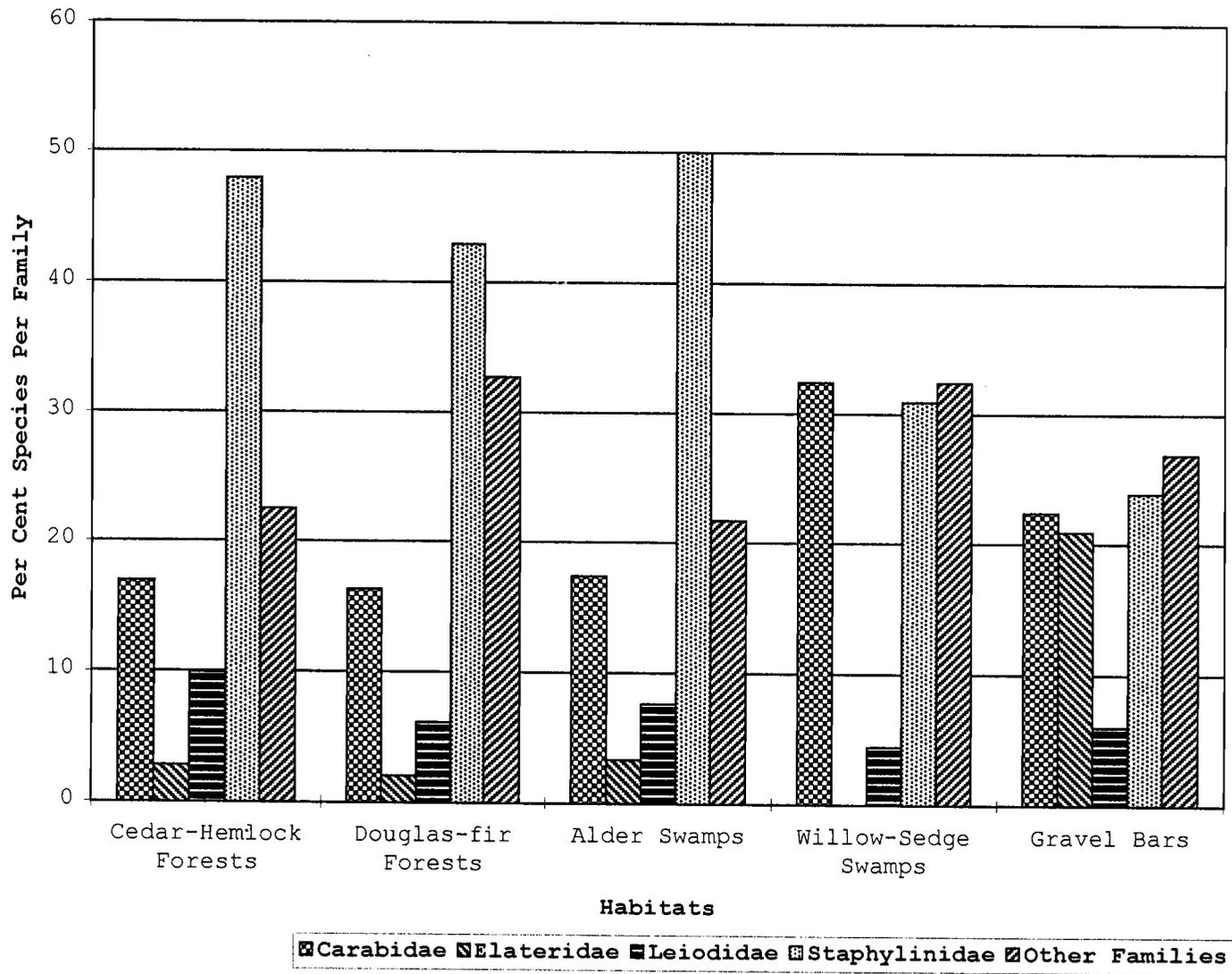


Figure 21. Beetle Family Relative Species Richness Per Habitat, 1995.

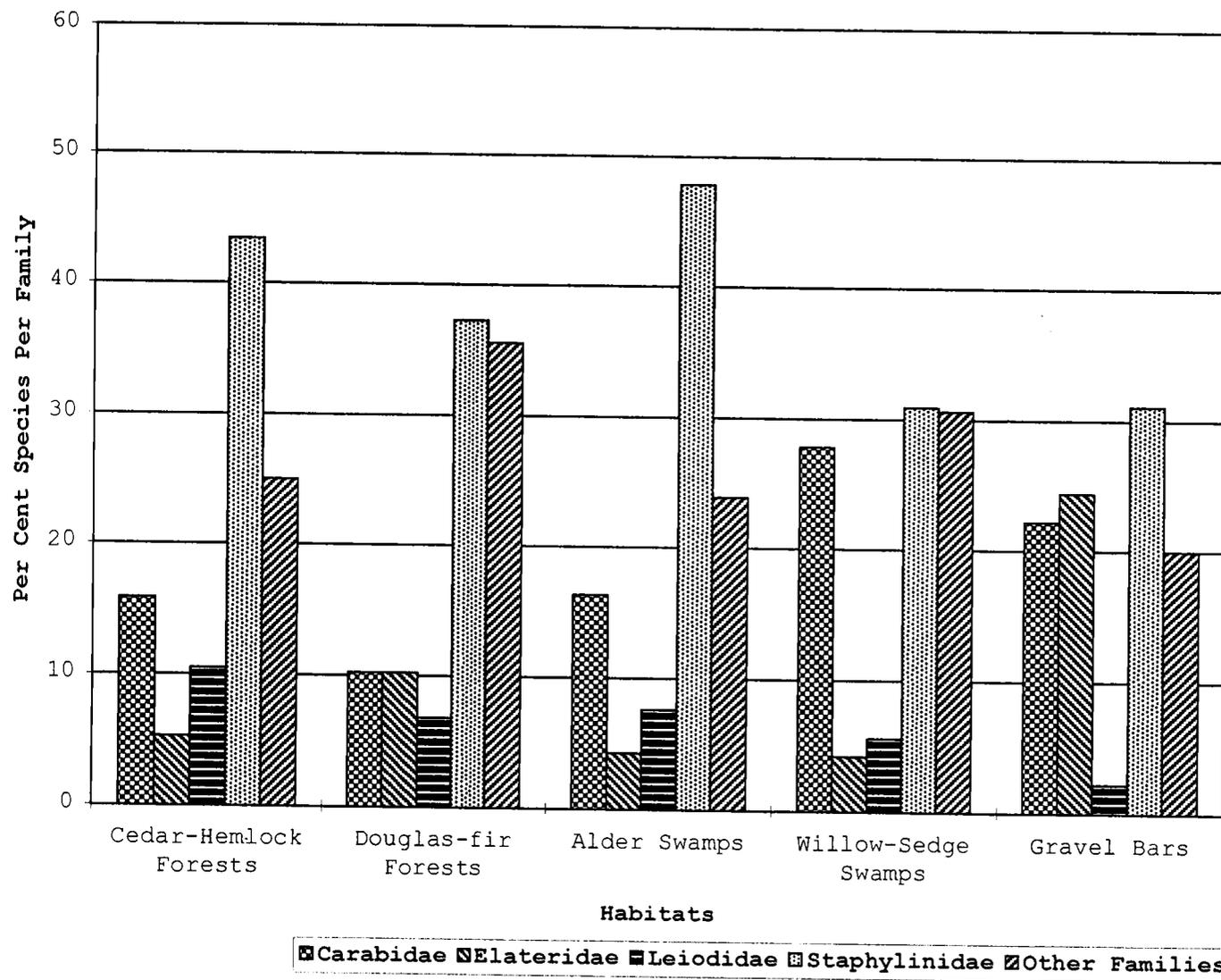


Figure 22. Beetle Family Relative Species Richness Per Habitat, 1996.

accounted for 2% of species richness in 1995 Douglas-Fir Forests and 10% in 1996, while Carabidae declined from 16% to 10% in this habitat. Elateridae were absent from Willow-Sedge Swamps in 1995 and comprised 4% of species in 1996.

SECTION 5: SPECIES-SPECIFIC PATTERNS

Ubiquitous and Abundant Species.

Only five species were found in all habitats (Table 1): one carabid, *Scaphinotus marginatus* (Fischer), and four staphylinids, *Lucifotychus cognatus* (LeConte), *Reichenbachia albionica* Motschulsky, *Tachinus basalis* Erichson, and *Tachinus crotchii* Horn.

Twenty species accounted for 51% of all beetle individuals collected, including Aleocharinae (Table 3). Excluding Aleocharinae, they comprised 62% of individuals. Of these species, 13 (65%) ranked within the twenty most abundant species each year. Eighteen of these species belonged to families exhibiting high species richness: Staphylinidae (8), Carabidae (5), and Elateridae (5). Only three of the five previously noted ubiquitous species were included within these twenty abundant species: the carabid, *S. marginatus*, and two staphylinids, *R. albionica* and *T. crotchii*. *Lucifotychus cognatus* tied for an abundance rank of 49 and *T. basalis*

Table 3. The Twenty Most Abundant Beetle Species.

AS = Alder Swamps, CHF = Cedar-Hemlock Forests, DfF = Douglas-fir Forests,
 GB = Gravel Bars, WSS = Willow-Sedge Swamps.

Habitats are listed for each species in order of numerical presence.

SPECIES	FAMILY	PREDOMINANT HABITATS	TOTAL FOR	RANK
			COMBINED YEARS Individuals (% Total)	Combined Years (1995, 1996)
<i>Eurygenius campanulatus</i> LeConte	Anthicidae	GB	479 (6)	2 (2, 4)
<i>Agonum brevicolle</i> Dejean	Carabidae	WSS	425 (5)	3 (4, 2)
<i>Pterostichus herculaneus</i> Mannerheim	Carabidae	DfF, CHF	88 (1)	17 (15, 16)
<i>Pterostichus neobrunneus</i> Lindroth	Carabidae	CHF, DfF	141 (2)	8 (8, 10)
<i>Scaphinotus angusticollis</i> (Fischer)	Carabidae	DfF, CHF	1036 (13)	1 (1, 1)
<i>Scaphinotus marginatus</i> (Fischer)	Carabidae	AS, CHF	102 (1)	14 (11, 19)
<i>Cardiophorus propinquus</i> Lanchester	Elateridae	GB	224 (3)	5 (3, 12)
<i>Ligmargus funebris</i> (Candeze)	Elateridae	GB	98 (1)	15 (7, 47)
<i>Zorochrus dispersus</i> (Horn)	Elateridae	GB	107 (1)	12 (10, 17)
<i>Zorochrus musculus</i> (Eschscholtz)	Elateridae	GB	291 (4)	4 (22, 3)
<i>Zorochrus</i> sp.	Elateridae	GB	122 (1)	10 (40, 5)
<i>Melanopthalma americana</i> (Mannerheim)	Latridiidae	WSS	68 (1)	20 (13, 29)
<i>Anthobium reflexicolle</i> (Casey)	Staphylinidae	AS	80 (1)	18 (27, 13)
<i>Dinothenarus pleuralis</i> (LeConte)	Staphylinidae	CHF, DfF	79 (1)	19 (16, 20)
<i>Eusphalerum pothos</i> (Mannerheim)	Staphylinidae	AS	93 (1)	16 (absent, 8)
<i>Lordithon fungicola</i> Campbell	Staphylinidae	AS, DfF, CHF	131 (2)	9 (9, 11)
<i>Proteinus collaris</i> Hatch	Staphylinidae	AS	189 (2)	6 (6, 7)
<i>Reichenbachia albionica</i> Motschulsky	Staphylinidae	WSS	104 (1)	13 (12, 14)
<i>Tachinus crotchii</i> Horn	Staphylinidae	AS	168 (2)	7 (5, 9)
<i>Tachinus semirufus</i> Horn	Staphylinidae	DfF, CHF	120 (1)	11 (43, 6)

tied for a rank of 36. The most abundant species was the carabid, *Scaphinotus angusticollis* (Fischer). This single species accounted for 1,036 specimens (Table 1), 13% of all beetles collected.

Habitats differed in the composition of their five most abundant species (Table 4). The proportion of total abundance per habitat represented by these species ranged from 33% in Alder Swamps to 71% in Gravel Bars. Most, but not all, of these species were also among the twenty most overall abundant species. Additional species were *Agonum ferruginosum* (Dejean) and *Loricera decempunctata* Eschscholtz (Carabidae), and the staphylinid, *Gabrius seattlensis* (Hatch). These two carabid species were only abundant in Willow-Sedge Swamps, while the staphylinid was only prevalent in Alder Swamps. Two of the overall "Top 20" species, the carabid, *S. marginatus*, and the elaterid, *Ligmargus funebris* (Candeze), were not dominant elements of any habitat.

"Rare" Species.

Of the total 290 species, 183 (63%) were represented by five or fewer individuals (Table 1). These "rare" species contributed only 369 (6%) of the beetles identified to species level. Ninety species (30%) were

Table 4. The Five Most Abundant Species of Each Habitat.

SPECIES	FAMILY	HABITATS										OVERALL RANK*
		Cedar-Hemlock Forests		Douglas-fir Forests		Alder Swamps		Willow-Sedge Swamps		Gravel Bars		
		Number	% Total	Number	% Total	Number	% Total	Number	% Total	Number	% Total	
<i>Eurygenius campanulatus</i>	Anthicidae									479	28	2
<i>Agonum brevicolle</i>	Carabidae							425	36			3
<i>Agonum ferruginosum</i>	Carabidae							51	4			27
<i>Loricera decempunctata</i>	Carabidae							43	4			28
<i>Pterostichus herculeanus</i>	Carabidae			46	4							17
<i>Pterostichus neobrunneus</i>	Carabidae	73	6	66	6							8
<i>Scaphinotus angusticollis</i>	Carabidae	459	40	518	49							1
<i>Cardiophorus propinquus</i>	Elateridae									224	13	5
<i>Zorochrus dispersus</i>	Elateridae									107	6	12
<i>Zorochrus musculus</i>	Elateridae									290	17	4
<i>Zorochrus</i> sp.	Elateridae									120	7	10
<i>Melanophthalma americana</i>	Latridiidae							67	6			20
<i>Anthobium reflexicolle</i>	Staphylinidae					67	5					18
<i>Dinothenarus pleuralis</i>	Staphylinidae	45	4									19
<i>Eusphalerum pothos</i>	Staphylinidae					89	6					16
<i>Gabrius seattlensis</i>	Staphylinidae					60	4					22
<i>Lordithon fungicola</i>	Staphylinidae			39	4							9
<i>Proteinus collaris</i>	Staphylinidae	35	3			154	11					6
<i>Reichenbachia albionica</i>	Staphylinidae							82	7			13
<i>Tachinus crotchii</i>	Staphylinidae					98	7					7
<i>Tachinus semirufus</i>	Staphylinidae	42	4	78	7							11
HABITAT TOTALS		654	57	747	70	468	33	668	57	1220	71	

represented by only single specimens. "Rare" species were the bulk of the 74 species which only occurred in 1995 and the 70 species absent in 1995.

Exotic Species.

Four of the beetle species collected are not indigenous to North America (Hatch 1953, 1957, 1971; Lindroth 1961-1969; Arnett and Thomas 2001): *Anisodactylus binotatus* (Fabricius) and *Calathus fuscipes* (Goeze) (Carabidae), *Onthophagus nuchicornis* (Linnaeus) (Scarabaeidae), and *Trichophya pilicornis* (Gyllenhal) (Staphylinidae). Four additional species, all Staphylinidae, are thought to be probable exotic species (Hatch 1957, Downie and Arnett 1996a): *Aleochara bilineata* Gyllenhal, *A. bimaculata* Gravenhorst, *Pseudopsis sulcata* Newman, and *Stenus morio* Gravenhorst. These species were predominantly found in the open habitats, i.e., Gravel Bars and Willow-Sedge Swamps (Table 1).

SECTION 6: TROPHIC PATTERNS

Individuals.

Abundance patterns of individuals in the various trophic categories varied among habitats (Figure 23). Predators had the greatest representation in all habitats, ranging from 47% (Alder Swamps) to 80% (Willow-Sedge Swamps) of all individuals. Most other categories were about 10% or less, except for detritivores in Gravel Bars (31%) and fungivores in Alder Swamps (26%).

Species.

Trophic category patterns for species generally mirrored those for individuals, with predatory species more prevalent than any other category in all habitats (Figure 24). Representation of species in this category varied from 47% in Cedar-Hemlock Forests to 65% in Willow-Sedge Swamps. The most abundant predator was *Scaphinotus angusticollis* (Fischer) (Carabidae), which was predominant in Cedar-Hemlock and Douglas-fir forests. Detritivores were more pronounced than with individuals, with most habitats having about 10% or more species in that category. *Eurygenius campanulatus* LeConte (Anthicidae) was the only common detritivorous species and was only found in Gravel Bars. Fungivores were also more

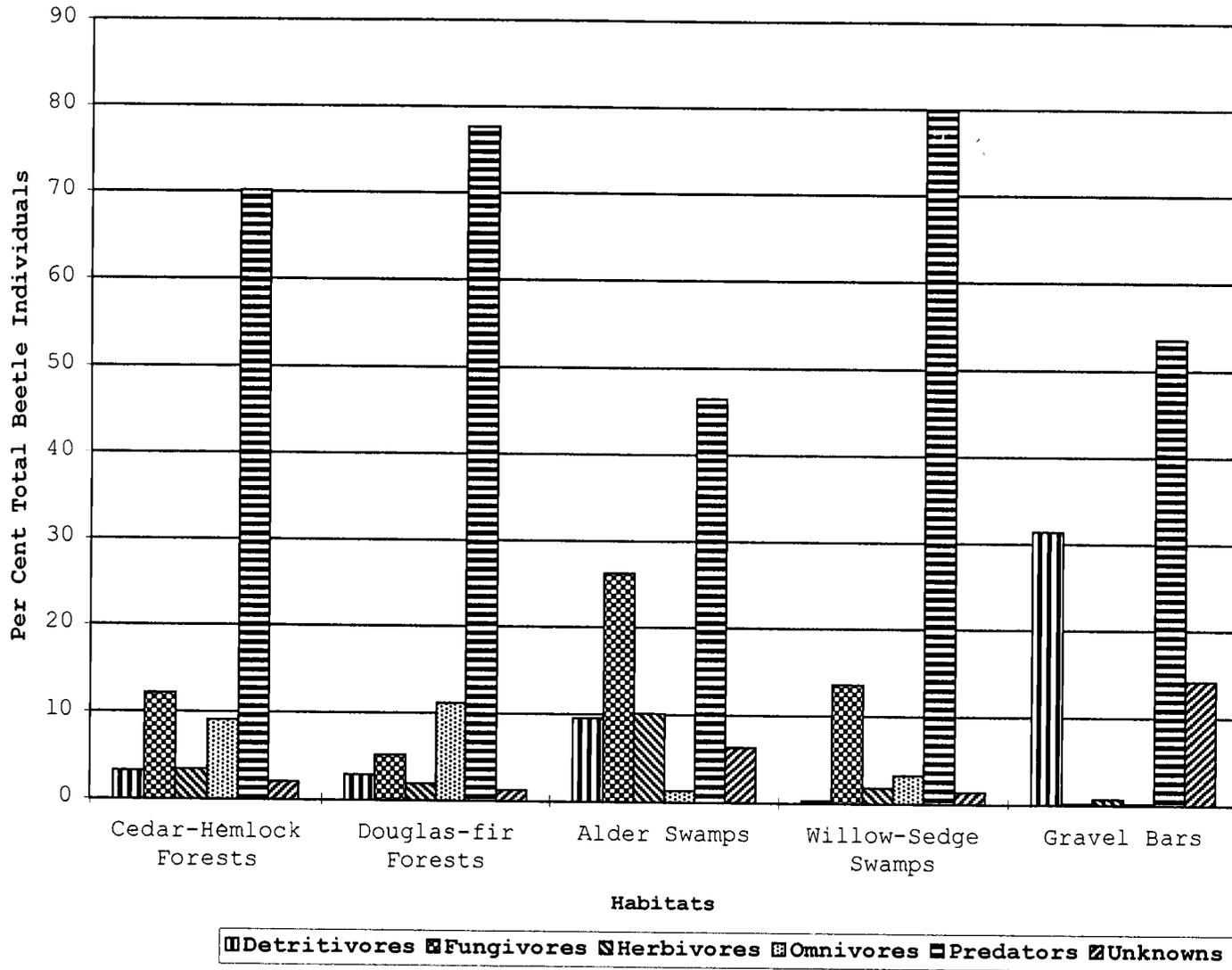


Figure 23. Per Cent Beetle Individuals in Trophic Categories Per Habitat.

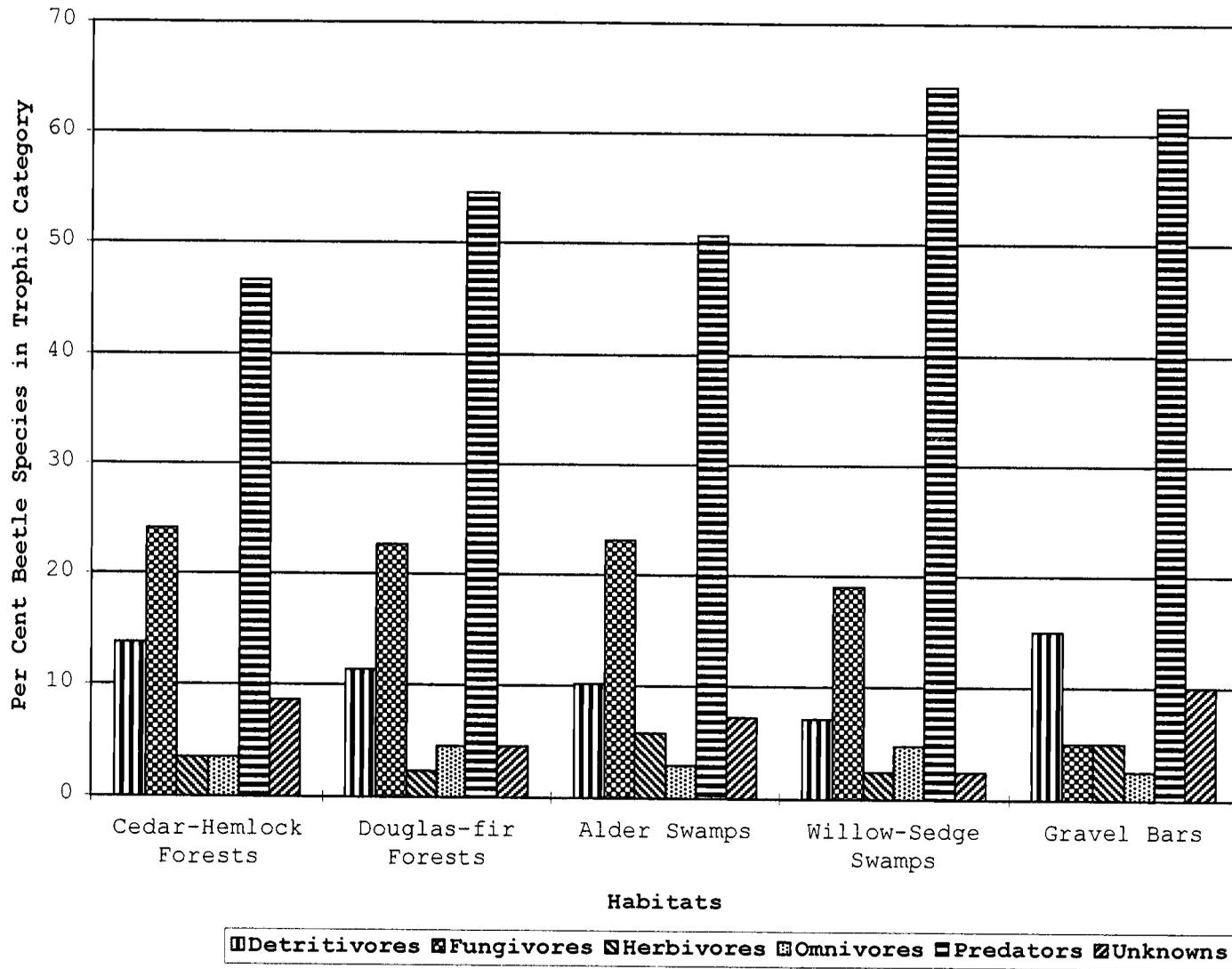


Figure 24. Per Cent Beetle Species in Trophic Categories Per Habitat.

pronounced than with individuals. All habitats but Gravel Bars had about 20% of all species in this category. The most abundant fungivore was *Proteinus collaris* Hatch (Staphylinidae), which was most prevalent in Alder Swamps, but was also found in Cedar-Hemlock Forests. The remaining categories were under 10%, other than unknowns (10%) in Gravel Bars. *Eusphalerum pothos* (Mannerheim) (Staphylinidae), a pollen-feeding species, was the only common herbivore. It was only found in Alder Swamps. The most abundant omnivore was *Pterostichus neobrunneus* Lindroth (Carabidae), common in both Cedar-Hemlock and Douglas-fir forests.

CHAPTER 4: DISCUSSION

SECTION 1: SAMPLING PROTOCOLS

Pitfall Trapping Biases and Limitations.

A discussion of the constraints imposed by the sampling method of this study, pitfall trapping, follows. These issues in no way detract from the utility of pitfall traps or the information that can be gleaned from this sampling method. No sampling method is free of bias (see Southwood 1978). However, the biases and limitations of pitfall trapping must always be considered when analyzing pitfall trap data.

Literature Review.

Pitfall trapping is a well-established method of sampling epigeal arthropods (Southwood 1978, Spence and Niemela 1994). Much of the extensive literature on this method is based upon carabid beetle research (e.g., Greenslade 1964, Stork 1990, Desender et al. 1994, Digweed et al. 1995, Niemela 1996), although it has been used to study a wide array of surface-active arthropods (e.g., Barber 1931, Doane 1961, Duffey 1962, Hayes 1970, Quinn et al. 1990, Abensperg-Traun and Steven 1995, and Table 5).

Table 5. Review of Selected Pitfall Trapping Literature.

*The Study Period is often the snow-free season or some lesser subset of the activity period of adults, rather than a full calendar year.

Literature Cited	Number of Traps Per Habitat or Site	Sampling Frequency (weeks)	Study Period (years*)	Taxa Sampled
Apigian & Wheelwright 2000	10	4	1	Carabidae
Falke et al. 2000	3-10	2	5	Carabidae
Schwerk 2000	1-18	4	1-6	Carabidae
Mico et al. 1998	8	1	2	Scarabaeidae
Blake et al. 1996	18	4	2	Carabidae
Desender 1996	3	2	6	Carabidae
Eyre et al. 1996	9	4	8	Carabidae
Huusela-Veistola 1996	3	1	3	Carabidae
Kinnunen et al. 1996	16-25	2	2	Carabidae
Luff 1996	20	1	1	Carabidae
Spence et al. 1996	6	2-4	4	Carabidae
Carcamo 1995	12	2	1	Carabidae
Carcamo et al. 1995	2-4	2	2	Carabidae
Michaels & McQuillan 1995	18	6	1	Carabidae
Eyre & Luff 1994	9	4	2	Carabidae
Georges 1994	4	4	2	Carabidae
Klenner 1994	5	3	1	Carabidae
McFerran et al. 1994	5	2-4	2	Carabidae
Nyilas 1994	5	2	2	Carabidae

Table 5 (continued).

Literature Cited	Number of Traps Per Habitat or Site	Sampling Frequency (weeks)	Study Period (years*)	Taxa Sampled
Sugg et al. 1994	5-26	2	5	Neuropteroidea
Niemela et al. 1993	6	2	2	Carabidae
Luff et al. 1992	9	4	3	Carabidae
Mossakowski et al. 1990	5	2-3+	1	Carabidae
Pizzolotto & Brandmayr 1990	5-10	4	3	Carabidae
Quinn et al. 1990	10	1	2	Tenebrionidae
Eyre et al. 1989	9	4	1	Carabidae, Curculionidae
Mader 1986	11	6	15	Carabidae
Niemela et al. 1985	15	4	1	Carabidae
Aitchison 1984	4-8	2	2	Araneae
Dulge 1984	5	4	1	Carabidae
Doane 1981	1	1	2	Carabidae
Quinn et al. 1981	10	1	2	Carabidae
Aitchison 1979, 1979a, 1979b, 1979c	8	1-2	2	Collembola, Coleoptera, Acari, Diptera, Hymenoptera
Baars 1979	3	1	7	Carabidae
Papp 1978	30	1/2	2	Coleoptera
Kirk 1971	6	1	4	Carabidae
Williams 1959	1	2	1	Invertebrates

Pitfall traps offer several advantages (Southwood 1978, Spence and Niemela 1994), some of which are particularly pertinent to projects with substantial resource constraints. Although these traps can be quite elaborate, very simple designs are often used and materials can be very inexpensive. Trap placement and maintenance is relatively simple and fast, so large numbers of traps are feasible, enabling sampling of relatively large areas. Pitfall traps using preservatives can sample continuously for long periods. Baits may also be used to target specific taxa (e.g., Mico et al. 1998, Assmann and Gunther 2000).

An extensive literature base addresses the protocols and limitations of this method (e.g., Southwood 1978, Adis 1979, Spence and Niemela 1994, Mommertz et al. 1996). The primary constraints of pitfalls are that they selectively sample surface-active arthropods (versus litter-dwelling or arboreal species) nor do they provide direct, unbiased measures of abundance. The latter characteristic is of particular concern. Pitfall catches are affected by numerous variables, including climatic and microclimatic conditions, habitat and vegetation structure, trap size and design, previous catches, and the intrinsic activity levels, hunger states, dispersal capacities, body sizes, genders and reproductive conditions, phenologies, and population densities of target individuals and taxa (Williams 1959, Greenslade 1964, Luff 1975, Southwood 1978, Adis 1979,

Best et al. 1981, Luff 1986, Perfecto et al. 1986, Morrill et al. 1990, Quinn et al. 1991, Neve 1994, Spence and Niemela 1994, Vermeulen 1994, Abensperg-Traun and Steven 1995, Mommertz et al. 1996, Baumgartner 2000, Fournier and Loreau 2000).

Necrophagous Insects.

The analytical consequences of the often abundant, yet incidental, necrophagous (carrion-feeding) insects, such as blowflies (Diptera: Calliphoridae) and burying beetles (Coleoptera: Silphidae), must be considered when dealing with pitfall trap data. These insects are attracted to, and feed upon, carrion. Relatively long periods between pitfall trap collections may result in samples which effectively act as baits for necrophagous species, especially traps that incidentally capture vertebrates (Evans 1969) and those with dilute preservative.

As mentioned under methods of analysis, all known necrophagous beetles were excluded from analyses, following the rationale of Brenner (2000). Carrion is an unpredictable, patchy and ephemeral resource, leading to intense competition between necrophages (Crowson 1981, Lawton and Hassell 1984, Ratcliffe 1996). As a result, necrophages are often capable of detecting carrion at considerable distances, as much as two miles away in some

species of the silphid genus, *Nicrophorus* (Ratcliffe 1996). An unfortunate consequence of this wonderful sensory capacity is that such insects are strongly attracted to pitfall traps once the captured organisms begin decaying (e.g., Evans 1969). Preservatives are rarely perfect and, in any event, become increasingly diluted with rain and the body fluids of captured organisms. Necrophagous beetles are usually grossly disproportionately abundant in pitfall traps (Brenner 2000, LaBonte, unpublished). Of the beetles collected via pitfall traps in BBCRNA habitats, 34% (4,191) were necrophages, which vastly exceeds their non-trap encounter rate in these habitats (LaBonte, unpublished). Furthermore, necrophagous beetles may be attracted to traps from far outside the sampled habitat, rendering them suspect in any small-to-modest scale faunal analysis.

All species of Silphidae, *Nicrophorus* spp. and *Thanatophilus lapponicus* (Herbst), collected in this study are necrophagous, as are the Leiodidae, *Catops* spp. and *Catoptrichus frankenhauseri* (Mannerheim). These species were excluded from analysis. Some Staphylinidae are probably necrophagous, especially those species in the subfamily Aleocharinae. It is uncertain whether these beetles feed upon carrion or upon those insects which are true necrophages. Furthermore, it is unknown which, if any, Aleocharinae are attracted to carrion. I decided to err on the side of caution and retain all

Staphylinidae for analysis. However, since the bulk of Aleocharinae were not determined beyond subfamily, most were already excluded from any analyses below the family level.

Beetle Responses to Preservatives.

There is evidence that ethylene glycol, a standard preservative used in pitfall traps, attracts some species or genders of insects (Holopainen 1990), as is true of some other preservatives (Luff 1968). Preservatives may also repel some species (Southwood 1978). To the best of my knowledge, there is no published documentation about any attractive or repellent qualities of the preservative used in the BBCRNA study, propylene glycol. However, it seems likely that it would have such effects on at least some beetle taxa. Investigation of this phenomenon would provide information valuable to researchers using pitfall traps.

Target Taxa of Pitfall Traps.

Target taxa of pitfall traps are, of necessity, primarily those species active upon the substrate surface. It was not surprising that the abundant and speciose families in this study included the Carabidae

and Staphylinidae, two families notable for their preponderance of epigeal species in temperate zones. There was no *a priori* expectation of the abundance of Anthicidae and Elateridae in Gravel Bars, although adults of these families are often found under rocks, in litter, or upon substrate surfaces. Of the eight families contributing 1% or more of the total individuals, either the families or the species representing them were associated with soil or litter habitats (Table 2). Nor is it surprising that all ubiquitous species (Table 4) and almost all abundant species, such as those in the "Top 20" (Table 3) (with the possible exception of *Eusphalerum pothos* - see species profiles), were soil and litter inhabitants.

Of the 33 families contributing less than 1% of the total individuals, 70% (23) were exemplified by adults normally found in habitats other than soil or litter (Table 2). With a few exceptions, non-soil/litter inhabiting families represented those families present only in 1995 or 1996. I considered such taxa incidental, in the sense of Gaston (1994). The Corylophidae, Histeridae, and Sphaeritidae were the only "rare" families with ground or litter inhabiting species. Corylophidae are minute beetles not only found in litter but are often in association with fungi under bark (White 1983). The combination of very small size and association with subcortical habitats may have rendered members of this family less susceptible to pitfall traps.

Sphaeritidae and most Histeridae are associated with dung and carrion (White 1983) and may not be readily collected with unbaited pitfall traps.

The relationship between the sampling method and collection of the 183 "rare" species is less straightforward. Although almost all species in the incidental families were also "rare", these taxa contributed only 43 (24%) of the total "rare" species. The balance of "rare" species were from soil or litter inhabiting families. Whether the apparent rarity of most of these species is real or is an artifact of pitfall trap susceptibility or sampling periods remains an open question.

Sampling bias and differential species susceptibility ensure that even the most vigorous pitfall trapping scheme will detect only some fraction of the total beetle biodiversity present at the BBCRNA (see final section of this chapter). However, such sampling selectivity may be a blessing in disguise. A serious hindrance to insect biodiversity studies is the limited number of practicing taxonomists available (Lattin 1993, New 1995). Over a hundred families and thousands of species of beetles are known from the Pacific Northwest (Hatch 1953, 1957, 1963, 1965, 1971). Specialists capable of identifying components of such an extensive fauna are often overwhelmed by previous demands upon their expertise, lack the time to deal with large numbers of specimens, or simply don't exist. On the other hand,

based upon this study, only a few key families and relatively few abundant beetle species were detected by pitfall trapping. BBCRNA and National Park researchers and land managers could focus taxonomic efforts upon these taxa. The modest number of abundant taxa may make it feasible to develop "in-house" identification expertise through training and consultation with a few taxonomic authorities.

Sampling Intensity.

The range of traps per habitat or site (these aspects were not always clear from the materials and methods sections of the cited papers) from thirty-seven studies using pitfall trapping in faunal surveys ranged from one to thirty (Table 5). Ten or fewer traps per habitat were utilized in 76% (28) of these studies. Thus, the number of traps per habitat in the BBCRNA study appeared typical of faunal surveys using pitfall traps.

Sampling Frequency.

The sampling frequency in Table 5 ranges from one-half to six weeks. A four-week sampling frequency was indicated for 35% (13) of the studies, while 59% (22) sampled at intervals less than every four weeks. BBCRNA

sampling was thus less frequent than that of the majority of studies cited in Table 5. While more frequent sampling would have been desirable, the remote location of and difficulty of access to the BBCRNA sites did not allow that option. North Cascades National Park staff, who serviced the traps, had to travel four hours to the trailhead at the entrance to the BBCRNA (by auto, boat, and foot), and then hike up to eight miles (one way), often through difficult terrain without trails, to acquire trap samples. Sample acquisition generally took a full week.

Sampling Period.

It is clear from the literature in Table 5 that most pitfall trap studies were conducted during the snow-free seasons (where appropriate) or some smaller subset of a full calendar year. The sampling season, mid-June through mid-October, at the BBCRNA was primarily dictated by the snow-free season of the BBCRNA, from May through mid-October as a rule. While valuable information about winter-active and early season taxa can be gained through trapping at those times, it was not possible for this study. Hiking through miles of deep snow prior to snow melt was not feasible. Furthermore, pitfall traps normally fare poorly during snow melt. They are often

swamped by the melting snow or displaced by snow melt and the freezing and thawing that often occurs during this period.

Bear activity further constrained the practical sampling season. During the first year of this study, traps were initially placed in May. However, sample destruction by bears from early May to early June was so extensive (up to 70% of traps per habitat) it was pointless to sample during that time. Safety considerations for personnel servicing the traps also led to the decision to avoid May-to-June sampling.

Study Duration.

The study periods of the literature cited in Table 5 ranged from one to fifteen years or seasons. Of these, 73% (27) were conducted through two or fewer years/seasons, with 40% (15) performed for two years/seasons. The duration of the BBCRNA study thus appears typical of invertebrate faunal surveys.

Sampling Effort.

There was little difference between habitats in the number of trap days (Figure 5), a measure of sampling effort. There were no apparent relationships between

sampling effort and patterns of habitat abundance (Figures 6, 7), species richness (Figure 9), and diversity indices (Figures 10,11). While no comparative species curves reached asymptotes, rates of species accumulation were declining for all habitats (Figure 25), suggesting that sampling of reasonably abundant and pitfall-vulnerable species was becoming relatively complete for most habitats. This is supported by examination of Table 1, which shows that almost all of the seventy additional species collected in 1996 were represented by fewer than five individuals. Thus, "new" species were virtually all "rare". The only striking exception to this pattern was *Eusphalerum pothos*, with no individuals captured in 1995 and 93 collected in 1996. As discussed in the species profile below, traps yielding *E. pothos* may have been unintentionally biased by being placed adjacent to skunk cabbage which subsequently flowered, attracting large numbers of this floricolous species.

SECTION 2: FAMILY AND SPECIES PROFILES

Families and Species to be Discussed.

Most of the 41 families found during this study contributed relatively few individuals or species to the beetle fauna of the BBCRNA. Families other than

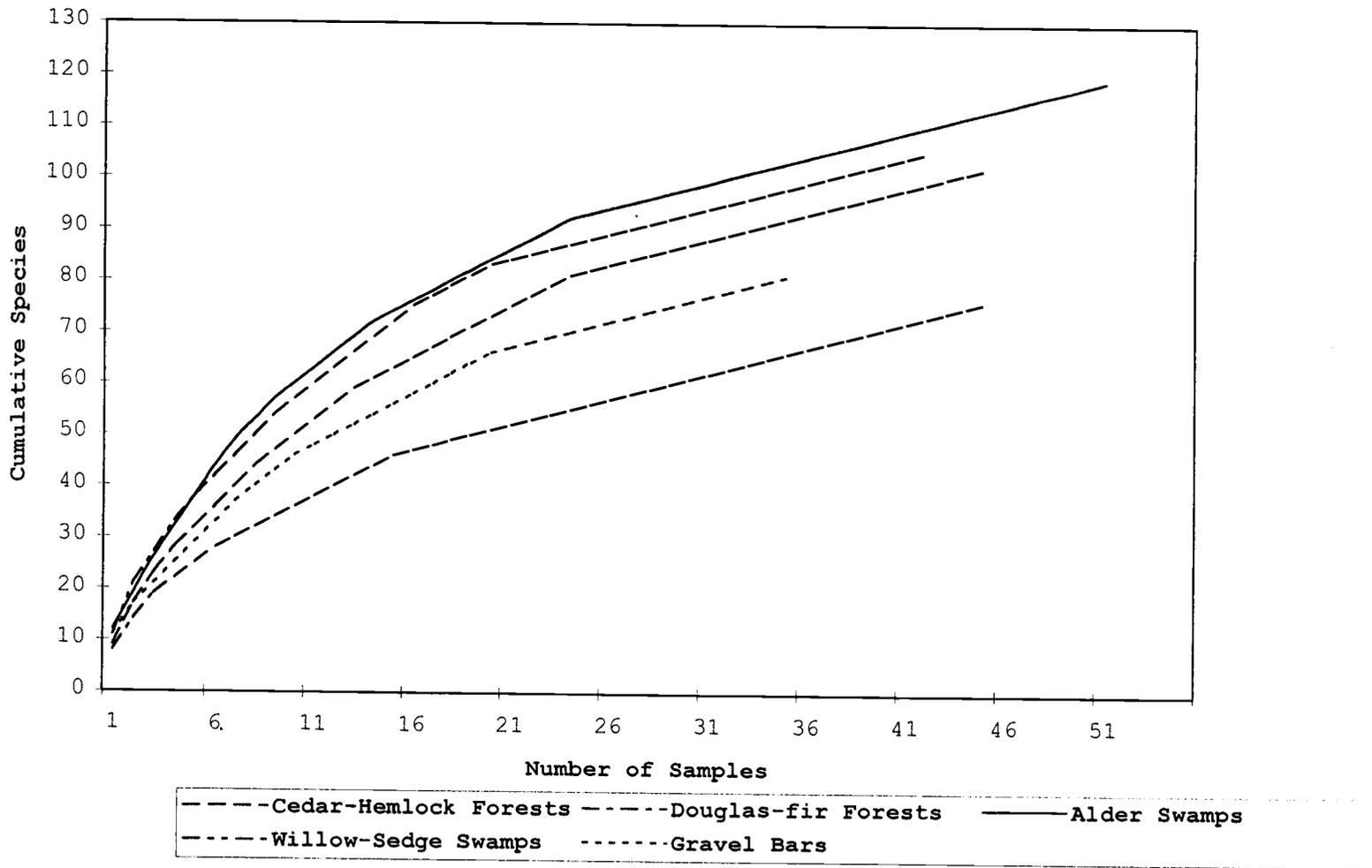


Figure 25. Comparative Habitat Species Curves.

Anthicidae, Carabidae, Elateridae, and Staphylinidae contributed only 8% of total individuals (Figure 14), with per habitat contributions of 3% (Gravel Bars) to 18% (Willow-Sedge Swamps) (Figure 16). The relative contributions of these "other" families to species richness were greater than for individuals. Species of families other than Carabidae, Elateridae, Leiodidae, and Staphylinidae accounted for 35% of all species (Figure 19), with per habitat contributions of 26%-34% (Figure 20). Moreover, 23 (64%) of the 36 "other families" were represented by species whose primary adult habitat is not in soil and litter (Table 2). Inhabitants of the soil and litter are the targets of pitfall traps (see discussion of sampling). Although the Leiodidae was a relatively species-rich family (20 species, Table 1), the aggregate numbers of this family constituted less than 1.5% of all individuals and this family will not be discussed. Consequently, the following discussion is restricted to the biology of and significance to the BBCRNA of the four abundant or species-rich families: Anthicidae, Carabidae, Elateridae, and Staphylinidae. An exception was made for the Latridiidae because a species of this family was among the twenty most abundant species (Table 3). A general caveat is that remarks about the degree of knowledge about family biology and taxonomy are with respect to North America. In many cases, the depth and quality of knowledge for most beetle families is much greater in other parts of the world, e.g., Europe.

A comprehensive treatment of the 290 species of beetles collected during the BBCRNA study is beyond the scope of this dissertation. Species profiles will be provided for the twenty most abundant species (Table 3) as well as several additional species with noteworthy biologies. A discussion of exotic species found in the BBCRNA and the first record for one BBCRNA species from the lower 48 states of the U.S.A. will follow the species profiles. These accounts enabled finer resolution analyses of BBCRNA beetle spatiotemporal abundance and diversity patterns than would have been available from higher taxonomic levels. Species-specific data also aided in the formulation of hypotheses regarding the phenomena responsible for the perceived patterns of BBCRNA beetle abundance and diversity.

Anthicidae: Ant-like Flower Beetles.

***Eurygenius campanulatus* LeConte.**

Anthicidae are a somewhat heterogeneous family now including genera that were once placed in the Pedilidae (*Eurygenius* Laferte-Senectere) or in the Pyrochroidae (*Ischalia* Pascoe) (Lawrence and Newton 1995). This is not a particularly diverse family in North America, with about 215 species in North America north of Mexico (Poole and Gentili 1996) and with about 30 in the Pacific Northwest (Parsons, LaBonte, and Miller, unpublished). Anthicidae are most closely related to several other

families (Aderidae and Scaptiidae) in the same general lineage as the Tenebrionidae (Lawrence and Newton 1995). Downie and Arnett (1996b) address the Northeastern North American fauna, while Hatch (1965) treats the Pacific Northwestern species.

Most North American adult anthicids are fairly small, ~2-4 mm long, although *Eurygenius campanulatus* adults are up to 11 mm in length. Adults are slender, with rounded or squared heads and pronota which are distinctly more narrow than either head or abdomen, accounting for the common name of the family. Little has been published on the biology of anthicids. General accounts can be found in Young (1991) and White (1983). The following information is derived from the treatment in Young (1991). Adult anthicids are often found on flowers or foliage, hence the common name for the family. Many species are associated with the decaying vegetation on the ground surface of open areas, such as sand dunes, ocean beaches and the shores of bodies of water. Adults of most species are probably detritivorous, although some are predators and others may only feed upon nectar and pollen. Most larvae are believed to be detritivorous or mycetophagous in the decaying vegetation where they are found. Adults of the genus *Ischalia* are nocturnal, resting on foliage or under bark during the day (Young 1975). The larvae of this genus are found under bark and in rotting wood, presumably feeding upon fungi therein

although they may be facultative predators. Adults of most other anthicids are at least partly diurnal.

Anthicidae were the fourth most abundant family in BBCRNA pitfalls (Table 2). However, only three species of this family were collected (Table 1). With the exception of *Ischalia vancouverensis* Harris, which was found only in Alder Swamps and Cedar-Hemlock Forests, the vast majority of anthicids (97%) were collected from Gravel Bars (Table 1). A single species, *Eurygenius campanulatus* LeConte, accounted for 479 (94%) of the anthicids found (Table 1). The phenological pattern of this family (Figure 15) matched that of Gravel Bars (Figure 8). It also matched the pattern of the other abundant Gravel Bar family, the Elateridae (Figure 15).

Distribution: *Eurygenius campanulatus* has been recorded from Alberta, British Columbia, Idaho, Washington, and Oregon (Hatch 1965, Bousquet 1991).

Habitat: Little has been published on the habitat of this species. It has been collected under rocks and on flowers in open habitats with sandy and gravelly soils, both near and distant from open water (LaBonte, unpublished). Larvae of related species are known from plant detritus, often in very moist areas, but also from beach sand (White 1983).

Trophic data: Since adults frequent flowers, they may feed upon pollen and nectar, although they may also be

detrivorous or omnivorous (Young 1991). Larvae are presumed to either be direct detritivores of plant detritus and litter, or to perhaps feed upon the fungi associated with this resource (Young 1991).

BBCRNA significance: This species was the second most abundant BBCRNA beetle, with 479 individuals (Table 3). Most specimens, 76%, were collected in 1995. It was only found in the Gravel Bars, where it was the most abundant species, comprising 27% of all beetles. Like *Scaphinotus angusticollis*, such abundance may be more apparent than real, instead reflecting idiosyncratic vulnerability to pitfall trapping. However, adult *E. campanulatus* have not been observed to be particularly active (LaBonte, personal observation) nor are they greatly larger than many other common Gravel Bar beetles, e.g., many elaterids. Furthermore, Hatch (1965) lists this species as common. This study's vegetation inventory revealed few flowering plants on the Gravel Bars, making it more likely that adult *E. campanulatus* are detritivores or omnivores. Presumably the same would apply to the larvae. This species contributed the vast majority of detrivorous individuals (over 90%) found in the Gravel Bars (Figure 23).

Carabidae: Ground or Carabid Beetles.

Carabid beetles are one of the most diverse beetle families, with about 40,000 species worldwide (Bousquet and Laroche 1993). They are well represented in the Pacific Northwest. About 500 species are known from Oregon (Parsons, LaBonte, and Miller, in prep.). Carabids are related to many aquatic beetle families, such as Amphizoidae, Dytiscidae and Gyrinidae (Crowson 1981). The tiger beetles, often placed in their own family of Cicindelidae, are now regarded as specialized members of the Carabidae (Bousquet and Laroche 1993). As a result of several regional works (Hatch 1953, Lindroth 1961-1969) and many taxonomic revisions, the composition of the Pacific Northwest carabid fauna is well understood.

Adult carabids vary greatly in size and shape, with North American species ranging from 1.2-40 mm in length. Most species in the Pacific Northwest are black or brown, but a few genera, including *Cicindela*, have numerous brightly colored species. A good treatment of carabid biology and ecology is Thiele (1977). There are also several compendia of carabid papers covering a wide range of subjects, e.g., Erwin et al. (1979), den Boer (1986), Stork (1990), Desender et al. (1994), Niemela (1996), and Brandmayr et al. (2000). A substantial proportion of the Pacific Northwest carabid fauna is comprised of exotic species indicative of disturbed or anthropogenic habitats

(Hatch 1953, Spence 1990). Most of these species are indigenous to western Europe (Lindroth 1957).

Sterotypical carabids are portrayed as generalist predators of small invertebrates and are regarded as important beneficial predators in agroecosystems (Borrer et al. 1989). However, many carabids have more restricted diets, specializing upon springtails (Thiele 1977), slugs and snails (Greene 1975, Thiele 1977), or millipedes (LaBonte 1983, unpublished). Several genera, e.g., *Brachinus* Weber and *Lebia* Latreille, are even parasitic as larvae (Thiele 1977). Many carabids include substantial amounts of plant matter in their diet, mainly in the form of seeds and fruits, and some taxa may be almost solely phytophagous (Johnson and Cameron 1969, Hengeveld 1980, Larochelle 1990). Several of the carabid genera and species most typical of Pacific Northwest forests have been recorded eating Douglas-fir seeds in captivity (Johnson et al. 1966).

Carabidae were the second most abundant family in BBCRNA pitfalls (Table 2). Carabids were prominent, to varying degrees, in all BBCRNA habitats (Figures 16, 20). *Scaphinotus angusticollis* (Fischer), was the most abundant beetle species collected in the BBCRNA, accounting for 13% (1,036) of all individuals (Table 3). Four other carabid species were among the top twenty most abundant BBCRNA beetles (Table 3). Carabidae contributed relatively few individuals to Alder Swamps and Gravel Bars, but comprised over 40% of the abundance in Douglas-

fir and Cedar-Hemlock Forests (Figure 16). Members of this family were numerically dominant in Willow-Sedge Swamps, with 59% of the individuals collected. Abundance patterns for carabids as a whole (Figure 15) did not match that of any particular habitat, but closely approximated that for the entire BBCRNA study area (Figure 8). The July and September peaks were similar to those observed for several groups of woodland Carabidae in Arkansas (Allen and Thompson 1977) and England (Evans 1969).

The proportion of Carabidae in Gravel Bars, 12%, was similar to that of this family (4-19%) in non- or pre-flooded riparian habitats along the Rio Grande River in New Mexico (Ellis et al. 2001). Although at least some of the sampled Gravel Bars in the BBCRNA had clearly flooded during the winter of 1995, it is unknown whether all were. This is unfortunate, as it would otherwise be possible to compare the flood response of this family to that found at the Rio Grande, where Carabidae comprised 32-50% of the beetles in post-flood habitats (Ellis et al. 2001).

This family had the second greatest species diversity of the study locale, with 55 species, 19% of the total species collected (Figure 19, Table 1). Carabid species representation was least in Douglas-fir Forests (12%) and greatest in Gravel Bars (21%) and Willow-Sedge Swamps (28%) (Figure 20).

***Agonum brevicolle* Dejean.**

Distribution: This species has been documented from British Columbia south to California, east to Nevada (Bousquet and Laroche 1993).

Habitat: Little has been published on the habitat of this species. In British Columbia, it has been recorded from marshes of *Carex* spp. and *Typha latifolia*, on soft, organic soil (Lindroth 1961-1969). Kavanaugh (1992) found *A. brevicolle* was restricted to marshes and bogs below 250 m elevation in the Queen Charlotte Islands. I've found this species abundantly along the vegetated margins of a montane (1,185 m elevation) lake on the west slopes of the Oregon Cascades (LaBonte, unpublished). Members of the subgenus in which this species has been placed, *Agonum* Bonelli, are often prominent in similar wetland habitats (Lindroth 1961-1969; LaBonte, unpublished). Larvae presumably live in the same habitat as the adults.

Trophic data: Nothing has been published on the feeding habits of this species. Adults and larvae of related species are believed to primarily be predators of small invertebrates, although some plant material may be consumed as well (Dawson 1965, Hengeveld 1980, Forsythe 1982, Laroche 1990).

BBCRNA significance:

This species ranked third in abundance, with 425 individuals (Table 3). It was found only in the Willow-Sedge Swamps (Table 1). It was the most abundant species in this habitat, constituting 34% of the individuals collected. Most specimens, 73%, were collected in 1996. The abundance of this species certainly contributed to the overwhelming dominance of predatory individuals in Willow-Sedge Swamps (Figure 23). Unlike *Scaphinotus angusticollis* (see below), its abundance chronology closely matched the overall pattern for Willow-Sedge Swamps (Figure 8), although removal of this data made October the lowest abundance month, rather than the second-to-lowest. Also unlike *S. angusticollis*, there is no reason to suspect trapping bias. This species is no larger nor more active than many other beetles found in Willow-Sedge Swamps (LaBonte, personal observation).

***Blethisa oregonensis* LeConte.**

This species was not among the top twenty abundant beetles, with only twenty-three collected. Discussion of *B. oregonensis* is included because the foraging behavior of the adult underscores the linkage of aquatic and terrestrial ecosystems in riparian zones.

Distribution: Bousquet and Larochelle (1993) recorded this species from British Columbia south to Oregon, east to Idaho.

Habitat: *Blethisa oregonensis* is found along the margins of standing bodies of water, such as lakes, ponds, riverine backwaters, and in marshes and bogs; on soft, wet, organic soil, generally amid or adjacent to dense vegetation (Lindroth 1961-1969; LaBonte and Johnson 1989; LaBonte, unpublished). It is also found in sphagnum mats in bogs (LaBonte, unpublished).

Trophic data: No trophic data have been published for this species. Congeners have eaten freshwater shrimps and mealworm larvae (Tenebrionidae: *Tenbrio molitor* L.) in captivity (Larochelle 1990). Both adults and larvae are presumed to be exclusively predaceous upon small invertebrates.

BBCRNA significance: This species was only found in the Willow-Sedge Swamps at BBCRNA (Table 1). The vast majority of specimens, 87%, were collected in 1995.

Members of this genus, including *B. oregonensis*, are known to submerge themselves upon disturbance by crawling down emergent plant stems or debris and remaining submerged for several minutes (Arens and Bauer 1987, LaBonte and Johnson 1989). This behavior has been interpreted as an adaptation to seasonal flooding of their riparian habitats (Arens and Bauer 1987). However, it may also function as a predator-escape response (LaBonte and Johnson 1989). More germane to the BBCRNA

and considerations of trophic linkages between aquatic and terrestrial realms, voluntary immersions of *B. oregonensis* have also been observed, leading to the suggestion that these beetles may forage underwater (LaBonte and Johnson 1989). Such behavior has been reported for several other carabids (Adis 1982, Thiele 1977).

***Loricera decempunctata* Eschscholtz.**

As with *Blethisa oregonensis*, this species was not among the twenty most abundant beetles, with fifty-three individuals collected (Table 1). It is included in this discussion because *L. decempunctata*, along with several other species of beetles found in the BBCRNA, is believed to be a specialist predator. Specialist predators may have an ecological effect disproportionate to their relative abundance (New 1991), which is one of the desirable aspects of such species when used for biological control (Debach 1974).

Distribution: The known range of this species extends from Alaska south to northwestern California, primarily west of the Cascade Crest (Kavanaugh 1992).

Habitat: *Loricera decempunctata* has been documented from a wide variety of moist habitats, on organic substrates, exposed or deeply shaded, including bogs, marshes, and the margins of streams, ponds, and lakes (Kavanaugh

1992). It is not restricted to the vicinity of open water (LaBonte, unpublished; Lindroth 1961-1969).

Trophic data: No trophic data have been published for this species. Both adults and larvae of congeners selectively prey upon Collembola, although they are known to feed upon other arthropods (Larochelle 1990).

Detailed analysis of the Holarctic *L. pilicornis* (F.) reveals adult behavioral and morphological adaptations for catching such elusive prey (Bauer 1982). The segments of the basal half of the antennae have coarse, long, ventrally-directed setae and there are combs of similar setae along the lateral and apical margins of the venter of the head. Upon encountering a collembolan within range, a beetle rapidly lowers its antennae on either side of the prey until the antennae are in contact with the substrate. The collembolan is effectively "corraled" by the antennal and ventral head setae.

Congeners of several other BBCRNA Carabidae are also known to specialize upon Collembola (Hengeveld 1980), although their morphological and behavioral means of prey capture differ from *Loricera* (Bauer 1982). *Leistus* spp. have a large central concavity on the venter of head, formed in part by the pronouncedly ventrally concave mandibles, lined by rows of coarse setae along the ventral lateral and apical margins of the head. Although prey capture behavior for this genus has not been documented, the beetles presumably clap their heads down over prey, trapping them. *Notiophilus* spp. are very

different in appearance from species of *Leistus* and *Loricera*. These compact, "bullet-shaped" beetles have short antennae and extremely large, bulbous, compound eyes. A *Notiophilus* lies in wait for a collembolan, triangulates the prey's position, and then rapidly darts out and grabs the prey in its mandibles (Bauer 1977).

BBCRNA significance: *Loricera decempunctata* was relatively abundant only in Willow-Sedge Swamps (81% of all specimens), although a few specimens were found in Alder Swamps and one in Cedar-Hemlock Forests (Table 1). This species was slightly more abundant in 1996 (60% of individuals) than 1995. *Leistus ferruginosus* Mannerheim was almost as abundant as *Loricera decempunctata* (48 specimens), but was most prevalent in Cedar-Hemlock Forests (60% of individuals) and Alder Swamps (38% of individuals). Only three *N. sylvaticus* Eschscholtz were collected, two in Cedar-Hemlock Forests and one in Douglas-fir Forests.

These BBCRNA species presumably have prey selectivities similar to that documented for their congeners. This may not necessarily be so. Examination of the gut contents of several Oregon *Leistus ferruginosus* revealed no discernable collembolan remains, although dipteran fragments were abundant (LaBonte, unpublished). Nonetheless, carabids that were presumptive collembollan specialists were present in all habitats except Gravel Bars. Collembola tend to be a minor or virtually absent element in Gravel Bars (Merritt

and Cummins 1984, Hering 1998), except right at the water margin (LaBonte, personal observations).

***Pterostichus herculaneus* Mannerheim.**

Distribution: This species has been documented from British Columbia south to Oregon, east to Idaho and Montana (Bousquet and Larochelle 1993). It is almost certainly in California, as *P. herculaneus* is known from southwesternmost Oregon and there are California specimens in the California Academy of Sciences collection identified as other species (LaBonte, unpublished).

Habitat: *Pterostichus herculaneus* is a somewhat eurytopic species. In the Willamette Valley of Oregon, it is found in oak/Douglas-fir savanna, forest margins, deciduous to coniferous forests, from dry to moist conditions; often, but not exclusively, in dense and closed-canopy stands (Lindroth 1961-1969; LaBonte, unpublished). This species is generally present at low to moderate elevations, from sea level to ~1,400 m, although specimens from southern Oregon were found up to ~1,750 m (LaBonte, unpublished).

Adults of *P. herculaneus* and related species are primarily litter and soil surface dwellers, but can frequently be found under the bark of dead (especially fallen) trees or in decaying coarse woody debris.

(LaBonte, unpublished). Larvae are undescribed, but are presumably to be found in litter or within the upper soil horizons.

Trophic data: *Pterostichus herculaneus* has been observed feeding upon Douglas-fir seeds in the laboratory (Johnson et al. 1966). Otherwise, no trophic data have been published for this species. Based predominantly upon European literature, adults of *Pterostichus* spp. have been documented as feeding upon fruits, vegetables, seeds, miscellaneous plant materials, and various invertebrates, including mites, earthworms, molluscs, opilionids, Collembola, insect larvae and eggs, etc. (Fox and MacLellan 1956, Davies 1953, Tod 1973, Hengeveld 1980, Forsythe 1982, Larochele 1990). Adults of species related to *P. herculaneus* are relatively unselective predators of small and moderate-sized invertebrates (LaBonte, unpublished). Adults of *P. herculaneus* are frequently found feeding at banana and apple baits set for *Scaphinotus* spp. (LaBonte, unpublished). Adults are probably predominantly predaceous upon various invertebrates, but opportunistically eat fruit, seeds, and vegetation. Larvae of other *Pterostichus* spp. are apparently entirely predaceous (Thiele 1977, Larochele 1990).

BBCRNA significance:

This species was seventeenth in abundance, with 88 individuals (Table 3). It was found in all habitats except Willow-Sedge Swamps (Table 1). Most individuals

were from Douglas-fir (52%) and Cedar-Hemlock (30%) forests, with Alder Swamps contributing 16%. There was little between-year variation in abundance in these habitats. The two individuals found in Gravel Bars were almost certainly strays from adjacent forested habitats.

This species belongs to a subgenus of *Pterostichus*, *Hypherpes* Chaudoir, with great diversity in the western United States. About 70 species are recognized (Bousquet and Larochelle 1993). *Hypherpes* is among the most taxonomically challenging groups of North American *Pterostichus*. Many species can only be confidently identified via the male genitalia.

Species of *Hypherpes* have a rather uniform set of characteristics presumably associated with the forest habitat of most members: absent dorsal elytral setae, fused elytra, and extreme brachyptery. Adults overwinter, remaining active throughout the winter in moderate climates (LaBonte, unpublished). Hand collecting and other pitfalling studies indicate that members of this subgenus are among the most numerous macro-insects of the epigeal fauna of Pacific Northwestern coniferous forests (LaBonte, unpublished).

***Pterostichus neobrunneus* Lindroth.**

Distribution: The known range of *P. neobrunneus* extends from British Columbia south to Oregon (Bousquet and Larochelle 1993).

Habitat: This species is less eurytopic than *P. herculaneus*. It is apparently restricted to open or closed-canopy mesic or xeric coniferous forests (Lindroth 1961-1969; LaBonte, unpublished). *Pterostichus neobrunneus* is abundant in Oregon from moderate elevations (~1,500 m) up to the timber limit (LaBonte, unpublished). It is not surprising to find it at the lower elevation BCCRNA, given the well known pattern of elevational depression of life zones with increased latitude.

As with *P. herculaneus*, adults are primarily litter and soil surface dwellers, but can frequently be found under the bark of dead (especially fallen) trees or in decaying coarse woody debris. (LaBonte, unpublished). Larvae are undescribed, but are presumably to be found in litter or within the upper soil horizons.

Trophic data: No trophic data have been published for *P. neobrunneus*. The preceding comments on the trophic relationships of *P. herculaneus*, which belongs to the same subgenus as *P. neobrunneus* (Bousquet and Larochelle 1993), presumably apply equally well to this species.

BBCRNA significance:

This species was eighth in abundance, with 141 individuals (Table 3). Like *P. herculeanus*, most specimens were found in Cedar-Hemlock (52%) and Douglas-fir (47%), with a few specimens from Alder Swamps (Table 1). This species was absent from the other habitats. Also like *P. herculeanus*, there was little interyear variation in abundance.

***Scaphinotus angusticollis* (Fischer).**

Distribution: This species is known from Alaska to northern California, mainly west of the Cascades, but east of the Coast Ranges in southern British Columbia and to the east slopes of the Cascades in Washington and Oregon (Kavanaugh 1992).

Habitat: *Scaphinotus angusticollis* is found in coniferous and mixed mesic forests, from sea level to timberline, depending upon the latitude (Kavanaugh 1992, LaBonte 1998). During the day, the predominantly crepuscular or nocturnal adults can be found under logs and other fallen coarse woody debris, as well as under the bark of dead standing or fallen logs (LaBonte, personal observation). The larvae are found under similar cover or within the litter layer (LaBonte, personal observation).

Trophic Data: *Scaphinotus* spp. are persistently referred to as strict molluscivores feeding solely upon snails and slugs (e.g., Lindroth 1961-1969, Thiele 1977). This may be true of adults of some subgenera, e.g., *Neocychnus* Roeschke (LaBonte, unpublished) and larvae (Greene 1975; LaBonte, unpublished). It is not so for adults of most Pacific Northwest species (LaBonte 1998), including *S. angusticollis*. Although adults of western U.S. *Scaphinotus* spp., including *S. angusticollis*, will readily attack and consume small to modest-sized slugs and snails (Greene 1975; Digweed 1993; LaBonte, unpublished), there is ample evidence they prey upon a wide variety of invertebrates, including congeneric and conspecific adults (e.g., Larochelle 1972, 1990). Adults may also be facultative frugivores, as appears to be the case for several species of Carabidae (Larochelle 1990, Hill and Knisley 1992). They are readily captured at fruit baits (apple, banana, peach) and adults have been maintained in culture for months on huckleberries and other berries (LaBonte, unpublished).

BBCRNA significance: This species was the most abundant of BBCRNA beetles, with 1,036 individuals, or 13% of all non-necrophagous beetles collected (Table 3). It was about equally abundant in Cedar-Hemlock (44% of total *S. angusticollis*) and Douglas-fir (50%) forests. Relatively few individuals were found in Alder Swamps (6%). It was absent from the other habitats. There was relatively

little interyear variation in the abundance of this species (Table 1).

Scaphinotus angusticollis was also the numerically dominant species in both Cedar-Hemlock and Douglas-fir forests (Table 1), comprising 40% and 49%, respectively, of the total beetles in these habitats. The influence of this single species was so great that removal of its data shifted abundance peaks from September (Figure 8) to August for Cedar-Hemlock Forests and to July for Douglas-fir Forests.

The great apparent abundance of this species was almost certainly an artifact of the sampling biases of pitfall traps. Based upon extensive hand and bait collecting experience with *Scaphinotus* spp. in the Pacific Northwest, while *S. angusticollis* can be quite common, it has not been observed to be numerically dominant, let alone to such an overwhelming degree (LaBonte, unpublished). With regard to carabid taxa, *Pterostichus* (*Hypherpes*) spp. are generally much more abundant. Several forays in the Big Beaver Creek habitats yielded similar results (LaBonte, personal observation). Instead, it is probable that these large (amongst the largest Big Beaver Creek beetles) and highly active beetles are especially vulnerable to pitfalls. These characteristics are known to increase the susceptibility of insects to this sampling method (Spence and Niemela 1994). However, despite such caveats, this species probably has a significant role in the Big Beaver

Creek forested habitats since it is abundant, large, active and relatively long-lived as an adult.

***Scaphinotus marginatus* (Fischer).**

Distribution: *Scaphinotus marginatus* has the greatest range of any western species of the genus. It is known from the outer Aleutian Islands and Alaskan Peninsula south to northwestern California, east to Alberta, Montana, and Wyoming (Bousquet and Laroche 1993, Lindroth 1961-1969).

Habitat: This species is probably the most eurytopic *Scaphinotus* in the Pacific Northwest (LaBonte 1998). It can be found in urban gardens, alpine talus slopes, steppe riparian woodlands, oak and oak-Douglas fir savannah, open and closed-canopy deciduous forests, mixed and coniferous forests and forest margins (Kavanaugh 1992, LaBonte 1998). The elevational range extends from sea-level to at least 2,300 m (LaBonte 1998). Adults and larvae are found in the same situations as are *S. angusticollis*.

Trophic data: Adults and larvae of this species readily feed upon modest-sized slugs and snails in captivity (Greene 1975; Laroche 1990; Digweed 1993; LaBonte, unpublished), as well as having been observed feeding upon slugs and snails in the field (Laroche 1990; LaBonte, unpublished). However, adults have also been

observed feeding upon fly eggs (Larochelle 1972), mealworm larvae (Larochelle 1990; LaBonte, unpublished) and small caterpillars (LaBonte, unpublished). Related species have been documented as feeding upon a wide variety of invertebrates, including congeners and conspecifics (Larochelle 1990). As with *S. angusticollis*, adult *S. marginatus* may be facultative frugivores, as they are readily captured at fruit baits (LaBonte, unpublished).

BBCRNA significance: This species was much less abundant than *S. angusticollis*, with 102 individuals and ranking fourteenth in abundance (Table 3). As it was present in all habitats, it was one of the five ubiquitous BBCRNA species. However, it was only abundant in two habitats, with 51% of all specimens from Alder Swamps and 31% from Cedar-Hemlock Forests. The single specimen from Gravel Bars was probably a stray from an adjacent more heavily vegetated site. This species demonstrated little interyear variation in abundance.

It is possible that the apparent lesser abundance of *S. marginatus* relative to *S. angusticollis* is a sampling artifact. This species is somewhat less active (LaBonte, personal observation) and much smaller than *S. angusticollis*, which may render it less susceptible to pitfalling. However, hand collecting and baiting both seem to indicate that it is often much less common than *S. angusticollis* (LaBonte, unpublished).

Elateridae: Click Beetles or Wireworms.

Elateridae are a distinctive family with many common, conspicuous, and agriculturally important species. The North American species diversity is substantial, with 928 species known (Poole and Gentili 1996). The Pacific Northwest probably has several hundred species (Hatch 1971), but the distributions of most species are poorly known. Elateridae are related to Buprestidae and several other families of that lineage (Lawrence and Newton 1995). There are no comprehensive taxonomic treatments of the North America species. Pacific Northwestern species are treated in Hatch (1971), while Downie and Arnett (1996a) address the Northeastern North American species. Distributional data on Pacific Northwestern species are often limited to that found in Hatch (1971).

Adult elaterids are elongate and dorsoventrally flattened. North American species range from ~2-45 mm in length. Most adults are dark concolorous, although many have elytra patterned with contrasting pale and dark colors, while some are resplendently metallic.

The common name of "click beetles" arises from the remarkable ability of adults to flip themselves into the air starting from a position with the dorsum resting upon a surface. A prong at the posterior of the ventral prothorax fits into a groove between the mid-coxae when

the anterior of the body is raised from the surface. A projection in the groove prevents the prong from contacting the bottom of the depression until contraction of the pro- and mesothoracic muscles creates sufficient tension to suddenly and sharply drive it home. The resulting energy released against the surface hurls the beetle as much as 30 cm into the air, performing one or more full rotations en route back to the surface (Klausnitzer 1983). This remarkable process functions both as a means of escaping predators and of righting these beetles when they've fallen from vegetation.

Elaterid biology is generally poorly known, with the exception of some economically important species associated with agricultural systems. General treatments of elaterid biology can be found in Becker (1991) and White (1983). The following information on adult elaterids is derived from Becker (1991). Adults are most often associated with foliage and flowers. Most appear to be at least partly diurnal. They can be extremely common. Adult feeding behavior is poorly known, but some are known to feed upon leaves, flowers and pollen, generally doing little significant damage. Many adults may not feed at all.

Elaterid larvae, commonly referred to as "wireworms", are usually found in the soil, in litter or in rotting wood (White 1983). Many of the soil dwellers are root feeders, accounting for the economic significance of some species (Becker 1991, Swan and Papp

1972). Those found in litter or rotting wood are usually predatory, presumably feeding upon a variety of small invertebrates (P.J. Johnson, personal communication). The feeding behavior of most species is unknown and the preceding generalizations are based upon relatively few species (P.J. Johnson, personal communication). Predation is particularly associated with a subfamily, the Denticollinae (P.J. Johnson, personal communication), that includes some of the most diverse genera in North America. Most of the BBCRNA species in this study are members of that subfamily.

Elateridae were the third most abundant family in BBCRNA pitfalls (Table 2). Elateridae were insignificant components of all habitats except Gravel Bars, where they accounted for 53% of all beetles (Figure 16). The Elateridae were also among the most speciose BBCRNA families, with 23 species (Table 1). Elateridae were minor contributors to species diversity, 3%-8%, in all habitats except Gravel Bars, 17% (Figure 20). Species of Gravel Bars were the only abundant elaterids (Table 1). The pattern of elaterid abundance (Figure 15) closely matched that of Gravel Bars (Figure 8), where this family was numerically dominant.

***Cardiophorus propinquus* Hatch.**

Distribution: Hatch (1971) recorded this species from British Columbia, Idaho and Washington.

Habitat: Larvae are soil dwellers (Becker 1991). Adults in this genus have often been collected from open, often xeric, habitats, frequently under rocks resting upon loose or sandy/gravelly soil (Hatch 1971; Crowson 1981; LaBonte, personal observation). This species has been found along streams at altitudes ranging from approximately sea level up to about 1,200 m (Hatch, 1971).

Trophic data: Larvae of the subfamily to which this species belongs (Cardiophorinae) are presumably predominantly predaceous, but may be facultatively herbivorous (P.J. Johnson, personal communication). The BBCRNA vegetation inventory revealed few plants on the Gravel Bars, so larvae of *C. propinquus* may well be predaceous (LaBonte 1998). Adult trophic relationships are uncertain, although *Cardiophorus* spp. are often found on flowers and foliage (Hatch 1971, Downie and Arnett 1996a). At least one species has been recorded as damaging the buds and blossoms of fruit trees (White 1983). This illustrates one of the problems with attempts to conveniently "pigeon-hole" some beetles into a single trophic category.

BBCRNA significance: This species was the fifth most abundant BBCRNA beetle, with 224 individuals (Table 3).

Most specimens, 73%, were collected in 1995. This species was only found in Gravel Bars (Table 1).

***Ligmargus funebris* (Candeze).**

Distribution: This species was recorded from southern British Columbia south to Oregon and east to western Montana (Hatch 1971), as well as California and western Nevada (Horn 1891).

Habitat: Both larvae and adults of *L. funebris*, and related species, are usually found near streams under rocks and debris (Hatch 1971). Adults can be common under stones in gravel bars (LaBonte, personal observation).

Trophic data: Larvae are predaceous (P.J. Johnson, personal communication). Adult trophic relationships are uncertain.

BBCRNA significance: This species was fifteenth in abundance, with 98 individuals (Table 3). Most specimens, 88%, were collected in 1995 (Table 1). This species was only found in Gravel Bars (Table 1).

***Zorochrus dispersus* (Horn).**

Distribution: Hatch (1971) did not treat species of this group (under *Negastris* Thomson) separately. Horn (1891)

recorded *Z. dispersus* from Nevada, Washington and, dubiously, Nova Scotia.

Habitat: Larvae of this genus are found in soil (Becker 1991, under *Hypolithus* Eschscholtz). Adult *Zorochrus* spp. are often found under stones or debris along the margins of streams and lakes (Crowson 1981, White 1983, Downie and Arnett 1996a; in all, under *Hypolithus* spp.). Adults of this genus can be common under stones in gravel bars (LaBonte, personal observation).

Trophic data: Larvae are predaceous (P.J. Johnson, personal communication). Adult trophic relationships are uncertain.

BBCRNA significance: *Zorochrus dispersus* was twelfth in abundance, with 107 individuals (Table 3). A slight majority of individuals, 57%, was found in 1995 (Table 1). This species was found only in Gravel Bars (Table 1).

***Zorochrus musculus* (Eschscholtz).**

Distribution: Although Hatch (1971) did not provide specific distribution data for this species group, he indicated this species, and related species, are part of the Pacific Northwest's montane, subalpine, or alpine faunas. Horn (1891) recorded this species from Alaska.

Habitat: Larvae of this genus are found in soil (Becker 1991, under *Hypolithus* Eschscholtz). Adult *Zorochrus* spp. are often found under stones or debris along the

margins of streams and lakes (Crowson 1981, White 1983, Downie and Arnett 1996a; in all, under *Hypolithus* spp.). Adults of this genus can be common under stones in gravel bars (LaBonte, personal observation).

Trophic data: Larvae are predaceous (P.J. Johnson, personal communication). Adult trophic relationships are uncertain.

BBCRNA significance: This species was fourth in abundance, with 291 individuals (Table 3). The vast majority of individuals, 88%, were collected in 1995 (Table 1). All but one individual (in an Alder Swamp) were found in Gravel Bars (Table 1).

***Zorochrus* sp.**

This species may be undescribed. However, the group of Elateridae to which this genus belongs is in great need of revision and no comprehensive keys to the North American species exist (P.J. Johnson, personal communication). As no specific determination was made, no data were available regarding this species, other than that acquired during the BBCRNA study.

Distribution: Other than the BBCRNA records, the range of this species is unknown.

Habitat: This species was only collected from BBCRNA Gravel Bars (Table 1). The habitat is presumably similar to that of other species in this genus.

Trophic data: There are no trophic data available for this species, but it presumably has trophic relationships similar to other species in the genus.

BBCRNA significance: This species was tenth in abundance, with 122 individuals (Table 3). Most specimens, 86%, were collected in 1996 (Table 1). Almost all individuals were found in Gravel Bars, although two were found in Willow-Sedge Swamps (Table 1).

Latridiidae: Minute brown scavenger beetles.
***Melanophthalma americana* (Mannerheim).**

There are no comprehensive treatments of the North American fauna of this family. Hatch (1961) addresses the species of the Pacific Northwest, and Downie and Arnett (1996b) treat the northeastern North American species.

Adult latridiids are tiny, between 1-3 mm in length, are generally various shades of brown, have clubbed antennae and coarsely faceted eyes, possess coarsely punctate elytral striae and the elytra are thinly clothed with long setae. Little has been published about the biology of this family. The following general statements are derived from White (1983). Latridiids are predominantly associated with moldy animal and plant substances and some species are common in animal nests. Adults and larvae primarily feed upon mold spores. Members of this family are frequently found where grain

or other foodstuffs are stored, presumably because moldy material is present. Adults are commonly swept from vegetation or found in litter.

Distribution: Hatch (1961) recorded *M. americana* from British Columbia south to Oregon and east to Idaho. Downie and Arnett (1996b) also recorded this species from California, as well as Indiana and Pennsylvania.

Habitat: Hatch (1961) states that this species was reared from logs of subalpine fir and could be readily collected from vegetation. *Melanophthalma distinguenda* Comolli was commonly collected from conifer forest vegetation, along with some less abundant congeners, in the H.J. Andrews Experimental Forest in the western Oregon Cascades (Parsons et al. 1991).

Trophic data: No data on the trophic relationships of this species have been published. Presumably, larvae and adults feed upon spores or conidia of various fungi like most other members of this family (Lawrence 1991, Crowson 1984).

BBCRNA significance:

This species was twentieth in abundance, with 68 individuals (Table 3). Most specimens, 65%, were collected in 1995 (Table 1). Other than one specimen, collected in an Alder Swamp, all specimens were found in Willow-Sedge Swamps (Table 1). Although four other species (including two additional *Melanophthalma* spp.) of

this family were collected during the BBCRNA study, *M. americana* was the only common species.

Staphylinidae (Rove beetles).

The Staphylinidae are among the most taxonomically and biologically diverse families of insects. This family is not only the most speciose beetle family in North America, with about 4,100 species, but it also appears to be the most speciose of all North American insect families (Poole and Gentilli 1996, Newton et al. 2001). The known Pacific Northwestern species number between 450-500 species (Parsons, G., J.R. LaBonte, and J.C. Miller, unpublished). However, the taxonomy and species distributions of this family are so poorly known it is certain there are many species present which are not yet recorded from this area.

The boundaries of this family have recently been significantly expanded (Lawrence and Newton 1995, Newton et al. 2001), now including species formerly in families such as Clambidae and Scaphidiidae. The entire family of Pselaphidae has now been subsumed within the staphylinids. Other families within the staphylinid lineage include the Leiiodidae, Ptiliidae and Silphidae (Lawrence and Newton 1995). As a whole, Staphylinidae are among the most taxonomically challenging beetle families.

There are no comprehensive species-level North American treatments of the Staphylinidae. The only Pacific Northwest family-breadth taxonomic work is the dated treatment in Hatch (1957). There are a number of recent revisions of various North American genera, particularly in the subfamilies Omaliinae and Tachyporinae (e.g. Campbell 1973, 1978, 1979, 1982, 1991; Smetana 1971). A generic key to the entire North American (north of Mexico) genera has just been published (Newton et al. 2001). There are still a great many staphylinid taxa in desperate need of revision or good keys, especially the Aleocharinae, a notably taxonomically recalcitrant group.

Archetypal adult staphylinids have a very distinctive appearance: elongate in general body form, with a square or round head distinct from the pronotum, elongate or round pronotum, short legs, short and unclubbed antennae, and the most distinctive feature, short elytra exposing most of the slender abdomen. However, short elytra are shared by some members of other families, while some staphylinids have elytra long enough to completely (or nearly so) cover the abdomen (this is characteristic of an abundant and diverse subfamily, the Omaliinae). Many staphylinids are quite "stocky", while those formerly in the Pselaphidae often have clubbed antennae. Most staphylinids are quite small, under 5-6 mm, but many members of the subfamily Staphylininae are 10-12 mm long, with some species over 20 mm in length.

Most staphylinids are brown or black, but some species are maculate and a few have metallic coloration.

Staphylinids are remarkably varied with regard to their biology and ecology (see Crowson 1981, White 1983, Frank 1991, Newton 1991). They occur in virtually all habitats, although there are relatively few species associated with foliage (there are several genera which are flower associates). Rove beetles can be found along the margins of bodies of water, burrowing in soil and substrates, in the rocky and sandy intertidal zones, in and on carrion and dung, in bird and mammal nests, in and on fungi, under bark, in decaying wood, amid litter, and in the nests of ants and termites. Larvae and adults are generally presumed to have similar habitat preferences although larvae are believed to be restricted to higher moisture regimes than adults (Frank 1991).

Other than in a general sense, our knowledge of North American staphylinid biology, ecology, and taxonomy is rather scant. There is no comprehensive source for general North American staphylinid biology, although Newton et al. (2001) provide at least brief biological data for most treated genera and some species. Moore and Legner (1975) listed only about 3% of the North American species as even partially investigated. This is undoubtedly at least partly due to the absence of comprehensive keys for many staphylinid genera. Crowson (1981), Frank (1991), and Newton et al. (2001) offer some information from a world-wide perspective, while Newton

(1984) provides some data on fungivorous species. Recent taxonomic treatments often contain at least some biological and ecological data (e.g., Newton et al. 2001).

Although staphylinids are stereotypically regarded as generalist predators of invertebrates (e.g., Borror et al. 1989), this is not true for a great many species. Some are truly fungivorous, such as many Aleocharinae and Phloeocharinae (e.g. species of *Megarathrus* Curtis and *Proteinus* Latreille), while several genera of Omaliinae are believed to feed upon pollen, e.g., species of *Eusphalerum* Kraatz (Newton 1984). Association with a potential food resource does not imply that a staphylinid feeds upon it. Many staphylinids associated with carrion, dung or fungi in fact prey upon the maggots and adult flies utilizing these materials, e.g. species of *Tachinus* Gravenhorst (Campbell 1973). Several staphylinid genera are specialized predators. Some species of *Aleochara* Gravenhorst are parasitoids of fly pupae, some of the former Pselaphidae are mite specialists and all Steninae are specialized predators of springtails (Crowson 1981). It is best to recognize that the diets of most staphylinid species are more a matter of conjecture, supposition and extended generalization than of verified knowledge. Larvae, in general, presumably feed upon the same food as adults (Frank 1991, Newton 1991).

Staphylinidae were the most abundant beetles in Park pitfalls, accounting for 43% of all beetles (Figure 14, Table 2). Staphylinidae were prominent in all sampled Park habitats, except Gravel Bars (Figures 16, 20). This family was numerically dominant in Cedar-Hemlock and Douglas-fir forests (~50% of individuals in each habitat) and overwhelmingly dominant in Alder Swamps, with 78% of all beetles collected therein (Figure 16).

This was also the most diverse BBCRNA beetle family, with 92 species, 31% of all beetle species (Figure 19, Table 1). The species count is conservative, as only a few of the taxonomically recalcitrant Aleocharinae could be determined to species. Staphylinidae had the greatest species representation in all habitats, ranging from 31% (Gravel Bars and Willow-Sedge Swamps) to 48% (Alder Swamps). 1996 staphylinid species representation increased in Douglas-fir Forests, Cedar-Hemlock Forests, and Alder Swamps. The abundance pattern for Staphylinidae (Figure 15) most closely approximated those of Cedar-Hemlock and Douglas-fir forests (Figure 8), where this family was numerically co-dominant with Carabidae (Figure 16). This overall abundance pattern for the family was not reflected in Alder Swamps (Figure 8), where this family was overwhelmingly numerically dominant (Figure 16). However, this pattern was similar to those of several forest species of Staphylinidae in England (Evans 1969).

***Anthobium reflexicolle* (Casey).**

Distribution: Hatch (1957) recorded this species from British Columbia south to Oregon, east to northern Idaho.

Habitat: *Anthobium reflexicolle* has been found in mouse nests, while congeners are known from fungus and carrion (Hatch 1957). *Anthobium sinuosum* Hatch was abundant in conifer forest vegetation at the H.J. Andrews Experimental Forest in the western Oregon Cascades (Parsons et al. 1991).

Trophic data: Larvae and adults of this genus are presumably predaceous (Newton et al. 2001). Adults of some members of the subfamily (Omaliinae) in which *Anthobium* spp. are placed are recorded as sometimes damaging flowers (Frank 1991). Some omaline genera are believed to feed upon pollen (Newton 1984, Newton et al. 2001).

BBCRNA significance: This species was eighteenth in abundance, with 80 individuals (Table 3). It was found in three habitats, Alder Swamps, Cedar-Hemlock Forests, Gravel Bars (Table 1). Alder Swamps contributed the vast majority, 87%, of individuals, and 81% of those were collected in 1996 (Table 1).

***Dinothenarus pleuralis* (LeConte).**

Distribution: The known range of *D. pleuralis* is from British Columbia south to Oregon and east to Utah (Moore and Legner 1975). Hatch (1957) recorded *D. pleuralis* as common. This species was formerly placed in the genus *Staphylinus* Linnaeus (Newton et al. 2001).

Habitat: Virtually nothing has been published on the biology of *D. pleuralis*. This species was recorded as uncommonly found on the soil surface and beneath the litter layer in conifer forests in the H.J. Andrews Experimental Forest in the western Oregon Cascades (Parsons et al. 1991).

Trophic data: Larvae and adults of *Staphylinus* spp. and related genera, e.g. *Dinothenarus* Thompson, are generalist predators upon a wide array of invertebrates, including slugs and snails, worms, and the larvae and adults of many insects (Balduf 1935).

BBCRNA significance:

With 79 individuals, *D. pleuralis* ranked nineteenth in abundance (Table 3). It was only found in the forested habitats, but was only abundant in Cedar-Hemlock Forests, 57%, and Douglas-fir Forests, 37% (Table 1). There was virtually no difference in abundance between years (Table 1).

***Eusphalerum pothos* (Mannerheim).**

Distribution: Hatch (1957) recorded this species from British Columbia south to western Oregon and east to southeastern Idaho.

Habitat: No habitat data for *E. pothos* were provided by Hatch (1957). Adult *Eusphalerum* spp. have frequently been observed in very large numbers on the spadices of skunk cabbage (*Lysichitum americanum*) in forested swamps (LaBonte, personal observation).

Trophic data: Adults of *Eusphalerum* spp. are known to feed upon pollen (Newton 1984, Newton et al. 2001), which is supported by the large numbers observed on skunk cabbage spadices (LaBonte, personal observation). Larval diets are unknown (Newton et al. 2001).

BBCRNA significance: This species was sixteenth in abundance, with 93 individuals (Table 3). Except for four individuals found in Gravel Bars, it was otherwise only found in Alder Swamps (Table 1). All specimens were collected in 1996 (Table 1).

It is not surprising that this species was found in Alder Swamps, since the BBCRNA vegetation inventory found skunk cabbage to be among the dominant herbaceous plants of this habitat. Skunk cabbage was rarely a significant component of trap sites in the other habitats. However, the abundance of *E. pothos*, and its absence in 1995, may be an example of trapping bias. The great majority of Alder Swamp specimens, 81%, were collected in a single

trap on a single date, and another 18% were similiarly collected in another trap. These traps may have been coincidentally placed adjacent to flowering skunk cabbage plants.

***Lordithon fungicola* Campbell.**

Distribution: This is a widespread transcontinental species found from Alaska south to California and New Mexico, east to Labrador, Newfoundland and the eastern seaboard (Campbell 1982). Prior to the description of *L. fungicola* in 1982, individuals of this species were generally identified as *L. obsoletus* (Say) (e.g. Hatch 1957), an eastern U.S. species (Campbell 1982).

Habitat: Adults have been found in a wide variety of fungi, including *Polyporus* (Campbell 1982). Adult *Lordithon* spp. are often abundant in fungi in forested areas (LaBonte, personal observation).

Trophic data: The strong association with fungi led to the assumption that adults and larvae of *Lordithon* spp. were fungivorous. However, this was erroneous (Campbell 1982, Newton et al. 2001). Both adults, and probably larvae, are predators of fly larvae feeding upon fungi, e.g., Mycetophilidae. Larvae may be partially or facultatively mycetophagous (Campbell 1982).

BBCRNA significance:

Lordithon fungicola was ninth in abundance, with 131 individuals (Table 3). It was found in all habitats except Willow-Sedge Swamps, although only five specimens were found in Gravel Bars (Table 1). This species was approximately evenly distributed among the three forested habitats and was essentially no more abundant in 1995 than in 1996 (Table 1). Its absence from non-forested habitats can presumably be attributed to the absence of suitable fungi.

***Proteinus collaris* Hatch.**

Distribution: *Proteinus collaris* has been recorded only from western Washington State (Hatch 1957, Moore and Legner 1975).

Habitat: Little has been published on the biology of the genus. Larvae and adults of *Proteinus* spp. are normally associated with a wide variety of decaying soft fungi, as well as dung, carrion and rotting vegetation (Newton 1984). In Seattle, WA, *P. collaris* was collected from alder litter and pine litter in late winter (Hatch 1957).

Trophic data: Although associated with the resources listed above, the trophic role of this genus is unknown. Adults and larvae are presumably largely detritivorous or fungivorous, perhaps sometimes predaceous (Newton et al. 2001).

BBCRNA significance:

This species was the most abundant staphylinid, ranking sixth in overall abundance, with 189 individuals (Table 3). *Proteinus collaris* was present only in Alder Swamps and Cedar-Hemlock Forests (Table 1). Most specimens, 81%, were found in Alder Swamps. There was little difference in abundance between years (Table 1).

***Reichenbachia albionica* Motschulsky.**

The subfamily to which this species belongs, the Pselaphinae, was generally treated as a separate family until recently (Lawrence and Newton 1995, Newton et al. 2001). Adults are in part distinguished from other Staphylinidae by their small size, compact bodies, clubbed or asymmetric antennae, inflexible abdomens, and often with one or more large frontal foveae sported between the eyes. *Reichenbachia albionica* is typical in all the above respects, verging upon rotundity and only 1-1.5 mm long.

Distribution: The known range of this species extends from Alaska south to northern California and east to Idaho (Chandler 1997).

Habitat: Adults have been collected around cattails, from cottonwood and leaf litter, from leaf litter beside sloughs and by sweeping introduced grasses (Chandler 1997).

Trophic data: Little has been written about the biology of the genus, but, like most other pselaphines (Chandler 1997), larvae and adults of *Reichenbachia* spp. are presumed to be predators of small invertebrates, such as mites.

BBCRNA significance:

Reichenbachia albionica was thirteenth in abundance, with 104 individuals (Table 3). Although this species was one of the five ubiquitous BBCRNA species, it was represented by only a few individuals in all habitats except Willow-Sedge Swamps, 79%, and Alder Swamps, 17% (Table 1). There was virtually no difference in abundance between years (Table 1).

***Stenus morio* Gravenhorst.**

As with several of the carabid species discussed, this species was not among the twenty most abundant beetles, with thirty-two individuals collected (Table 1). Although five other *Stenus* species were found in BBCRNA traps, none approximated *S. morio* in abundance. The aggregate numbers of all *Stenus* spp. were still modest, only totalling fifty-seven individuals. *Stenus* spp. (*S. morio* will serve as an exemplar for the genus) are included in this discussion because, along with several species of carabids found in the BBCRNA, they are

believed to be specialist predators of Collembola, as detailed below.

Members of *Stenus* and the related genus, *Dianous* Samouelle, are also notable for a remarkable defensive strategy (Crowson 1981, Klausnitzer 1981). When threatened by a human (and presumably other potential predators) while on shore, these beetles run onto the surface film of adjacent water. They then release terpenes from pygidial glands, which greatly lowers the surface tension of the water surface behind them. The unreduced surface tension pulls the beetles forward at speeds of 0.75 m/s over distances of 10-15 m.

Distribution: This species has a Holarctic distribution, from Alaska, the Yukon and Northwest Territories south to British Columbia and east to New Brunswick (Bousquet 1991). More southerly records include Idaho and eastern Washington south to California (Hatch 1957), as well as Indiana and Michigan (Downie and Arnett 1996a). Bousquet (1991) indicates that *S. morio* is a naturally Holarctic species, while Downie and Arnett (1996a) state it is a European species accidentally introduced in North America.

Habitat: No habitat data have been published for this species in North America. Many species are found along the margins of ponds, lakes, streams and rivers, and amid wetlands such as marshes and wet meadows (Hatch 1957). Members of this genus can be abundant in such habitats (Hatch 1957; LaBonte, personal observations). They are

generally associated with relatively lush vegetation (LaBonte, personal observations).

Trophic data: *Stenus* spp., and those of the related genus, *Dianous* Samouelle, are believed to be specialized predators of Collembola (Klausnitzer 1981), although they may also feed upon other arthropods (Newton et al. 2001). Adults have morphological adaptations reminiscent of larval dragonflies, with large and protruding compound eyes providing binocular vision and a long, protrusible labium with grasping appendages at its apex (Crowson 1981, Klausnitzer 1981).

BBCRNA significance:

Stenus morio was only found in Willow-Sedge Swamps, with 72% of individuals collected in 1995 (Table 1). Except for two individuals found in Alder Swamps, the other *Stenus* spp. were also collected only in Willow-Sedge Swamps. About half of the individuals of these other species were collected in 1995 and the rest in 1996.

It is not surprising that *Stenus* spp. were not trapped in the other BBCRNA habitats. Cedar-Hemlock and Douglas-fir forests were not normally trapped at the shore margins which *Stenus* spp. inhabit. In Gravel Bars, the trap locations were also distant from the water margins. These locations were generally dry during the trapping period, as well as being more-or-less devoid of Collembola, which are generally hygrophilic.

***Tachinus crotchii* Horn.**

Distribution: The distributions of *Tachinus* spp. are much better understood than those of most North American staphylinid taxa because of several revisions by Campbell (1973, 1988). This species is distributed from southern British Columbia (Queen Charlotte Islands) to central California, from the Cascade Crest to the west (Campbell 1973, 1988).

Habitat: Most *Tachinus* spp. are associated with decaying organic matter, such as leaf litter, rotting mushrooms and fungi, carrion and dung (Campbell 1973). Most specimens of *T. crotchii* were collected from cow or human dung; however, many were found in rotting *Boletus* spp. mushrooms, wolverine dung, a compost heap, and decaying plant material (Campbell 1973, 1988). Although *T. crotchii* was uncommonly collected at the H.J. Andrews Experimental Forest in the western Oregon Cascades, some congeners were abundantly collected from conifer forest litter at that locale (Parsons et al. 1991).

Trophic data: Larvae and adults are apparently predominantly predaceous upon insect larvae found in the resources listed above (e.g., fly larvae) (Campbell 1973). Larvae of *Tachinus* spp. may be at least facultatively mycetophagous (Campbell 1973).

BBCRNA significance:

Tachinus crotchii was seventh in abundance, with 168 individuals (Table 3). It was one of the five ubiquitous BBCRNA species (Table 1). However, this species was only found abundantly in Cedar-Hemlock Forests, 58%, and Douglas-fir Forests, 17%. There was little difference in abundance between years (Table 1). Campbell (1988) stated that *T. crotchii* is one of the most abundant species of this genus in western North America.

***Tachinus semirufus* Horn.**

Distribution: *Tachinus semirufus* is known from Alaska (Glacier Bay) south along the Coast Range to central California and east to south central British Columbia and central Nevada (Campbell 1973, 1988).

Habitat: Adults are usually collected from decomposing plant material and rotting mushrooms (Campbell 1973). This species was commonly collected from conifer forest litter at the H.J. Andrews Experimental Forest in the western Oregon Cascades (Parsons et al. 1991).

Trophic data: The trophic relationships are similar to those of *T. crotchii*.

BBCRNA significance: This species was eleventh in abundance, with 120 individuals (Table 3). Unlike *T. crotchii*, it was only found in the Douglas-fir and Cedar-Hemlock forests (Table 1). Most specimens, 65%, were

collected from Douglas-fir Forests. Almost all individuals, 87%, were collected in 1996 (Table 1).

Exotic Species.

An important measure of the quality and health of a given natural system is the prevalence of exotic species. From the conservation viewpoint, such species can be biological pollutants degrading the quality of otherwise relatively pristine habitats and competitively stressing or excluding indigenes. They can also be viewed from a biogeographical perspective as foreign elements "tainting" native faunas. In either sense, it was relatively encouraging that the BBCRNA yielded only eight known or probable exotic beetle species and only a total of forty-eight individuals thereof (if *Stenus morio* is counted as an exotic species). To place this data in a broader context, approximately 260 exotic beetle species (including both intentionally and accidentally introduced species) are known from Oregon alone (Parsons, LaBonte, and Miller, unpublished). On the other hand, to find any exotic species in such a remote and virtually pristine area is sobering.

Whether the propagules of these species arrived at the BBCRNA via active or passive dispersal is unknown. All of these species are capable of flight. The North Cascades Highway, a possible route from which such

species could spread, is only about 10 km south of the BBCRNA. On the other hand, humans could have transported "contaminated" materials, such as hay for horses, into the area, given the association of all these species with dung and/or litter/plant detritus (Hatch 1957, 1971; Lindroth 1961-1969, Arnett and Thomas 2001). The Park revegetation program may have been another avenue of introduction. Native plants are raised outside the Park, in Marblemount, and then transplanted to various locations in the Park. I found *Calathus fuscipes*, one of the BBCRNA exotic species, in Sedro Woolley, just west of Marblemount. Soil and litter associated exotic species resident in the Marblemount vicinity could be easily spread throughout the Park via such programs.

Closing or substantially limiting such pathways of introduction to prevent further exotic incursions may not be feasible. Maintenance of relatively barren roadsides is necessary for automobile safety. Unfortunately, the resulting habitat is ideal for many exotic species (see Spence and Spence 1988, Spence 1990), enabling them to spread throughout an area via the network of roads. It also seems unlikely that pack or riding livestock fodder could be rendered free from exotic species apt to be found in this material. Even if this could be done practically and without endangering the health of these animals, use of such feed reduces their foraging impacts upon Park vegetation. Obviously, it would also be desirable for revegetation facilities to be located in

Park areas devoid of exotic ground or soil dwelling species. This approach is probably impractical. It would be possible to drench the soil and root masses of transplants with pesticides prior to relocation. However, this raises numerous other issues, such as Park staff safety and pesticide contamination of hitherto pristine areas. Unfortunately, there appear to be no easy solutions to curtailing the encroachment of exotic beetles or other exotic invertebrates in the Park. This problem is further compounded by the prospect that some BBCRNA and Park habitats may be innately susceptible to exotic colonization.

With two exceptions, all the BBCRNA exotic species or presumptive exotics were found in the open habitats (Table 1). *Anisodactylus binotatus*, *Onthophagus nuchicornis*, and *Stenus morio* were collected from Willow-Sedge Swamps, *Aleochara bilineata* was found in Gravel Bars and Willow-Sedge Swamps, and *Aleochara bimaculata* and *Trichophya pilicornis* were trapped only in Gravel Bars. *Pseudopsis sulcata* is known from forest litter (Parsons et al. 1991, Arnett and Thomas 2001) and its association with Alder Swamp habitat is not surprising. The association of *C. fuscipes* with the forested Alder Swamp habitat is somewhat anomalous, as this European species typically inhabits open, anthropogenic sites in North America (Lindroth 1961-1969).

Open BBCRNA habitats may be inherently vulnerable to colonization by soil and litter dwelling exotic beetles.

Most species of Carabidae exotic to North America inhabit anthropogenic, open habitats (Spence and Spence 1988, Spence 1990) and this appears to hold for other exotic beetles inhabiting soil and litter (see generic treatments in Arnett and Thomas 2001). Furthermore, successfully established exotic carabid species may be specialists of temporary habitats maintained by frequent disturbance (Spence and Spence 1988). At least one such species established in the Pacific Northwest, *Elaphropus parvulus* (Dejean), is known from open, riparian habitats with similar natural high disturbance regimes, i.e., seasonal flooding (LaBonte and Nelson 1998). If this pattern holds true for exotic litter and soil associated exotic beetles in general, open BBCRNA habitats maintained by frequent disturbances, such as Gravel Bars, may be particularly prone to colonization by exotic beetle species.

The ultimate impact of these exotic species upon the indigenous BBCRNA beetle fauna is unknown. Many introduced Carabidae not only favor disturbed, anthropogenic habitats, but appear to be more or less restricted to such environments (Spence and Spence 1988, Spence 1990). Theoretically, such species should not be able to colonize relatively pristine habitats, although this may not be true of habitats with high disturbance regimes. The risk of competitive displacement of indigenes by exotics appears slight (Spence 1990). However, there is evidence that some exotic beetle

species are invading relatively pristine, low disturbance habitats and possibly displacing indigenes (Niemela and Spence 1994, LaBonte and Nelson 1998). The anticipated negligible impact of exotic soil and litter dwelling beetles upon native beetles may thus be more presumptive than actual.

New Continental U.S.A. Record.

At least one of the species collected during this project represents a significant new distributional record. *Agonum consimile* Gyllenhal (Carabidae) has never been recorded from the continental U.S.A. (lower 48 states) (Bousquet and Laroche 1993), although it has been found in southern British Columbia (Lindroth 1961-1969). This circumpolar species has previously been recorded from the margins of standing waters with rich vegetation of *Carex* spp. and non-*Sphagnum* mosses (Lindroth 1961-1969). At the BBCRNA, it was found in Alder Swamps (1 specimen) and Willow-Sedge Swamps (4 specimens) (Table 1). These habitats are clearly equivalent to those from which this species has been previously recorded. Considering how little is known of the BBCRNA and North Cascades National Park beetle faunas, new state, regional, and country species records are only to be expected.

SECTION 3: SPATIAL AND TEMPORAL BEETLE ABUNDANCE AND DIVERSITY

Distinctive patterns of BBCRNA beetle spatiotemporal abundance and diversity were presented in the results chapter. These patterns will be discussed below, generally in the order presented in the results, i.e., individuals, species, families, and trophic categories. Where appropriate, possible explanations for these results are presented and discussed. As emphasized earlier, the biases and limitations of pitfall trapping should always be kept in mind during the ensuing discussion.

Patterns of Individual Abundance.

Annual Overall Abundance.

Overall abundance of BBCRNA beetle individuals, both raw and standardized (Figure 7, Table 1), increased between years by 15%. Given the perceived propensity of insects to fluctuate greatly in abundance (e.g., Price 1984), this seems quite modest. However, that perspective is based primarily upon changes in the abundance of individual species and is probably inappropriately applied to an entire fauna. Among 290 species, it is not unexpected that variations in the

abundance of any one species (unless these changes were of considerable magnitude) would yield little overall change in abundance. Given that only two data points exist for the BBCRNA beetle fauna, it is best not to make too much of this apparent consistency.

Annual Abundance Patterns of Individuals Among Habitats.

There were substantial differences in abundance of individuals, both absolute and standardized, among the habitats, with the exception of the Cedar-Hemlock and Douglas-fir forests, which were virtually identical (Figures 6, 7). The relative rank of those habitats exhibiting differences was consistent between years and overall. Given the stereotypical perception of great annual variability of insect abundance, this consistency was not anticipated. As with the overall BBCRNA beetle abundance consistency, it is best not to place undue emphasis upon these abundance rankings without further monitoring. There were no *a priori* expectations as to the ranking of any particular habitat, nor do I have any satisfactory explanations for the rankings, other than perhaps for the similarities in the Cedar-Hemlock and Douglas-fir forests, which will be addressed later.

With one exception, all habitats exhibited greater beetle abundance in 1996, especially the Cedar-Hemlock and Douglas-fir forests. Gravel Bars, on the other hand, had a rather substantial decline in abundance that year.

Lacking data from years prior to 1995, explanations for this pattern must be speculative. Big Beaver Creek experienced heavy spring floods in 1996, before traps were placed that year. Many of the Willow-Sedge Swamp sites were also inundated because of extensive beaver dam building that spring.

The effects of flooding on the abundance of terrestrial riparian beetles in North America are not well documented. However, flooding did not affect the overall abundance of Rio Grande riparian epigeal forest floor beetles (Ellis et al. 2001). If all BBCRNA habitats experienced flooding to a similar degree as those in Ellis et al. (2001), which is unknown, the response was an overall increase in beetle abundance (Figure 14), rather than a steady state. Differences in response between two such geographically and historically distinct riparian faunas would not be unexpected, especially since the sampled stretch of the Rio Grande is no longer subject to natural flood regimes.

One possible explanation for the 1996 increases was that the beetles of the habitats with greater topographic relief (all those which were forested) benefited from the deposition of organic materials. However, this explanation requires a rapid numerical response among species. Although little is known of the life cycles of most BBCRNA beetle species, the majority are probably univoltine, as is true of most Nearctic Carabidae and Staphylinidae, making such a rapid response unlikely.

A better explanation for this pattern is a concentration effect. Traps were placed after flood waters had receded along the main channels, and to a lesser degree, in the Willow-Sedge Swamp. The traps were often placed relatively near water margins, as would be expected for efforts to sample riparian habitat associations. A common response of water-margin inhabiting beetles to flooding is to flee to nearby higher relief inundation refugia (Anderson 1968, Adis et al. 1986, Zulka 1994). There is a good possibility that traps would have thus been placed in or near zones of beetle concentration greater than the average 1995 densities. A related phenomenon may have also been involved. Post-flooding immigration into previously flooded habitats appears typical of hygrophilous and riparian carabids (Andersen 1968, Nelson 1988, Adis et al. 1986, Adis et al. 1990, Lindroth 1992, Zulka 1994, Bonn 2000, LaBonte, unpublished). Waves of returning immigrants moving through trap areas could have contributed to a greater catch. Both of these phenomena would have resulted in a net effective increase in beetle activity, which would be expressed with pitfall traps as increased trap catches.

A possible explanation for the 1996 decline in abundance in Gravel Bars is that the beetles of this set of habitats suffered mortality or were displaced downstream by the scouring floods that occurred along the main channels of Big Beaver Creek, where this habitat

type is found. It has been suggested that riparian beetles are "perennial pioneers" which continually recolonize their habitats (Holeski and Graves 1978, Holeski 1984, LaBonte and Nelson 1998), since these habitats, especially gravel and sand bars, are at least in part created and maintained by frequent intense floods (Gregory et al. 1991, Malanson 1993). Similar "cyclic colonization" may be typical of insects inhabiting seasonally and perennially flooded wetlands (Adis et al. 1986, Batzer and Wissinger 1996, Bonn 2000). There would necessarily be a lag in abundance between recolonizations. Such a lag was seen for Carabidae in post-flood habitats at the Rio Grande, although it was not certain whether this was a function of recruitment or numerical response (Ellis et al. 2001).

The other habitat types would not have been affected in this manner. Probably only the margins of the higher relief habitats would have been scoured. Although low relief, the Willow-Sedge Swamp sites were gradually inundated rather than scoured, both because of the nature of beaver dam inundation and because of their separation from the main channels (Gregory et al. 1991) of Big Beaver Creek. Many water-margin inhabiting beetles have behavioral, morphological, and physiological adaptations enabling them to readily survive even lengthy inundations (Andersen 1968, Evans et al. 1971, Adis 1982, LaBonte and Johnson 1989, Landry 1994, Zulka 1994, Fuelhaas 2000) that do not disrupt their shelters or refugia.

Inundation was thus less likely than scouring flooding to cause declines in beetle abundance.

Monthly Abundance Patterns Among Habitats.

Distinct monthly abundance patterns were found among all habitats but the two conifer forests (Figure 8). Although there is not much published data on the phenologies of most beetle families, considerable information of this nature has been amassed about the Carabidae of temperate regions (e.g., Thiele 1977, Makarov 1994), which enables speculation as to the ecological significance of the BBCRNA patterns. However, caution must be used in too freely applying these conclusions to other beetle families, let alone faunas comprised of many families. Carabidae may not be good analogues of other families and much of this information is based upon the intensive studies that have been made of northern European species. Also, the reproductive categories into which Carabidae have been placed have been challenged as too simplistic (e.g., Makarov 1994). Furthermore, there is some evidence a given population of a species may shift back and forth between activity patterns in response to microclimatic and weather conditions (Thiele 1977). Consequently, the following remarks must be regarded with caution. The lack of

abundance data prior to and after the sampling period also limits the strength of any inferences.

Both Gravel Bars and Willow-Sedge Swamps had unimodal abundance patterns with the greatest abundance in July, followed by rapid declines, closely approximating the phenological patterns exhibited by species of Carabidae classified as "spring breeders" (Thiele 1977). These species overwinter as adults, breeding in spring and early summer, after which most adults die or aestivate. Carabid faunas of temperate riparian and wetland habitats are dominated by "spring breeder" species (Thiele 1977, Zulka 1994, Bonn 2000, Fuelhaas 2000). It is thought that this reproductive strategy may be adaptive because adults can either escape or withstand seasonal flooding better than larvae (e.g., Andersen 1968, Thiele 1977, Zulka 1994, Fuelhaas 2000), although there is some evidence that larvae and other life stages can tolerate at least some flooding (Andersen 1968). Conceivably, similar selective pressures would operate upon species in other families of beetles in these habitats.

The two conifer forest habitats had essentially identical monthly abundance patterns strongly peaking in September (Figure 8). These patterns are strongly reminiscent of the predominant reproductive strategy of carabid species of temperate forested habitats, "autumn breeding" (Thiele 1977, Dulge 1994). Species in this reproductive category may exhibit early, but relatively

low, activity from overwintering adults, with peak adult activity during late summer and fall. The September peaks may have been strongly influenced by the superabundant *Scaphinotus angusticollis* (see species profiles). Although the reproductive category of this species has not been firmly established (LaBonte 2000), Greene (1975) found that three other Pacific Northwestern species of *Scaphinotus* all exhibited phenologies fitting the "autumn breeder" category. Thiele (1977) speculated that temperate forest carabid species may be selected for reproduction during the period when the forest floor microclimate is warmest. The October declines may have been due to the substantially cooler ambient temperatures of that month relative to the three prior months (NOAA 1995, 1996). Of course, this explanation presumes that patterns observed in Carabidae also apply to members of other beetle families.

Alder Swamps had a bimodal abundance pattern, with one peak in July and another in September, almost appearing to be a hybrid of the two previous patterns. The expectation, based upon the temperate carabid reproductive categorizations (while considering all the prior caveats) would be that this habitat would instead exhibit a unimodal pattern similar to the two conifer forest habitats. However, Thiele (1977, p. 249) makes the intriguing observation that the proportion of "spring breeder" carabid species increases in "damp to wet" forests. Based upon the habitat parameter surveys

performed at the BBCRNA (in August), Alder Swamp soils were characterized as wet, versus dry soils for the conifer forest habitats (see methods chapter). If Thiele's generalization is applicable to BBCRNA habitats and the overall beetle fauna, it may provide at least a partial explanation of the abundance pattern of Alder Swamps. It may have been selectively advantageous for species inhabiting hydric forests subjected to even infrequent and modest inundations to be in the adult stage during such events.

Species-level Patterns.

The virtually invariant number of total species per year was not anticipated. Whether this is a consistent pattern resulting from the interaction of the sampling protocols and the actual species richness of the BBCRNA habitats sampled is unknown and cannot be ascertained without further monitoring. As mentioned in the discussion of sampling effort, the differences in annual species composition were almost completely attributable to "rare" species. This was not unexpected, as probability dictates that "rare" species should form the bulk of species turnover.

The total of 290 beetle species from the BBCRNA samples is reasonably impressive, considering that very few, if any, had been previously documented from this

locale. Many more beetle species undoubtedly remain to be recorded from the BBCRNA. For instance, 824 beetle species have been recorded from another montane Cascadian forest locale, the H.J. Andrews Experimental Forest ("the Andrews") in Oregon (Parsons et al. 1991). However, the Andrews total was the result of varied sampling techniques over many years. Approximately half of the Andrews beetle species were those normally found in aquatic habitats, foliage, flowers, or trees (Parsons et al. 1991), habitats poorly sampled by pitfall traps. Furthermore, it would be unlikely that any pitfall sampling regime in a reasonably diverse set of habitats would yield more than a substantial fraction of the total species richness in only two years. This is supported by the species accumulation curves (Figure 25). Even after two decades of pitfall trapping in the Andrews, previously unrecorded species continue to be found via this method (Parsons, LaBonte, and Miller, unpublished).

Abundance of BBCRNA beetle individuals was disproportionately in favor of just a few species (Tables 1, 3). Although there were no *a priori* expectations in this regard, the BBCRNA data fits the well known pattern of numerical dominance which is expressed in many species abundance data sets (e.g., Magurran 1988).

The relative consistency of the species composition of the twenty most abundant species between years (Table 3) was somewhat surprising when considering the often great fluctuations in abundance thought to be typical of

many insect populations (e.g., Price 1984). As with the results for annual overall abundance, too much weight should not be placed upon the BBCRNA data, as it only covers a two-year span. Furthermore, abundance data should not necessarily be accepted at face value. Allowances for sampling bias should always be considered. However, my studies of western Oregon and Washington Carabidae indicate that the relative abundance of many epigeal silvan species has remained more-or-less constant over several decades (LaBonte, unpublished data). These "Top 20" species, or at least the thirteen species so ranked in both years, may be particularly useful for tracking BBCRNA beetle responses to climate change and other disturbances.

Species Compositions and Habitats.

Given the habitat parameters denoted in the methods chapter, as well the myriad unmeasured aspects of available resources, structure, microclimate, etc., differences in species composition among the sampled BBCRNA habitats were expected. However, the exact nature and degree of these differences could not *a priori* be predicted.

Most habitats had profound differences in species composition (Tables 1, 4). This was exemplified by the composition of the five most abundant species per habitat

(Table 4), which were almost unique for each habitat. Exceptions were one species shared between Alder Swamps and Cedar-Hemlock forests and three species shared between Cedar-Hemlock and Douglas-fir forests. Even the latter very similar habitats had differences in "Top 5" species composition and the proportions of individuals represented by such species.

Habitats also varied in the degree of shared and unique species with more than five total individuals ($n = 107$) (see Table 1). Gravel Bars and Willow-Sedge Swamps shared only ten such species, while Alder Swamps and Cedar-Hemlock Forests shared 51. Gravel Bars had the greatest proportion of unique species. Of the 40 species in this habitat with five or more individuals, 16 (40%) were found only in Gravel Bars. Willow-Sedge Swamps followed with 13 (31%) unique species, then Alder Swamps with 5 (7%). Cedar-Hemlock and Douglas-fir Forests both lacked unique species.

In counterpoint to the unique species, the five ubiquitous species were found in all of the habitats. However, none of these species were equally abundant throughout the habitats (Table 1). All were represented by only a few individuals in one or more habitats. Such records may represent no more than incidental occurrences, in the sense of Gaston (1994).

The representation of "rare" species (total individuals of five or less) also varied among habitats (see Table 1). The proportion of these species per

habitat was greatest in the open habitats. "Rare" species were 59% of the beetle fauna of Willow-Sedge Swamps and 51% of Gravel Bar species were "rare". The forested habitats all had 43% "rare" species. These data are similar to those of a study of woodland beetles in England, where approximately 50% of the species were rare (Evans 1969). Of course, some of the "rare" species may have been common in unsampled BBCRNA habitats and were thus incidental species (Gaston 1994) in the sampled habitats. Phenological sampling bias may also be an explanation for the apparent rarity of these species. Many Pacific Northwestern beetle species are most common, or at least most active, during the winter and early spring (e.g., Nelson 1988; LaBonte 1994, unpublished), before BBCRNA traps were placed.

All the sampled BBCRNA habitats exhibited some changes in species composition between years (Table 1). As with abundance, species associations of these habitats may have been influenced by flooding during 1996. Flooding has been documented as affecting riparian arthropod assemblages. For instance, Ellis et al. (2001) found that flooding altered riparian community compositions. Different taxa exhibited different responses to flooding, some decreasing and some increasing, presumably as a consequence of differing adaptations and vulnerabilities to flooding. Alluvial carabid assemblages have also been shown to vary depending upon the character of floods (e.g., duration,

frequency, and intensity), among other factors (Sustek 1994). If flooding was a factor in the observed changes in species compositions between years, the effects would be expected to be most profound in the habitat most drastically affected by flooding. This appeared to be the case with the Gravel Bars.

Of the BBCRNA habitats sampled, Gravel Bars exhibited some of the greatest changes in species composition and abundance between years. Absolute abundance for most beetle species declined in Gravel Bars, mirroring the overall decline in abundance for the habitat (Table 1). Except for two carabids, *Cicindela depressula* Casey and *C. oregona* LeConte (both up to 14 mm in length), all large abundant or moderately abundant Gravel Bar beetle species declined. The abundance of most small species remained unchanged or increased. Two small species of Elateridae, *Zorochrus* sp. and *Z. musculus* (Eschscholtz) (both ~3 mm in length), increased between six- and eight-fold. Presuming that both large and small species remained *in situ* during scouring floods, as can be the case (e.g., Andersen 1968), larger species may have been more vulnerable to disruption of their shelters. Smaller species could have had more secure refugia deeper within the smaller interstitial spaces denied to larger species (e.g., Andersen 1968).

Biodiversity Indices and Habitats.

Habitats also differed in species richness and the values of two diversity indices (Figures 9, 10, 11). As with abundance and species composition, there were no prior expectations of a particular pattern. Perhaps most surprising were the almost invariant values for some habitats and the stability of the relative standings of the habitats between years. However, some interyear differences were observed.

Douglas-fir Forests demonstrated strong increases in both the Shannon-Weiner and Simpson's 1-D indices (Figures 10, 11). These results may have been largely due to the greatly reduced absolute and relative abundance of *Scaphinotus angusticollis* in 1996. In 1995, this species comprised 50% (n = 318) of the total individuals of this habitat, while it was only 21% (n = 200) of the total in 1996 (Table 1). Combined with the greater species richness in 1996 (Table 1), the probability that a given individual would represent a previously uncounted species would have been increased, increasing the values of these indices.

The small decline in the Shannon-Weiner index in Gravel Bars versus the invariant Simpson's 1-D index may be a consequence of the greater sensitivity of the Shannon-Weiner index, a Type I heterogeneity index, to rare species (Ludwig and Reynolds 1988, Magurran 1988, Krebs 1989). Of the 59 species with five or fewer total

individuals in Gravel Bars (73% of the total species richness), 36 (61%) were present only in 1995. Although several common species sharply declined in abundance in 1996, several others greatly increased, perhaps resulting in little net change to a Type II index such as the Simpson's 1-D. Type II indices are most sensitive to changes in representation of common species (Ludwig and Reynolds 1988, Magurran 1988, Krebs 1989). Gravel Bars also were the only habitat to exhibit reduced species richness in 1996 (Figure 9), from 67 to 45, a decline of 33%. As discussed earlier, these changes may have been the result of flooding during 1996.

Although the Willow-Sedge Swamps showed an increase in species richness in 1996, both diversity indices exhibited substantial declines. This may have been a consequence of the much greater numerical dominance of *Agonum brevicolle* in 1996. The contribution of this species to the annual total abundance more than doubled in 1996, from 21% (n=117) to 44% (n=308) (Table 1). This effectively reduced the probability of any given individual representing an uncounted species, thus lowering the values of these indices. It is possible that *A. brevicolle*'s increased abundance was in response to the inundation of the Willow-Sedge Swamps early in 1996.

The evenness index, J' , varied little between years, other than to show a small decline in 1996 for all habitats. Although increased relative abundance of

species that were numerically dominant in 1995 could account for these changes, no such simple pattern appeared generally evident. A possible exception was the Willow-Sedge Swamp habitat, with greatly increased abundance of *Agonum brevicolle*, as previously noted. While some species became more abundant in 1996, others became less so, or even absent. Whether these changes were due to the 1996 flooding and inundation is uncertain. Most habitats also had greater species richness in 1996, but most of the "new" species were rare, which should have had little effect upon evenness index values.

Family Abundance Patterns Among Habitats.

Overall relative representation of the "Big Four" families varied among habitats, although Cedar-Hemlock and Douglas-fir forests appeared virtually identical (Figure 16). Differences were most pronounced between forested and open habitats. Staphylinidae were dominant in forested habitats (overwhelmingly so in Alder Swamps), which, in part, may have been based upon the abundance of fungivores or species associated with fungi (see Newton et al. 2001). Most such Staphylinidae were almost entirely absent from the open habitats. The co-dominance of Carabidae in the two conifer forests was largely based upon the prevalence of *Scaphinotus angusticollis*, which

was much less abundant in the Alder Swamps (Table 1). The dominance of Carabidae in Willow-Sedge Swamps was primarily due to *Agonum brevicolle* (Table 1). The abundant species of Anthicidae and Elateridae were only found in Gravel Bars (Table 1), so these families were negligible components of the other habitats.

There were substantial changes in relative abundance of the "Big Four" families among years for habitats other than Alder Swamps and Willow-Sedge Swamps (which exhibited little change) (Figures 17, 18). Although the precise changes were somewhat different, in 1996 both of the conifer forest habitats showed an increase in Staphylinidae and a corresponding decline in Carabidae. Absolute abundance of most species of Carabidae in these habitats did not decline (Table 1), so the apparent decline of this family was actually largely a consequence of the increased absolute abundance of Staphylinidae. Increased staphylinid abundance in 1996 appeared to be mainly the result of substantial increases in the abundance of fungivorous or fungi-associated species. It would have been interesting to know whether the increases in these species could be correlated with a greater standing crop of fungi in 1995 (or 1996) than the prior year (s). Unfortunately, this information was not available.

Some of the greatest changes in family representation between years occurred in the Gravel Bars (Figures 17, 18). The absolute and relative abundance of

Anthicidae decreased by more than 50% in 1996. Elaterid absolute abundance increased by about 25% and relative abundance increased by over 60%. As previously discussed under individual and species abundance patterns, 1996 flooding may have been responsible for this variability, since Gravel Bars were the habitats most likely to be strongly affected by this perturbation. Although riparian taxa have been shown to respond differentially to flooding (Ellis et al. 2001) and flood characteristics (Sustek 1994), whether flooding was a factor in the changes in family abundance between 1995 and 1996 is unknown.

Trophic Patterns.

Predominance of Predators in BBCRNA Habitats.

The marked predominance of predators in all of the sampled BBCRNA habitats (Figures 23, 24) was not unexpected. This was at least partially a consequence of the sampling method, because of the susceptible taxa and the portion of the habitats sampled. As discussed above under the review of pitfall trapping, it would be expected that predominantly epigeal families (at least in temperate regions) such as Carabidae and Staphylinidae would be well represented when pitfall traps are used. These families in large part consist of predators, with

some notable exceptions (e.g., Carabidae in grasslands and floricolous Staphylinidae). Herbivores would be expected to be uncommon, as they would be most often represented by stray individuals falling from or crawling between host plants. This expectation was borne out by the BBCRNA data.

It is possible that predatory beetle species could also be more susceptible to pitfall trapping. Within trophically diverse families, predatory species may be larger or more active than species relying upon more sedentary resources. As discussed earlier, such traits render insects more vulnerable to pitfall traps.

Scaphinotus angusticollis is a prime example of a large, active, presumably predominantly predaceous beetle that may be predisposed to capture by pitfall traps (see species profiles). Thus, when using pitfall data, habitats with such species may exhibit apparent rather than actual epigeal predator dominance.

While acknowledging the possibility that epigeal predator dominance of the sampled BBCRNA habitats may be to some extent an artifact of the sampling method and species specific susceptibilities thereto, predators are probably a dominant trophic element in these riparian habitats. A study of the riparian beetles of a small stream in the Oregon Coast Range, mostly in gravel and sand bars, found that ~42% of the individuals were predaceous (Hering 1998). This was very similar to the proportion of predators in BBCRNA Gravel Bars, while the

other BBCRNA habitats had higher proportions of predators (Figure 23). The Hering study did not utilize pitfall traps, so trapping bias would not have been a factor. Predators were also numerically dominant in the riparian beetle faunas of alpine floodplains in Germany (Hering and Plachter 1997).

There were no *a priori* expectations as to the trophic categories of any ubiquitous species. All five ubiquitous species were predators. It might be expected that polyphagous predators would exhibit relatively great habitat breadth, providing that their abiotic tolerances were not exceeded in a given habitat. Unfortunately, little published detailed information exists regarding the breadth of the specific diets and habitat selectivities of these species. Some data suggests *Scaphinotus marginatus* is polyphagously predaceous as an adult and it may be facultatively omnivorous (see species profiles). Such dietary breadth may enable this species to exploit a variety of habitats. In contrast, two of the ubiquitous species of Staphylinidae, *Tachinus basalis* and *T. crotchii*, may specialize upon insects feeding upon decaying organic matter (see species profiles), a resource which is probably prevalent in most habitats.

Trophic Patterns Among Habitats.

Other than the overwhelming abundance of predators, habitats varied with regard to the relative representation of individuals (Figure 23) and species (Figure 24) in the six trophic categories. The three forested habitats were all quite similar (especially in proportions of species), while Gravel Bars and Willow-Sedge Swamps were not particularly so, other than in their preponderance of predators. Other than Gravel Bars, BBCRNA habitats were also similar in the proportions of fungivore and detritivore species.

The basis for the trophic similarities among BBCRNA habitats was presumably largely a consequence of the similar resources available to litter and substrate dwelling beetles, which are primarily detritus, fungi, and other consumers (Crowson 1981). It was no surprise that herbivores were notably insignificant components of all habitats, since the litter and soil/substrate zones are largely devoid of primary producers, other than algae, lichens, and mosses. Even Willow-Sedge Swamps, which had graminaceous plants in direct contact with these zones, had few herbivores. The aforementioned sampling biases of pitfall traps probably contributed to the similarities in trophic patterns among habitats as well.

Gravel Bars were unique among the sampled habitats in having very few fungivores (Figure 23, 24). The reason

for few fungivorous species in this habitat appears obvious. The soils of this habitat are exposed, seasonally dry and flooded, and have little organic matter. Thus, these habitats are probably not conducive to the production of the fungi upon which fungivores are dependent.

Gravel Bars were also the only habitat with a large proportion of detritivorous individuals, more than 30% (Figure 23). A study of the beetles of gravel and sand bars along a small stream in Oregon yielded similar results, with detritivores accounting for 34% of all individuals (Hering 1998). Active gravel bars are notable for having little endogenous primary productivity, with energy and nutrient input largely derived from adjacent terrestrial or aquatic habitats. Active gravel bars are thus similar to abyssal, dune, and alpine aeolian ecosystems, which are also reliant upon exogenous productivity and are dominated by detritivores and predators (e.g., Mann et al. 1980, Edwards 1987, Crawford 1988). Although relatively little has been published about the trophic relationships of terrestrial gravel bar insects, some species of beetles found in active gravel bars apparently rely predominantly upon exogenous animal and plant detritus (Hering and Plachter 1997, Hering 1998).

Similarities Between The Conifer Forest Habitats.

The following analysis incorporates data from the array of abundance and diversity patterns addressed in this study, rather than focusing upon a single type of pattern or a single taxonomic level. The analysis also emphasizes similarities instead of differences between habitats.

Although there were some differences, the Cedar-Hemlock and Douglas-fir forests appeared very similar in many aspects. Annual and seasonal abundance patterns (Figures 6, 7, 8), individual trophic patterns (Figure 23), annual family diversity patterns (Figure 13), and relative family abundance (Figure 16) were virtually identical. Species trophic patterns (Figure 24) were extremely similar. Of the seven "top 20" species at least relatively abundant in either habitat, only one (*Scaphinotus marginatus*) was not so in both (Table 3). Species compositions also were similar between the two habitats. Cedar-Hemlock and Douglas-fir forests shared three of the five most abundant species in each habitat. Only one such species was shared among other habitats, *Proteinus collaris* between Alder Swamps and Cedar-Hemlock Forests (Table 4). Neither habitat had any unique species (Table 1).

The similarities between the patterns of beetle abundance and biodiversity in these conifer forest habitats may be founded in beetle responses to habitat

characteristics other than plant species composition or the availability of specific foods. For example, microclimate is well known to be a critical component of terrestrial arthropod habitats (Cloudsley-Thompson 1962). Carabidae, in particular, have been shown to select habitats based primarily upon structure, moisture, and microclimate rather than upon plant species composition as distinct from these factors (Thiele 1977, Plachter 1986, Luff et al. 1989, Epstein and Kulman 1990, Georges 1994). If Carabidae are representative of the greater BBCRNA soil and litter beetle fauna, the latter (possibly excepting trophic specialists) may respond to habitat characteristics in a similar manner. Support for this generalization is provided by Ottesen (1996), where terrestrial alpine beetle communities appeared to be more a function of soil moisture and other habitat characteristics, rather than associations with particular plants.

An absence of dietary constraints may be the basis for such habitat selection strategies. Most detritivorous beetles are thought to be broadly polyphagous (Crowson 1981), as is believed to be the case for many predaceous or omnivorous species of Carabidae (Thiele 1977). Predators, and to a lesser degree, detritivores, were predominant in all BBCRNA habitats, including the conifer forests. Hence, habitat selection by polyphagous soil and litter beetles, driven by similarities in structural and abiotic characteristics of Cedar-Hemlock and Douglas-

fir forests, may be responsible for the great similarities in beetle abundance and diversity patterns displayed by these habitats.

The data from this study suggest it may be justifiable to consider treating these two coniferous forest habitats as essentially identical for future BBCRNA terrestrial riparian beetle survey and monitoring efforts. This would be the case both from an ecological perspective as well as from the desire to conserve the normally restricted resources available for terrestrial arthropod biodiversity studies.

SECTION 4: APPLICATIONS AND FUTURE STUDIES

At the heart of bioinventory studies are lists. These lists can be short or extensive, depending upon the nature and extent of the study. At its core, this study of the habitat associations of riparian beetles at the Big Beaver Creek Research Natural Area in the North Cascades National Park in Washington, generated a list: 290 species of beetles from five habitats. Such lists have value as ends in themselves. The documentation of almost 300 beetle species, along with their habitat associations, adds significantly to the knowledge of the biota of BBCRNA and the Park, as well as to the general knowledge of the beetle fauna of the Pacific Northwest. At least some biological and ecological insights have

been provided about the sampled beetle species and associations. For most BBCRNA beetle species, prior to this study there was little or no documentation of even the most basic habitat data, let alone data on associated species. Of course, this list, in and of itself, is merely a foundation from which much more information can be extracted.

The greatest value of bioinventory and biodiversity studies is not the simple listing of species or taxa, the habitats in which they are found, and their numbers therein. Potentially, a vast array of biological data can be available from even a simple list of organisms, enabling exploration of hypotheses regarding the processes integral to community structure, etc. For instance, the disciplines of taxonomy and ecology were bridged by the trophic categorizations (where possible) of the 290 beetle species found in this study. Recognition that the terrestrial riparian beetle associations of the BBCRNA (and presumably those of other locales) are dominated by predators and detritivores may greatly aid our understanding of nutrient and energy flows from purely terrestrial to aquatic ecosystems and vice versa. Awareness of the trophic roles of abundant beetle species may aid in determining their use as "indicator" species. Predatory and detritivorous riparian beetles may prove useful in postulating, predicting, or detecting the impacts of disturbances upon riparian and adjacent habitats. Their intermediate trophic positions

may enable these species to integrate and magnify ecological perturbances rippling through food webs.

This study also underscored the value of examining spatiotemporal patterns of abundance and diversity at different taxonomic scales. Different patterns were discernable at the levels of beetle individuals in general, species, and families. Such information may be quite useful, as ecological changes may be expressed idiosyncratically, depending upon the biological organizational level. For instance, introduction of an exotic species may have little impact on overall beetle abundance, but may have profound effects upon the distribution and abundance of a particular species or family.

The data acquired in this study provided feedback regarding the sampling protocols. One primary objective of the study was to determine whether the sampling methodology, which was intended to be conservative of materials and labor, could detect differences in the beetle associations of the selected habitats. There seems little doubt that this was achieved, since numerous differences, as well as some similarities, were found among the beetle associations of the sampled habitats. Such baseline data may enable the Park to determine the impacts of environmental perturbances or to otherwise assess the "environmental health" of riparian habitats. These results offer the promise that similar studies (perhaps using other sampling methods in concert) could

be mounted in the future, either further monitoring of the BBCRNA or other watersheds in the Park. These methods could certainly be utilized to examine non-riparian habitats as well.

The precise protocols of the sampling and identification procedures may prove very useful to the Park. Recognition that known necrophages are probably not useful for habitat analyses will enable Park personnel, once trained by a taxonomist, to save time when sorting samples by discarding these taxa prior to mounting and labeling. Since over 4,000 (34%) of the total beetles collected during this study were known necrophages, this could have resulted in a relatively great investment of time and labor. Fortunately, during the processing of the first year's samples, I recognized the potential resource drain represented by these taxa and recommended dealing with them in a much more cost effective manner.

Recognition that bears were extremely damaging to pitfall samples early in the snow free season in the BBCRNA (and presumably elsewhere in the Park) prevented wasting survey efforts at that time of year, as well as reducing the risk of bear encounters for Park personnel servicing traps. However, if logistic difficulties can be resolved, it may be worth placing traps at least sporadically during the late fall, winter, and early spring to detect and study those beetle species (and other insects) most active during those periods.

Although the trap design appeared relatively effective, traps in very wet habitats, such as the early season Willow-Sedge Swamps, tended to be disrupted by fluctuating water levels. This was also true for traps in other wetland habitats not addressed in this study, such as sphagnum bogs. Perhaps traps specifically designed for such wetland habitats (e.g., Dormann 2000) would be more effective and less susceptible to water disturbance. Similar considerations may be necessary for any traps placed in snow.

It has been explicitly acknowledged that pitfall traps selectively sample from the greater array of epigaeic insects and other arthropods. If a goal of the Park is to accumulate a more complete inventory of the terrestrial invertebrates within Park boundaries, other sampling methods should be utilized. These would be limited primarily by the resources available, since many (but not all) of these methods are more time and personnel consumptive than pitfall traps. Beating and sweeping vegetation, sifting litter or using Tullgren funnels, use of interception or lure traps (e.g., Lindgren funnel traps), black light trapping, and "hand collecting" can all be extremely productive. As suggested above, collecting during periods other than those of this study may also yield many additional species. Obviously, the same would be true of sampling additional habitats.

Another consideration would be for the Park to increase the frequency of sampling or the intensity of trapping. While increased investments in resources would be required, not only would there be the possibility of detecting additional species, but the resolution of subsequent analyses would be increased. For instance, these approaches would provide more precise phenological information, which could then be used to test some of the assumptions derived from this study.

Because of this study, the Park received several additional assets. Several other habitat association studies at BBCRNA were made possible by the collection of non-coleopteran taxa in the pitfall traps. These included ants (Hymenoptera: Formicidae) (Glesne 2000), true bugs (Hemiptera: Heteroptera) (Lattin 1997), and spiders (Arachnida: Araneae) (Glesne 1998). Since the major investment of field labor and specimen preparation had already taken place for the beetle project, these constituted "value added" outcomes. With luck, planning, and determination, similar opportunities may be available with almost any bioinventory effort.

The Park also gained a valuable reference collection vouchering the species determined in this study. Voucher collections are a necessary adjunct to any bioinventory project. Such reference material enables identifications to be verified in the future, not only in the event that some determinations are regarded as dubious, but also to enable identifications to be properly updated in the

event of revisionary work. This collection can also be used as a reference to aid Park personnel in the identification of beetles from the BBCRNA, other Park environs, and other Park studies. In this case, the voucher collection also formed the nucleus of a Park entomological collection housed at Park facilities. There it can not only be expanded over time through additional vouchering, but can also serve as an educational tool for Park visitors.

Not only were Park personnel trained in the basics of pitfall trapping protocols, but they were also exposed to techniques of insect specimen preparation, enabling them to expand and maintain the Park entomological collection. Furthermore, to the degree possible in the time allotted, they were trained to function at a limited level as "parataxonomists" capable of distinguishing common beetle families, as well as some of the abundant and distinctive beetle species. Development of such taxonomic infrastructure can be extremely useful to organizations engaging in biodiversity studies. Once staff have acquired the basic knowledge and skills necessary to perform as parataxonomists, the opportunity exists for these to be expanded and honed through interaction with taxonomic experts. This "in house" expertise may free the Park to some extent from dependence upon the often limited availability of taxonomists to identify specimens from large numbers of

samples (see comments under the section on sampling protocols).

Outside of issues directly pertaining to sampling methodology, some of the information gathered in this study may have immediate implications for future Park management. For instance, there had been no previous recognition of Alder Swamps and Gravel Bars as habitats with great species richness, and, in the case of Gravel Bars, great faunal uniqueness as well. These habitats may have formerly been dismissed as having no particular management significance. During the otherwise exhaustive plant community mapping used as the basis for site selection in this study, Gravel Bars were not mapped - after all, these habitats normally lack substantial vegetation. According to Park personnel, Alder Swamps have hitherto been notable primarily for the difficulty of travel through them. Although not directly a management issue, the many similarities among the terrestrial riparian beetle faunas of the Cedar-Hemlock and Douglas-fir forests of the BBCRNA may support treating these habitats as virtually identical for any future riparian beetle studies. This approach would conserve the often limited resources available for insect biodiversity projects.

Another case in point is the unexpected detection of several exotic species of beetles in the otherwise virtually pristine habitat of BBCRNA (see discussion of exotic beetles in the species profiles section). These

findings provide a baseline for monitoring the future effects of these species upon their taxonomic or ecological equivalents in vulnerable habitats, as well as alerting Park personnel to the presence of these alien elements. Furthermore, Park staff are now aware that current revegetation and recreational practices may aid the dispersal of such species throughout the Park, and that certain habitats may be inherently vulnerable to the establishment of exotic insects. While there may not be any practical means of curbing the ingress of such species, awareness of the pathways through which they may enter the Park could enable the development of strategies to address this problem.

Ideally, future Park studies of the BBCRNA terrestrial riparian beetle faunas may shed some light on the stability, consistency, and causes of the patterns of abundance and diversity observed in this study. Aspects such as the apparent phenological dichotomy between open and forested riparian habitats, the dominance of the "Big Four" families and the "Top 20" species, responses of riparian beetles to perturbances such as flooding, and trophic patterns all would be worthy of further investigation. A particularly worthwhile endeavor, albeit not particularly glamorous, would be to study the diet of the abundant riparian beetle species, including gut content analyses. Even basic dietary data, such as whether a given species is truly predominantly predatory or not, would go far to increase our understanding of the

ecological roles and significance of these insects. Exploration of the responses and adaptive strategies of terrestrial riparian beetles to flooding may also amply repay investigatory efforts. The means by which these beetles deal with scouring floods versus gradual inundation may prove extremely interesting.

The information gained through this study may have ramifications far beyond the boundaries of the BBCRNA and North Cascades National Park. The BBCRNA study could provide a model for terrestrial arthropod bioinventory and biodiversity projects in other national parks and public lands. The sampling methodology and protocols were specifically designed to be conservative of materials and the efforts of the staff implementing and maintaining the study.

Furthermore, many of the riparian beetle species and the habitats in which they were found exist throughout the Pacific Northwest, as well as other areas. The BBCRNA data on these species and those associated with them in the sampled habitats may be applicable to the other locales in which they are found. Comparison of the abundance and diversity patterns observed at the BBCRNA with those of other locales could provide understanding of whether these patterns are idiosyncratic to the BBCRNA or if they represent more general aspects of terrestrial riparian insect biology. For instance, latitudinal comparisons of terrestrial riparian beetle faunas, such as those of the BBCRNA with those of the Andrews

Experimental Forest in the central Cascades of Oregon, would likely prove very informative.

This study has provided a modest baseline from which further entomological investigations at the Big Beaver Creek Research Natural Area and the North Cascades National Park could be launched. This largely pristine landscape, with its rich ecological and geological diversity, offers a wealth of opportunities for advancing our knowledge of the insect fauna of this locale and the Pacific Northwest. I hope my efforts will encourage other entomologists to take advantage of this unique and beautiful resource.

CHAPTER 5: LITERATURE CITED

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