AN ABSTRACT OF THE DISSERTATION OF

Holly K. Ober for the degree of Doctor of Philosophy in Forest Science and Wildlife Science presented on November 7, 2006.
Title: Functional Relationships Among Vegetation, Nocturnal Insects, and Bats in Riparian Areas of the Oregon Coast Range.

Abstract approved:____

John P. Hayes

Vegetation provides food for many insects, and many insects serve as food for bats. We investigated the linkages among these three trophic levels in riparian areas throughout the Oregon Coast Range by examining the influence of vegetation cover, composition, and structure on the activity of nocturnal insects and bats, the influence of insect abundance on activity of bats, and the diets of bats.

Vegetation characteristics at the stream reach spatial scale explained more variation in bat activity than did vegetation characteristics measured at larger spatial scales. Vegetation characteristics most closely associated with bat activity varied among species of bat, included both canopy and shrub attributes, and apparently operated through constraints imposed by vegetation structure on bat flight capabilities rather than through regulation of the distribution of insect prey abundance.

The two orders of insects most frequently consumed by bats were Lepidoptera and Diptera. Three species of bat fed predominantly on small insects likely of aquatic origin, and activity of these species was correlated with local abundance of small insects. The seven remaining species of bat fed predominantly on larger, terrestrial insects, and their activity was not correlated with local abundance of insects.

Variation among stream reaches in the number of captures and biomass of the six most commonly captured orders of insects (Diptera, Lepidoptera, Trichoptera, Ephemeroptera, Coleoptera, and Hymenoptera) was better explained by cover of deciduous canopy than by any other vegetation characteristic investigated. The number of captures and biomass of these insects increased as deciduous canopy cover increased. Canopy composition explained variation in macro-moth community composition as well: species richness and cover of canopy trees and of shrubs were associated with variation in moth species composition. Number of moths captured, biomass, and Shannon's species diversity were greater in deciduous- than conifer-dominated stream reaches.

Deciduous shrub and canopy trees play an important role in the determination of nocturnal flying insect abundance and community composition. Management activities that promote deciduous vegetation in riparian areas in this region are likely to help maintain biodiversity and abundance of nocturnal insects, which in turn serve as food resources for bats.

Functional Relationships Among Vegetation, Nocturnal Insects, and Bats in Riparian Areas of the Oregon Coast Range

by
Holly K. Ober

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APPROVED:

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Head of the Department of Fisheries and Wildlife

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Holly K. Ober, Author

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CHAPTER 1 - INTRODUCTION

Conservation of biodiversity has become recognized as a necessary element of ecologically sustainable forest management (Naeem et al. 1994, Carey and Curtis 1996, Christensen et al. 1996, Hunter 1999). Priorities have shifted from timber production to ecosystem management on forested public lands in the Pacific Northwest, making maintenance of biodiversity a more substantive objective, and raising concerns about the impact of land management activities on biodiversity (Christensen et al. 1996, Simberloff 1999, Hobbs et al. 2002). Accurate assessment of the influence of forest management activities on biodiversity requires additional knowledge of the distribution and abundance of many taxa. Furthermore, development of sustainable forest management strategies requires making predictions regarding responses of specific species to vegetation changes, which is possible only when basic ecological relationships between plants and animals are understood. As expanding human populations put additional pressure on remaining forest resources, understanding patterns of biodiversity within forests and, more specifically, the ecological linkages between vegetation and unfamiliar animal taxa, is more critical to planning vegetation management strategies than ever before (Ehrlich and Wilson 1991, Simberloff 1999).

Influence of Vegetation on Animals

Vegetation affects animals through two primary pathways: by providing resources and by imposing constraints on resource acquisition. Vegetation provides structural elements of habitat required by many animals, such as sites for roosting, perching, and nesting, as well as cover for protection from predators and the weather. Vegetation also provides a direct energy source for primary consumers and an indirect energy source for secondary consumers. At the same time, vegetation can act as a constraint to resource acquisition by animals when vegetation architecture restricts animal behavior by hindering animal movements.

The influence of structure and composition of vegetation on patterns of abundance and diversity of birds is well established (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981, Rice et al. 1984, Hagar et al. 1996), as is the influence of these factors on diurnal insect abundance and diversity (Murdoch et al. 1972, Lawton 1983, Lewinsohn et al. 2005). However, relationships between vegetation and nocturnal animals have rarely been investigated.

I chose to examine the influence of riparian vegetation on bat foraging activity using a food web approach to understand the functional relationships between bats and their habitat. Due to the role of nocturnal flying insects as a nutritional resource for bats, I expected insect abundance to influence spatial patterns of bat activity. Similarly, due to the role of vegetation as a nutritional resource for insects, I expected vegetation to influence spatial patterns of insect abundance. Furthermore, I expected the insight gained from examination of these two relationships to elucidate causal factors underlying observed associations spanning non-adjacent trophic levels (e.g., between vegetation and bats).

Linkages Among Bats, Insects, and Vegetation in Riparian Areas

Riparian areas are an important habitat component for bats in forests. Bat activity in temperate forested landscapes tends to be high over ponds, lakes, and rivers (Lunde and Harestad 1986, Krusic et al. 1996, Parker et al. 1996, Walsh and Harris 1996, Vaughan et al. 1997, Seidman and Zabel 2001), where insect abundance is relatively high (Thomas 1988, Brigham et al. 1992), and lower within forest stands (Thomas 1988, Erickson and West 1996, Parker et al. 1996, Grindal and Brigham 1998, Grindal et al. 1999, Humes et al. 1999). Despite consistent evidence that bats in forested landscapes spend the majority of their flight time in riparian areas, little effort has been expended to investigate factors influencing bat foraging activity in riparian ecotones. The few studies that have examined the influence of vegetation bordering streams on bat activity have compared number of bats captured in streams surrounded by stands of different ages and tree species (Perkins and Cross 1988), use of streams bordered by clear-cut and intact riparian vegetation (Hayes and Adam 1996), and use of streams with and without riparian vegetation (Warren et al. 1999). These studies have enriched understanding of bat habitat use, but more research is needed before predictions can be made regarding potential influences of riparian vegetation management on bat foraging activities.

Several characteristics of bats make them an important component of faunal diversity in temperate forest ecosystems. First, bats often comprise a large proportion of a region’s mammalian biodiversity. As the second-most speciose order of mammals (following Rodentia), bats often contribute substantially to mammalian species richness

(Kunz and Pierson 1994). For example, 15% of all mammal species native to the Oregon Coast Range (10 of 65) are bats (Hayes and Hagar 2002). Second, due to their low reproductive rates and presumed low population densities, many species of bat are classified as needful of special conservation attention (Racey and Entwistle 2003). In western Oregon, 43% of the species of forest-dwelling mammals that are considered rare, threatened, endangered, or sensitive are bats (Hayes and Hagar 2002). Third, as the only organisms that consume nocturnal flying insects, bats fill an irreplaceable role in food webs.

Invertebrates also contribute substantially to forest biodiversity. Arthropods comprise 65-70% of species in forests (Langor and Spence 2006) and provide a diverse array of ecosystem services (Kim 1993, Miller 1993), yet little attention has been devoted to invertebrate ecological research in forests relative to vertebrates. The host-specificity and the limited range of movements of many of these organisms make them sensitive to small-scale environmental conditions (Smith and Remington 1996). This has led to the suggestion that many insects could make ideal candidates for monitoring responses to vegetation management activities (Ricketts et al. 2002, Langor and Spence 2006). However, understanding of the relationships between vegetation and insects in temperate forests remains limited.

In the following chapters I explore the influence of vegetation structure and composition on activity of bats and nocturnal insects (Fig. 1.1). I examine the influences of:

(1) riparian vegetation on nocturnal insect abundance and biomass (chapter 2)

(2) riparian vegetation on species composition of macro-moths (chapter 3)

(3) nocturnal insect abundance on bat activity (chapter 4)

(4) riparian vegetation on bat activity at multiple spatial scales (chapter 5).

In combination, these chapters provide insight into the dynamics of the food webs that link plants to nocturnal insects to bats in the Oregon Coast Range, and provide information on the potential effect of riparian forest management activities on these inconspicuous components of Coast Range biodiversity.

Contributions of Coniferous and Deciduous Vegetation

Chapters 2 through 5 are linked by the underlying objective of determining the relative contributions of coniferous and deciduous vegetation to bats and nocturnal insects. Currently, the basal area of deciduous trees exceeds that of coniferous trees along second- and third-order streams in the Oregon Coast Range (Pabst and Spies 1999). Few large conifers exist in these riparian areas partly because natural disturbances that commonly occur in riparian areas within the region, such as flood events and debris flows, tend to favor pioneering species such as red alder over long-lived conifers. In addition, timber harvest prior to adoption of the Oregon Forest Practices Act in 1972 decreased conifer density near streams throughout the region (Minore and Weatherly 1994, Hibbs and Bower 2001). After disturbance, vacancies in growing space tend to be filled by rapidly sprouting hardwoods and shrubs, which prevent the subsequent regeneration of conifers (Minore and Weatherly 1994, Hibbs and Giordano 1996). Large conifers are essential to pool formation and thus to fish (House and Boehne 1987, Bilby and Ward 1991, Bilby and Bisson 1992), so management regimes planned for areas throughout the Oregon Coast Range prioritize conversion of riparian vegetation from hardwoods to conifers (Oregon Department of Forestry 1994, Beechie et al. 2000). If natural regeneration of conifers in riparian areas throughout the region continues on its current trajectory, riparian stands are forecasted to follow a successional pathway leading to shrub-dominated communities (Minore and Weatherly 1994, Hibbs and Bower 2001). Given the large acreage of riparian habitat currently under federal and state ownership in the Pacific Northwest, forest management practices on public lands have the ability to affect these trajectories throughout much of the region. As part of a larger study conducted by the Cooperative Forest Ecosystem Research program (CFER) examining the influence of vegetation on various aspects of riparian food webs, this research attempts to elucidate the unique roles of coniferous and deciduous vegetation in food webs involving nocturnal insects and bats.

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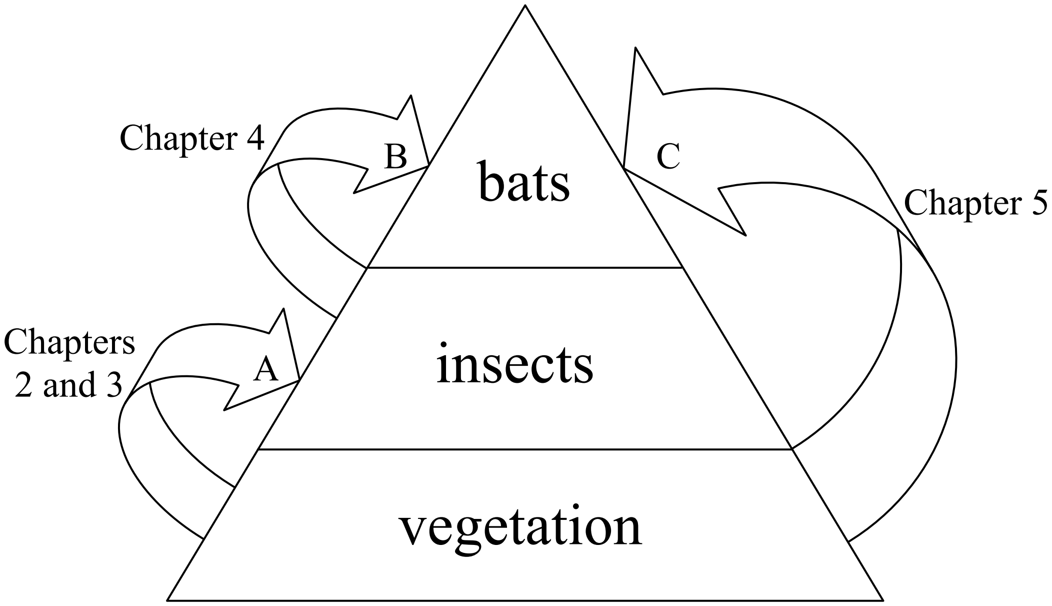
Figure 1.1. Schematic of the riparian food web investigated. Arrows dipict relationships between trophic levels. Chapters 2 and 3 explore the relationships depicted by arrow A, chapter 4 examines the relationships depicted by arrow B, and chapter 5 investigates the relationships depicted by arrow C.



CHAPTER 2 - INFLUENCE OF RIPARIAN VEGETATION ON NOCTURNAL FLYING INSECTS

Abstract

We examined small-scale relationships between riparian vegetation and nocturnal flying insects (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera) in the Oregon Coast Range. Using an information theoretic approach, we evaluated models representing five hypotheses developed to explain mechanisms underlying associations between plants and insects. Our data demonstrated stonger support for the resource quality hypothesis, which predicts that insect abundance and biomass increase with the cover of deciduous vegetation, than for the resource diversity, resource abundance, resource concentration, and stream cover hypotheses. We conclude that deciduous vegetation is an important habitat element for nocturnal flying insects in the region. This research contributes to the growing body of evidence that demonstrates deciduous trees provide important resources for both terrestrial and aquatic organisms in riparian areas of coniferous forests.

Introduction

Vegetation provides nutritional resources for phytophagous insects. The tremendous biomass of plant material in terrestrial ecosystems represents a vast food resource for these insects (Strong et al. 1984), but diversity in chemical composition among vegetative species severely restricts the diet of each insect species to a small number of plant species (Holloway and Hebert 1979, Strong et al. 1984, Mattson and

Scriber 1987). This diet specificity leads to a strong coupling between variation in plant species distributions and variation in the distribution and abundance of phytophagous insects (Hunter and Price 1992, Price 1992, Barbehenn et al. 1999).

Relationships between plants and diurnal insects at small spatial scales have been the subject of research attention for decades. Associations have been reported between species diversity of insects and species diversity of plants (Murdoch et al. 1972, Knops et al. 1999), species diversity of insects and structural complexity of plants (Murdoch et al. 1972, Wettstein and Schmidt 1999), species richness of insects and leaf biomass (Marques et al. 2000), species richness of insects and species richness of plants (Haddad et al. 2001, Panzer and Schwartz 1998), insect abundance and plant biomass (Haddad et al. 2001, Knops et al. 1999, Polis et al. 1997), insect abundance and species richness of plants (Haddad et al. 2001), and insect abundance and species diversity of plants (Knops et al. 1999). Although these studies have provided strong evidence of relationships between characteristics of plants and abundance or diversity of insects, unified principles governing relationships between plants and insects have not emerged from these efforts (Lewinsohn et al. 2005). One reason for this lack of consensus is that researchers have generally not employed analyses enabling evaluation of the relative strength of associations between vegetation characteristics and insect abundance or diversity. As a result, debate continues regarding which vegetative factors are most influential to insect abundance or diversity (Lewinsohn et al. 2005).

In recent years, concern about the influence of land management activities on biodiversity has risen, but efforts to assess how forest management activities influence biodiversity have been hampered by inadequate knowledge of relationships between plants and animals (Dobson 2005). Increased understanding of which local vegetation characteristics are most influential to abundance and biomass of nocturnal insects in forests of the Pacific Northwest would be useful for land managers concerned about biodiversity of these organisms as well as those vertebrates that depend on them for food (Chapter 4). Thus, the primary objective of our research was to determine which vegetative characteristics were most strongly associated with abundance and biomass of nocturnal flying insects in riparian areas of the Oregon Coast Range. Results should enable land managers to make more accurate predictions regarding the potential impacts of riparian vegetation management actions on nocturnal insect communities.

Research Approach

Most insects are phytophagous during some or all portions of their lifecycle (Strong et al. 1984). Two characteristics typical of phytophagous species, diet specificity and a limited scale of movements, result in a high likelihood of insects remaining in close proximity to their host plants (Smith and Remington 1996). Consequently, we anticipated strong associations between local vegetation and the abundance and biomass of insects. We developed five hypotheses to explain mechanisms underlying the relationships between vegetation and insects, used these hypotheses to formulate candidate models (Table 2.1), and then evaluated the strength of evidence for each using an information-theoretic approach. The underlying concept from which all hypotheses originated was that vegetation quantity, quality, or distribution determines patterns of insect abundance and biomass.

Increases in habitat structural complexity coincide with increases in plant species richness. Habitat structural complexity is a determining factor of potential niche space for insects, with greater structural complexity allowing for greater insect abundance (Knops et al. 1999, Haddad et al. 2001). Thus, the **resource diversity hypothesis** predicts that insect abundance and biomass within a stream reach will increase as the vegetative species richness bordering that stream reach increases.

Plants may determine the carrying capacity for phytophagous insects by limiting food availability (Price 1992) and by regulating the number of eggs female insects are able to oviposit (Dempster 1983). Consequently, increased vegetative cover may lead to increased abundance and biomass of insects (Polis et al. 1997, Knops et al. 1999, Haddad et al. 2001). Thus, the **resource abundance hypothesis** predicts that insect abundance and biomass within a stream reach will increase as the cover of riparian vegetation bordering that stream reach increases.

Species-specific factors, such as foliar nutrient content and secondary defense compound concentrations, influence the palatability and quality of food that vegetative species provide to insects (Ohgushi 1992). The immense diversity in chemical composition of foliage among plant species leads to a high degree of diet specificity among phytophagous insect species (Ehrlich and Raven 1964, Renwick and Chew

1994). Deciduous foliage generally has higher nitrogen content (which is a limiting nutrient for many herbivorous insects) and lower lignin content (which inhibits herbivory of many insects) than coniferous foliage, making deciduous foliage a higher quality food resource for many insects (Mattson and Scriber 1987, Ohgushi 1992, Friberg and Jacobsen 1994). Deciduous vegetation tends to support a greater diversity and abundance of certain types of terrestrial insects (Holloway and Hebert 1979, Robinson et al. 2000, Allan et al. 2003) and aquatic insects (Anderson and Cummins 1979, Piccolo and Wipfli 2002). Thus, the **resource quality hypothesis** predicts that insect abundance and biomass within a stream reach will increase as the cover of deciduous foliage bordering that stream reach increases.

Optimal foraging theory predicts that residence time within a particular habitat patch will vary as a function of the rate of energy gain within the patch relative to the rate outside the patch; organisms should stay in a patch as long as it is more profitable for them to stay than it is for them to travel to and forage in a different patch (Charnov 1976, Stephens and Krebs 1986). Accordingly, phytophagous insects should spend long periods of time in patches containing high densities of plants that provide food resources (Root 1973, Feeny 1976, Miller and Stricker 1984, Andow 1991, Long et al. 2003). Many species of phytophagous insects consume more than one species of closely related plants, but few are capable of consuming taxonomically distant species, such as representatives from both gymnosperms and angiosperms (Holloway and Hebert 1979, Robinson et al. 2000). Therefore, we consider areas dominated by either coniferous or by deciduous plant species likely to be inhabited for longer periods of time than areas with plants of both types mixed together. Thus, the **resource concentration hypothesis** predicts that insect abundance and biomass will peak in stream reaches bordered by vegetation dominated by coniferous or by deciduous vegetation and will decrease as the riparian vegetation composition tends towards an even mixture of the two vegetation types.

Sunlight influences abiotic factors, such as temperature and humidity, and biotic factors, such as plant growth. The forest canopy intercepts sunlight, causing lower temperatures and greater humidity levels below, whereas gaps in the forest canopy allow sunlight to penetrate, promoting growth of understory plants (Ford and Newbould 1977), aquatic plants that thrive in direct sunlight (Murphy 1998), and insect species reliant on these plants (Hawkins et al. 1982). The removal of canopy cover can influence both terrestrial (Collier and Smith 2000, Hamer et al. 2003) and aquatic insects (Bilby and Bisson 1992, Kiffney et al. 2003). Thus, the **stream cover hypothesis** predicts that insect abundance and biomass within stream reaches will increase as canopy cover directly over the stream channel decreases.

Methods

Study Area

The Oregon Coast Range is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1973). The terrain is steep and rugged, with a dense network of streams throughout. Elevation ranges from sea level to

1250 m. Common riparian overstory species are Douglas-fir (*Psuedotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and western redcedar (*Thuja plicata*). The understory tree layer is dominated by vine maple (*Acer circinatum*) and hazelnut (*Corylus cornuta*), and the shrub layer by salmonberry (*Rubus spectabilis*) and swordfern (*Polystichum munitum*).

The northern and southern boundaries of our study region were the Columbia River and the southern border of the Coos River sub-basin, and the eastern and western boundaries were the Pacific Ocean and the Willamette Valley, delineating a region that is approximately 300 km (190 miles) north to south (Fig. 2.1). Within the boundaries of 17 watersheds located throughout this region we selected one conifer- and one deciduous-dominated stream reach. To locate these stream reaches we generated random UTM coordinates and determined the nearest point on a second- or third-order stream for each point using 1:24,000 scale topographic quadrangle maps. Points were dropped from consideration if they (1) were not on either public property or private property to which access had been granted, (2) were on or within 2 km of a stream reach already selected, (3) had vegetation completely obstructing the airspace directly over the stream (which would hinder the transmission of light from traps), or (4) were not 3-7 m wide and >0.5 m deep. To reduce logistical constraints, we divided the study area into three subregions and focused our work within the central subregion in 2002, the southern subregion in 2003, and the northern subregion in 2004 (Appendix A). We sampled two of the stream reaches from a single watershed each year to assess inter-annual variability in number of insects captured.

Insect Sampling

We captured nocturnal insects using black light traps (Bioquip Inc., Rancho Dominguez, CA) with 12-watt fluorescent black light tubes, powered with 12-volt marine gel-cell batteries. Traps were placed 0.5 m off the ground within 2 m of the stream edge, in a location that maximized visibility from all directions. A “no-pest strip” (Hotshot, Newport Beach, CA) was placed in the bottom of each trap as a killing agent.

To account for temporal variability within a summer, we visited all stream reaches once during each 2-week period between mid-June and early September, for a total of five visits to each stream reach each summer. Each night, we began trapping within 30 min of sunset and ceased 0-30 min after sunrise. In the morning, insects were removed from traps, placed in labeled plastic boxes, and stored at -10ºC until analysis.

In the laboratory, we sorted all insects to order and measured their body lengths from the anterior of the head to the posterior of the last abdominal segment (antennae and cerci excluded) to the nearest mm using a dissecting microscope. We estimated insect biomass using previously published length-mass equations (Appendix B). Directly weighing insects requires lengthy processing time and typically gives inaccurate results due to changes in biomass as storage time increases and as carbohydrates are lost from specimens during defrosting (Burgherr and Meter 1997, Benke et al. 1999, Martin 2001). For as many orders as possible, we used length-mass equations derived from insects in forested ecosystems of the Pacific Northwest (western Oregon, Judy Li, personal communication; coastal, northern California, Sabo et al. 2002). For those orders not included in these studies, we used equations from other published records (Benke et al. 1999, Sample et al. 1993). Biomass estimates may lack precision for some species of Lepidoptera due to inter-specific differences in body widths.

Vegetation Sampling

At each location where we deployed insect traps, we sampled vegetation throughout a 30 m x 60 m plot (Fig. 2.2). We estimated species richness, cover, and composition in 30 m x 30 m plots on each side of the stream and estimated canopy cover directly over the stream.

Vegetative species richness

We recorded all species of woody shrubs and understory trees (trees with ≤5 cm DBH) that occurred in three 2 x 10 m subplots located at each end and the center of each plot (Fig. 2.2), and tallied the number of species across all 18 subplots as an index of shrub species and understory tree species richness for the stream reach. Western swordfern (*Polystichum munitum*) was recorded as a shrub because it is a perennially erect plant that contributes substantial biomass year-round throughout the study region, and due to its stature, vinemaple was recorded as an understory tree. We determined richness of canopy trees by tallying number of species of trees >5 cm DBH throughout the entire 30 x 60 m plot. We summed richness of shrubs, understory trees, and canopy trees (accounting only once for those species that occurred in >1 vegetation layer) as an index of richness of all woody species.

Vegetation cover

We determined cover of shrubs and understory trees by visually estimating the percentage of each of the eighteen 2 x 10 m subplots that was covered by shrubs and understory trees. We estimated canopy tree cover from the center of each of the 18 subplots using a moosehorn densiometer (Garrison 1949). Each cover estimate was made independently by two observers and then averaged. We used the mean of measurements from all 18 subplots as an index of shrub, understory tree, and canopy tree cover for the stream reach, and summed all three estimates to arrive at an index of total woody vegetative cover for the stream reach. We determined deciduous vegetative cover in a manner identical to that described above, with the exception of limiting measurements to deciduous species rather than including all vegetative species.

Vegetation concentration

We measured DBH of each tree >5 cm DBH within the entire 30 x 60 m plot and calculated the basal area of all coniferous and deciduous trees separately. We used the ratio of deciduous basal area / total basal area as an index of the vegetation composition of the stream reach; a ratio of 0 describes a site where all trees are coniferous and a ratio of 1 describes a site where all trees are deciduous. We then calculated the absolute value of this proportion subtracted from 0.5 so that the resultant number was between 0 and 0.5. Values near zero indicate a site contains an even mix of coniferous and deciduous vegetation (low resource concentration), and values near 0.5 indicate either a site contains nearly exclusively coniferous trees or nearly exclusively deciduous trees (high resource concentration).

Canopy cover over the stream

We used a moosehorn densiometer to determine percent cover of trees in the canopy layer directly over the stream channel at seven points located at 5 m intervals along the 30 m stream reach. We used the mean of these values as an index of canopy cover over the stream.

Statistical Analyses

We analyzed data for insects in the six most commonly captured orders: Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera. We used the total number of individuals captured of a given order per stream reach per night averaged over five sampling nights, and estimated biomass of all individuals captured of a given order per stream reach per night averaged over five sampling nights as our two response variables.

We developed statistical models to represent each of our five hypotheses. For three of these hypotheses (resource diversity, resource abundance, and resource quality), the possibility existed that all three vegetation strata (shrubs, understory trees, or canopy trees) combined or one vegetation stratum alone was responsible for driving associations between vegetation characteristics and insects. To facilitate our ability to provide information to siviculturalists regarding which component of riparian vegetation was most influential to patterns of insect abundance and biomass we therefore undertook a preliminary model selection step to determine which of four options (shrub, understory tree, canopy tree, or the sum of all three combined) was most strongly related to the number of captures and biomass of each insect order for each of these three hypotheses. We used the model receiving the most support in this preliminary model selection step for number of captures and for biomass of each insect order in the subsequent analysis that compared the degree of support from the data for each of the five hypotheses relative to one another. In this second model selection step we included one model to represent each of the five original hypotheses, using the most relevant vegetation stratum determined in step one for the resource diversity, resource abundance, and resource quality hypotheses, and the null model (intercept only model). We did not include quadratic terms because (1) we had no biological reasons to expect such relationships, (2) the presence of such trends would be difficult to detect given the relatively small size of our samples, and (3) the number of potential models would be exceedingly large if we included both linear and non-linear trends for each hypothesis. All response variables were natural log transformed to more closely meet assumptions of statistical models.

We used a model selection approach to rank models according to their likelihood, given the data (Burnham and Anderson 2002). We found no evidence of overdispersion and therefore used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank models. We placed all models in rank order according to the difference between the AIC_c score of each model and the lowest AIC_c score of all models for that order (ΔAIC_c), and considered all models with $\Delta AIC_c \leq 2.0$ to have substantial empirical support. We used Akaike weights, w_i, to evaluate the relative likelihood of each model relative to the others. All analyses were conducted in SAS (v9.1) using PROC REG.

We tallied the number of times a model representing each of the original hypotheses had $\Delta AIC_c \leq 2.0$ to obtain an indication of which of our hypotheses best explained number of captures and biomass of the riparian nocturnal flying insect community. This approach was preferable to a single analysis with all orders combined because it provided equal weighting for each order of insect; in a single collective analysis orders with many individuals would be weighted more heavily than orders with fewer individuals and orders with individuals of high biomass would be weighted more heavily than orders with individuals of lesser biomass.

Results

On average, we captured 733 insects per stream reach per night. The orders of insects most commonly captured were Diptera (68.2% of individuals), Lepidoptera (13.3%), and Trichoptera (11.6%) (Table 2.2). The six most commonly captured orders (Diptera, Lepidoptera, Trichoptera, Ephemeroptera, Coleoptera, and Hymenoptera) comprised 98.4% of all individuals captured. No statistically significant inter-annual differences were found for number of captures of any of the six most common orders of insects in sites repeatedly measured each year (*p*>0.35 for all ANOVA comparisons among years for each insect order at each site), so we assume the effect of year was negligible.

In the preliminary model selection step we found that no single vegetative stratum emerged as the primary driver behind associations between vegetation characteristics and number of captures or biomass of insects. Relationships were strongest between insects and the shrub layer in 5 cases, the understory tree layer in 8 cases, the canopy tree layer in 16 cases, and all vegetation layers combined in 7 cases (Table 2.3).

In the subsequent model selection step, when we ranked models pertaining to the five hypotheses according to their ability to explain variation in number of captures and biomass of each order of insect, we found evidence in support of all five hypotheses (Tables 2.4, 2.5, Appendices C, D). The three orders of terrestrial insects (Lepidoptera, Coleoptera, and Hymenoptera) were highly associated with canopy foliage. Five of the eight models for these three orders with $\Delta AIC_c \leq 2.0$ included explanatory variables pertaining to percent deciduous canopy cover, two models reflected stream channel canopy cover, and one model reflected resource concentration (a measure of canopy composition heterogeneity). These results demonstrate strong linkages between these insects and cover and composition of trees in the canopy. Patterns were less clear for insects with aquatic origins (Trichoptera, Ephemeroptera, and Diptera). The null model had $\Delta AIC_c<2$ for biomass of Ephemeroptera and number of captures of Diptera.

Models that included deciduous canopy cover received substantial support for number of captures of Ephemeroptera and for biomass of Diptera and the only model that received substantial support for number of captures and biomass of Trichoptera included cover of all deciduous vegetation. Thus, cover of deciduous vegetation appears to be important to all three insect orders with aquatic origins.

When we tallied the number of times a model representing each of the original hypotheses received substantial support according to the model selection criteria ($\Delta AIC_c \leq 2.0$) for any insect order (omitting models with which the null model was strongly competing), the resource abundance, resource diversity, and resource concentration hypotheses received one tally each, the stream channel cover hypothesis received two tallies, and the resource quality hypothesis received 10 tallies (Table 2.6). Models with deciduous canopy cover as an explanatory variable received substantial support for biomass of Diptera ($r^2 = 0.14$, $w_i = 0.40$), number of captures of Ephemeroptera ($r^2 = 0.10$, $w_i = 0.25$), number of captures ($r^2 = 0.17$, $w_i = 0.61$) and biomass ($r^2 = 0.14$, $w_i = 0.40$) of Coleoptera, number of captures ($r^2 = 0.28$, $w_i = 0.76$) and biomass ($r^2 = 0.20$, $w_i = 0.67$) of Hymenoptera, and number of captures ($r^2 = 0.11$, $w_i = 0.43$) and biomass ($r^2 = 0.28$, $w_i = 0.91$) of Lepidoptera, although the proportion of variance explained by deciduous cover was relatively low in each of these cases. Models with total deciduous cover as an explanatory variable received substantial support for number of captures ($r^2 = 0.18$, $w_i = 0.72$) and biomass ($r^2 = 0.20$, $w_i = 0.79$) of Trichoptera.

Discussion

Predictions made by the resource quality hypothesis received considerably more support than did predictions made by any of the other four hypotheses we examined. Models with deciduous canopy cover as an explanatory variable received substantial support for biomass of Diptera, Coleoptera, Hymenoptera, and Lepidoptera as well as for number of captures of Coleoptera, Ephemeroptera, Hymenoptera, and Lepidoptera. Models with total deciduous cover as an explanatory variable received substantial support for number of captures and biomass of Trichoptera. The six orders of insects we investigated represented 98.4% of all insects captured in black light traps, and are likely to comprise the majority of the nocturnal flying insect community within riparian areas throughout the region. Therefore, we interpret these findings as an indication that deciduous vegetation is an important habitat component for nocturnal flying insects in the region.

The resource quality hypothesis predicts that the abundance and biomass of insects increase with amount of deciduous vegetative cover. High diversity in chemical composition of foliage has spurred coevolution of a variety of digestive and behavioral adaptations in insects, such that most insect species are restricted to feeding on a limited number of plant species (Mattson and Scriber 1987). Due to disparate digestive adaptations required to process coniferous needles and deciduous leaves, few caterpillars can feed on the foliage of both (Holloway and Hebert 1979, Hammond and Miller 1998, Robinson et al. 2000). In general, deciduous foliage is more palatable than is coniferous foliage to herbivores; deciduous leaves have higher mineral content, lower lignin content, and fewer resins than does coniferous foliage (Triska et al. 1975, Feeny 1976, Mattson and Scriber 1987). Furthermore, deciduous foliage generally contains more nitrogen than does conifer needles; nitrogen is the most limiting nutrient for growth and survival of many insects (Mattson and Scriber 1987, Barbehenn et al. 1999). Red alder, the dominant deciduous tree species in riparian areas throughout the region, has foliage with unusually high nitrogen content, making it a valuable food resource for many phytophagous species (Iversen 1974).

Vegetation also influences aquatic emergent insects during the aquatic phase of their lifecycle through the input of leaf litter into streams. Deciduous foliage dominates allochthonous organic input to forested streams (Bilby and Bisson 1992, Hart 2005). This foliage represents a valuable food resource for aquatic emergent insects during the aquatic phases of their life cycles because it tends to contain lower concentrations of substances that prohibit the microbial activity that necessarily precedes consumption of leaf litter by aquatic invertebrates than does coniferous foliage (Triska et al. 1975). Streams in the Pacific Northwest that are bordered by deciduous trees tend to contain more organic matter, enhanced microbial activity, and greater biomass of leaf-shredding invertebrates relative to streams bordered by coniferous trees (Bilby and Bisson 1992, Piccolo and Wipfli 2002, Allen et al. 2003).

The remaining hypotheses received fairly little support from the data. The resource abundance hypothesis predicts that cover of riparian vegetation in a stream reach is coupled with abundance and biomass of insects. This association has been demonstrated for a variety of taxa and ecosystems, including spiders in forests (Halaj et al. 1998), beetles in fields (Knops et al. 1999, Haddad et al. 2001), and entire insect communities on islands (Polis et al. 1997). However, in our study, the resource abundance hypothesis received substantial support only for explaining variation in number of captures of Ephemeroptera, and in this case the proportion of variance explained was fairly low ($r^2 = 0.11$) as was the weight of evidence in favor of this model (0.23).

The resource diversity hypothesis predicts that riparian vegetative species richness is coupled with number of captures and biomass of insects because niche heterogeneity increases exponentially with plant species richness (Lawton 1983). Although such relationships have been reported in other ecosystems (Polis et al. 1997, Knops et al. 1999, Haddad et al. 2001), relationships between plant species richness and insects in our study were not strong. The resource diversity hypothesis only received substantial support for explaining variation in number of captures of Ephemeroptera, and in this case the proportion of variance explained was fairly small ($r^2 = 0.13$), as was the weight of evidence in favor of this model (0.34).

The resource concentration hypothesis predicts that abundance and biomass of insects increase with the dominance of the riparian vegetation along a continuum from an even mixture of coniferous and deciduous trees to 100% coniferous or 100% deciduous vegetation. Because dense patches of host plants provide a predictable, available food supply (Root 1973, Miller and Stricker 1984, Strong et al. 1984), this hypothesis could be particularly relevant to terrestrial phytophagous insect orders. However, the resource concentration hypothesis only received substantial support for explaining variation in biomass of Diptera, and in this case the proportion of variance explained was fairly small ($r^2 = 0.15$), as was the weight of evidence in favor of this model (0.42).

The stream channel cover hypothesis predicts that abundance and biomass of insects are highly associated with canopy cover directly over the stream. Alterations in riparian canopies influence aquatic insect communities (e.g., Bilby and Bisson 1992, Kiffney et al. 2003), and composition of diurnal Lepidoptera differs between gaps and heavily shaded areas in forests (Hamer et al. 2003), leading to the prediction that canopy cover would be influential to abundance and biomass of insects. In our study, the stream cover hypothesis was relatively ineffective at explaining variation in abundance or biomass of aquatic emergent insects, but models reflecting this hypothesis received substantial support for explaining variation in biomass of Coleoptera and number of captures of Lepidoptera. In both cases, however, these models explained a fairly small proportion of variance and the weight of evidence in favor of these models was fairly low ($r^2 = 0.13$, $w_i = 0.33$ for biomass of Coleoptera; $r^2 = 0.06$, $w_i = 0.17$ for number of captures of Lepidoptera).

Conclusions and Management Implications

Abundance and biomass of nearly all insects investigated was more strongly associated with cover of deciduous trees than with any other factor investigated. This study adds to a growing body of evidence indicating that in riparian areas of coniferous forests, deciduous vegetation plays an important role for many terrestrial and aquatic organisms (McComb et al. 1993, Gomez and Anthony 1996, Whiles and Wallace 1997, Wipfli 1997, Piccolo and Wipfli 2002, Allen et al. 2003, Premdas 2004, Romero et al. 2005). In the Oregon Coast Range, riparian areas with low densities of large conifers are predicted to follow successional pathways leading to shrub-dominated communities (Minore and Weatherly 1994, Hibbs and Bower 2001). If shrub-dominated communities become more prevalent across riparian areas throughout the Oregon Coast Range ecoregion, results of this study suggest that vegetation management prescriptions that enhance cover of deciduous trees may become necessary if management goals include maintenance of biodiversity and abundance of invertebrates. Such management actions would also confer benefits to vertebrates dependent upon nocturnal insects as a food resource.

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Figure 2.1. Map of Oregon Coast Range, showing the location of 34 stream reaches where insects were sampled.

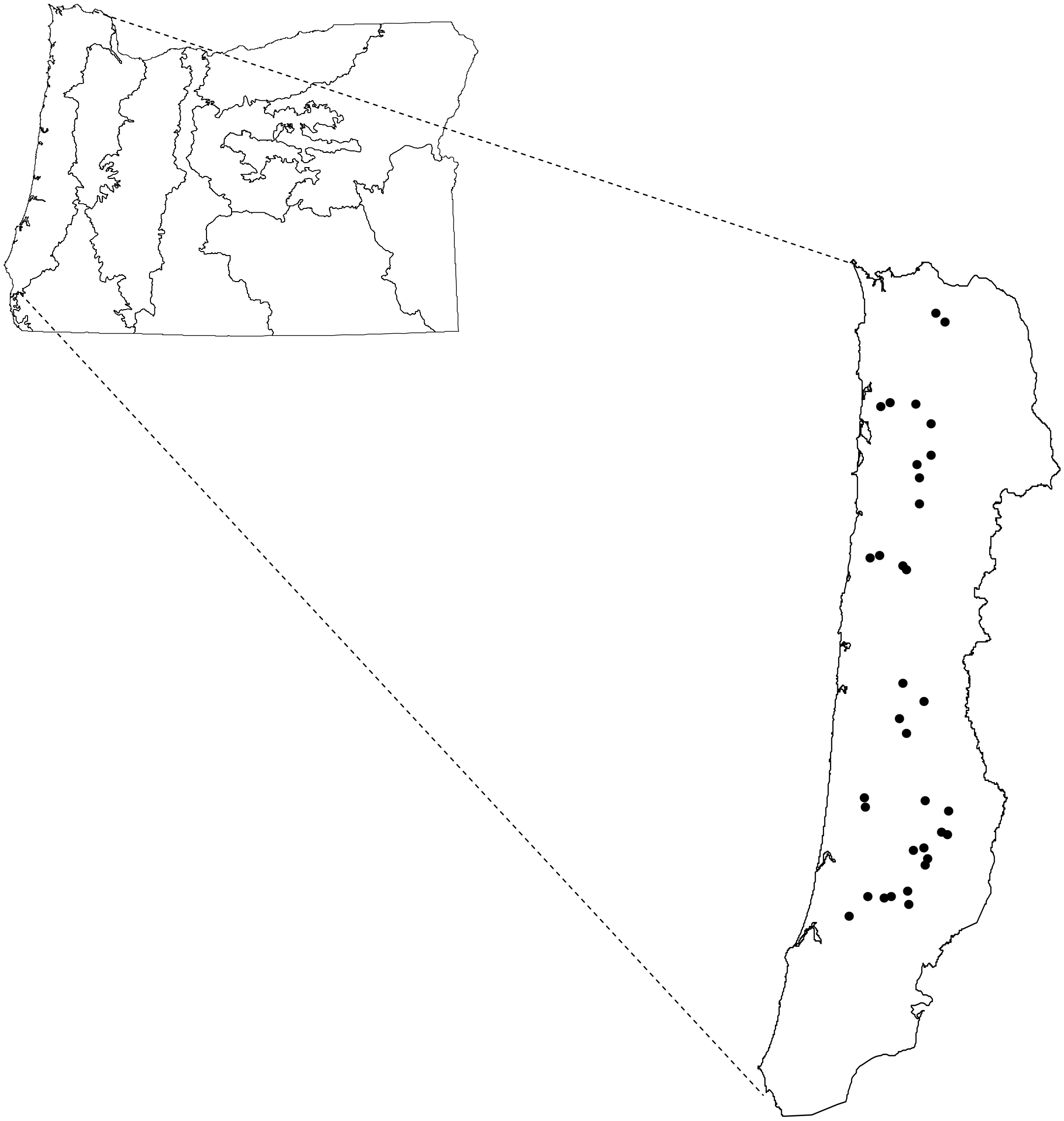

Figure 2.2. Vegetation sampling plots. We identified and measured DBH for all trees >5 cm DBH within the entire 30 x 60 m plot. Within each of the eighteen 10 x 2 m subplots, we recorded each species of shrub and understory tree, estimated percent cover of shrubs and understory trees, and estimated height of shrubs. At the 18 locations indicated by gray circles we measured canopy cover.

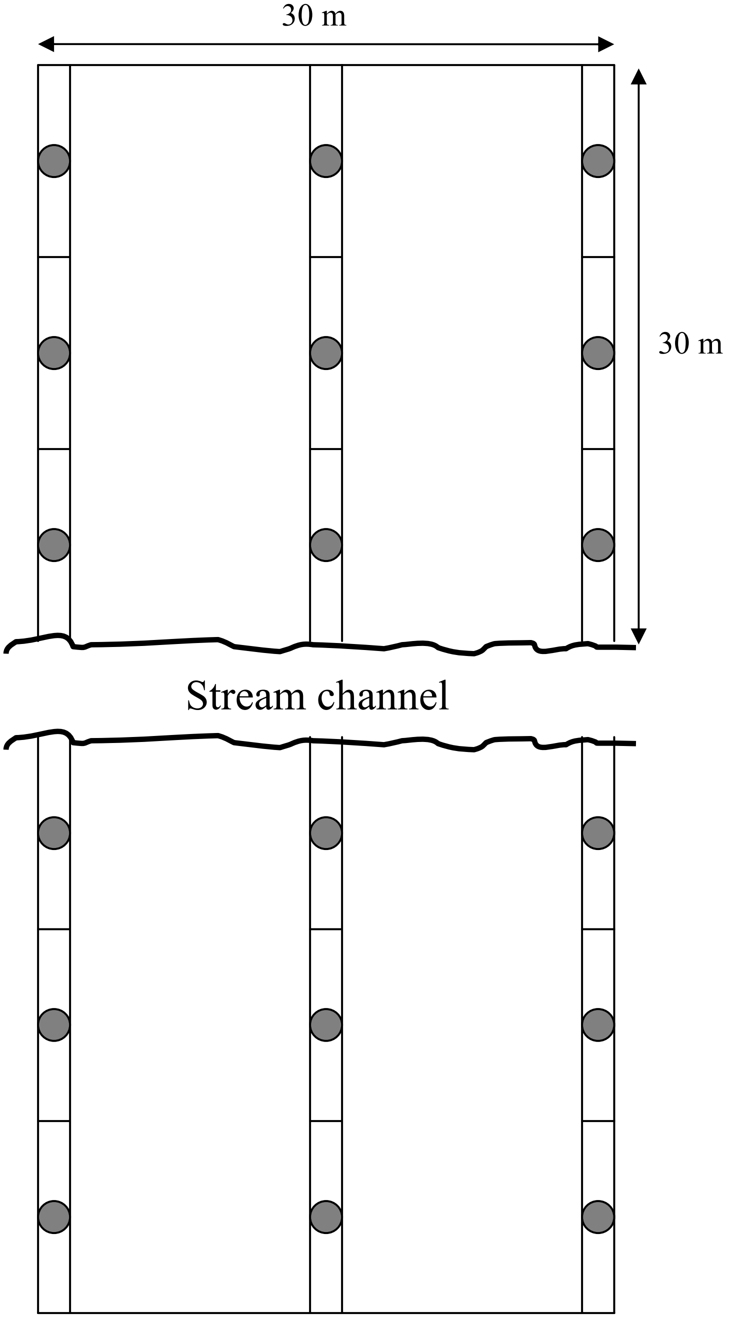

Table 2.1. Relationships between riparian vegetation and number of captures or biomass of nocturnal flying insects predicted by *a priori* hypotheses and the linear models associated with each.

Hypothesis	Predicted relationship	Model structure
Resource diversity	Positive effect of vegetative species richness	$\beta_0 + \beta_1$(vegetative species richness)
Resource abundance	Positive effect of vegetative cover	$\beta_0 + \beta_1$(percent vegetative cover)
Resource quality	Positive effect of deciduous vegetative cover	$\beta_0 + \beta_1$(percent deciduous cover)
Resource concentration	Positive effect of homogeneity of vegetation composition	$\beta_0 + \beta_1(\lvert 0.5 - \text{deciduous basal area/total basal area}\rvert)$
Stream channel cover	Positive effect of canopy cover over the stream channel	$\beta_0 + \beta_1$(canopy cover over stream)

Table 2.2. Number of individuals and biomass per stream reach per night of common orders of nocturnal flying insects captured in black light traps in the Oregon Coast Range, summers 2002-2004.

	No. of individuals			Biomass (mg)		
Order	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Coleoptera	6.7	1.01	0 - 98	62.8	10.99	0 - 1216.1
Diptera	517.6	83.76	7 - 9969	184.2	16.99	3.9 - 1239.0
Ephemeroptera	26.7	5.98	0 - 657	13.3	3.92	0 - 587.4
Hemiptera	0.2	0.04	0 - 3	0.1	0.07	0 - 15.0
Homoptera	2.4	0.37	0 - 29	0.8	0.29	0 - 37.8
Hymenoptera	4.5	0.47	0 - 40	5.2	0.70	0 - 60.6
Lepidoptera	85.1	12.92	1 - 1551	1778.9	145.04	6.2 - 9669.1
Neuroptera	0.1	0.04	0 - 4	4.7	1.71	0 - 138.7
Plecoptera	3.5	0.93	0 - 135	22.5	5.84	0 - 869.1
Trichoptera	78.8	7.69	1 - 605	146.7	14.59	0.6 - 1064.8

Table 2.3. Tallies of the number of times a candidate model with an explanatory variable pertaining to each of the 3 different vegetative strata ranked highest in comparison to those with explanatory variables pertaining to other vegetative strata during the preliminary model selection step for each of the six most common orders of insects in riparian area of the Oregon Coast Range.

Insect order	Shrub	Understory tree	Canopy tree	All vegetation strata combined
Coleoptera	0	0	4	2
Diptera	1	2	3	0
Ephemeroptera	2	2	2	0
Hymenoptera	2	0	3	1
Lepidoptera	0	0	4	2
Trichoptera	0	4	0	2
total	**5**	**8**	**16**	**7**

Table 2.4. Strongly competing candidate models ($\Delta AIC_c \leq 2.0$) relating number of captures of orders of insects to characteristics of vegetation in riparian areas of the Oregon Coast Range, summers 2002-2004. Sign indicates whether the regression coefficient was positive or negative.

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Coleoptera	deciduous canopy cover	+	0	0.61	0.17
Diptera	shrub species richness	-	0	0.27	0.08
	deciduous canopy cover	+	0.1	0.26	0.08
	null		1.1	0.15	-
Ephemeroptera	shrub species richness	-	0	0.34	0.13
	deciduous canopy cover	+	0.6	0.25	0.10
	understory tree cover	+	0.8	0.23	0.11
Hymenoptera	deciduous canopy cover	+	0	0.76	0.28
Lepidoptera	deciduous canopy cover	+	0	0.43	0.11
	stream channel canopy cover	+	1.8	0.17	0.07
Trichoptera	total deciduous vegetation cover	+	0	0.72	0.18

Table 2.5. Strongly competing candidate models ($\Delta AIC_c \leq 2.0$) relating biomass of orders of insects to characteristics of vegetation in riparian areas of the Oregon Coast Range, summers 2002-2004. Sign indicates whether the regression coefficient was positive or negative.

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Coleoptera	deciduous canopy cover	+	0	0.38	0.14
	stream channel canopy cover	+	0.3	0.33	0.13
Diptera	concentration	+	0	0.42	0.15
	deciduous canopy cover	+	0.1	0.40	0.14
Ephemeroptera	shrub species richness	-	0	0.29	0.10
	deciduous canopy cover	+	0.4	0.24	0.09
	null		1.4	0.15	-
Hymenoptera	deciduous canopy cover	+	0	0.67	0.20
Lepidoptera	deciduous canopy cover	+	0	0.91	0.28
Trichoptera	total deciduous vegetation cover	+	0	0.79	0.20

Table 2.6. Number of times a candidate model with an explanatory variable pertaining to each of the 5 different hypotheses ranked either highest or within $\Delta \mathrm{AIC}_c \leq 2.0$ of the highest ranked model during the primary model selection step for each of the six most common orders of insects in riparian area of the Oregon Coast Range.

Insect order	Resource diversity	Resource abundance	Resource quality	Resource concentration	Stream channel cover
Coleoptera			2		1
Diptera			1	1	
Ephemeroptera	1	1	1		
Hymenoptera			2		
Lepidoptera			2		1
Trichoptera			2		
total	**1**	**1**	**10**	**1**	**2**

CHAPTER 3 – MACRO-MOTH BIODIVERSITY IN RIPARIAN AREAS OF THE OREGON COAST RANGE

Abstract

Insufficient knowledge of the distribution and habitat associations of inadequately studied taxa limits abilities to predict influences of forest management activities on biodiversity. We examined spatial patterns of diversity in moth community composition in riparian areas of the Oregon Coast Range, using canonical correspondence analysis to assess how macro-moth community composition varied with local vegetation and geographical factors. The ordination axis that accounted for the greatest amount of variation in moth community composition among sites represented a gradient in north-south orientation, shrub species richness, and elevation; the second axis represented a gradient in east-west orientation and shrub cover; the third axis represented a gradient in canopy tree composition and cover. As this last factor was the one most likely to be altered by forest management activities, we further investigated the influence of canopy composition on moths by comparing measures of moth abundance and diversity between stream reaches dominated by coniferous and deciduous trees. Number of captures, biomass, Shannon's species diversity, and patchiness of species distributions were greater in deciduous-dominated stream reaches, but rarefied species richness was greater in conifer-dominated stream reaches, and Simpson's dominance was similar between forest types. If maintenance of biodiversity is a priority within these forests, we recommend vegetation management activities for

riparian areas that maintain or enhance heterogeneity of vegetative cover, species richness, and composition across broad spatial scales, and we suggest that conservation efforts cover a range in latitude, longitude, and elevation.

Introduction

Concern regarding influences of land management activities on biodiversity has risen in recent years, as conservation of biodiversity has become recognized as a necessary element of ecologically sustainable forest management (Carey and Curtis 1996, Christensen et al. 1996, Hunter 1999). Maintenance of biodiversity is one goal of ecosystem management, the approach currently shaping management practices across most land owned by federal agencies (Christensen et al. 1996, Simberloff 1999, Spies and Martin 2006). Efforts to assess how forest management activities influence biodiversity are challenging due to inadequate knowledge of the current distribution and abundance of many taxa. Furthermore, development of sustainable forest management strategies requires making predictions regarding the potential responses of specific species to vegetation changes, which is possible only after basic ecological relationships between plants and animals are understood (Dobson 2005). As expanding human populations put additional pressure on remaining forest resources, understanding patterns of biodiversity within forests and, more specifically, the ecological linkages between vegetation and unfamiliar animal taxa, is more critical to planning vegetation management strategies than ever before (Ehrlich and Wilson 1991, Simberloff 1999).

In comparison with vertebrates, forest invertebrates have received relatively little research attention. This is alarming, given that 65-70% of species in forests are arthropods (Langor and Spence 2006). Some species of insects could be strongly influenced by vegetation management activities because their host-specificity and their limited range of movements make them sensitive to small-scale environmental conditions (Smith and Remington 1996, Niemela 1997, Ricketts et al. 2002, Langor and Spence 2006). The predominance of phytophagy among moths has led to the conjecture that moths could be particularly susceptible to changes in vegetation (Holloway 1984, Luff and Woiwod 1995, Kitching et al. 2000). Compositional differences in communities of macro-moths have been noted in forests subjected to different coarse-scale disturbances (Burford et al. 1999, Summerville et al. 2004).

Insufficient knowledge of distributions of moth species in forests of the Pacific Northwest and factors governing these distributional patterns makes predicting the influence of forest management activities on nocturnal Lepidoptera impossible. Therefore, the first objective of our study was to gather information on macro-moth species occurrence throughout the Oregon Coast Range ecoregion. Our second objective was to examine patterns of macro-moth community composition. The large number of species of moths in forests of the Pacific Northwest renders a species-specific management approach for moths challenging or impractical. Information on which environmental factors are most strongly associated with distributional patterns would enable forest managers to identify priority sites for moth conservation; a small number of sites distributed along each of the gradients that accounted for large amounts of variability in moth community composition could potentially enable conservation of maximum species diversity with minimal investment. An understanding of which vegetation factors are most strongly associated with distributional patterns would enable more accurate predictions of potential effects of forest management activities. We therefore examined how differences in vegetation and geography among sites correlated with differences in macro-moth species composition among sites, and identified which of these factors accounted for the greatest variation in moth community structure. Because number of captures and biomass of macro-moths (at an ordinal level) were strongly associated with deciduous canopy cover (Chapter 2), we further investigated the influence of canopy composition on macro-moths by comparing number of captures, biomass, species richness, species diversity, and species dominance between stream reaches dominated by coniferous trees and by deciduous trees.

Methods

Study Area

The Oregon Coast Range is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1973). The terrain is steep and rugged, with a dense network of streams throughout. Elevation ranges from sea level to 1250 m. Common riparian overstory species are Douglas-fir (*Psuedotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and western redcedar (*Thuja plicata*). The understory is dominated by vine maple (*Acer circinatum*) and hazelnut (*Corylus cornuta*), and the shrub layer by salmonberry (*Rubus spectabilis*) and swordfern (*Polystichum munitum*).

The northern and southern boundaries of our study region were the Columbia River and the southern border of the Coos River sub-basin respectively, and the western and eastern boundaries were the Pacific Ocean and the Willamette Valley respectively. This delineates a region approximately 300 km (190 miles) north to south. We conducted research in pairs of randomly selected stream reaches within 17 watersheds located throughout this region.

We randomly selected stream reaches that were dominated by either coniferous or deciduous trees. To locate these stream reaches we generated random UTM coordinates and determined the nearest point on a second or third order stream for each point using 1:24,000 scale topographic quadrangle maps. Points were dropped from consideration if they (1) were not on either public property or private property to which access had been granted, (2) were within 2 km of a stream reach already selected, (3) were on a stream where a reach had already been selected, (4) had vegetation completely obstructing the airspace directly over the stream (which would hinder the transmission of light from traps), or (5) were not 3-7 m wide and >0.5 m deep.

Over the course of three summers we monitored macro-moth activity in 17 pairs of stream reaches (Fig. 3.1, Appendix A). We investigated 5 pairs of stream reaches in the central Coast Range in 2002, 6 in the southern Coast Range in 2003, and 6 in the northern Coast Range in 2004. We sampled two of the stream reaches from a single watershed each year to assess inter-annual variability in number of moths and biomass of moths captured.

Lepidoptera Sampling

We used black light traps (Bioquip, Inc.) with 12-watt fluorescent black light tubes, powered with 12-volt marine gel-cell batteries, to capture nocturnal Lepidoptera. We placed traps 0.5 m off the ground within 2 m of the stream edge, in a location that maximized visibility from all directions. A “no-pest strip” (Hotshot, Newport Beach, CA) was placed in the bottom of each trap as a killing agent. We activated traps within 30 min of sunset and deactivated them 0-30 min after sunrise. In the morning, we removed insects from traps, placed them in labeled plastic boxes, and stored them at -10ºC until analysis.

We identified all macro-moths to species in the laboratory. We used the number of individuals of each species captured per site per night as an index of abundance. To estimate biomass of macro-moths captured, we used a previously published length-mass equation (Sample et al. 1993; Appendix B) because weighing insects directly requires lengthy processing time and typically gives inaccurate results due to changes in biomass as storage time increases and as carbohydrates are lost from specimens during defrosting (Burgherr and Meter 1997, Benke et al. 1999, Martin 2001). We measured body lengths of five randomly selected individuals of each species to the nearest mm, from the anterior of the head to the posterior of the last abdominal segment. In instances where we had <5 individuals of a species, we measured body lengths of specimens from the Oregon State University Arthropod Collection (Cordley Hall, Corvallis, OR). Our biomass estimates may be inaccurate for some species due to inter-specific differences in body widths.

We accounted for potential temporal variability in the composition of Lepidopteran communities within a summer (Devries and Walla 2001, Summerville and Crist 2003, 2005) by sampling each pair of stream reaches once during every 2-week period between mid-June and early September. Five visits to each stream reach each summer yielded 190 samples.

Vegetation Sampling

At each location where we deployed insect traps, we sampled vegetation throughout a 30 x 60 m plot (Fig. 3.2). We estimated species richness, cover, and composition in 30 m x 30 m plots on each side of the stream and estimated canopy cover directly over the stream.

Vegetative species richness

We recorded all species of woody shrubs and understory trees (trees with ≤5 cm DBH) that occurred in three 2 x 10 m subplots located at each end and the center of each plot (Fig. 3.2), and tallied the number of species across all 18 subplots as an index of shrub species and understory tree species richness for the stream reach. Western swordfern (*Polystichum munitum*) was recorded as a shrub because it is a perennially erect plant that contributes substantial biomass year-round throughout the study region, and due to its stature, vinemaple was recorded as an understory tree. We determined richness of canopy trees by tallying number of species of trees >5 cm DBH throughout the entire 30 x 60 m plot. We summed richness of shrubs, understory trees, and canopy trees (accounting only once for those species that occurred in >1 vegetation layer) as an index of richness of all woody species.

Vegetative cover

We determined cover of shrubs and understory trees by visually estimating the percentage of each of the eighteen 2 x 10 m subplots that was covered by shrubs and understory trees. We estimated canopy tree cover from the center of each of the 18 subplots using a moosehorn densiometer (Garrison 1949). Each cover estimate was made independently by two observers and averaged. We used the mean of measurements from all 18 subplots as an index of shrub, understory tree, and canopy tree cover for the stream reach.

Tree species composition

We measured the DBH of each tree >5 cm DBH within the entire 30 x 30 m plot on each side of the stream, and calculated the basal area of coniferous and deciduous trees separately. We used the ratio of deciduous basal area / total basal area as an index of the vegetation composition of the stream reach; a ratio of 0 describes a site where all trees are coniferous and a ratio of 1 describes a site where all trees are deciduous.

Statistical Analyses

To determine the potential effect of year in our analyses, we used ANOVA to compare mean number of moths and mean biomass of moths captured per night among years for each stream reach measured all three years of the study. We found no statistically significant inter-annual differences in biomass (*p*>0.27) or number (*p*>0.23) of moths captured in stream reaches repeatedly measured each year. Hence, we assumed the effect of year was negligible.

Factors Governing Moth Community Composition

We used canonical correspondence analysis (CCA) to examine how variation in moth community composition was related to differences in vegetation and geography among stream reaches. CCA is a direct gradient approach that describes community variation with respect to measured environmental variables, and is founded on the idea that spatial variation in the abundance of species among sites reflects the habitat preferences of each species (Harvey 1996). CCA positions sites along environmental gradients on the basis of similarities in species composition and environmental variables. Synthetic ordination axes are created using linear combinations of those environmental variables that explain the most variance in species composition (ter Braak 1987). The first axis orders species and sites to produce the maximum possible correlation between site and species scores. This process is repeated for creation of subsequent axes, with each additional axis orthogonal to previous axes. Explanatory variables can be highly intercorrelated and species can have linear or nonlinear relationships with environmental gradients (Palmer 1993).

Relationships between environmental factors and number of captures of each species of moth can be portrayed as a biplot, with species and sites represented as points and environmental variables by arrows. The location of sites and species relative to arrows indicates the environmental characteristics of sites and the habitat associations of species, respectively (Palmer 1993). Axes are scaled so that species scores are weighted mean site scores, enabling interpretation of relationships between environmental variables and species points, and site scores are centered and standardized to unit variance (McCune and Grace 2002). The direction an arrow points indicates the maximum correlation between species composition and the environmental variable that arrow represents, arrow length is proportional to the importance of that variable in influencing community structure, and angles between arrows represent the degree of correlation between environmental variables (ter Braak 1987). The position of a species relative to arrows indicates characteristics of the realized niche for that species (Palmer 1993). Species with low scores for the first two axes (positioned near the origin of the plot) tend to have general habitat requirements and widespread distribution, whereas those with higher scores on one or both axes (located farther from the origin) tend to have more specific habitat requirements and tend to be less common (Harvey 1996).

We performed CCA using PC-ORD (v4.4; MJM Software, Inc.). The first input matrix consisted of data for number of captures of each moth species pooled across all five sampling nights at each stream reach, after removing those species that occurred in only one stream reach. The second input matrix consisted of seven variables describing vegetation (species richness of shrubs, understory trees, and canopy trees; cover of shrubs, understory trees, and canopy trees; and canopy composition) and three variables describing geography (xUTM, yUTM, and elevation). To test the null hypothesis that moth species composition was not more strongly correlated to environmental variables than was expected by chance, we computed 1000 Monte Carlo permutations of the data and compared observed correlations to those from randomized runs (McCune and Grace 2002).

Comparisons of Moth Communities between Conifer- and Deciduous-dominated Stream Reaches

We tested the null hypothesis that the mean difference in number of moths captured per night or biomass of moths captured per night between conifer- and deciduous-dominated stream reaches was zero using repeated measures ANOVA in SAS (v9.1).

For each stream reach sampled, we estimated species diversity with the Shannon Index (H′) and species dominance with the Simpson Index (D) (Magurran 1988). We computed these indices using EcoSim (v7.72; Gotelli and Entsminger 2001), after pooling samples from all five visits to each site. We tested the null hypothesis that the mean difference in H′ and D between paired sites was equal to zero using paired *t*-tests in SAS.

Comparisons of raw species richness between sites could be misleading if species accumulation curves have not yet reached an asymptote (Gotelli and Colwell 2001, Willott 2001). A plot of number of species against number of individuals collected suggested that our data had not yet reached an asymptote, so we used rarefaction to predict the expected number of species in random sub-samples of various sizes. By repeatedly sampling from the entire pool of individuals captured per habitat at random and plotting the mean number of species represented within sub-samples of different sizes, rarefaction produces smooth curves that enable comparisons of species richness between habitats when densities of individuals differ between those habitats (Gotelli and Colwell 2001). Using EstimateS (v7.5, Colwell 2005), we produced individual-based and sample-based rarefaction curves.

For individual-based curves, we pooled data from all visits to deciduous-dominated sites, repeatedly re-sampled these data randomly, and plotted the number of expected species against the number of individuals sampled. We then repeated this process with data from conifer-dominated sites. These two curves show the number of species expected when a given number of individuals are sampled from each of the two habitats throughout the study region, assuming individuals are distributed at random among sites.

If species are not randomly distributed across habitats, then individual-based curves will overestimate expected species richness (Gotelli and Graves 1996). Thus, we computed sample-based curves by first pooling data from all 5 visits to each stream reach to arrive at a list that reflected summer-wide number of captures for each species for each stream reach (here referred to as a “sample”). We then randomized data among groups of samples from the same habitat (conifer- or deciduous-dominated) and plotted the expected number of species against the number of individuals sampled from each habitat. The number of species estimated by sample-based curves is always lower than estimates from individual-based curves because fewer species are represented when random selection is from a group of pooled samples than when random selection is from all samples collected throughout the entire habitat (Gotelli and Colwell 2001). Comparisons of the magnitude of difference between an individual-based and a sample-based curve for one habitat versus another provides an indication of how patchily distributed species are in one habitat relative to the other (Gotelli and Colwell 2001).

Results

We captured 9,514 moths from 13 families, 153 genera, and 233 species (Appendix E). The majority of individuals were from the Geometridae (*n*=5,510; 57.9%) and Noctuidae families (*n*=1,786; 18.8%). Most species were rare (Figs. 3.3, 3.4); 28% of the species captured were represented by only 1 (40 species), 2 (16 species), or 3 (10 species) captures. The 12 most common species (*Perizoma grandis*, *Iridopsis emasculata*, *Venusia cambrica*, *Lophocampa maculata*, *Sabulodes aegrotata*, *Ceratodalia gueneata*, *Nadata gibbosa*, *Macaria signaria*, *Lophocampa argentata*, *Oligocentria semirufescens*, *Diarsia esurialis*, and *Achytonix epipaschia*) comprised >50% the total individuals captured, but only 5% of species richness. On average, we collected 51.9 (±3.98) individuals per stream reach per night. Mean body length was 14.7 (±0.04) mm.

Factors Governing Moth Community Composition

We rejected the null hypothesis that there was no relationship between species and environment; the eigenvalue for the first ordination axis was significantly higher than would be expected by chance ($p = 0.001$). Species-environment correlations (measures of how well the extracted variation in community composition was explained by environmental variables), were high (Pearson correlation=0.966 for axis 1; 0.955 for axis 2; 0.932 for axis 3). However, eigenvalues associated with each ordination axis (measures of the amount of variation in the species composition data explained by the combination of environmental variables that comprise that axis), were fairly low; the first three axes explained 10.2%, 6.6%, and 3.3% of the variation respectively. The gradient represented by each axis can be inferred from the canonical coefficients and correlation coefficients of each environmental variable (Harvey 1996) (Table 3.1, Fig. 3.5). The first axis represents a gradient in north-south orientation, shrub species richness, and elevation, such that sites located at the left side of the plot tend to be more northerly, higher in elevation, and have relatively low shrub species richness. The second axis represents a gradient in east-west orientation and shrub cover, such that sites located at the lower edge of the plot tend to be more westerly and have relatively high shrub cover. The location of species relative to axes and sites indicates their habitat associations and distributions, respectively. The third axis (not represented in the biplot) represents a gradient in canopy composition and canopy cover extending from highly deciduous with a relatively high percent cover to highly coniferous with a relatively low percent cover.

Comparisons of Moth Communities between Conifer- and Deciduous-dominated Stream Reaches

We captured most species in greater numbers in deciduous-dominated stream reaches than in conifer-dominated stream reaches (Fig. 3.6). Of 111 species captured ≥10 times, only 27 species were captured more frequently in conifer-dominated than in deciduous-dominated stream reaches, whereas 78 species were captured more frequently in deciduous-dominated than in conifer-dominated stream reaches. In addition, of species captured ≥10 times, 40 species were captured at least twice as often in deciduous-dominated as in conifer-dominated stream reaches, and only 11 species were captured twice as often in conifer-dominated as in deciduous-dominated stream reaches. The median number of captures in deciduous-dominated stream reaches (35.5 individuals) was 17% higher than the median number of captures in conifer-dominated stream reaches (20.4 individuals; 95% CI from 13 to 23% more; t_{16}=4.08, *p*=0.0009). The median biomass of macro-moths captured in deciduous-dominated stream reaches (484.6 mg) was 14% more than the median biomass of macro-moths captured in conifer-dominated stream reaches (342.8 mg; 95% CI from 12 to 18% more; t_{16}=2.76, *p*=0.0014). Shannon's Index of species diversity (H′) was greater in deciduous-dominated stream reaches (2.94 ± 0.089) than in conifer-dominated stream reaches (2.76 ± 0.102; $\bar{x}$ difference = 0.18, 95%CI from 0.04 to 0.33; t_{16}=2.65, *p*=0.017). Of the 13 families captured, only 6 were captured in conifer-dominated stream reaches, whereas 12 were represented in samples from deciduous-dominated stream reaches. Simpson's Index of species dominance (D) was similar between stream reaches with different canopy types ($\bar{x}$ difference = 0.009, 95%CI from -0.06 to 0.04; t_{16}=0.37, p=0.713).

Comparisons of estimates of richness based on all individuals captured from stream reaches with each canopy type show that deciduous-dominated stream reaches had lower richness than did conifer-dominated stream reaches for sub-samples of all sizes (Fig. 3.7). Comparisons between individual-based and sample-based curves for each canopy type show that relative patchiness of the distribution of species within each canopy type was fairly similar, but slightly more patchy in the deciduous-dominated stream reaches (Fig. 3.7).

Discussion

Conservation emphases have shifted in recent years from a single species approach to a focus on biodiversity of entire communities (Carey and Curtis 1996, Christensen et al. 1996, Hunter 1999, Dobson 2005). The design of effective conservation strategies under this approach requires knowledge of spatial patterns in species composition so that efforts can be directed toward preserving areas that harbor representative samples of regional biodiversity. We found that macro-moths are speciose in the Oregon Coast Range, and that most of the species encountered are rare. The high species richness of moths in the region makes a fine-filter approach to conservation, tailored to fit individual species, impractical. However, the rarity of most species in the region, coupled with strong habitat preferences and potentially restricted distributions of some species, suggests a coarse-filter conservation strategy that aims to protect a large number of species in a diverse array of ecosystems might not adequately encompass all native species of macro-moths. A meso-filter approach that focuses on conserving specific ecosystem elements critical to the survival of particular species in the matrix between reserves is sometimes used as a complement to coarse-filter approaches (Hunter 2005). Our results suggest that riparian shrubs may be an important habitat element for moths, so management of shrubs may serve as a meso-filter conservation approach for moths in this region.

Each of the spatial factors investigated contributed to the separation of moth communities: north-south, east-west, and elevation gradients. Although local vegetation factors were also highly correlated with these two axes, the ability of spatial location to explain appreciable variance in moth community composition suggests that moth species were not distributed homogeneously throughout the region. This suggests that ensuring adequate representation of regional variation in species composition requires conservation efforts across the province, so that a range of latitudes, longitudes, and elevations are included.

Although biodiversity of invertebrates has not been thoroughly studied, ecological diversity within the Oregon Coast Range ecoregion is generally perceived to be high, due to the environmental diversity promoted and maintained by complex patterns of vegetation, geology, soils, and climate (Spies et al. 2002). Climatic diversity across the province varies along north-south and east-west gradients due to shifts in temperatures, humidity, and precipitation associated with prevailing weather patterns

(Spies et al. 2002). These climatic gradients were reflected in patterns of moth community composition. The first ordination axis differentiated species favoring southern, low elevation sites with high shrub species richness from those favoring northern, high elevation sites with low shrub species richness. In riparian areas of the Oregon Coast Range, dominance of salmonberry in the understory is highest in the north, and decreases southward (Pabst and Spies 1999). Warmer, drier summers in southern Oregon coincide with less competition from salmonberry to promote greater shrub species richness. The second ordination axis differentiated species favoring western sites with high shrub cover from species favoring eastern sites with low shrub cover. Sites located west of the Coast Range Divide experience limited annual variability in temperatures due to proximity to the Pacific Ocean, and generally have cooler, wetter climates than sites located to the east (Spies et al. 2002). Both of these climatic gradients were reflected in turnover of species composition in moth communities, suggesting that climatic patterns may be ultimately responsible for producing regionally distinct species assemblages of moths.

Local vegetation factors (shrub species richness, shrub cover, canopy composition, and canopy cover) were associated with variation in moth community composition as well. These findings affirm other studies that have indicated moths are vulnerable to changes in vegetation composition and cover (Holloway 1984, Luff and Woiwood 1995, Kitching et al. 2000), and indicate that forest management activities that alter riparian vegetation have the capacity to impact moth community composition.

Uniform vegetation management strategies implemented across a broad spatial scale could be especially detrimental to macromoth biodiversity in the region.

The contributions of shrub species richness and shrub cover in differentiating moth communities, as revealed by the first two axes of the CCA, corroborates previous findings that understory vegetation is an important determinant of moth community structure in forested ecosystems. Strong relationships between species richness of shrubs and richness of Geometrids or all moths collectively have been reported in both temperate and tropical forests (Chey et al. 1997, Intachat et al. 1997, Usher and Keiller 1998, Beck et al. 2002). In this study, the correlation between species richness of shrubs and Geometrids was weak (r = 0.03), as was the correlation between species richness of shrubs and all moths (r = 0.20). However, results of the CCA suggest that turnover in moth species composition among sites is associated with variation in shrub species richness and cover.

Two sources of information provide evidence of the influence of canopy composition on moth communities: (1) the third ordination axis reflects a gradient in canopy composition and cover ranging from highly deciduous with high percent cover to highly coniferous with low percent cover, and (2) the comparisons made between conifer- and deciduous-dominated stream reaches indicate significantly greater number of captures, biomass, and species diversity in deciduous-dominated stream reaches, but greater species richness (after rarefaction) and less patchiness in species distributions in conifer-dominated stream reaches. Variation in nutrient content and in the type and concentration of chemical defense compounds in foliage of different plant species has prompted insect species to develop specialized adaptations. Many species of insects are dietarily restricted to a limited number of closely related plant species (Holloway and Hebert 1979, Mattson and Scriber 1987). It follows that few moths have the capacity to feed on taxonomically distinct taxa such as angiosperms and gymnosperms (Holloway and Hebert 1979). Deciduous foliage is generally considered a higher quality food resource because it tends to have higher nitrogen content (a limiting nutrient for many phytophagous insect species), whereas conifer needles tend to have more resins and higher concentrations of lignin (inhibitory compounds) (Triska et al. 1975, Feeny 1976, Mattson and Scriber 1987, Ohgushi 1992, Friberg and Jacobsen 1994). Thus, diversity and abundance of invertebrates (Anderson and Cummins 1979, Piccolo and Wiplfi 2002, Allan et al. 2003) and moths in particular (Holloway and Hebert 1979, Hammond and Miller 1998) supported by deciduous foliage exceeds that supported by coniferous foliage. According to previously published records, 54% of Lepidopteran species associated with one or more of the species of plants occurring in our study region feed only on deciduous trees or shrubs, whereas only 9% of species associated with one or more of the plant species occurring within our study region feed only on conifers (Robinson et al. 2000). In sum, it appears as though variation in the cover and diversity of deciduous vegetation is important to variation in the diversity of macro-moths in forests of the Oregon Coast Range.

Conclusions and Management Implications

As one of the most productive forest ecosystems in the world, the Pacific Northwest experiences considerable pressure to produce timber. Interest in devising cost-effective strategies to conserve biodiversity throughout the region has risen in recent years (Polansky et al. 2001, Lichtenstein and Montgomery 2003). Our data suggest that when maintenance of biodiversity in these forests is a priority, conservation efforts covering a range in latitude, longitude, and elevation will be necessary to ensure representation of regional variation in macro-moth species composition. Characteristics of trees in the canopy and shrubs accounted for variation in moth species composition, suggesting that riparian management activities that alter either of these vegetative strata have the capacity to influence moth communities. However, shrub characteristics accounted for more variation in moth species composition than did canopy characteristics. Because of this we conclude that moths are more likely to respond to management activities that alter shrubs than to those that alter the canopy. Given that species-specific habitat preferences of moths were evident across gradients of vegetative cover, species richness, and composition, maintaining heterogeneity of these characteristics across broad spatial scales will likely be necessary for maintenance of moth species communities. Thus, we recommend riparian vegetation management prescriptions that strive to enhance heterogeneity in shrub species richness, shrub cover, canopy composition, and canopy cover across broad spatial scales.

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Figure 3.1. Map of 34 stream reaches where macro-moths were sampled in the Oregon Coast Range.

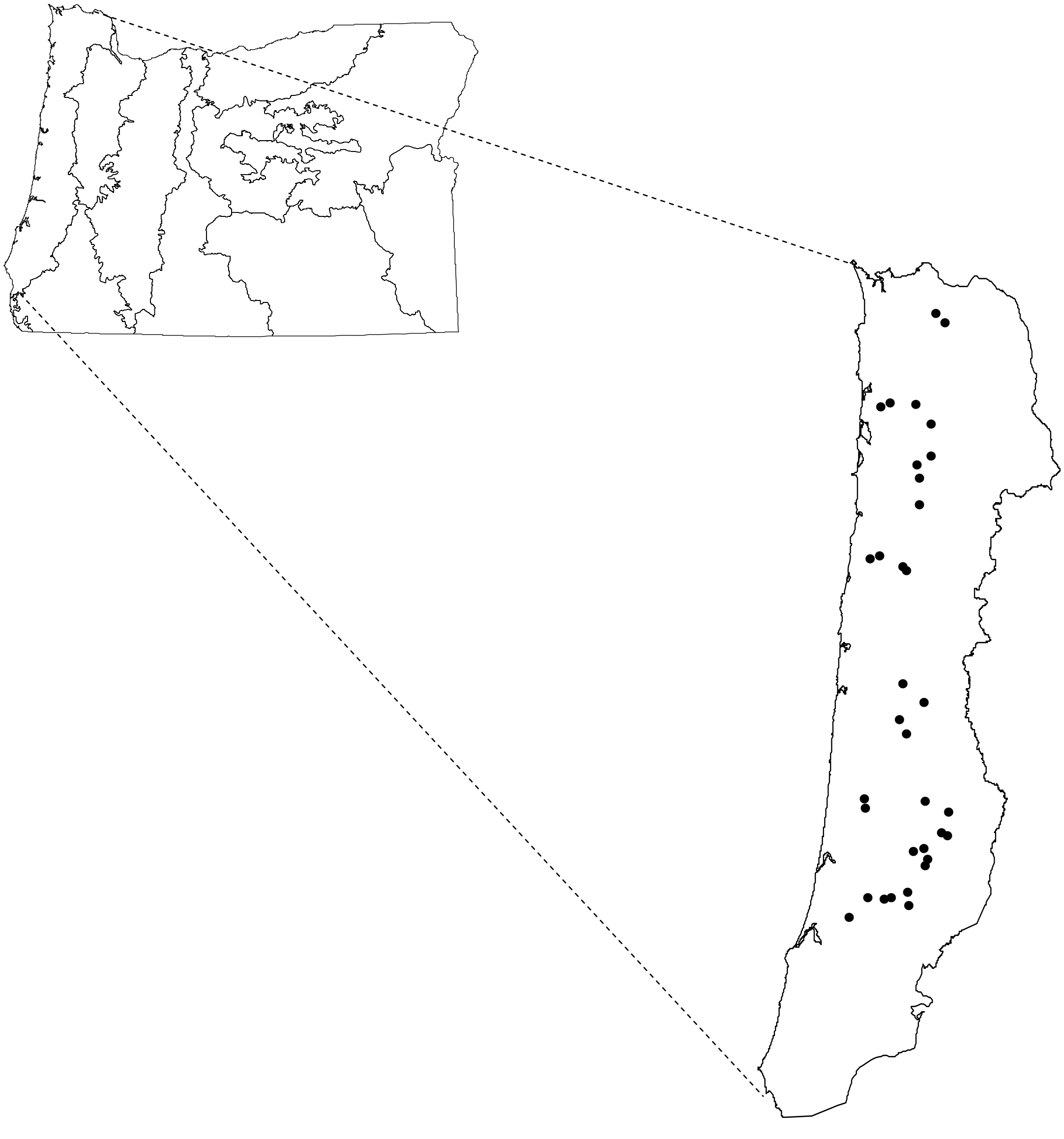

Figure 3.2. Vegetation sampling plots. We identified and measured DBH of all trees >5cm DBH within the entire 30 x 60 m plot. Within each of the eighteen 10 x 2m subplots, we recorded each species of shrub and understory tree, estimated percent cover of shrubs and understory trees, and estimated height of shrubs. At the 18 locations marked by gray circles we measured canopy cover.

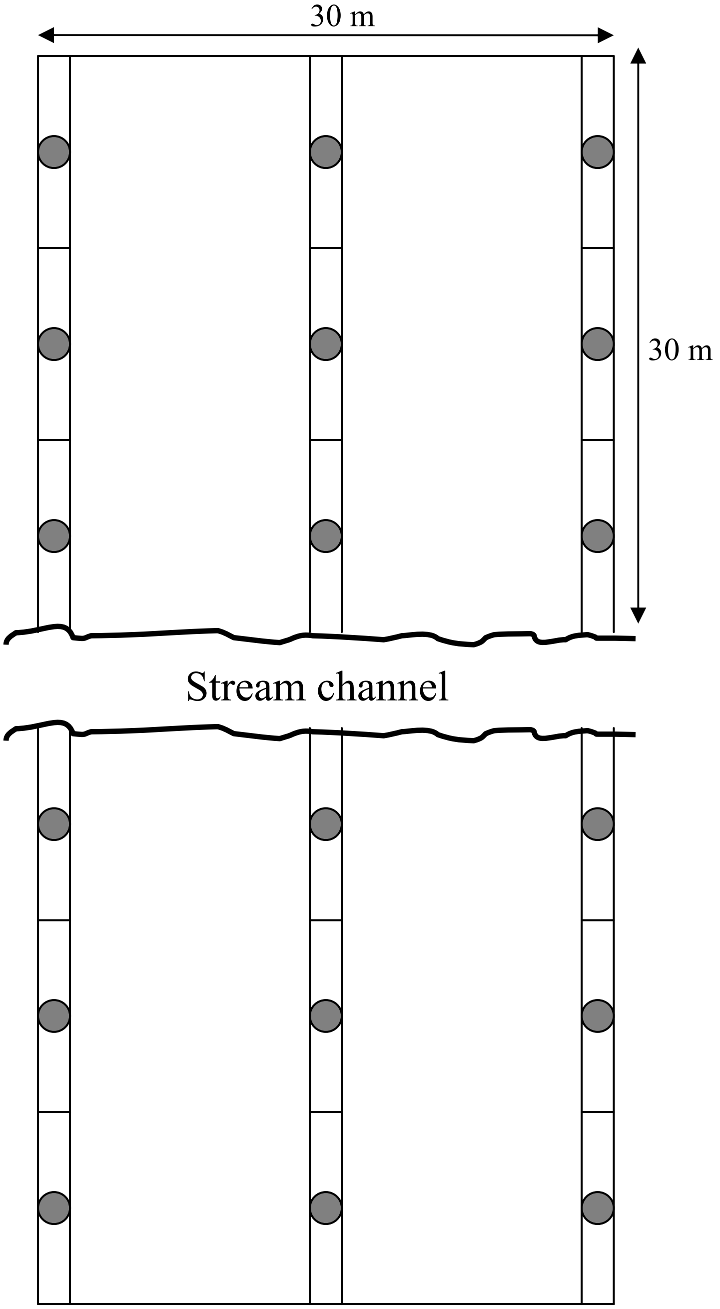

Figure 3.3. Number of captures of each species of macro-moth in the Oregon Coast Range, summers 2002-2004, with species ordered relative to number of captures.

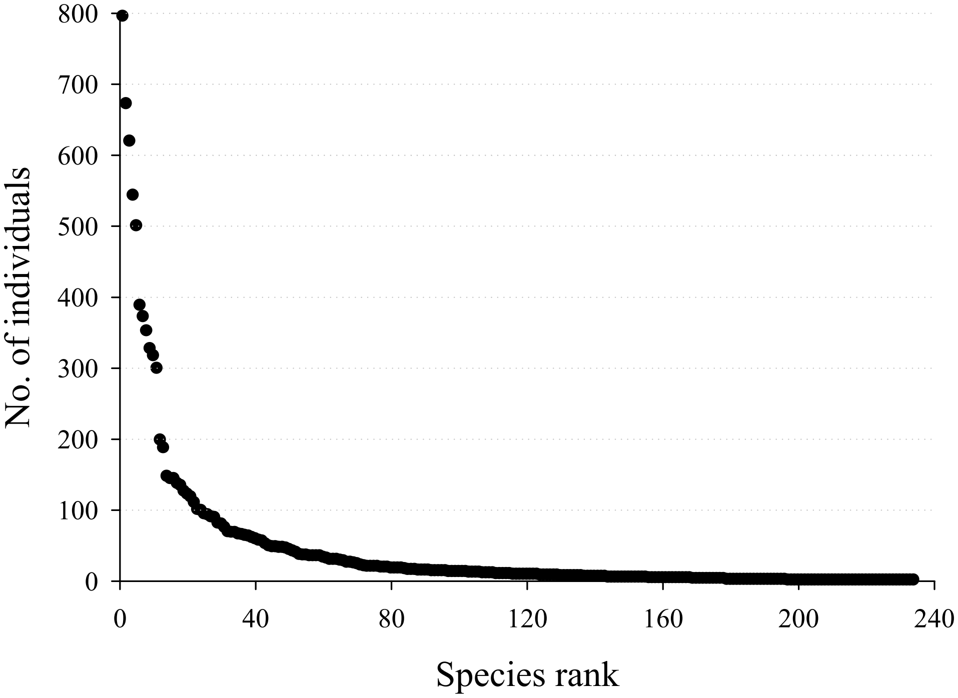

Figure 3.4. Number of captures per species of macro-moth in the Oregon Coast Range, summers 2002-2004.

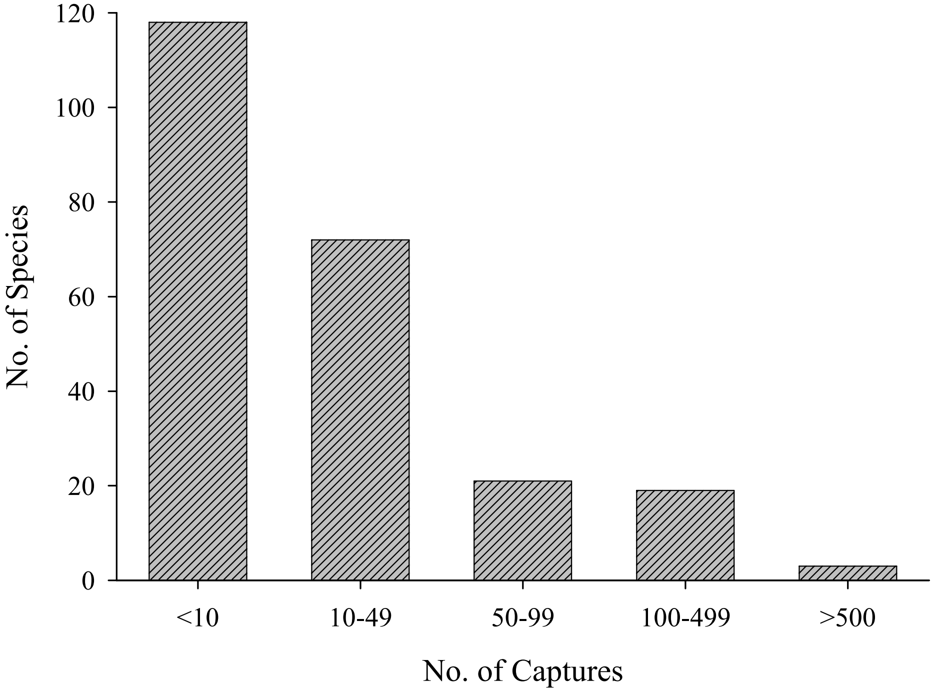

Figure 3.5. CCA ordination diagram with species (represented by pluses), sites (filled circles), and environmental variables highly correlated with the first two axes (arrows). Angles between arrows represent the degree of correlation among environmental variables, arrow length is proportional to the rate of change of the environmental variable in the direction the arrow points, and the location of sites and species relative to arrows indicate the environmental characteristics of sites and the habitat associations of species, respectively.

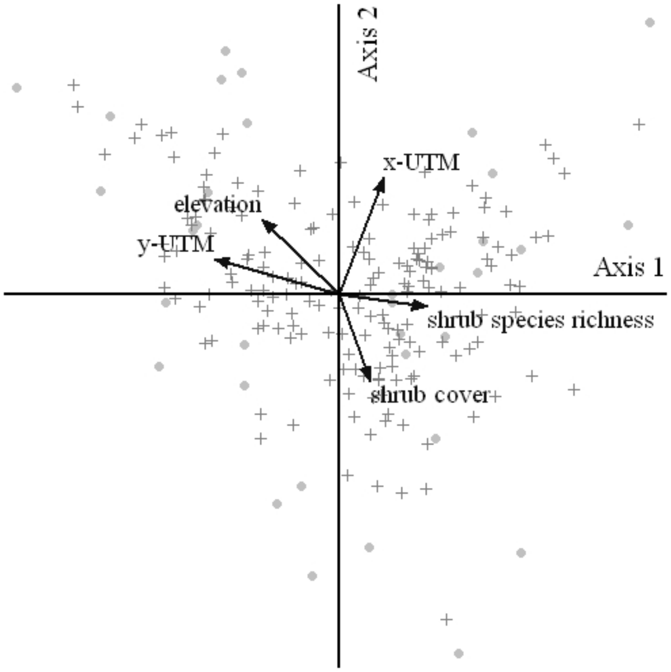

Figure 3.6. Number of captures of each species of macro-moth in conifer-dominated (gray bars) and deciduous-dominated (black bars) stream reaches throughout the Oregon Coast Range, summers 2002-2004. Species are ordered relative to number of captures in deciduous-dominated stream reaches.

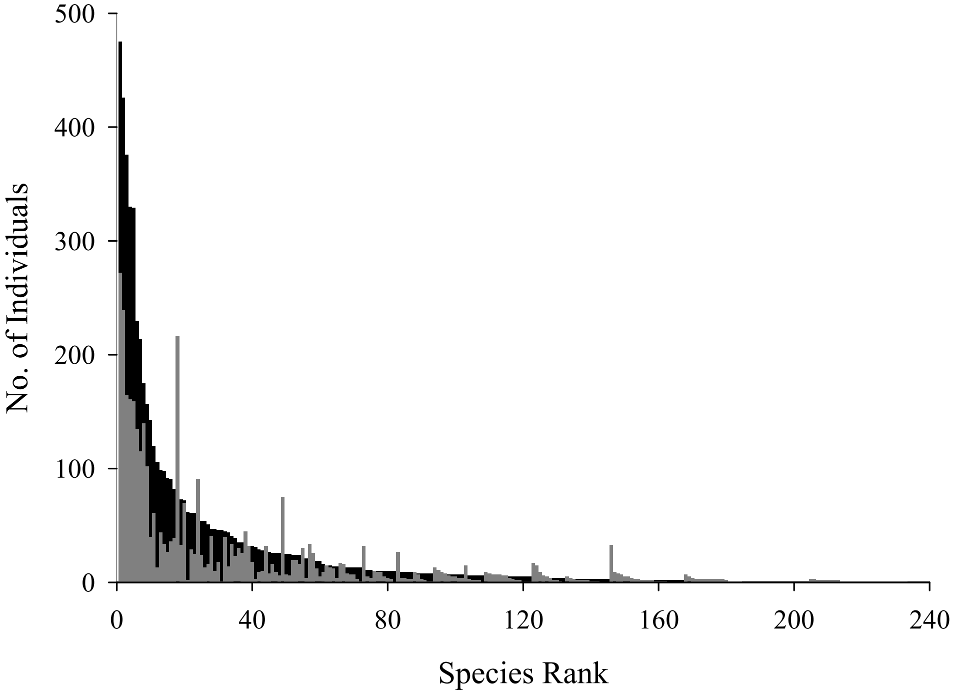

Figure 3.7. Individual-based (solid lines) and sample-based (dashed lines) rarefaction curves of the macro-moth communities of conifer-dominated (gray lines) and deciduous-dominated (black lines) stream reaches of the Oregon Coast Range. Curves are scaled to the number of individuals to facilitate comparisons of the number of species between stream reaches with different canopy types.

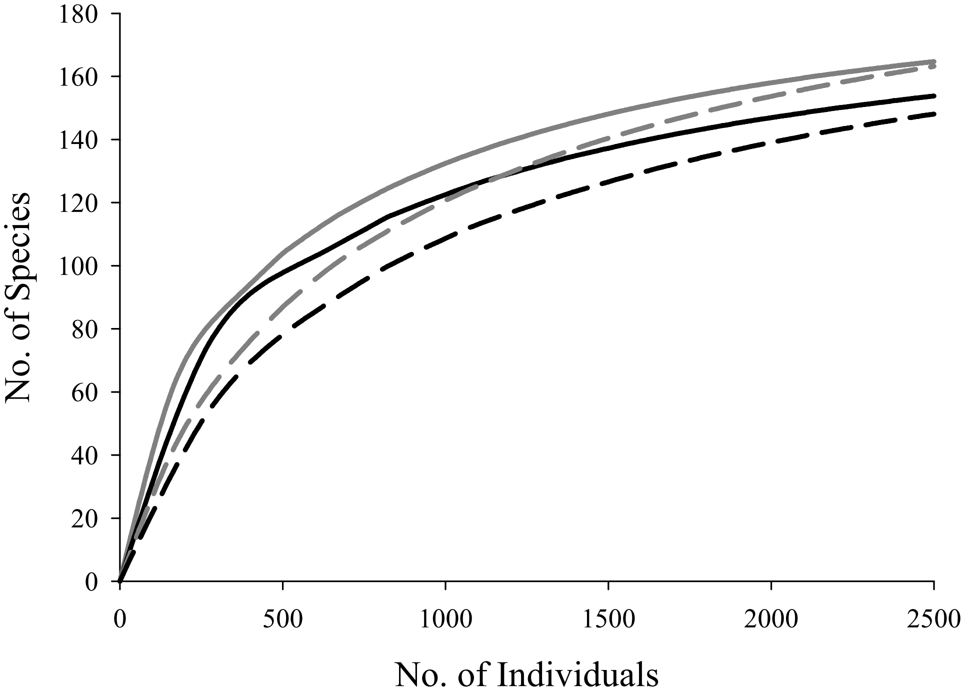

Table 3.1. Intraset correlations between explanatory variables and ordination axes resulting from the canonical correspondence analysis, describing the relative magnitude and importance of each environmental variable in structuring the macro-moth species composition ordination.

	Correlations		
Explanatory variable	Axis 1	Axis 2	Axis 3
y-UTM	-0.823	0.234	-0.231
x-UTM	0.291	0.771	-0.289
elevation	-0.512	0.493	0.437
shrub cover	0.206	-0.575	0.255
shrub species richness	0.577	-0.079	0.404
understory cover	-0.461	0.296	-0.064
understory species richness	-0.012	0.431	0.242
canopy cover	-0.232	0.171	-0.566
canopy species richness	-0.040	0.226	-0.204
canopy composition	-0.190	-0.224	-0.708

CHAPTER 4 – BAT PREY SELECTION IN THE OREGON COAST RANGE

Abstract

We examined relationships between bat activity and food resource abundance. We hypothesized that as a consequence of the high mobility and high energetic demands of insectivorous bats, a high correlation would exist between the distribution of their activity and the abundance of potential insect prey. We captured and obtained guano from 337 free-flying individuals throughout the Oregon Coast Range over the course of three summers, and identified prey remains within guano samples to determine which insect taxa bats consumed. The two orders of insects most frequently consumed by bats were Lepidoptera and Diptera. Three species of bat fed predominantly on small insects likely of aquatic origin (Diptera and Trichoptera). The seven remaining species of bat fed predominantly on larger, terrestrial invertebrates (Lepidoptera, Coleoptera, Hemiptera, Araneae). We also monitored bat and insect activity simultaneously in 26 stream reaches throughout the region to determine if there was an association between bat activity and abundance of potential insect prey. We used both model selection and multivariate analyses to determine whether variability in activity of bats was more strongly associated with number of captures of those orders of insects comprising the majority of their diet or to number of captures of insects within particular size classes, or independent of both. Associations were strongest between activity of small *Myotis* species and abundance of insects 0-2 mm in body length,

suggesting that local abundance of small insects in riparian areas influences the location of foraging activity of these bats.

Introduction

Distribution and abundance of prey strongly influence distributions of predators (Kareiva and Odell 1987, Lima 2002, Sabo and Power 2002, Harwood et al. 2003). Variability in densities of prey in conjunction with the energetic expense of locating and capturing prey often results in congregations of predators in areas with high concentrations of prey (Curio 1976, Fauchald et al. 2000, Houghton et al. 2006). Highly mobile predators are able to track fluctuations in prey densities over space and time, and tend to spend longer periods of time in areas where food was recently consumed (Kareiva and Odell 1987, Bernstein et al. 1991).

Mobility is a key characteristic underlying ability to track variation in the distribution of food resources (Kotliar and Wiens 1990, Bernstein et al. 1991). Consequently, volant predators ought to be able to track changes in distributions of prey closely. Accordingly, bat activity is often correlated with insect abundance (Anthony et al. 1981, Avery 1985, Racey and Swift 1985, de Jong and Ahlen 1991, O'Donnell 2000, Kusch et al. 2004). However, the strength of this association varies, and in some cases, this pattern does not exist or occurs under a limited range of conditions (Lunde and Harestad 1986, Ekman and de Jong 1996, Rautenbach et al. 1996, Grindal and Brigham 1999, Verboom and Spoelstra 1999, Meyer et al. 2004). Variation in findings may be due in part to the metric commonly used to describe insect abundance (total number of insects captured). Only a subset of insects are potential prey for a given species of bat, so total number of insects captured may be too coarse a metric to effectively reflect food resources available to particular species of bats, resulting in weak associations.

Knowledge regarding relationships between insect characteristics and foraging ecology of bats is needed to better understand the associations between bat activity and insect abundance. Most studies of bat prey selection focus on taxa of insects consumed. However, size may be a more important determinant of bat prey selection (Anthony and Kunz 1977, Belwood and Fullard 1984, Barclay 1985, Aldridge and Rautenbach 1987). Determining the relative importance of insect size and taxon in bat prey selection is difficult because insect size and taxon are generally partially confounded. We know of no study that has formally compared the strength of the associations of bat activity with prey taxon and prey size under field conditions. Our specific objectives were to determine (1) the taxonomic composition of the diet of bats in the Oregon Coast Range, and (2) relative strength of association of bat activity with abundance of insects of commonly consumed taxa or abundance of insects of particular size classes.

Methods

Study Area

We conducted our study throughout the Oregon Coast Range, a region extending approximately 300 km from north to south. The terrain is steep and rugged, with a dense network of streams throughout. Elevation ranges from sea level to 1250 m. The area is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1973). Dominant riparian vegetation includes Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), western redcedar (*Thuja plicata*), vine maple (*Acer circinatum*), hazelnut (*Corylus cornuta*), salmonberry (*Rubus spectabilis*), and swordfern (*Polystichum munitum*).

Bat Diets

Field and Laboratory Procedures

In 2002, we used mist nets to capture bats in second and third-order stream reaches (as determined by 1:24,000 scale topographic quadrangle maps). Due to extremely low capture success ($\bar{x} = 1.1 \pm 0.23$ bats captured per 10 hour night of mist netting effort). In 2003 and 2004 we used H-nets (Waldien and Hayes 1999) and hoop nets to actively net bats while they visited the undersides of bridges to night-roost.

After capture, we held bats in cloth bags for ~1 hr, then recorded data on sex, age, and species before each bat was released. We took biopsy samples from each *Myotis yumanensis* and *M. lucifugus* to obtain genetic confirmation of species identification (Scott 2005). After bats were released, we stored accumulated guano from each bag in a labeled plastic vial and placed these in the freezer within 10 hours of collection.

In the laboratory, we teased apart guano in a Petri dish containing 95% ethyl alcohol. All pellets collected from an individual bat were treated as one sample. We identified food items to order using a dissecting microscope, comparing invertebrate fragments in guano pellets to reference mounts made of invertebrates collected nearby. All samples were processed by the author.

Percent Volume and Frequency of Occurrence

We visually estimated percentage of each sample composed of each invertebrate order (percent volume), and then calculated the mean percent volume for each order for all individuals of a given species of bat ([sum of individual volumes of invertebrate order / total volume of all samples] x 100). We also calculated the frequency of occurrence of each order for each species of bat ([number of samples in which a particular invertebrate order occurred / total number of samples for that species of bat] x 100).

Bat Activity and Insect Captures

Field and Laboratory Procedures

We monitored bat and insect activity in 26 randomly selected stream reaches. To reduce logistical constraints imposed by sampling throughout the Oregon Coast Range each summer, we divided the area into subregions and conducted fieldwork at 12 stream reaches in the southern subregion in 2003, and 12 stream reaches in the northern subregion in 2004. We monitored two additional stream reaches both years to assess inter-annual variation in insect and bat activity. Each night we measured bat and insect activity in one stream reach dominated by deciduous trees and one stream reach dominated by coniferous trees. Each stream reach was sampled from sunset until sunrise once during every 2-week period between mid-June and early September, for a total of five all-night visits to each stream reach each summer.

We captured nocturnal flying insects using black light traps (Bioquip Inc., Rancho Dominguez, CA) with 12-watt fluorescent black light tubes, powered with 12-volt batteries. Traps were placed 0.5 m off the ground within 2 m of the stream edge, in a location selected to maximize visibility from all directions. Previous studies in Pacific Northwest forests have demonstrated either a lack of vertical stratification of insects (Jackson and Resh 1989, Schowalter and Ganio 1998) or greatest abundance of herbivorous insects in the understory (Shaw et al., *in press*), reducing the need to monitor insects at multiple heights above the ground. A “no-pest strip” (Hotshot, Newport Beach, CA) was placed in the bottom of each trap as a killing agent. We began trapping within 30 min of sunset and ceased 0-30 min after sunrise. In the morning, insects were removed from traps, placed in labeled plastic boxes, and stored at -10°C until analysis. In the laboratory, we sorted all insects to order and measured insect body lengths from the anterior of the head to the posterior of the last abdominal segment (antennae and cerci excluded) to the nearest mm using a dissecting microscope. We used the number of individuals captured per stream reach per night as an index of abundance of insects at that stream reach.

We assessed bat activity by recording echolocation calls of free-flying bats. We used calibrated (Larson and Hayes 2000), automated Anabat II detectors with Anabat zero crossings analysis interface modules (Titley Inc., Balina, Australia) to record echolocation calls. We activated detectors within 30 min of sunset and deactivated them 0-30 min after sunrise. The position of echolocation detectors at each stream reach was constant among visits. We placed echolocation detectors within 2 m of the stream edge, at an elevation 0.5 m above the surface of the stream, at a 30° angle oriented with the microphone aligned parallel to the main axis of the stream and pointing upstream. We believe this orientation maximized the period of time within which bats flying along the stream corridor were within the cone of detection of the detector. Because the attraction of insects to lights may increase bat activity (Fenton and Morris 1976, Bell 1980, Hickey and Fenton 1990, Adams et al. 2005), we placed detectors and black light traps within ca. 2 m of each other, so that all sites were similarly influenced by this factor.

We used recordings to obtain an index of bat activity rather than to quantify abundance of bats (Hayes 2000). We used Analook (v4.9j) to view recorded bat echolocation call sequences. We quantified bat activity by determining the number of minutes per stream reach per night during which echolocation calls were recorded, using the criteria outlined in Appendix F. We could not categorize all echolocation calls to species due to similarities in calls among species with similar ecomorphology. Instead, we partitioned calls into phonic groups consisting of species with similar call characteristics. Echolocation calls were categorized into one of six groups: *M. lucifugus*/*M. volans* (MYLU/MYVO); *M. californicus*/*M. yumanensis* (MYCA/MYYU); *M. evotis*/*M. thysanodes* (MYEV/MYTH); *Corynorhinus townsendii*

(COTO)*; Eptesicus fuscus/Lasionycteris noctivagans*/*Lasiurus cinereus* (EPFU/LANO/LACI); or unidentifiable (Appendix F).

Data Analysis

To determine the potential effect of year in our analyses, we used *t*-tests to compare the mean number of insects captured per night between years for each stream reach measured both years of the study. We found no statistically significant inter-annual differences in the number of captures of each of the six most abundant orders of insects ($p>0.35$). We used similar analyses to compare the mean number of minutes during which bat echolocation calls occurred per night among years for each site. We found no statistically significant inter-annual differences in overall bat activity in stream reaches repeatedly measured each year ($p>0.30$). Hence, we assumed the effect of year was negligible and pooled data across years for all subsequent analyses.

Model Selection

We developed multiple working hypotheses to reflect the two factors we hypothesized to be most likely to govern bat prey selection (insect taxon and insect size class). We hypothesized that if bats select prey items primarily on the basis of taxon, then bats of a given species should congregate in areas with high abundances of taxa of insects most commonly consumed. This hypothesis leads to the prediction that bat activity within a stream reach will increase with abundance of insects of preferred taxa. Alternatively, we hypothesized that if bats select prey items primarily on the basis of insect body size, then bats should congregate in areas with high abundances of insects within their preferred prey size class. This hypothesis leads to the prediction that bat activity within a stream reach will increase with abundance of insects in the preferred insect prey size class.

We developed regression models reflecting variations of these hypotheses (Table 4.1). For each phonic group, we assessed models reflecting the number of captures of each of the three insect orders consumed in greatest quantities by these bats (as determined via the guano analyses), the number of captures of small (0-2 mm), medium (3-6 mm), or large (≥7 mm) insects, and the number of captures of all insects. We also considered the relative likelihood of the null model (intercept only model) to evaluate the usefulness of the explanatory variables in predicting bat activity. The only taxon-specific model we included for *C. townsendii* reflected number of captures of Lepidoptera, due to the high degree of dietary specialization on Lepidoptera by this species.

We used the number of minutes which contained echolocation calls per stream reach per night, averaged over five sampling nights, as an index of bat activity. We used the number of individual insects captured per stream reach per night, averaged over five sampling nights, as an index of insect abundance. We natural log transformed explanatory and response variables to better meet assumptions of statistical models, and checked the data for severe outliers and evidence of nonlinear relationships before analysis. We did not include quadratic equations because (1) there was no evidence of such trends when we checked graphs of residuals, (2) there was no biological basis for suspecting such relationships, and (3) the number of candidate models would be large relative to our sample sizes if we included models with and without quadratic terms.

We used a model selection approach to rank models according to their likelihood, given the data (Burnham and Anderson 2002). We found no evidence of overdispersion, and therefore used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank models. We placed all models in scaled rank order according to the difference between the AIC_c score of each model and the lowest AIC_c score of all models for that phonic group (ΔAIC_c), and considered all models with $\Delta AIC_c \leq 2.0$ to have substantial empirical support. We used Akaike weights, w_i, to evaluate the relative likelihood of each model, and evidence ratios (w_1/w_2), as the relative evidence in favor of one model over another. All analyses were conducted in SAS (v9.1) using PROC REG.

Multivariate Analyses

We used a multivariate approach to determine if the abundance of one or a few orders of insects was highly correlated with activity of phonic groups. Canonical Correlation Analysis (CANCORR) is an extension of multiple regression and correlation analysis that is commonly used in ecological studies to relate the abundance of multiple species of a particular taxon with multiple explanatory variables. CANCORR helps summarize redundancy among variables by describing the major ecological relationships between two sets of related variables (McGarigal et al. 2000), finding the linear combination of explanatory variables that produces the largest correlation with the second set of variables. Using CANCORR, moderate correlations among explanatory or response variables do not hamper analyses (Afifi et al. 2004). We also employed canonical redundancy analysis to determine the proportion of variation in the original bat activity data accounted for by the canonical variates derived from the insect data during the CANCORR.

The data for the CANCORR consisted of activity levels of the five bat phonic groups and number of captures of the six most commonly captured insect orders (Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera). We natural log transformed number of captures of insects and number of minutes of activity of bats to meet assumptions of normality and checked for severe outliers and evidence of nonlinearity. We examined pair-wise correlations among all explanatory and all response variables to identify potential sources of multicollinearity problems, and dropped Ephemeroptera from further analyses due to the high correlation with abundance of Diptera (r=0.756) (ter Braak 1995, McGarigal et al. 2000). Analyses were conducted in SAS (v9.1) using PROC CANCORR.

We repeated this analysis using insects categorized by body length. Comparisons of results of the canonical redundancy analyses were used to assess relative importance of size and taxa in explaining variability in bat activity.

Results

Bat Diets

We analyzed 337 guano samples from 10 species of bats (Tables 4.2 and 4.3). Fifteen invertebrate orders were identified in bat guano, with ten orders (Lepidoptera, Diptera, Coleoptera, Isoptera, Trichoptera, Araneae, Hemiptera, Neuroptera, Homoptera, and Hymenoptera) comprising the majority of the diets of bats. These ten orders occurred in >20% of samples of ≥2 species of bat, whereas the remaining orders (Orthoptera, Acari, Psocoptera, Plecoptera, and Ephemeroptera) were consumed less regularly. Lepidoptera and Diptera were the two most prevalent prey items in bat diets. Spiders and mites were the only non-insect and also the only non-volant taxa consumed.

Lepidoptera figured prominently in the diets of the majority of bat species. We found Lepidoptera in >75% of samples in each species and in all samples from 6 species (Table 4.3). *C. townsendii* and *M. volans* showed particularly strong affinities for Lepidoptera, with the former feeding nearly exclusively on this order. *M. evotis* and *M. thysanodes* consumed a varied diet that contained large proportions of Lepidoptera, Araneae, and Coleoptera. *E. fuscus* fed predominantly on Coleoptera, Lepidoptera, and Hemiptera. The three smallest species in the bat community, *M. lucifugus, M. yumanensis,* and *M. californicus*, fed appreciably more on invertebrates that likely had aquatic origins, Diptera and Trichoptera.

Bat Activity and Insect Captures

We captured a mean of 815 insects per stream reach per night using black light traps (SE = 116.5). The most commonly captured orders of insects were Diptera (74.5% of individuals), Trichoptera (12.2%), and Lepidoptera (11.9%; Table 4.4).

Insect body length ranged in size from 1 to 50 mm, with the distribution of body lengths skewed heavily toward smaller sizes ($\bar{x}$=3.8 mm, median=2 mm). Distributions of body lengths varied greatly among orders of insects (Fig. 4.1).

Bat activity was extremely variable among stream reaches and species. The number of minutes per night during which activity occurred within a single stream reach varied from a low of 3 to a high of 524. The majority of activity was from bats in the two phonic groups containing small *Myotis* species (MYCA/MYYU and MYLU/MYVO; Table 4.5).

Model Selection

The models with the lowest AIC_c score for the MYCA/MYYU and MYLU/MYVO phonic groups were number of captures of insects in the small size class (Table 4.6, Fig. 4.2, Appendix G). For the MYLU/MYVO phonic group, the weight of evidence in favor of the model with number of captures of small insects being best given the data and the models tested was 0.67, which was >3 times the weight of evidence in favor of the next highest ranked model and >11 times the weight of evidence in favor of any remaining model. The proportion of variance explained by the top ranked model was 0.47. For the MYCA/MYYU phonic group, the weight of evidence in favor of the model with number of captures of small insects being best given the data and the models tested was 0.58, 2.5 times the weight of evidence in support of the model with abundance of Diptera, >5 times the weight of evidence in support of the model with number of captures of all insects, and >14 times the weight of evidence in favor of any remaining model. The proportion of variance explained by the model with number of captures of small insects was 0.26 and by the model with number of captures of Diptera was 0.21.

For the remaining phonic groups (MYEV/MYTH, COTO and EPFU/LANO/LACI), the null model either had the lowest AIC_c score or had $\Delta AIC_c < 2$. This suggests that none of our explanatory variables were strongly related to activity of these bat species or that we had inadequate data to arrive at conclusive results.

Multivariate Relationships

In the CANCORR relating bat activity to number of captures of insects from different orders, the first canonical correlation was 0.84, suggesting a strong correlation between the first canonical variate derived for the number of captures of insects and the first canonical variate derived for bat activity. This high correlation indicates that stream reaches that had high scores on the first insect variate also had high scores on the first bat variate. Correlations for the second, third, fourth, and fifth canonical variates did not significantly differ from zero.

When variables are somewhat intercorrelated (as was the case with our data), examination of correlation coefficients between the original variables and the derived canonical variates is useful for quantifying the strength and direction of the association between the two sets (Afifi et al. 2004). These correlations suggested that activity of bats from the MYLU/MYVO phonic group were strongly related to the first canonical bat variate and number of captures of Diptera and Trichoptera were strongly related to the first canonical insect variate (Table 4.7), implying that the strongest correlation between activity of any phonic group and any insect order was the correlation between these groups. However, the variance in the bat data accounted for by the first bat canonical variate (16%) and the variance in the insect data accounted for by the first insect canonical variate (34%) was relatively low.

Canonical redundancy analysis provides a measure of the average proportion of variance in the original data that is accounted for by the derived canonical variates. The first canonical insect variate accounted for only 11% of the variance in the original bat data, suggesting that the linear combination of explanatory variables with the greatest correlation with bat activity was not very effective at explaining variability in bat activity among stream reaches.

When we repeated the analysis using abundance of insects categorized by size class rather than taxa, the first canonical correlation was 0.81, suggesting a high degree of correlation between the first canonical variate derived for the insect abundances and the first canonical variate derived for the bat activity. The remaining canonical variates had correlations that were not significantly different from zero.

Correlations between the canonical variates and the original variables suggested that activity of bats in the MYLU/MYVO and MYCA/MYYU phonic groups were strongly related to the first canonical bat variate and number of captures of small insects were strongly related to the first canonical insect variate (Table 4.7). These results imply that activity of bats in these two phonic groups was highly correlated with number of captures of insects 0-2 mm in body length. In this analysis, amount of variance in bat activity accounted for by the first canonical bat variate was higher than in the previous approach (25% versus 16%), as was the amount of variance in the insect abundance data set accounted for by the first canonical insect variate (50% versus 34%).

Canonical redundancy analysis estimated that the first canonical insect variate accounted for 17% of the variance in the original bat data, suggesting it was more effective at explaining overall variability in bat activity then was the insect variate derived in the previous analysis when insects were categorized by taxon (which explained 11%).

Discussion

Bat Diets

Food habits of each species of bat in the Oregon Coast Range were similar to those reported for the same species in other geographic locations. For example, studies across North America have found that the diet of *E. fuscus* consists of a large proportion of Coleoptera, that *M. lucifugus* feeds on a heterogeneous diet that includes Diptera and Trichoptera, and that the diet of *C. townsendii, M. volans,* and *M. evotis* is predominantly Lepidoptera (Whitaker 1972, Black 1974, Belwood and Fenton 1976, Whitaker et al. 1977, 1981, Brigham and Saunders 1990, Barclay 1991, Brigham et al. 1992, Syme et al. 2001, Whitaker 2004). One difference between previous reports of bat diets and results from Oregon is the prominence of Lepidoptera in the diet of some species. *M. lucifugus* (Buchler 1976, Barclay 1991, Adams 1997, Syme et al. 2001) and

E. fuscus (Whitaker 1972, 1995, 2004, Brigham and Saunders 1990, Hamilton and Barclay 1998) rarely consume Lepidoptera elsewhere but do so in Oregon. The prevalence of Lepidoptera in diets in the Oregon Coast Range may be due to their preponderance; Lepidoptera ranked first in biomass and third in number of captures of all nocturnal flying insect orders captured via black light traps (Table 4.4). Another difference between the diets of bats in the Oregon Coast Range and those in other regions is the greater prevalence of spiders in the diets of nearly all bat species. Black light traps are not an effective means of collecting spiders, so we do not have information on their relative abundance. Irrespective of their abundance, it is surprising that spiders comprised a sizeable proportion of the diets of several bat species, including species considered to be aerial insectivores (Verts and Carraway 1998). As spiders are flightless, bats may be obtaining prey by gleaning. Many bat species that generally are categorized as either gleaners or aerial-hawkers may in fact employ both foraging strategies at different times, as circumstances demand (Fenton and Bell 1979, Fenton 1990, Faure and Barclay 1994). Alternatively, because previous studies in Oregon and Alaska have also reported higher consumption of spiders by bats in this region than is commonly reported for them elsewhere in North America (Whitaker et al. 1977, Whitaker and Lawhead 1992), spiders in this region may be more susceptible to predation by bats through means other than gleaning, such as while ballooning or while suspended in open areas (Best et al. 1997, Schulz 2000).

Discrepancies between the rank-order of prey items when measured as percent volume versus the rank order of prey items when measured as frequency of occurrence can be insightful. For example, Isoptera ranked fourth in percent volume across all bats collectively, but eighth in frequency of occurrence. This implies that Isoptera were not consumed by many individual bats, but those bats that did eat Isoptera consumed them in large volumes. The tendency of winged termites from all colonies in an area to leave nests simultaneously promotes outbreeding in termites (Weesner 1965), and also provides an opportunistic food resource for bats (Redford and Dorea 1984). Although bats may only encounter these aggregations on rare occasions, they appear to take advantage of profitable feeding opportunities during rare events (Gould 1978). For example, Isoptera consumption was evident in only 26 samples collected during 2003; 22 of these samples were collected over four consecutive nights in August, with average volume exceeding 50% per sample. When a prey type occurs in high abundance, the relative search costs and handling costs of feeding on that prey type are reduced, making it more profitable for predators to feed on many individuals of the abundant prey type (Westoby 1977, Fenton 1990).

Hemiptera, on the other hand, ranked seventh in percent volume across all bats collectively, but third in frequency of occurrence. This suggests that Hemiptera were consumed by more individual bats than were most orders of insects, but usually in small volumes. Hemiptera were not abundant among black light captures. Although we cannot rule out the possibility that black light traps did not effectively sample

Hemiptera, the high frequency of occurrence but low volume of occurrence suggests that bats may have an affinity for these insects, regularly consuming them when they are encountered. The high nitrogen content of Hemiptera relative to other invertebrates (Studier and Sevick 1992, Fagan et al. 2002) may make them a particularly valuable food resource.

Bat Activity and Insect Captures

Our hypothesis that high mobility and high energetic demands of bats would lead to high correlations between bat use of stream reaches and the abundance of potential invertebrate prey was only partially supported. Through two separate analyses we found that the strongest association between bat activity and number of captures of insects was that between the activity of small *Myotis* species and number of captures of small insects. Both analyses also suggested the lack of an association between number of captures of insects of any category investigated and activity of larger bat species as analyzed using phonic groups.

There are strong links between morphology, flight patterns, echolocation call structure, and feeding behavior of bats (Norberg and Rayner 1987, Barclay and Brigham 1991, Bogdanowicz et al. 1999, Schnitzler and Kalko 2001). Morphology influences flight capabilities, which in turn constrains the ecological roles bats can fill by limiting their ability to forage in certain habitats (Norberg and Rayner 1987). Similarly, body size influences the frequency of echolocation calls bats are able to produce, which in turn constrains both the size of prey bats can detect and the range over which they can detect them (Barclay and Brigham 1991, Bogdanowicz et al. 1999, Schnitzler and Kalko 2001, Jones and Rydell 2003). These eco-morphological relationships can explain many of the associations between bat and insect activity we observed.

Activity of the smallest species in the Oregon Coast Range bat community (*M. californicus, M. yumanensis,* and *M. lucifugus*) was most strongly associated with number of captures of insects in the small size class. Low wing loading, low aspect ratios, and rounded wing tips allow these species to perform more maneuverable flight patterns than other species (Norberg and Rayner 1987). This enables them to more effectively pursue small insects, which tend to be agile fliers (Nachtigall 1968, Dudley 2002). The high frequency echolocation calls of *M. californicus, M. yumanensis,* and *M. lucifugus* are also better suited for locating small targets at close range than for finding larger targets at greater distances (Schnitzler and Kalko 2001, Jones and Rydell 2003). Finally, the relatively small size of their heads and gapes sets an upper limit to the size of prey these bats can successfully capture (Fenton 1989). Thus, these bats possess a combination of traits that predisposes them to specialize on small prey. In our traps, 99% of the insects in the small size class (0-2 mm) were Diptera, so activity of these bat species was also highly correlated with number of captures of Diptera. The fact that insects in the small size class were nearly exclusively Diptera indicates that bats morphologically constrained to foraging on small insects have little choice but to feed on insects of this order. Unfortunately, this high correlation between number of captures of Diptera and number of captures of small insects (r = 0.968) hindered our ability to differentiate whether bats were selecting prey on the basis of size or taxon through the model selection approach.

Despite a high degree of similarity in echolocation call characteristics with *M. lucifugus*, the fourth bat species in the two phonic groups whose activity was highly correlated with number of captures of small insects, *M. volans*, differs from the other three both dietarily and morphologically. *M. volans* in our study region consumed predominantly Lepidoptera, which tend to be larger in size than Diptera (Fig. 4.1). *M. volans* has a larger body size and longer wings with more pointed tips than the other bats in these phonic groups, which hinders the foraging abilities of this species in "cluttered" habitats available to the other bats in these phonic groups (Norberg and Naynor 1987, Fenton 1990). We suspect that *M. volans* probably produced a small proportion of the calls we recorded for the MYLU/MYVO phonic group.

In contrast, *C. townsendii* has large wings suited for slow flight in habitats cluttered by obstacles (Norberg and Rayner 1987), and generally hunts prey by flying slowly in close proximity to vegetation (Kunz and Martin 1982, Fellers and Pierson 2002) using short-duration, low-intensity echolocation calls to locate insects at close range. This time-intensive foraging strategy likely results in the capture of fewer individual insects, necessitating the selection of larger prey items so that energetic demands are met (Curio 1976). Activity of *C. townsendii* was extremely low throughout our study area; no echolocation calls were recorded at most sites on most nights. For this reason, no models received substantially more support than the null.

M. evotis and *M. thysanodes* in the study region consumed a diverse diet, a large proportion of which was invertebrates from orders poorly represented in light trap samples, that we did not include in statistical analyses, such as Araneae and Homoptera. These bat species tend to forage within the canopy (Whitaker et al. 1977, Maser 1998), using a combination of aerial-hawking and substrate gleaning to obtain prey (Barclay 1991, Faure and Barclay 1994). Black light traps were not an effective means of sampling those insects in the canopy foliage gleaned by bats. This was likely the reason for the lack of association we found between activity levels of this phonic group and number of captures of insects included in our analyses.

The remaining phonic group contains species that each feed predominantly on different taxa. *E. fuscus* fed mostly on Coleoptera and Hemiptera, *L. noctivagans* on Lepidoptera and Diptera, and *L. cinereus* on Lepidoptera and Hemiptera. This disparity likely accounts for the lack of strong associations between the activity of this phonic group and number of captures of any insect taxon. This problem was compounded by the relative paucity of activity of these species. Associations may have been more likely to emerge if we were able to tease apart echolocation calls made by each of these three species.

The lack of association between number of captures of large insects and activity of *E. fuscus*, *L. noctivagans*, and *L. cinereus* was unexpected because the morphology and echolocation calls of these taxa should predispose them to specialize on larger prey items (Barclay 1985, Barclay and Brigham 1991, Jones and Rydell 2003). One potential explanation for the lack of association between activity of these species and number of captures of any of the insect categories we examined is that these species have a greater tendency than others in the Oregon bat community to fly above the forest canopy (Whitaker et al. 1977, 1981, Maser 1998), where they most likely feed on insects that were not effectively sampled by the black light traps we placed 0.5 m above the ground.

Alternatively, the fast flight speeds of *E. fuscus*, *L. noctivagans*, and *L. cinereus* may facilitate a high encounter rate with insects so that these bats are able to maintain energy balance in habitats with lower insect abundances than is possible for slower-flying bats with lower insect encounter rates (Aldridge and Rautenbach 1987). Furthermore, if these species select larger prey, the number of prey items required to meet energetic demands may be low enough that it is not profitable for these species to expend energy searching for areas with high prey concentrations, in contrast to those bat species that feed on smaller prey items which provide so little energy per unit that bats specializing on them must locate areas with high abundances of prey in order to meet energetic demands (Aldridge and Rautenbach 1987). Furthermore, the greater distances these larger species fly per night (Brigham 1991, Campbell et al. 1996, Mattson et al. 1996) may lead to less localization of foraging efforts than is typical of smaller, slower-flying species that use smaller nightly ranges (Brigham et al. 1997, Waldien et al. 2000, Weller and Zabel 2001). This would in turn lead to lesser correlations between activity of these large bats and local insect abundance than is typical of smaller bats.

One final explanation for the lack of association between number of captures of large insects and activity of *E. fuscus*, *L. noctivagans*, and *L. cinereus* is simply the paucity of data from these bats. The small number of calls detected from these species resulted in low power to detect patterns.

Results of the multivariate analyses corroborated patterns uncovered by univariate analyses, while also providing additional insight into the question of whether bats were selecting prey on the basis of size or taxon. In agreement with the model selection, the strongest correlation revealed by canonical correlation analysis was between number of captures of small insects and activity of bats in the MYLU/MYVO and MYCA/MYYU phonic groups. Results also revealed that the strongest correlation between activity of bats and number of captures of insect taxa was weaker than the strongest correlation between activity of bats and and number of captures of insects categorized by size class. This suggests that these bats were likely selecting foraging areas on the basis of abundance of small insects rather than abundance of insects of any particular order of insect.

In summary, we found only partial support for our hypothesis that high mobility and high energetic demands of bats would lead to high correlations between bat use of stream reaches and the abundance of potential invertebrate prey. The strongest association between bat activity and number of captures of insects was that between the activity of small *Myotis* species and number of captures of small insects, while no associations were found between number of captures of insects of any category investigated and activity of larger bat species as analyzed using phonic groups. Although we cannot rule out the possibility that the lack of associations between activity of the larger bat species and number of captures of insects was due to the low activity of these bats, we suggest that the distribution of smaller bats within riparian areas of the Oregon Coast Range is more closely linked to patterns of insect abundance than is that of larger bats.

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Figure 4.1. Percentage of individuals within each of three size classes for insects captured in black light traps in riparian areas of the Oregon Coast Range, summer 2003 and 2004.

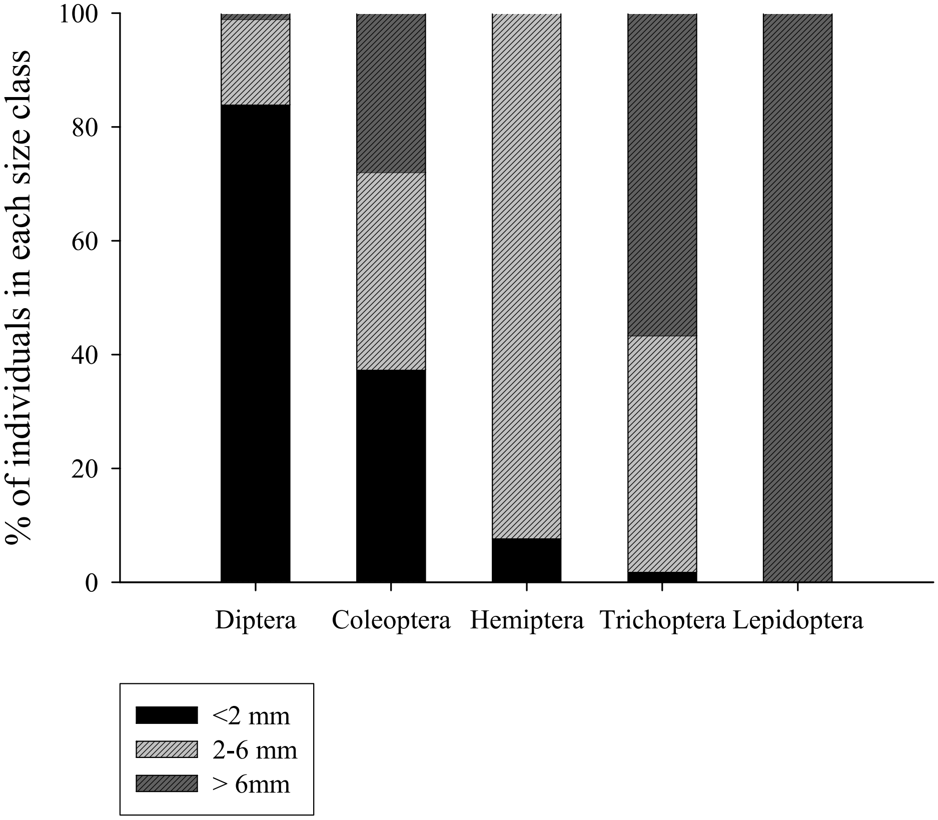

Figure 4.2. Relationships between bat activity and number of captures of insects for models that received substantial support in the model selection procedure ($\Delta AIC_c \leq 2.0$). X-axes portray mean number of insects captured per stream reach per night, ln transformed. Y-axes portray mean number of minutes during which bat activity was recorded per stream reach per night, ln transormed. A: Activity of MYLU/MYVO versus number of captures of small insects. B: Activity of MYCA/MYYU versus number of captures of small insects. C: Activity of MYCA/MYYU versus number of captures of Diptera.

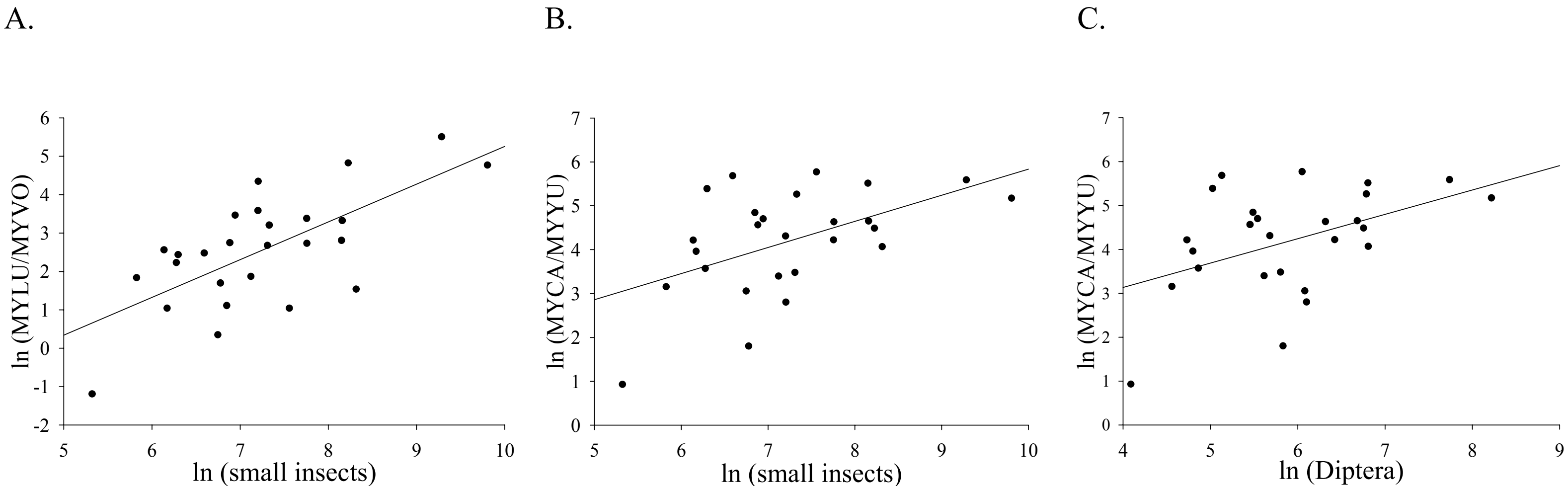

Table 4.1. Relationships between insect abundance and activity of bats predicted by hypotheses and the linear model associated with each.

Hypothesis	Predicted relationship	Model structure
Insect size	Positive effect of abundance of small insects	$Y = \beta_0 + \beta_1$(no. of captures of insects with body length 0-2 mm)
	Positive effect of abundance of medium insects	$Y = \beta_0 + \beta_1$(no. of captures of insects with body length 3-6 mm)
	Positive effect of abundance of large insects	$Y = \beta_0 + \beta_1$(no. of captures of insects with body length $\geq$7 mm)
Insect taxon	Positive effect of abundance of Coleoptera	$Y = \beta_0 + \beta_1$(no. of captures of Coleoptera)
	Positive effect of abundance of Diptera	$Y = \beta_0 + \beta_1$(no. of captures of Diptera)
	Positive effect of abundance of Hemiptera	$Y = \beta_0 + \beta_1$(no. of captures of Hemiptera)
	Positive effect of abundance of Lepidoptera	$Y = \beta_0 + \beta_1$(no. of captures of Lepidoptera)
	Positive effect of abundance of Trichoptera	$Y = \beta_0 + \beta_1$(no. of captures of Trichoptera)
All insects	Positive effect of abundance of all insects	$Y = \beta_0 + \beta_1$(no. of captures of all insects)

Table 4.2. Mean percent volume of food items identified in fecal pellets of each species of bat in the Oregon Coast Range, summers 2002-2004. LACI = *Lasionycteris noctivagans*; COTO = *Corynorhinus townsendii*; LANO = *Lasiurus cinereus*; EPFU = *Eptesicus fuscus*; MYCA = *Myotis californicus*; MYYU = *Myotis yumanensis*; MYLU = *Myotis lucifugus*; MYEV = *Myotis evotis*; MYTH = *Myotis thysanodes*; MYVO = *Myotis volans*. Sample sizes (number of samples per species) appear in parentheses.

	LACI (2)	COTO (4)	LANO (4)	EPFU (67)	MYCA (15)	MYYU (70)	MYLU (26)	MYEV (23)	MYTH (20)	MYVO (106)
Lepidoptera	40	95	24	29	30	11	15	35	21	72
Diptera	0	0	24	2	30	31	33	5	9	5
Coleoptera	5	1	8	37	8	1	5	12	14	1
Isoptera	3	0	1	9	5	12	5	5	1	10
Trichoptera	3	0	10	3	7	22	25	3	2	0
Araneae	3	4	0	0	2	10	6	20	24	6
Hemiptera	18	0	16	13	5	6	4	14	5	3
Neuroptera	3	0	14	4	7	2	4	3	2	1
Homoptera	25	0	0	1	1	2	2	0	19	1
Hymenoptera	3	0	4	2	5	1	1	1	1	0
Orthoptera	0	0	0	0	0	0	0	1	4	0
Acari	0	0	0	0	0	1	1	0	0	0
Psocoptera	0	0	0	0	1	0	0	0	0	0
Plecoptera	0	0	0	0	0	<1	<1	0	0	0
Ephemeroptera	0	0	0	0	0	<1	0	0	0	0
Unknown	0	0	0	0	0	<1	0	0	0	0

Table 4.3. Frequency of occurrence of food items identified in fecal pellets of bats in the Oregon Coast Range, summers 2002-2004. LACI = *Lasionycteris noctivagans*; COTO = *Corynorhinus townsendii*; LANO = *Lasiurus cinereus*; EPFU = *Eptesicus fuscus*; MYCA = *Myotis californicus*; MYYU = *Myotis yumanensis*; MYLU = *Myotis lucifugus*; MYEV = *Myotis evotis*; MYTH = *Myotis thysanodes*; MYVO = *Myotis volans*. Sample sizes (number of samples per species) appear in parentheses.

	LACI (2)	COTO (4)	LANO (4)	EPFU (67)	MYCA (15)	MYYU (70)	MYLU (26)	MYEV (23)	MYTH (20)	MYVO (106)
Lepidoptera	100	100	100	97	100	83	77	100	90	100
Diptera	0	0	100	42	100	94	96	61	65	37
Hemiptera	100	0	100	79	47	31	27	57	40	33
Araneae	50	75	0	3	40	59	50	91	90	42
Trichoptera	50	0	100	28	67	90	96	35	15	3
Coleoptera	100	25	100	91	53	10	23	78	75	10
Neuroptera	50	0	100	57	73	17	38	35	25	14
Isoptera	50	0	25	28	7	26	15	13	10	19
Hymenoptera	50	0	50	22	40	16	15	9	15	5
Homoptera	50	0	0	7	7	9	12	4	40	5
Acari	0	0	0	3	0	17	12	0	0	0
Orthoptera	0	0	0	0	0	0	0	17	30	0
Psocoptera	0	0	0	0	7	3	0	4	0	0
Plecoptera	0	0	0	0	0	1	4	0	0	0
Ephemeroptera	0	0	0	0	0	1	0	0	0	0
Unknown	0	0	0	0	0	1	0	0	0	0

Table 4.4. Number of individuals and biomass per stream reach per night of common orders of nocturnal flying insects captured in black light traps in the Oregon Coast Range, summers 2003-2004.

	No. of individuals			Biomass (mg)		
Order	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Coleoptera	5.4	0.66	0 - 43	56.2	12.55	0 - 1216.1
Diptera	627.1	115.66	7 - 9969	191.6	20.25	5.7 - 1239.0
Ephemeroptera	29.6	6.51	0 - 437	12.5	2.68	0 - 203.3
Hemiptera	0.2	0.05	0 - 3	0.1	0.03	0 - 1.5
Homoptera	3.3	0.49	0 - 29	0.8	0.27	0 - 6.6
Hymenoptera	5.1	0.53	0 - 40	6.1	0.92	0 - 60.6
Lepidoptera	68.1	6.66	1 - 420	1885.2	177.68	11.66 - 9669.1
Neuroptera	0.1	0.04	0 - 3	5.2	2.21	0 - 138.7
Plecoptera	3.8	1.24	0 - 135	25.1	7.88	0 - 869.1
Trichoptera	79.9	8.92	1 - 605	148.4	17.26	2.3 - 1064.8

Table 4.5. Number of minutes during which activity occurred per stream reach per night for bats in riparian areas of the Oregon Coast Range, summer 2003 and 2004.

Phonic group	$\bar{x}$	SE	Range
MYLU/MYVO	32	6.1	0 - 470
MYCA/MYYU	111	9.8	0 - 411
MYEV/MYTH	2	0.3	0 - 21
COTO	0.3	0.1	0 - 6
EPFU/LANO/LACI	0.9	0.2	0 - 18
all bats	169	11.4	3 - 524

Table 4.6. Candidate models relating bat activity to number of captures of insects of different orders and size classes in riparian areas of the Oregon Coast Range, summer 2003 and 2004. Only models that received substantial empirical support ($\Delta AIC_c \leq 2.0$) are listed. For each phonic group, models are ranked according to Akaike's Information Criteria adjusted for small sample sizes (AIC_c) and Akaike weights(w_i).

Phonic group	Explanatory variable in model	ΔAIC_c	w_i	Proportion of variance explained
MYLU/MYVO	number of small insects	0	0.67	0.47
MYCA/MYYU	number of small insects	0	0.58	0.26
	number of Diptera	1.9	0.23	0.21
MYEV/MYTH	null model	0	0.30	-
	number of Coleoptera	1.2	0.16	0.05
COTO	number of medium insects	0	0.39	0.15
	number of large insects	1.5	0.19	0.10
	null model	1.7	0.17	-
EPFU/LANO/LACI	number of Hemiptera	0	0.27	0.10
	null model	0	0.27	-

Table 4.7. Standardized correlation coefficients between original variables and the derived canonical variates resulting from the canonical correlation analysis. The original variables in the first analysis were number of minutes during which activity of bat phonic groups occurred and number of captures of insects categorized by order, and for the second analysis were number of minutes during which activity of bat phonic groups occurred and number of captures of insects categorized by size class. Correlation coefficients show the strength of relationships between the original bat variables and the derived bat variates, and between the original insect variables and the derived insect variates.

	Correlation Coefficient	
Original Variables	1st analysis	2nd analysis
Bat data set		
MYLU/MYVO	0.516	0.694
MYCA/MYYU	0.197	0.552
MYEV/MYTH	-0.150	-0.091
COTO	-0.420	-0.152
EPFU/LANO/LACI	-0.209	0.085
Insect data set		
Coleoptera	0.169	-
Diptera	0.650	-
Hymenoptera	0.396	-
Lepidoptera	-0.050	-
Trichoptera	0.766	-
small insects	-	0.794
medium insects	-	0.399
large insects	-	0.438

CHAPTER 5 – INFLUENCE OF VEGETATION ON USE OF RIPARIAN AREAS BY BATS AT MULTIPLE SPATIAL SCALES

Abstract

Research on habitat use by bats typically occurs at a single, small spatial scale, despite recent work demonstrating the importance of considering multiple spatial scales when investigating vertebrate habitat selection. We measured bat use of 118 stream reaches located throughout the Oregon Coast Range and measured vegetation characteristics at three spatial scales surrounding each of these locations. We used an information-theoretic approach to determine vegetation characteristics most closely related to bat activity, and a multilevel modeling approach to determine the amount of variation in bat activity occurring at different spatial scales. Vegetation characteristics measured at the smallest spatial scale explained more variation in bat activity than did vegetation characteristics at larger spatial scales, suggesting that small-scale forest management activities that alter cover of shrubs or canopy trees within riparian areas have the capacity to influence bat foraging habitat selection. The influence of vegetation on bat activity varied by bat species, and apparently operated more strongly through constraints imposed by vegetation architecture on bat foraging abilities than through regulation of the distribution of insect prey abundance. Given the differences in foraging constraints among species, maintaining heterogeneity in riparian vegetation conditions may be a useful tactic for providing foraging habitat for all species. We therefore caution against the implementation of uniform riparian vegetation management prescriptions across large geographical areas.

Introduction

Species respond to ecological processes that operate concurrently at multiple spatial scales (Wiens 1989). When examining the response of an organism to environmental heterogeneity, consideration should be given to the temporal scale appropriate to the ecological process of interest and the spatial scale within which the organism of interest operates during that time period (Addicott et al. 1987). Because most ecological phenomena are affected by processes occurring at multiple spatial scales, investigations of ecological processes are most illuminating when they encompass several spatial scales (Levin 1992).

Animals may make habitat selection decisions in a hierarchical fashion, considering different spatial scales at each stage (Johnson 1980, Orians and Wittenberger 1991). The relevance of multiple spatial scales has been demonstrated in habitat selection studies of a variety of vertebrate taxa, including mammals (Fisher et al. 2005, Bowyer and Kie 2006), birds (Wiens et al. 1987, Lawler and Edwards 2006), amphibians (Russell et al. 2005, Stoddard and Hayes 2005), and fish (Torgersen and Close 2004, Eikaas et al. 2005). Despite the evidence that habitat selection occurs at multiple scales, research on bat foraging activity has typically focused on a single, fine spatial scale, although this trend appears to be changing (Zimmerman and Glanz 2000, Erickson and West 2003, Loeb and O'Keefe 2006, Yates and Muzika 2006). If bats respond to multiple spatial scales when selecting habitat, use of a multi-scale approach to investigate foraging activity by bats could be more informative than the single-scale approach typically employed.

We hypothesized that vegetation was most likely to influence bats at three spatial scales: the watershed, nightly activity area, and stream reach. We reasoned that vegetation composition at the scale of the watershed could influence selection of nightly activity areas, that vegetation composition at the scale of the nightly activity area could influence selection of stream reaches, and that vegetation cover, composition, or structure at the stream reach scale could influence habitat selection at this scale. More specifically, we hypothesized that vegetation at the stream-reach scale could influence bat foraging activity through one of two pathways: (1) by determining the distribution of insect prey, or (2) by imposing structural restrictions on potential flight paths of bats, limiting their ability to acquire prey. We anticipated nutritional linkages between vegetation and bats because all ten species of bat occurring in western Oregon are insectivorous (Whitaker et al. 1977, 1981), and the majority of the insects these bats consume are phytophagous during some or all portions of their life cycle (Strong et al.1984). We reasoned that most potential prey items for bats would be located within close proximity to their host plants, due to the food specificity and the relatively small scale of movements characteristic of many of these organisms (Smith and Remington 1996). In addition, we reasoned that bat activity would be focused in locations where foraging opportunities were most profitable, as predicted by optimal foraging theory (Charnov 1976, McNair 1982), due to the high mobility of bats and the high energetic demands necessitated by their small size and energetically demanding mode of locomotion (Speakman and Thomas 2003). Thus, vegetation bordering stream reaches could influence bat activity indirectly through regulation of the distribution of insect prey. On the other hand, vegetation bordering stream reaches could influence bat activity directly by physically obstructing flight space. Previous studies have shown that vegetation architecture imposes structural restrictions on potential flight paths used by bats, limiting the ability of certain species to forage in certain habitats (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Crome and Richards 1988, Adams 1996, Bradshaw 1996, Grindal 1996, Grindal and Brigham 1998).

Differences in morphology and echolocation calls among species are likely to result in species-specific responses to vegetation. Morphology, flight patterns, echolocation call structure, and feeding behavior of bats are strongly linked (Norberg and Rayner 1987, Barclay and Brigham 1991, Bogdanowicz et al. 1999, Schnitzler and Kalko 2001). Morphology indirectly constrains the ecological roles bats can fill by influencing flight capabilities, which in turn restricts the ability of bats to forage in certain habitats (Norberg and Rayner 1987). Similarly, body size indirectly constrains both the size of prey bats can detect and the range over which they can detect them by limiting the frequency of echolocation calls bats are capable of producing (Barclay and Brigham 1994, Bogdanowicz et al. 1999, Schnitzler and Kalko 2001, Jones and Rydell 2003). These ecomorphological relationships are likely to lead to differences in microhabitat use among species.

The primary goal of this study was to determine which relationships between vegetation and bats were strongest. This information will enable land managers planning vegetation manipulations to better predict the influence of their actions on bats. Our objectives were to determine which vegetation characteristics were most closely related to bat activity at each of three spatial scales, whether the effect of vegetation characteristics at one spatial scale on bat activity influenced the effect of vegetation characteristics on bat activity at other spatial scales, which of the three spatial scales explained the greatest amount of variability in bat activity, and whether these patterns varied among species.

Theoretical Framework

We proposed several competing mechanistic hypotheses to explain underlying associations between vegetation and bats. We formulated candidate models to reflect each of these hypotheses and used an information-theoretic approach to rank them according to the weight of evidence for each.

Small Spatial Scale

The high degree of host specificity of many phytophagous insect species (Smith and Remington 1996, Robinson et al. 2000) may result in a strong coupling between vegetative and insect species richness (Murdoch et al. 1972, Panzer and Schwartz 1998, Knops et al. 1999). Increased prey species richness can in turn confer benefits to predators, such as increased food resource reliability and opportunities to obtain a diversity of nutrients (Petchey 2000). Thus, the **resource diversity hypothesis** predicts that bat activity within a stream reach will increase as the vegetative species richness bordering that stream reach increases.

By limiting availability of food (Price 1992) and oviposition sites (Dempster 1983), plants may determine carrying capacity of phytophagous insects. Accordingly, increased foliage volume may increase abundance or biomass of insects. Thus, the **resource abundance hypothesis** predicts that bat activity within a stream reach will increase as the amount of foliage bordering that stream reach increases.

Deciduous foliage is generally considered a higher quality food resource for phytophagous insects than is coniferous vegetation, due to higher concentrations of nutrients and lower concentrations of secondary defense compounds (Mattson and Scriber 1987, Ohgushi 1992). In comparison with coniferous foliage, deciduous foliage supports a greater abundance and diversity of certain insects in terrestrial (Holloway and Hebert 1979, Allen et al. 2003) and aquatic (Anderson and Cummins 1979, Piccolo and Wipfli 2002) environments. Thus, the **resource quality hypothesis** predicts that bat activity within a stream reach will increase as the amount of deciduous foliage bordering that stream reach increases.

Interspecific differences in wing morphology and body size among bats result in differences in flight abilities and consequently foraging behavior among species (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Crome and Richards 1988, Adams 1996, Bradshaw 1996, Grindal 1996, Grindal and Brigham 1998). Smaller, more agile, slow-flying species with soft echolocation calls are capable of intricate flight patterns and capturing prey at close range, and are therefore equally well suited to forage in cluttered or open habitat. Larger, less maneuverable, faster-flying species with loud echolocation calls are able to detect insects at long range in open habitats but are unable to make quick changes in direction while flying, so these bats are better suited for foraging in relatively open areas. Sensitivity to habitat structural complexity for these larger species should therefore lead to an inverse relationship between their activity and vegetative clutter. Thus, the **flight space hypothesis** predicts that bat activity within a stream reach will decrease as the amount of open airspace over that stream reach decreases.

Several species of bats forage close to the surface of water (Whitaker et al. 1977, Maser 1998). Vegetation that obstructs this airspace hinders the ability of these bats to forage effectively. Thus, the **stream surface obstruction hypothesis** predicts that bat activity within a stream reach will decrease as the obstruction of airspace at the surface of the water increases.

Intermediate Spatial Scale

If habitat selection occurs at multiple spatial scales, then vegetation composition of the landscape in which a stream reach is embedded may influence likelihood of use (Russell et al. 2005, Stoddard and Hayes 2005). Deciduous foliage provides higher quality food than coniferous foliage for many phytophagous insects, and abundance and diversity of insects tend to be greater near deciduous as compared to coniferous foliage. If bats select habitat at the scale of their nightly activity area, then vegetation composition within the landscape surrounding a particular stream reach may influence relative use of particular stream reaches. Thus, the **nightly activity vegetation**

composition hypothesis predicts that bat activity within a stream reach will increase as the amount of deciduous vegetation in the nightly activity area surrounding that stream reach increases.

Optimal foraging theory predicts that average residence time within each patch increases with cost of travel between patches of foraging habitat (Stephens and Krebs 1986). This implies that the amount of time animals spend in a patch increases with rarity of patches of foraging habitat across the landscape (McNair 1982). If coniferous and deciduous vegetation each offer unique prey items important in the diets of bats, the rarity of conifer- or deciduous-dominated reaches relative to that in the nightly activity area of a bat may influence the relative use of each. Thus, the **nightly activity vegetation rarity hypothesis** predicts that bat activity within a stream reach will increase with the relative rarity of the vegetation type in the nightly activity area surrounding that stream reach.

Large Spatial Scale

This hypothesis is a variant of the nightly activity vegetation composition hypothesis, but the relationship is manifested at a larger spatial scale. If bats make habitat-selection decisions at the scale of the watershed, then vegetation composition of the entire watershed may influence decisions regarding habitat use at the nightly-activity-area or stream-reach scales. Thus, the **watershed vegetation composition hypothesis** proposes that vegetation composition of the entire watershed influences habitat use decisions made by bats at smaller spatial scales.

This hypothesis is a variant of the watershed vegetation composition hypothesis, but considers riparian vegetation only. Previous studies have shown that bat foraging activity in forested regions of the Pacific Northwest is highest in riparian areas (Lunde and Harestad 1986, Brigham et al. 1992, Parker et al. 1996, Seidman and Zabel 2001). If bats forage predominantly on insects that originate and reside in these riparian areas, then consideration of vegetation at the larger scale should be limited to vegetation composition in riparian areas only. Thus, the **watershed riparian buffer vegetation composition hypothesis** proposes that riparian vegetation composition throughout the entire watershed influences habitat use decisions made by bats at smaller spatial scales.

Methods

Study Area

The terrain of the Oregon Coast Range is steep and rugged, with a dense network of streams throughout. Elevation ranges from sea level to 1250 m. The area is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1973). Dominant riparian canopy species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and western redcedar (*Thuja plicata*). The understory tree layer is dominated by vine maple (*Acer circinatum*) and hazelnut (*Corylus cornuta*), and the shrub layer by salmonberry (*Rubus spectabilis*) and swordfern (*Polystichum munitum*).

The northern boundary of our study region was the Columbia River, the southern boundary was the southern border of the Coos River sub-basin, the western boundary was the Pacific Ocean, and the eastern boundary was the Willamette Valley (Fig. 5.1). This region is approximately 300 km (190 miles) north to south, and contains 64 5th-field Hydrologic Units (HUCs). HUCs are topographically defined drainages organized in a nested hierarchy by size such that HUCs of any given level within a physiographic area are similar in size (Dzurik and Theriaque 1996). The 5th field HUCs in the study region range in size from 45 km^2 to 670 km^2 (17 miles^2 to 258 miles^2), and will hereafter be referred to as watersheds.

Before randomly selecting watersheds within the study region, we omitted several that did not meet three *a priori* criteria. The three criteria for omission were: (1) extremely low densities of large conifers, (because the majority of bat species in the region roost in large conifers (Campbell et al. 1996, Brigham et al. 1997, Betts 1998, Ormsbee and McComb 1998, Waldien et al. 2000, Weller and Zabel 2001), and bat activity could be so low in areas with limited roost site availability that selection for the variables of interest in this study could be difficult to discern), (2) >50% coverage by the Sitka spruce (*Picea sitchensis*) vegetation type (because this project was part of a larger effort concerned with habitat selection patterns in the western hemlock vegetation zone only), and (3) >70% private property.

To reduce logistical constraints, we subdivided the region into three geographical subregions and focused most of our work each summer in one of these three subregions. To ensure our research encompassed a variety of vegetation conditions, we took a stratified-random selection of the watersheds remaining after omissions. We categorized each watershed according to the proportions of deciduous and coniferous vegetation in each using the Coastal Landscape Analysis and Modeling (CLAMS) database (Ohmann and Gregory 2002). We calculated the ratio of the number of pixels described as “broadleaf” to the sum of the number of pixels described as “conifer” plus “broadleaf” to categorize watersheds as “least deciduous” (those with ratios in the lowest third within a given year’s subregion), “moderately deciduous” (those with ratios in the middle third) and “most deciduous” (those with ratios in the highest third). We randomly selected two watersheds in each of these categories and each summer we worked in six watersheds, two of each vegetation type.

We randomly selected stream reaches with bankfull width 3-7 m wide and >0.5 m deep in each watershed. To locate these stream reaches we generated random UTM coordinates and determined the nearest point on a second or third order stream for each point using 1:24,000 scale topographic quadrangle maps. Points were dropped from consideration if they (1) were not on either public land or private property to which access had been granted, (2) were located along a stream on which another stream reach had already been selected, (3) were within 2 km of a stream reach already selected, (4) had vegetation completely obstructing the airspace over the stream (which would hinder the transmission of bat echolocation calls), or (5) were not 3-7 m wide and >0.5 m deep. Additional points were visited in a given watershed until 5-8 stream reaches exhibiting a range in vegetation composition (from purely deciduous to purely coniferous) were located (Fig 5.2).

We monitored bat activity at 118 stream reaches (Fig. 5.3). We investigated 41 stream reaches in 2002, 37 new stream reaches in 2003, and 40 new stream reaches in 2004 (Appendix A). We sampled eight of the stream reaches from a single watershed each year to assess inter-annual variability in bat activity within a watershed.

Bat Activity Sampling

We assessed bat activity by recording echolocation calls of free-flying bats at each stream reach once during each 2-week period between mid-June and early September, for a total of four visits per stream reach in 2002 and five visits per stream reach in 2003 and 2004. Echolocation calls of bats were recorded from sunset until sunrise using calibrated (Larson and Hayes 2000), automated Anabat II detectors with Anabat zero crossings analysis interface modules (Titley Inc., Balina, Australia). We used a blocked sampling design, simultaneously monitoring 5–8 stream reaches within a given watershed each night. It is not possible to distinguish number of individuals that produced calls, so we used recordings as an index of bat use rather than as an estimate of abundance (Hayes 2000).

The position of echolocation detectors at each stream reach was constant among visits. We placed echolocation detectors within 2 m of the stream edge, at an elevation 0.5 m above the surface of the stream, at a 30° angle oriented with the microphone aligned parallel to the main axis of the stream and pointing upstream. We believe this orientation reduced variation in rates of detection among sites due to habitat features while maximizing the time that bats flying along the stream corridor were detectable.

We used Analook (v4.9j) to view recorded sequences of bat echolocation calls. We quantified bat activity by determining the number of minutes per night during which echolocation calls were recorded using criteria outlined in Appendix F. We could not categorize all echolocation calls to species due to similarities in calls among species with similar ecomorphology. Instead, we partitioned calls into phonic groups consisting of species with similar call characteristics. Calls were categorized into one of six groups: *Myotis californicus*/*M. yumanensis* (MYCA/MYYU); *M. lucifugus*/*M. volans* (MYLU/MYVO); *M. evotis*/*M. thysanodes* (MYEV/MYTH); *Eptesicus fuscus/Lasionycteris noctivagans*/*Lasiurus cinereus* (EPFU/LANO/LACI); *Corynorhinus townsendii* (COTO); or unidentifiable bat calls (Appendix F).

Vegetation Sampling

We sampled vegetation along a 30 m length of stream extending 10 m downstream and 20 m upstream of each echolocation detector, and extending 30 m from the stream edge upslope on both sides of the stream (Fig. 5.4). We recorded vegetation measurements throughout the 30 x 60 m plot to estimate vegetative species richness, cover, and composition, and we recorded vegetation measurements over the stream channel to estimate open flight space.

Vegetative species richness at the stream-reach scale

We recorded all species of woody shrubs and understory trees (trees with ≤5 cm DBH) that occurred in three 2 x 10 m subplots located at each end and the center of the plot (Fig. 5.4), and tallied the number of species across all 18 subplots as an index of shrub species and understory tree species richness for the stream reach. Western swordfern (*Polystichum munitum*) was recorded as a shrub because it is a perennially erect plant that contributes substantial biomass year-round throughout the study region, and due to its stature, vinemaple was recorded as an understory tree. We determined richness of canopy trees by tallying number of species of trees >5 cm DBH throughout the entire 30 x 60 m plot. We summed richness of shrubs, understory trees, and canopy trees (counting those species that occurred in >1 vegetation layer only once) as an index of richness of all woody species.

Vegetative cover at the stream-reach scale

To determine cover of shrubs and understory trees, we visually estimated the percent coverage of shrubs and understory trees for each of the eighteen 2 x 10 m subplots. We estimated canopy tree cover from the center of each subplot using a moosehorn densiometer (Garrison 1949). Each estimate was made independently by two observers and averaged. We used the mean of measurements from all 18 subplots as an index of shrub, understory tree, and canopy tree cover for the stream reach, and summed all three estimates to arrive at an index of total vegetative cover for the stream reach. We determined deciduous vegetative cover at the stream-reach scale in a manner identical to that described above, limiting measurements to deciduous species rather than including all vegetative species.

Open airspace at the stream-reach scale

We quantified amount of open airspace along the 30 m stretch of stream by estimating the area of space within the “tunnel” created by riparian vegetation surrounding the stream reach (Fig. 5.5). To calculate the total area beneath the indigitating branches of trees in the canopy we multiplied the average distance between the base of the tree boles located closest to the stream on opposite sides of the stream (measured at 7 evenly spaced points along the 30 m stream reach; arrow a in Fig. 5.5) by the average height to the lowest branch containing foliage directly over the stream channel (arrow b). Second, we estimated the area within this tunnel occupied by shrubs. To calculate this we multiplied the average height of shrubs (estimated in 3 plots on each side of the stream; arrow c) by the total distance between tree boles less the width of the stream channel. Finally, we estimated the area of open flight space potentially available for bats by subtracting the area occupied by shrubs on each side of the stream from the area of the tunnel created by the interdigitating branches of canopy trees. The resulting index reflects the relative area of open airspace in the stream reach; low values are typical of stream reaches with limited space and high values of those with more open space.

Vegetation composition within nightly activity-areas

We used a circle of radius 1.5 km around each detector to approximate the area within which the activity of a single bat would likely occur on a given night, based on mean distances reported between the location of initial capture and subsequent roost sites from studies of bats in forests of the Pacific Northwest (Brigham 1991, Ormsbee 1996, Campbell et al. 1996, Vonhof and Barclay 1996, Brigham et al. 1997, Waldien et al. 2000, Weller and Zabel 2001, Evelyn et al. 2004). We characterized vegetation composition within the circle according to the proportion of deciduous versus coniferous vegetation using the CLAMS database as previously reported for watershed selection.

Vegetation composition rarity of the stream reach relative to the nightly activity-area

We measured the DBH of each tree within the entire 30 x 30 m plot on each side of the stream to determine the vegetation composition within stream reaches, and then calculated the basal areas of coniferous trees and deciduous trees separately. We used the ratio of basal area of deciduous trees to that of all trees as an index of vegetation composition of the stream reach. A value near 0 describes a stream reach where nearly all trees are coniferous and a value near 1 describes a stream reach where nearly all trees are deciduous. Basal area was used in these calculations because it is more highly correlated to leaf area and foliage biomass than is tree stem density (Avery and Burkhart 2002). We computed the absolute value of the difference between the vegetation composition at the stream-reach scale and the vegetation composition in the 1.5 km circle surrounding the detector, resulting in an index ranging from 0 and 1, with large values indicating rare stream reach vegetation composition relative to that of the surrounding region and small values indicating similar vegetation composition at the two scales.

Vegetation composition at the watershed scale and within riparian buffers at the watershed scale

We used the CLAMS database to characterize the vegetation composition of each watershed. We also determined vegetation composition within a 30 m buffer along all streams within each watershed.

Statistical Analyses

We compared activity of all bat species combined in stream reaches measured all three years of the study to determine if the effect of year could be dropped from consideration in our analyses. We found statistically significant inter-annual differences in overall bat activity in only one of nine stream reaches repeatedly measured each year (ANOVA; $p<0.05$). Hence, we assumed the effect of year on bat activity was negligible, and pooled data across all years for subsequent analyses.

The response variable we used for most phonic groups was mean number of minutes in which activity of bats was recorded pooled across all visits at a stream reach. However, little or no activity was recorded from bats in the COTO and EPFU/LANO/LACI phonic groups (range = 0-3 mins with activity per stream reach per night for COTO and 0-7 mins with activity for EPFU/LANO/LACI). Therefore, we reduced data from the EPFU/LANO/LACI phonic group to a binary, presence – absence response, and because the data for COTO were too sparse to permit accurate modeling we dropped this phonic group from further analyses.

Multilevel models (hierarchical linear models) allow the structure of data to be taken into account when sample units are nested within larger units and explanatory variables exist for the description of the smaller and the larger units (Bryk and Raudenbush 1992). Multilevel models allow testing of hypotheses about relationships occurring at the sample unit level (level-1), the larger unit level (level-2), and across levels. Multilevel modeling also corrects for biases in parameter estimates and standard errors resulting from clustering (Guo and Zhao 2000). Furthermore, multilevel analyses can be used to assess variation at each level by partitioning variance and covariance components among levels (Singer 1998).

We used multilevel models because several stream reaches were embedded within each watershed, and we had explanatory variables to describe both the stream reaches and the watersheds. We modeled vegetation characteristics measured at the stream-reach and nightly activity-area spatial scales as level-1 explanatory variables and vegetation characteristics of watersheds as level-2 explanatory variables. Our approach allowed the linear relationship between bat activity and vegetation characteristics at stream reaches or nightly activity areas to vary by watershed; each watershed was permitted to have a different regression model with its own intercept and slope.

We used model selection to rank candidate models according to their likelihood (Burnham and Anderson 2002). We developed statistical models to reflect each of the original seven hypotheses generated to explain variation in bat activity at the stream-reach and nightly activity-area scales (Table 5.1). For three of these hypotheses (resource diversity, resource abundance, and resource quality), the possibility existed that all three vegetation strata (shrubs, understory trees, or canopy trees) combined, or alternatively one particular vegetation stratum alone was responsible for driving associations between vegetation characteristics and bats. To facilitate our ability to provide information to forest managers regarding which component of riparian vegetation was most influential to patterns of bat activity, we conducted a preliminary model selection step (step one, Table 5.2) to determine which of four options (shrub, understory tree, canopy tree, or the sum of all three combined) was most strongly related to activity of each phonic group for each of these three hypotheses. Because inclusion of level-2 (watershed scale) explanatory variables in a model might influence the amount of variation explained by each level-1 explanatory variable, we modeled each relevant level-1 explanatory variable in combination with each level-2 explanatory variable in this first step. We used the model that received the most support for each phonic group during this first step in subsequent analyses comparing the degree of support for the seven hypotheses relative to one another. In the second model selection step we included one model to represent each of the hypotheses at the stream-reach or nightly activity-area scales. We also included a null model (intercept only model) to evaluate the usefulness of the explanatory variables in predicting bat activity. We did not include quadratic terms due to a lack of evidence of such relationships when graphs of residuals were examined and the lack of a biological basis to expect such relationships. When appropriate, response variables were natural log transformed to meet assumptions of statistical models more closely.

We found no evidence of overdispersion, and therefore used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank models. For each phonic group, we ordered all models according to the difference between the AIC_c score of each model and the lowest AIC_c score of all models for that phonic group (ΔAIC_c), and considered all models with $\Delta AIC_c \leq 2.0$ to have substantial empirical support. We used Akaike weights, w_i, to evaluate the likelihood of each model relative to the others, given the data.

In the third step, we determined whether or not level-2 explanatory variables accounted for enough variation in each of the strongly competing models to warrant inclusion in the models. We calculated the proportion of variance among watersheds as well as the proportion of variation in watershed means explained by each level-2 variable (Singer 1998, Goldstein et al. 2002). We decided *a priori* that any level-2 variable that explained ≥10% of the variance in the data at level-2 would be retained. If level-2 variables explained <10% of the variance, we removed watershed-scale variables from considerations and conducted a fourth and final model selection step among all models containing a single level-1 explanatory variable.

After the final model selection step, we checked the magnitude of effect sizes and determined whether or not 95% confidence intervals overlapped zero for regression coefficients in all models that received substantial support to determine if effects were meaningful. The amount of variance explained by models that received substantial support was estimated by calculating [1 - (residual variance of intercept-only model / residual variance of top-ranked model)] (Verbeke and Molenberghs 2000).

Numbers of minutes during which activity occurred per night from the MYCA/MYYU, MYLU/MYVO, and MYEV/MYTH phonic groups were modeled using maximum likelihood procedures for mixed models in PROC MIXED in SAS (v9.1). Presence/absence data for the EPFU/LANO/LACI and COTO phonic groups were modeled using maximum likelihood procedures for nonlinear mixed models in PROC NLMIXED in SAS (Wolfinger 1999, McMahon et al. 2006).

Results

We monitored bat activity during 5,540 hours and 604 detector nights. Activity varied among stream reaches and species. The number of minutes during which activity of any species occurred per stream reach per night varied from 4 to 371 (Table 5.3). The majority of identifiable calls (>99%) were from bats in the genus *Myotis* (Table 5.3). Activity of bats in the most frequently recorded phonic group, MYCA/MYYU, exceeded that of bats in the two least frequently recorded phonic groups, EPFU/LANO/LACI and COTO, by over 100 times.

No single vegetation stratum emerged as the primary driver behind associations between vegetation characteristics and bat activity (step one of model selection; Table 5.4). Although the shrub layer explained the highest amount of variation in bat activity more often than did other vegetative layers, no consistent patterns were observed among hypotheses for a particular phonic group or among phonic groups for a particular hypothesis.

Similarly, we found high variability across bat species when we ranked models that included explanatory variables reflecting the seven original hypotheses pertaining to level-1 variables in combination with each of the level-2 explanatory variables according to the strength of evidence for each (step two of model selection; Table 5.5). When we examined how variance was partitioned among levels, we found the majority of variance in bat activity occurred among stream reaches within watersheds (70-100%) rather than among watersheds (0 to 30%) (step three of model selection; Table 5.6). Watershed scale vegetation characteristics (level-2 explanatory variables) explained only 0 to 18% of variation in watershed means, indicating these variables explained very little of the overall variation in activity of any phonic group (0-18% of 0-30%). For the MYCA/MYYU phonic group, level-2 variables explained a substantial amount of variation, so no further model selection steps were taken for these bats. The sole model that received substantial support for MYCA/MYYU indicated that bat activity increased as percent cover of deciduous shrubs at the stream-reach scale decreased and varied with riparian buffer vegetation composition at the watershed scale, providing evidence in favor of the stream surface obstruction hypothesis. Watershed-scale characteristics (level-2 variables) explained ≤10% of the watershed-scale variation for the MYLU/MYVO, MYEV/MYTH, and EPFU/LANO/LACI phonic groups, so we proceeded to examine relationships exclusively at the smaller spatial scales for these phonic groups (step four of model selection; Table 5.7, Fig. 5.4). For the MYLU/MYVO phonic group, the only model to receive substantial support indicated that bat activity increased with the area of open space above the stream channel, providing evidence in favor of the flight space hypothesis. For the MYEV/MYTH phonic group, the only model that received substantial support indicated that bat activity increased with percent cover of trees in the canopy layer, providing evidence in favor of the resource abundance hypothesis. Two models received similarly high levels of support for the EPFU/LANO/LACI phonic group: the likelihood of bat presence increased as percent cover of trees in the canopy layer decreased, and as open airspace above the stream channel increased, providing evidence in favor of the flight space hypothesis.

Discussion

One of our objectives was to determine which spatial scale best explained variability in bat activity so we could assess the degree of concordance between the scale of typical forest management operations and the scale of vegetation characteristics most relevant to bat activity patterns. More variation in activity existed among stream reaches within watersheds (70-100%) than among watersheds (0-30%) for all phonic groups. We could not formally test relative variation in activity at the stream-reach and nightly-activity-area scales because both were level-1 variables in our multilevel models. However, variables at the stream-reach scale consistently explained more variation in activity than did variables at the nightly-activity-area scale. Thus, of the factors explored in our analyses, we conclude that vegetation factors at the stream-reach scale had greater influence on bat activity than did factors measured at either of the two larger spatial scales.

Landscape structure influences distributions of organisms in different ways, depending on characteristics of those organisms. As a result of their high vagility, bats can respond to habitat heterogeneity at fine spatial scales. This likely explains the relatively strong associations between activity and patterns of vegetation heterogeneity at the smallest spatial scale we investigated. This is consistent with findings of Erickson and West (2003) and Loeb and O'Keefe (2006), who reported that factors at smaller scales were more influential on activity of bats than factors at larger scales.

Watershed-scale attributes generally had a relatively weak influence on bat activity. Neither of the two watershed-scale variables we measured (vegetation composition of the entire watershed or of the riparian buffer throughout the watershed) explained appreciably more variation in bat activity than the other, based on similar ΔAICc scores for models containing the same level-1 variables but different watershed scale variables. This limits our ability to predict whether or not upslope forest management operations might influence bat activity within riparian areas.
However, 30% of the variation in activity of the MYCA/MYYU phonic group was among watersheds, and watershed-scale riparian buffer vegetation composition explained 18% of this variation. Thus, the activity of bats in this phonic group varied

among watersheds according to riparian vegetation composition, but ativity of bats in other phonic groups did not.

Different hypotheses emerged as the best explanation of variation in activity of different phonic groups, suggesting that bats in the Oregon Coast Range respond to vegetation in a species-specific manner. Bats from the MYEV/MYTH phonic group responded to vegetation characteristics in a manner consistent with the insect prey distribution explanation: the resource abundance hypothesis was the only model to receive substantial support for these bats. Bats from the three other phonic groups (MYCA/MYYU, MYLU/MYVO, and EPFU/LANO/LACI) were more strongly associated with vegetation characteristics in a manner consistent with the structural hindrance explanation: the stream surface obstruction and open flight space hypotheses received substantial support for these bats.

Myotis californicus and Myotis yumanensis

The model reflecting the stream surface obstruction hypothesis was the only model to receive substantial support for the MYCA/MYYU phonic group. This hypothesis predicts that bat activity increases as the amount of shrub foliage overhanging a stream reach decreases, due to the increased availability of foraging space for bats that feed along the surface of the water.

Both *M. yumanensis* and *M. californicus* forage over water (Black 1974, Brigham et al. 1992), often very close to the surface of streams and lakes (Whitaker et al. 1977, Maser 1998). The diet of these species includes a higher proportion of insects with aquatic lifestages than nearly all other co-occurring bat species (Chapter 4). Their strong connection to food resources of aquatic origin likely explains the fact that bats of these species comprised the majority of activity we recorded. Obstructions at the surface of the water hinder the ability of foraging bats to capture insects in this airspace. Foliage from salmonberry, the most abundant deciduous shrub in riparian areas throughout the study region, often overhangs the banks of streams, limiting bat access to the surface of the water along stream margins.

Myotis lucifugus and Myotis volans

The model reflecting the flight space hypothesis was the only model to receive substantial support for the MYLU/MYVO phonic group. The flight space hypothesis predicts that bat activity increases as the amount of open airspace directly above the stream channel increases, due to reduced interference of bat flight patterns from vegetative clutter.

We expected this hypothesis to be relevant to fast-flying species whose limited ability to alter flight directions in small spaces would restrict foraging success in stream reaches with small open air spaces above the stream channel. *M. volans* is the fastest flying species of *Myotis* in western Oregon (Verts and Carraway 1998), and tends to forage using rapid, direct flight patterns near the forest canopy or in the open (Whitaker et al. 1977, 1981, Fenton and Bell 1979, Saunders and Barclay 1992). The rapid flight of this species likely limits the foraging success and efficiency of these bats in cluttered habitats (Black 1974, Norberg and Rayner 1987).

The other species in this phonic group, *M. lucifugus,* has quite different flight capabilities and feeding habits than *M. volans*. *M. lucifugus* is a slower, more agile flier that tends to forage along the margins of vegetation as well as over water (Whitaker et al. 1981, Fenton and Bell 1979, Barclay and Brigham 1994), often in close proximity to the ground or the surface of water (Whitaker et al. 1977, Fenton and Bell 1979, Barclay 1991, Saunders and Barclay 1992). Unfortunately, we were unable to discern differences in calls between species that occupy such disparate ecological niches. Combining these two species into a single phonic group likely obscured details of associations between each species and vegetation. However, an affinity for open areas while foraging seems to be a common characteristic of these two species, as has been reported previously (Saunders and Barclay 1992).

Myotis evotis and Myotis thysanodes

The model reflecting the resource abundance hypothesis was the only model to receive substantial support for the MYEV/MYTH phonic group. The resource abundance hypothesis predicts that bat activity increases with the availability of food resources for phytophagous insects, as prey abundance is presumably associated with this factor.

M. evotis and *M. thysanodes* fly relatively slowly and forage close to the canopy (Whitaker et al. 1977), often among the trees (Maser 1998). They use a combination of aerial-hawking and substrate-gleaning to obtain food (Barclay 1991, Faure and Barclay 1994). Substrate-gleaning and hovering are relatively costly modes of foraging, and therefore are profitable only when energy returns from prey are high (Curio 1976). Given the affinity of these bats for the canopy, an increase in the volume of canopy foliage likely provides increased foraging substrates from which to obtain prey, which may in turn increase their foraging efficiency. The relationship between canopy cover and activity of these bats was the strongest relationship (greatest proportion of variance explained) of all phonic groups investigated.

Eptesicus fuscus, Lasionycteris noctivagans, and Lasiurus cinereus

The model reflecting the open air space hypothesis received substantial support for the EPFU/LANO/LACI phonic group, as did the model indicating that likelihood of presence of these bats increased as percent canopy cover decreased. The flight space hypothesis predicts that bat activity increases as the amount of open airspace directly above the stream channel increases, due to reduced interference on bat flight patterns from vegetative clutter.

We recorded relatively little activity of bats in the EPFU/LANO/LACI phonic group, likely reflecting the limited foraging these species do in the airspace monitored by our echolocation detectors. These species tend to avoid flying in cluttered habitats due to the hindrance their long wings impose on making quick turns in small spaces (Black 1974, Whitaker et al. 1981, Norberg and Rayner 1987). As the three fastest flying species in western Oregon (Verts and Carraway 1998) with the lowest frequency echolocation calls, these bats are adapted to detect insects in open habitats at long range and vegetative clutter precludes foraging success. Due to the constraints on foraging imposed by their morphology, these species are more likely to forage either in higher-order streams characterized by expansive open space above the water channel or above the forest canopy. Foraging above the forest canopy has previously been reported for these species in Oregon (Whitaker et al. 1977, 1981, Maser 1998).

There are two plausible explanations for the increased likelihood of presence of these species with decreasing canopy cover. First, these bats may have been selecting stream reaches that had large open flight spaces, which were stream reaches with limited canopy cover. The high degree of support for the model with open airspace above the stream channel provides evidence of the viability of this explanation. Alternatively, these bats may have been foraging above the canopy, and the increased likelihood of presence of these bats as canopy cover decreased was due to the greater chances of echolocation detectors recording calls from bats as the obstruction presented by foliage in the canopy layer decreased. This second explanation seems less likely than the first, given the limited ability of echolocation detectors to hear calls made by bats at the distances typically present between detectors and the upper canopy.

Scope and Limitations

We randomly selected watersheds from throughout the Oregon Coast Range and randomly selected stream reaches from all second and third order streams within each of these watersheds. Consequently, our results can be extrapolated to second and third order streams throughout the Coast Range, but may not be applicable to other areas or to other types of streams. We accounted for temporal variability in bat activity (Hayes

1997, 2000) by collecting data from sunset until sunrise each night, and by sampling each site once during each two-week period of the summer. Thus, results are applicable to the entire summer period but should not be extrapolated to other seasons.

Inferences regarding bat habitat use from bat echolocation monitoring are subject to several limitations. First, the number of minutes during which activity occurs for a particular phonic group provides no information on bat abundance; we use this metric as an index of relative use of each site to enable comparisons of use among sites. Second, interspecific differences in echolocation call intensities and frequencies result in variable detection probabilities among species, making comparisons of use among species tenuous; we draw comparisons among sites for the same species, but not among species. Third, echolocation detectors located near the ground cannot sample bat activity within or above the canopy in the forests we investigated; this study assessed bat use of the airspace below the foliage of canopy trees only. Fourth, data were pooled across sexes and across species within each phonic group, so some species-specific and all gender-specific patterns may have been masked.

Conclusions and Management Recommendations

Although we demonstrated associations between vegetation and nocturnal insect abundance (Chapter 2) and associations between nocturnal insect abundance and bat activity (Chapter 4), associations spanning from vegetation to bats along these nutritional pathways were not strong. Only bats from the MYEV/MYTH phonic group responded to vegetation characteristics in a manner consistent with the insect prey distribution explanation. Bats from the three other phonic groups (MYCA/MYYU, MYLU/MYVO, and EPFU/LANO/LACI) were more strongly associated with vegetation characteristics in a manner consistent with the structural hindrance explanation. This suggests that although vegetation may influence the distribution of nocturnal insects, and the distribution of nocturnal insects may influence the distribution of bat activity, the structure of vegetation has an impact on bat flight abilities that overrides these other effects. Thus, riparian areas that support high abundances of insects that could potentially serve as prey for bats are likely to get limited use by bats if the structure of the vegetation is such that bats are unable to efficiently forage there.

Vegetation features measured at the stream-reach scale were more influential than those at larger spatial scales in determining bat activity. This suggests that stand-scale riparian forest management operations have the capacity to influence bat foraging activity patterns, as suggested previously by Hayes and Adam (1996). We found a diversity of responses to small-scale vegetation characteristics among bat species, with activity of some species most strongly associated with shrub cover, others with canopy cover, and others with open space above the stream channel. Given these differences among species, the best strategy for the achievement of biodiversity conservation goals over broad spatial scales is likely maintenance or creation of a diversity of riparian vegetation conditions. We recommend that land managers planning to manipulate riparian vegetation strive to create diversity in shrub coverage, canopy coverage, and open space above the stream channel.

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Figure 5.1. Map showing 18 randomly selected watersheds (identified in white) in the Oregon Coast Range.

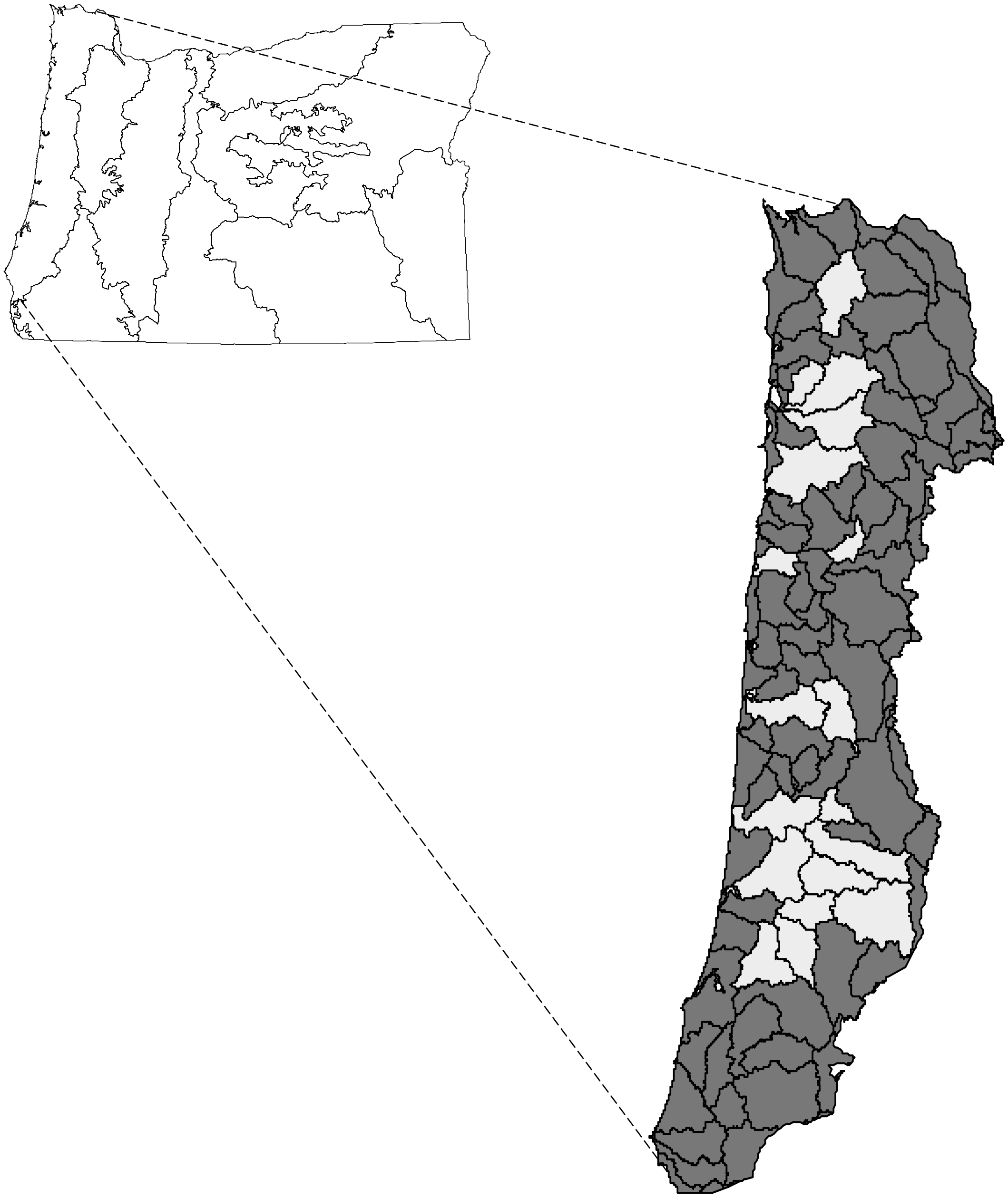

Figure 5.2. Detailed view of the location of 8 randomly selected stream reaches in an example watershed (the Upper Siuslaw River).

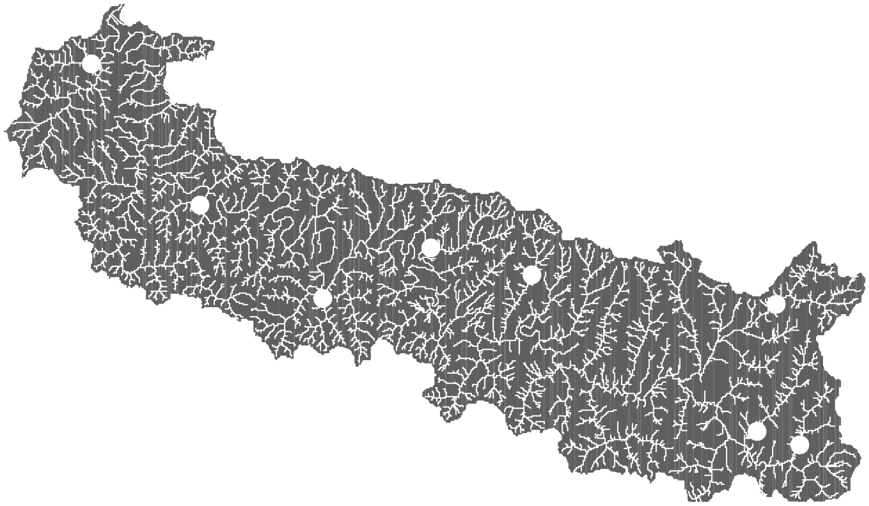

Figure 5.3. Map of 118 randomly selected stream reaches in the Oregon Coast Range.

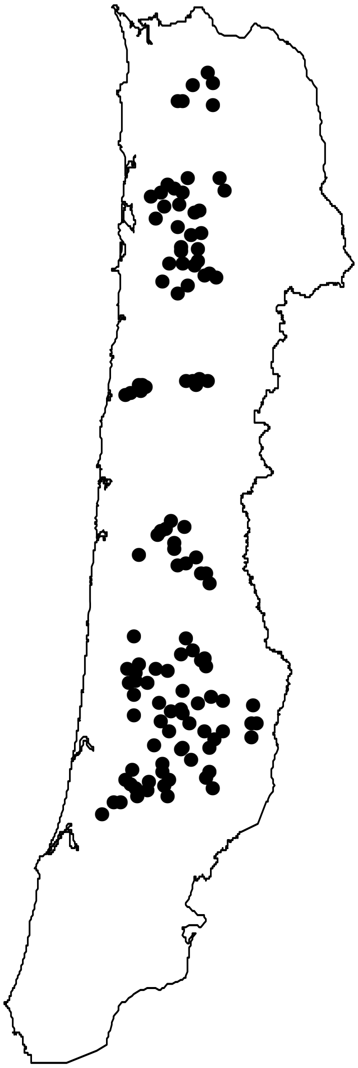

Figure 5.4. Vegetation sampling plots. We identified and measured DBH of all trees >5cm DBH within the entire 30 x 60 m plot. Within each of the eighteen 10 x 2m subplots, we recorded each species of shrub and understory tree, estimated percent cover of shrubs and understory trees, and estimated height of shrubs. At the 18 locations marked by gray circles we measured canopy cover.

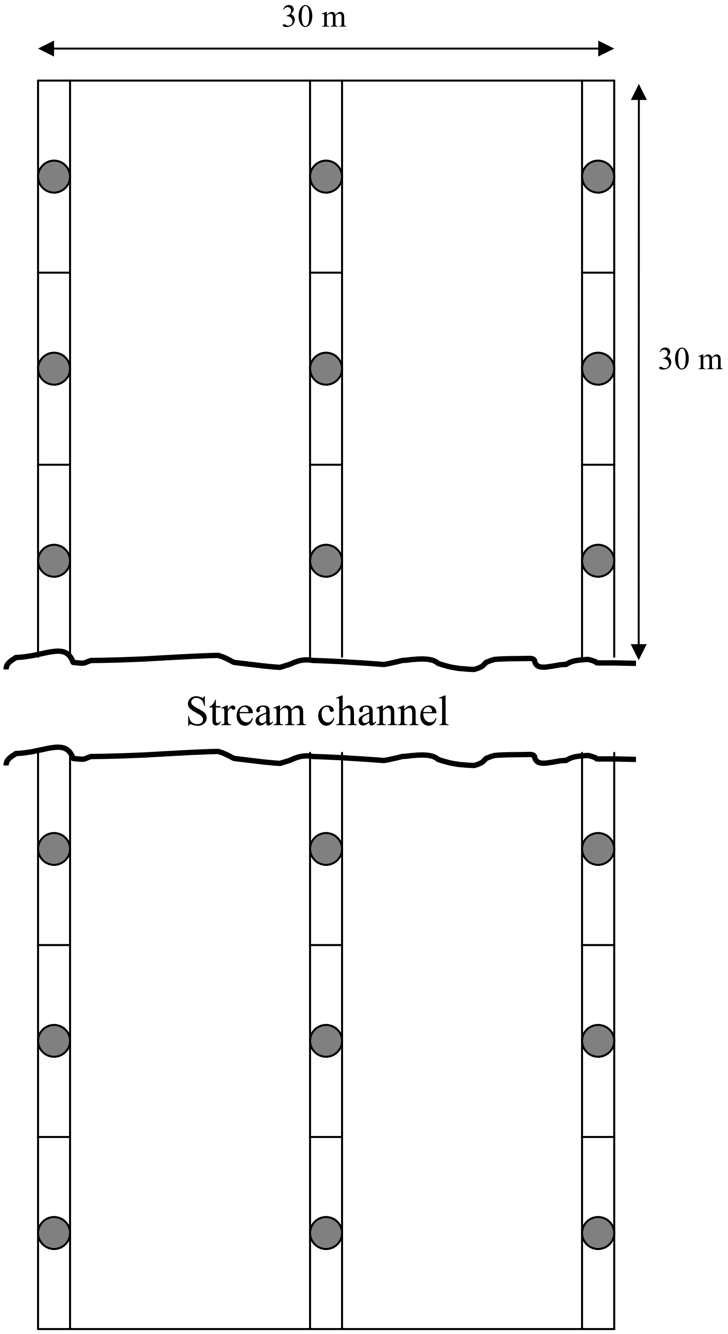

Figure 5.5. Description of open airspace calculations. First we calculated the area bordered by the lowest branches of canopy trees, the boles of trees closest to the stream margin, and the stream surface, to estimate the area of the "tunnel" of space created by canopy trees. Second, we determined the area within this tunnel that was occupied by shrubs. Finally, we subtracted the area occupied by shrubs from the area in the tunnel to determine the area of open flight space potentially available for bats.

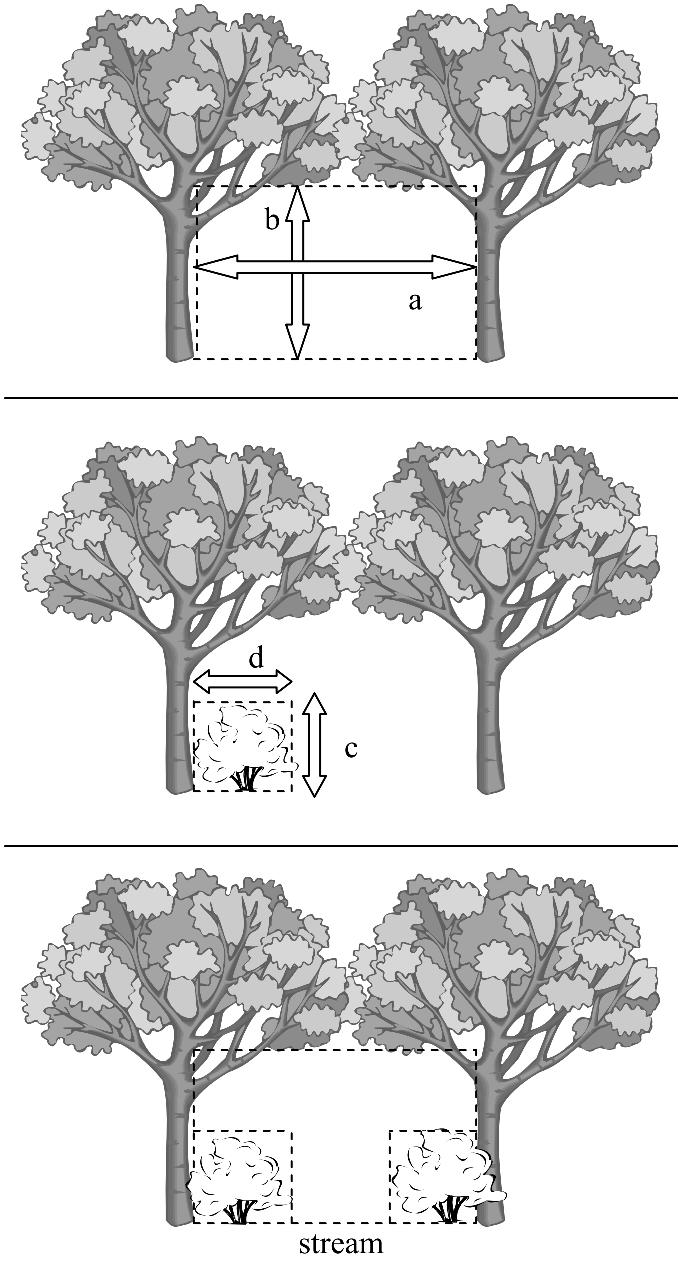

Figure 5.6. Relationships between bat activity and stream reach vegetation characteristics for models that received substantial support (ΔAICc≤2.0) after the final step of the model selection procedure. Y-axes portray the mean number of minutes during which bat activity occurred per stream reach per night, ln transformed. A: Activity of the MYCA/MYYU phonic group versus percent cover of deciduous shrubs. B: Activity of the MYLU/MYVO phonic group versus area of open airspace above the stream channel. C: Activity of the MYEV/MYTH phonic group versus percent cover of canopy trees.

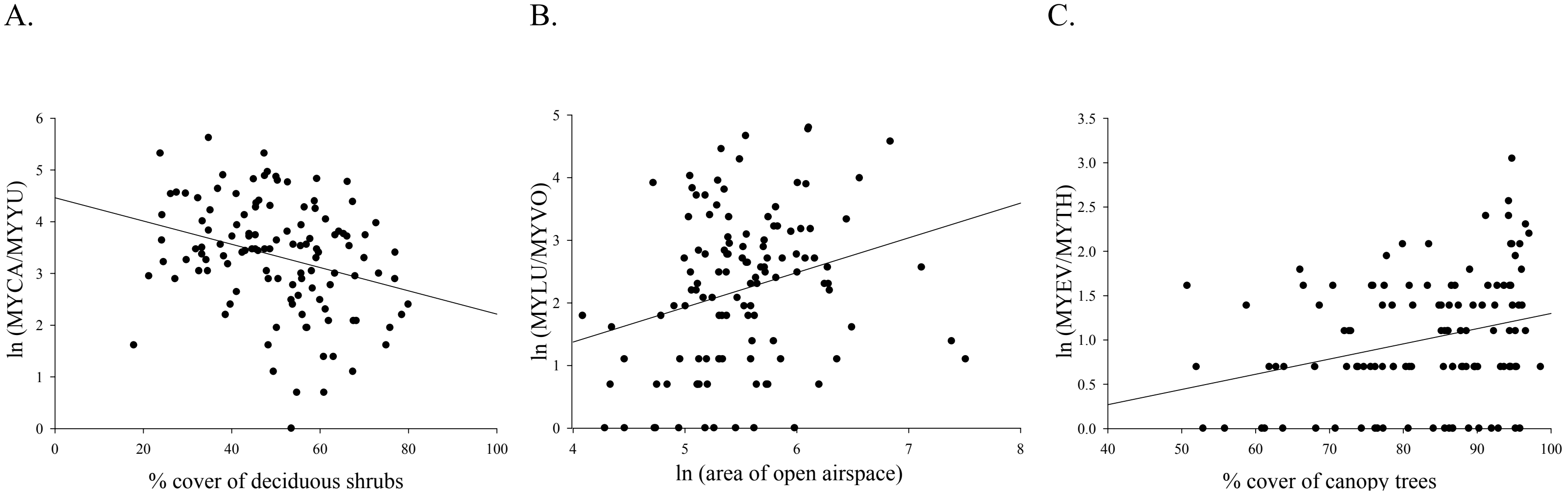

Table 5.1. Relationships between riparian vegetation and activity of bats predicted by *a priori* hypotheses and the linear models associated with each.

Hypothesis	Spatial scale	Predicted relationship	Model structure
Resource diversity	stream reach	Positive effect of vegetative species richness	$Y = \beta_0 + \beta_1(\text{species richness})$
Resource abundance	stream reach	Positive effect of vegetative cover	$Y = \beta_0 + \beta_1(\%\ \text{cover})$
Resource quality	stream reach	Positive effect of deciduous vegetative cover	$Y = \beta_0 + \beta_1(\%\ \text{deciduous cover})$
Open flight space	stream reach	Positive effect of open space above the stream channel	$Y = \beta_0 + \beta_1(\ln\ \text{area open space})$
Stream surface obstruction	stream reach	Negative effect of shrubs overhanging the stream channel	$Y = \beta_0 - \beta_1(\%\ \text{shrub cover})$ or $Y = \beta_0 - \beta_1(\%\ \text{deciduous shrub cover})$
Vegetation composition	nightly activity area	Positive effect of deciduous vegetative cover	$Y = \beta_0 + \beta_1(\text{proportion deciduous cover})$
Vegetation rarity	nightly activity area	Positive effect of divergence in vegetation composition between stream reach and surrounding area	$Y = \beta_0 + \beta_1(\lvert \text{stream reach vegetation composition - nightly activity area vegetation composition} \rvert)$
Vegetation composition	watershed	Vegetation composition throughout entire watershed influences relationships between smaller-scale vegetation patterns and bat activity	$\beta_0 = \gamma_{00} + \gamma_{01}W$ $\beta_1 = \gamma_{10} + \gamma_{11}W$
Vegetation composition	watershed	Riparian vegetation composition throughout entire watershed influences relationships between smaller-scale vegetation patterns and bat activity	$\beta_0 = \gamma_{00} + \gamma_{01}W$ $\beta_1 = \gamma_{10} + \gamma_{11}W$

Table 5.2. Description of steps followed in the model selection procedure.

Step	Objective	Approach	Outcome
1	For the resource diversity, resource abundance, and resource quality hypotheses, determine which vegetation strata (shrubs, understory trees, canopy trees, or all 3 combined) is most strongly related to the response variable when modeled in combination with each of the two level-2 explanatory variables.	For each of these three hypotheses, use model selection to determine which of the four potential sub-models ranks highest according to the weight of evidence for each when modeled in combination with each of the level-2 variables. Begin with 24 possible models.	For each of these three hypotheses, we retain two models for use in step 2: each contains one of the two possible level-2 variables in combination with the level-1 variable that pertains to the most relevant vegetation strata for that hypothesis.
2	Determine which of the seven hypotheses concerning level-1 variables are most strongly related to the response variable of interest when modeled in combination with each of the level-2 explanatory variables.	Fit all models containing one level-1 variable in combination with each level-2 variable plus the null model and use model selection to rank models according to the weight of evidence for each. Begin with 15 possible models.	Models are rank ordered according to the strength of evidence for each. Models with $\Delta AIC_c \leq 2.0$ are considered "strongly competing" and are retained for use in step 3.
3	Determine if the level-2 variable in each strongly competing model explains enough variation in the data to warrant continued inclusion in the model.	Calculate the proportion of variation explained by the level-2 variable in each strongly competing model.	If the proportion of variation explained by the level-2 variable <10%, conclude that inclusion of the variable is not warranted.
4	For those models where level-2 variables were dropped, determine which of the original hypotheses concerning level-1 variables are most strongly related to the response variable of interest.	Fit all models containing one level-1 variable plus the null model and use model selection to rank models according to the weight of evidence for each. Begin with eight possible models.	Models are rank ordered according to the strength of evidence for each. Models with $\Delta AIC_c \leq 2.0$ are considered "strongly competing" and are interpreted.

Table 5.3. Number of minutes during which activity occurred per stream reach per night for bats in riparian areas of the Oregon Coast Range, summers 2002-2004.

Phonic group	$\bar{x}$	SE	Range
MYCA/MYYU	44.2	4.23	0 - 275
MYLU/MYVO	17.2	2.17	0 - 120
MYEV/MYTH	2.5	0.27	0 - 20
EPFU/LANO/LACI	0.2	0.07	0 - 7
COTO	0.3	0.05	0 - 3
all bats	89.4	6.18	4 - 371

Table 5.4. Results of step 1 of the model selection procedure relating bat activity to vegetation characteristics in riparian areas of the Oregon Coast Range, summers 2002-2004. This step compared the weight of evidence in favor of models reflecting four different vegetative strata (shrubs, understory trees, canopy trees, or all strata combined) for each of three hypotheses (the resource diversity, resource abundance, and resource quality hypotheses). The stratum in the model that received most support is listed for each hypothesis for each phonic group.

Hypothesis	MYCA/MYYU	MYLU/MYVO	MYEV/MYTH	EPFU/LANO/LACI
Resource diversity	all strata	shrubs	understory trees	shrubs
Resource abundance	shrubs	all strata	canopy trees	canopy trees
Resource quality	shrubs	shrubs	understory trees	canopy trees

Table 5.5. Strongly competing candidate models ($\Delta AIC_c \leq 2.0$) from step 2 of the model selection procedure, relating bat activity to vegetation characteristics at multiple spatial scales in riparian areas of the Oregon Coast Range, summers 2002-2004. For each phonic group, we ranked all models containing one level-1 explanatory variable in combination with one level-2 explanatory variable plus the null model according to AIC_c. No results are shown for the EPFU/LANO/LACI phonic group because the amount of variation in bat activity at level-2 was negligible. All regression coefficients for level-1 explanatory variables were positive, with the exception of the coefficient for % cover of deciduous shrubs for the MYCA/MYYU phonic group.

Phonic group	level-2 explanatory variable	level-1 explanatory variable	ΔAIC_c	w_i
MYCA/MYYU	riparian buffer vegetation	% cover of deciduous shrubs	0.0	0.71
MYLU/MYVO	watershed vegetation	open space above stream channel	0.0	0.29
	riparian buffer vegetation	open space above stream channel	0.2	0.26
	watershed vegetation	activity area vegetation rarity	2.0	0.11
	riparian buffer vegetation	activity area vegetation rarity	2.0	0.11
MYEV/MYTH	riparian buffer vegetation	% cover of trees in canopy layer	0.0	0.39
	watershed vegetation	% cover of trees in canopy layer	0.0	0.39

Table 5.6. Partitioning of variance in bat activity among watersheds versus among stream reaches within watersheds, and proportion of variation explained by explanatory variables in models with the strongest evidence (according to AIC_c rankings) for each phonic group in the Oregon Coast Range, summers 2002-2004.

	% of total variation		% of within-level variation explained by "best" variable	
Phonic group	among watersheds	within watersheds	level-2	level-1
MYCA/MYYU	30.0	70.0	18.0	10.1
MYLU/MYVO	10.6	89.4	6.1	10.5
MYEV/MYTH	9.3	90.7	5.6	15.9
EPFU/LANO/LACI	trace	~100	trace	9.4

Table 5.7. Strongly competing candidate models ($\Delta AIC_c \leq 2.0$) after the fourth and final model selection step, relating bat activity to vegetation characteristics in riparian areas of the Oregon Coast Range, summers 2002-2004. Models were ranked according to AIC_c. Sign indictes whether the regression coefficients for level-1 explanatory variables were positive (+) or negative (-).

Phonic group	Explanatory variables in final model	Sign	w_i	Variance explained[a]
MYCA/MYYU	% cover of deciduous shrubs, riparian buffer vegetation	-	0.71	0.11
MYLU/MYVO	open air space above stream channel	+	0.55	0.10
MYEV/MYTH	% cover of trees in canopy layer	+	0.84	0.16
EPFU/LANO/LACI	% cover of trees in canopy layer	-	0.54	0.09
	open air space above stream channel	+	0.43	0.09

[a] Proportion of variance explained by the model under consideration relative to that of the null model (model with no effects).

CHAPTER 6 – GENERAL CONCLUSIONS

The overarching goal of this work was to gain a better understanding of how vegetation influences activity of bats and nocturnal flying insects in forested riparian areas of the Oregon Coast Range so that land managers planning vegetation manipulations might better predict the influence of their actions on these two components of biodiversity. We investigated relationships between plants and insects, between insects and bats, and between plants and bats.

Vegetation characteristics measured at the stream reach explained more variation in bat activity than did vegetation characteristics measured at larger spatial scales. Given the small scale of most forest management activities, these results suggest that forest management prescriptions that alter riparian vegetation have the capacity to influence bat foraging habitat selection. Vegetation factors most closely associated with bat activity varied by bat species, and appear to operate through constraints imposed by vegetation architecture on bat prey acquisition rather than through regulation of the distribution of insect prey abundance. Characteristics of shrubs were most influential for some species, whereas characteristics of the canopy were most influential to others, suggesting that manipulations to either of these vegetation layers could influence bat foraging activity.

Lepidoptera and Diptera were the two most common prey items consumed by bats. Bats grouped into two primary feeding groups: one fed primarily on small aquatic insects (*M. californicus*, *M. yumanensis,* and *M. lucifugus*), and the other on larger terrestrial insects (*Myotis evotis, M. thysanodes, M. volans*, *Corynorhinus townsendii, Eptesicus fuscus, Lasionycteris noctivagans*, and *Lasiurus cinereus).* Activity of the smaller bat species, whose diet is likely restricted to small prey items, was more closely linked to local prey abundance than was activity of larger bat species whose diet is likely less restricted by prey size.

Abundance and biomass of the six most commonly captured orders of nocturnal flying insects in riparian areas (Diptera, Lepidoptera, Trichoptera, Ephemeroptera, Coleoptera, and Hymenoptera) were highly associated with cover of deciduous vegetation. For all insect orders investigated, abundance and biomass increased as cover of deciduous vegetation increased. Associations between abundance and biomass of insects and cover of deciduous trees in the canopy exceeded those between abundance and biomass of insects and cover of trees in the understory or shrubs for most orders of insects. Variation in moth community composition was associated with variation in cover and composition of shrubs and canopy trees. Furthermore, number of captures, biomass, and Shannon's species diversity of moths were greater in deciduous-dominated stream reaches than in simultaneously sampled conifer-dominated stream reaches.

In sum, we discovered strong linkages between riparian vegetation, abundance of nocturnal insects, and activity of bats at small spatial scales. This work provides evidence that local riparian vegetation composition and cover are influential to both bats and nocturnal flying insects. Alteration of shrubs or canopy trees in riparian areas is likely to impact insect abundance and biomass, moth community composition, and bat activity. Prescriptions that alter canopy composition or cover appear likely to impact insects and larger species of bats (*Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus cinereus, Myotis evotis, M. thysanodes, M. volans,* and *M. lucifugus*), whereas prescriptions that alter shrub composition or cover appear likely to impact macro-moths and smaller species of bats (*M. yumanensis, M. californicus*). The positive relationship between cover of deciduous vegetation and abundance and biomass of insects suggests that alteration of riparian vegetation composition and cover could be influential to food webs involving bats in the Oregon Coast Range.

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APPENDICES

Appendix A. Descriptions of locations of stream reaches where data were collected.

Stream name	x-UTM	y-UTM	Taxa monitored	Year monitored	Ownership[a]
Alsea River	464240	4901620	bats	2002	BLM
Argue Crk	446320	4846270	bats	2003	BLM
Barn Crk	432760	4974800	bats	2002	STC
Bays Crk	442680	5015865	bats	2004	USFS
Bear Crk	430510	4981110	insects, bats	2002	STC
Bear Crk	454265	5014610	bats	2004	BLM
Bear Crk	458770	4856440	bats	2002, 03, 04	BLM
Beaver Crk	431080	4868380	bats	2002	USFS
Beaver Crk	441380	4856760	bats	2003	BLM
Beaver Dam Crk	471430	5050480	bats	2004	ODF
Bible Crk	455970	5006730	insects, bats	2004	BLM
Bickford Crk	431500	4821780	bats	2003	ODF
Blue Hole Crk	466180	4824660	bats	2003	BLM
Boulder Falls Crk	449750	4975755	insects, bats	2004	BLM
Bounds Crk	445600	4868850	bats	2002, 03,04	BLM
Briar Crk	445640	4906150	insects, bats	2002	BLM
Buck Crk	437100	4827120	bats	2003	BLM
Buck Crk	468040	4853100	insects, bats	2002, 03, 04	BLM
Bullrun Crk	440510	4920560	bats	2002	USFS
Butler Crk	442770	4833660	bats	2003	BLM
Camp Crk	445030	4821130	bats	2003	BLM
Carpenter Crk	441940	4849740	bats	2003	BLM
Cedar Crk	427210	4869400	bats	2002	USFS
Cedar Crk	427210	4869400	insects, bats	2003	USFS
Cedar Crk	452465	5049315	bats	2004	ODF
Cedar Crk	464555	5019040	bats	2004	WTC
Cedar Crk	458035	4976930	bats	2004	BLM
Clarence Crk	449640	5011650	bats	2004	USFS
Clear Crk	440065	5039920	bats	2004	ODF
Cleghorn Crk	458560	4845760	insects, bats	2003	BLM
Coleman Crk	460250	4905630	bats	2002	BLM
Company Crk	442060	5049280	bats	2004	ODF
Cougar Crk	428580	4826390	bats	2003	ODF
Cruiser Crk	462650	5029700	insects, bats	2004	ODF
Diamond Crk	435760	5051960	insects, bats	2004	ODF

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[a] BLM = Bureau of Land Management; CG = Campbell Group; ODF = Oregon Department of Forestry; OR = Olympic Resources; RR = Roseburg Resources; STC = Simpson Timber Company; USFS = United States Forest Service; WTC = Weyerhaeuser Timber Company

Stream name	x-UTM	y-UTM	Taxa monitored	Year monitored	Ownership
Doe Crk	470650	4857700	bats	2002, 03, 04	WTC
Dogwood Crk	464940	4859100	bats	2002, 03, 04	BLM
Douvre Crk	462425	5018340	bats	2004	BLM
Drift Crk	469250	5054775	bats	2004	ODF
East Bear Crk	444230	4922270	bats	2002	BLM
East Beaver Crk	446033	5022670	bats	2004	BLM
East Drift Crk	435260	4976200	bats	2002	STC
East Fork Trask Riv	458890	5023645	bats	2004	ODF
East Humbug Crk	452450	5083960	bats	2004	WTC
East Tom Foley Crk	464150	4840070	bats	2003	BLM
Edwards Crk	451230	5028940	bats	2004	ODF
Elk Crk	424200	4818980	bats	2003	ODF
Elk Crk	456335	5018795	insects, bats	2004	BLM
Fall Crk	427760	4864720	bats	2002	USFS
Fall Crk	427760	4864720	insects, bats	2003	USFS
Fish Crk	456600	4876660	bats	2002	BLM
Fish Crk	426150	4827500	bats	2003	ODF
Fitzpatrick Crk	449900	4825480	insects, bats	2003	BLM
Footlog Crk	429270	4831810	bats	2003	ODF
Grass Crk	432040	4912880	bats	2002	USFS
Greenleaf Crk	448890	4888330	insects, bats	2002	BLM
Hadsall Crk	432510	4871220	bats	2002	CG
Halfway Crk	453160	4844410	insects, bats	2003	BLM
Hamilton Crk	456580	5090490	bats	2004	ODF
Hawley Crk	484500	4856160	bats	2002, 03, 04	BLM
Headquarters Camp Crk	457380	5022300	bats	2004	ODF
Hembre Crk	455950	5033695	bats	2004	ODF
Honey Grove Crk	458650	4914430	insects, bats	2002	BLM
Horner Crk	432360	4976820	bats	2002	STC.
Joyce Crk	451715	5026995	bats	2004	ODF
Kansas Crk	449645	5036830	bats	2004	ODF
Kelly Crk	483400	4849410	bats	2002, 03, 04	WTC
Kentucky Crk	436400	4864060	bats	2003	USFS
Kilchis River	448680	5050920	bats	2004	ODF
Klickitat Crk	446550	4925890	bats	2002	BLM
Knapp Crk	453640	4881390	bats	2002	ODF
Knowles Crk	439640	4869510	bats	2002	CG
Little Camp Crk	443350	4825620	bats	2003	BLM
Little S. Fork Smith Riv	462130	4845820	bats	2003	BLM
Little Tom Foley Crk	456240	4835400	bats	2003	BLM
Lobster Crk	449250	4899640	insects, bats	2002	BLM
Lower Wildcat Crk	460930	4872770	bats	2002	BLM
Luchsinger Crk	442970	4830820	bats	2003	BLM
Marlow Crk	419200	4813700	insects, bats	2003	ODF

Stream name	x-UTM	y-UTM	Taxa monitored	Year monitored	Ownership
Michael Crk	460465	5034340	bats	2004	ODF
Mill Crk	453960	4978322	bats	2004	BLM
Mill Crk	451790	4861400	bats	2002, 03, 04	BLM
Nelson Crk	452100	4884660	insects, bats	2002	BLM
North Crk	428310	4974180	bats	2002	USFS
North Fork Jordan Crk	462490	5044380	insects, bats	2004	ODF
North Fork Mill Crk	448700	4917000	bats	2002	BLM
North Fork Sister Crk	451120	4854250	bats	2003	BLM
North Fork Soup Crk	436080	4823940	bats	2003	BLM
North Fork Wilson Riv	450360	5045280	bats	2004	ODF
North Tom Foley Crk	460480	4840930	insects, bats	2003	BLM
Northrup Crk	464880	5096030	insects, bats	2004	ODF
Oat Crk	459260	4867930	insects, bats	2002	BLM
Panther Crk	471760	4862860	insects, bats	2002	BLM
Paradise Crk	452210	4840140	bats	2003	BLM
Parker Crk	452600	4923240	bats	2002	BLM
Peach Crk	430070	4859420	bats	2003	USFS
Phipps Crk	459810	5042700	bats	2004	ODF
Pigeon Crk	454740	5025380	insects, bats	2004	ODF
Pine Crk	456625	4978565	bats	2004	BLM
Pollard Crk	458980	5028073	bats	2004	ODF
Quarry Crk	425910	4972680	bats	2002	USFS
Racks Crk	447400	4922890	insects, bats	2002	BLM
Record Crk	450150	4908430	bats	2002	BLM
Rogers Crk	454625	5055270	bats	2004	ODF
Saddle Butte Crk	459560	4837770	insects, bats	2003	BLM
Sager Crk	469490	5091680	insects, bats	2004	ODF
Sam Downs Crk	443390	5044040	bats	2004	ODF
Sawyer Crk	445650	4827950	bats	2003	BLM
Schoolhouse Crk	448250	4914720	bats	2002	BLM
Schroeder Crk	445380	5052930	bats	2004	ODF
Slander Crk	430840	4824190	bats	2003	ODF
Slick Rock Crk	435100	4982760	insects, bats	2002	USFS
Smith Crk	471210	4852260	insects, bats	2002, 03, 04	BLM
Smith River mainstem	470640	4846220	bats	2003	BLM
South Branch Crk	463385	4978670	bats	2004	BLM
South Fork Jordan Crk	457410	5041810	bats	2004	ODF
South Fork Miami Riv	440690	5054290	insects, bats	2004	ODF
South Fork Sister Crk	452090	4852830	bats	2003	BLM
South Fork Smith Riv	466720	4843260	bats	2003	BLM
South Fork Soup Crk	437800	4822530	insects, bats	2003	BLM
South Fork Trask Riv	451800	5022910	bats	2004	ODF
Spencer Crk	430280	4852090	bats	2003	BLM
Squaw Crk	463110	4828100	bats	2003	BLM
Squaw Crk	466115	5090660	bats	2004	ODF

Stream name	x-UTM	y-UTM	Taxa monitored	Year monitored	Ownership
Stanley Crk	465590	5082760	bats	2004	ODF
Sweden Crk	446780	4853930	bats	2003	BLM
Sweet Crk	431000	4865450	bats	2002	OR
Thistleburn Crk	464500	4831030	bats	2003	BLM
Thompson Crk	429950	4881790	bats	2002	USFS
Tilden Crk	437630	5048290	bats	2004	ODF
Tobe Crk	453820	4909430	bats	2002	BLM
Trout Crk	458400	4911580	bats	2002	BLM
Trout Crk	420990	4819570	bats	2003	ODF
Tucker Crk	485850	4848720	bats	2002, 03, 04	WTC
unnamed Crk	451020	4838770	bats	2003	BLM
Upper Wildcat Crk	463240	4870360	bats	2002	BLM
Vincent Crk	438930	4840630	bats	2003	BLM
Waggoner Crk	450640	4819610	insects, bats	2003	BLM
Walker Crk	451400	4875140	bats	2002	RR
Walker Crk	463925	5094885	bats	2004	ODF
Walker Crk	467670	5017100	bats	2004	BLM
Ward Crk	483670	4843370	bats	2003	BLM
Warden Crk	462390	4873810	bats	2002	BLM
Warnicke Falls Crk	447375	4977960	insects, bats	2004	BLM
W. Bear Crk	442430	4921620	bats	2002	BLM
W. Camp Crk	441750	4822750	insects, bats	2003	BLM
W. Drift Crk	433620	4976580	bats	2002	USFS
W. Fork Millicoma Riv	429040	4823080	insects, bats	2003	ODF
W. Fork Wilson Riv	454615	5053180	insects, bats	2004	ODF
W. Humbug Crk	449700	5083680	bats	2004	WTC
Williams Crk	462490	4905770	bats	2002	BLM
Wind Crk	459915	4979010	bats	2004	BLM
Yellow Crk	455490	4849160	bats	2003	BLM

Appendix B. Allometric equations used to estimate biomass (bm) of adult insects from body length measurements. Lengths are in mm and biomass estimates in mg.

Order	Equation	Study location	Source
Coleoptera	$bm = 0.04(length)^{2.64}$	CA	Sabo et al. 2002
Diptera	$bm = 0.04(length)^{2.26}$	CA	Sabo et al. 2002
Ephemeroptera	$bm = 0.046(length)^{2.6084}$	OR	Li, pers comm
Hemiptera	$bm = 0.0108(length)^{2.734}$	eastern states	Benke et al. 1999
Homoptera	$bm = 0.005(length)^{3.33}$	CA	Sabo et al. 2002
Hymenoptera	$bm = 0.056(length)^{1.56}$	CA	Sabo et al. 2002
Lepidoptera	$bm = 0.0065(length)^{3.122}$	WV	Sample et al. 1993
Mecoptera	$bm = 0.0544(length)^{1.919}$	WV	Sample et al. 1993
Neuroptera	$bm = 0.0113(length)^{2.570}$	WV	Sample et al. 1993
Orthoptera	$bm = 0.03(length)^{2.55}$	CA	Sabo et al. 2002
Plecoptera	$bm = 0.0074(length)^{2.4182}$	OR	Li, pers comm
Trichoptera	$bm = 0.0076(length)^{2.6715}$	OR	Li, pers comm

Appendix C. Candidate models relating number of captures per order of insect to vegetation characteristics in riparian areas of the Oregon Coast Range, summers 2002-2004, for Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera. Models were ranked according to Akaike's Information Criteria adjusted for small sample sizes (AIC_c). Sign indicates whether the regression coefficient was positive or negative.

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Coleoptera	deciduous canopy cover	+	0	0.61	0.17
	concentration	+	2.1	0.22	0.12
	null		4.7	0.06	-
	total vegetative cover	-	5.1	0.05	0.03
	stream channel canopy cover	+	5.4	0.04	0.03
	total species richness	-	6.7	0.02	0
Diptera	shrub species richness	-	0	0.27	0.08
	deciduous canopy cover	+	0.1	0.26	0.08
	null		1.1	0.15	-
	concentration	+	1.4	0.13	0.05
	canopy cover	+	1.5	0.13	0.03
	stream channel canopy cover	+	3.0	0.06	0
Ephemeroptera	shrub species richness	-	0	0.34	0.13
	deciduous canopy cover	+	0.6	0.25	0.10
	understory cover	+	0.8	0.23	0.11
	concentration	+	2.9	0.08	0.06
	null		3.2	0.07	-
	stream channel canopy cover	-	4.8	0.03	0.01

Appendix C (Continued).

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Hymenoptera	deciduous canopy cover	+	0	0.76	0.28
	stream channel canopy cover	+	2.7	0.20	0.22
	canopy cover	+	7.2	0.02	0.11
	shrub species richness	-	8.7	0.01	0.08
	null		9.8	0.01	-
	concentration	+	11.5	0.00	0.01
Lepidoptera	deciduous canopy cover	+	0	0.43	0.11
	stream channel canopy cover	+	1.8	0.17	0.07
	null		2.2	0.14	-
	canopy cover	+	2.4	0.13	0.04
	total species richness	+	3.4	0.08	0.02
	concentration	+	4.1	0.05	0
Trichoptera	total deciduous vegetation cover	+	0	0.72	0.18
	understory cover	+	3.9	0.10	0.07
	concentration	+	4.7	0.07	0.06
	null		5.1	0.06	-
	understory species richness	+	5.9	0.04	0.03
	stream channel canopy cover	-	6.9	0.02	0.01

Appendix D. Candidate models relating biomass of insects captured to vegetation characteristics in riparian areas of the Oregon Coast Range, summers 2002-2004, for Coleoptera, Diptera, Ephemeroptera, Hymenoptera, Lepidoptera, and Trichoptera. Models were ranked according to Akaike's Information Criteria adjusted for small sample sizes (AIC_c). Sign indicates whether the regression coefficient was positive or negative.

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Coleoptera	deciduous canopy cover	+	0	0.38	0.14
	stream channel canopy cover	+	0.3	0.33	0.13
	null		2.7	0.10	-
	canopy species richness	+	3.0	0.08	0.06
	canopy cover	+	3.2	0.08	0.06
	concentration	-	5.3	0.03	0
Diptera	concentration	+	0	0.42	0.15
	deciduous canopy cover	+	0.1	0.40	0.14
	null		3.1	0.09	-
	understory species richness	+	4.9	0.04	0.02
	understory cover	+	5.4	0.03	0.01
	stream channel canopy cover	+	5.5	0.03	0.01
Ephemeroptera	shrub species richness	-	0	0.29	0.10
	deciduous canopy cover	+	0.4	0.24	0.09
	null		1.4	0.15	-
	concentration	+	1.4	0.15	0.07
	understory cover	+	1.8	0.12	0.06
	stream channel canopy cover	-	3.6	0.05	0.01

Appendix D (Continued).

Order	Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
Hymenoptera	deciduous canopy cover	+	0	0.67	0.20
	stream channel canopy cover	+	3.1	0.14	0.13
	total vegetative cover	+	4.5	0.07	0.09
	shrub species richness	-	5.2	0.05	0.07
	null		5.3	0.05	-
	concentration	+	7.0	0.02	0.02
Lepidoptera	deciduous canopy cover	+	0	0.91	0.28
	stream channel canopy cover	+	5.2	0.07	0.17
	total vegetative cover	+	9.1	0.01	0.07
	null		9.2	0.01	-
	canopy species richness	+	10.8	0	0.03
	concentration	+	11.6	0	0.01
Trichoptera	total deciduous vegetation cover	+	0	0.79	0.20
	understory cover	+	4.8	0.07	0.09
	concentration	+	5.4	0.05	0.08
	null		5.7	0.05	-
	understory species richness	+	7.1	0.02	0.03
	stream channel canopy cover	-	8.0	0.01	0.01

Appendix E. Macro-moths captured in conifer- and deciduous-dominated stream reaches, Oregon Coast Range, summers 2002-2004.

Family	Species	Coniferous	Deciduous	Total
Arctiidae	*Arctia caja*	1	0	1
Arctiidae	*Clemensia albata*	36	91	127
Arctiidae	*Grammia ornata*	2	3	5
Arctiidae	*Lophocampa argentata*	216	79	295
Arctiidae	*Lophocampa maculata*	165	376	541
Arctiidae	*Pyrrharctia isabella*	5	7	12
Arctiidae	*Spilosoma vestalis*	9	2	11
Arctiidae	*Spilosoma virginica*	40	45	85
Arctiidae	*Tyria jacobeae*	33	2	35
Drepanidae	*Drepana arcuata*	16	51	67
Drepanidae	*Drepana bilineata*	2	3	5
Epiplemidae	*Callizzia amorata*	5	10	15
Geometridae	*Anagoga occiduaria*	15	6	21
Geometridae	*Anavitrinella pampinaria*	1	0	1
Geometridae	*Besma quercivoraria*	3	2	5
Geometridae	*Biston betularia*	13	106	119
Geometridae	*Cabera erythemaria*	9	5	14
Geometridae	*Campaea perlata*	33	73	106
Geometridae	*Caripeta aequaliaria*	0	3	3
Geometridae	*Caripeta divisata*	41	47	88
Geometridae	*Ceratodalia gueneata*	115	214	329
Geometridae	*Chlorosea banksaria*	3	1	4
Geometridae	*Coryphista meadii*	4	3	7
Geometridae	*Cyclophora dataria*	1	2	3
Geometridae	*Cyclophora pendulinaria*	44	99	143
Geometridae	*Drepanulatrix unicalcararia*	0	1	1
Geometridae	*Dysstroma citrata*	29	61	90
Geometridae	*Dysstroma ochrofuscaria*	6	7	13
Geometridae	*Dysstroma sobria*	45	33	78
Geometridae	*Dysstroma truncata*	16	24	40
Geometridae	*Ecliptopera silaceata*	34	19	53
Geometridae	*Ectropis crepuscularia*	0	2	2
Geometridae	*Elpiste lorquinaria*	9	8	17
Geometridae	*Elpiste metanemaria*	6	4	10
Geometridae	*Ennomos magnaria*	2	6	8
Geometridae	*Enypia packardata*	9	4	13
Geometridae	*Enypia venata*	9	10	19

Family	Species	Coniferous	Deciduous	Total
Geometridae	*Eppirhoe alternata*	18	32	50
Geometridae	*Euchlaena tigrinaria*	10	28	38
Geometridae	*Eudrepanulatrix rectifascia*	5	2	7
Geometridae	*Eulithis harveyata*	20	24	44
Geometridae	*Eulithis propulsata*	7	5	12
Geometridae	*Eulithis xylina*	20	24	44
Geometridae	*Euphyia unangulata*	26	35	61
Geometridae	*Eupithecia columbrata*	5	3	8
Geometridae	*Eupithecia cretaceata*	1	0	1
Geometridae	*Eupithecia graefii*	3	0	3
Geometridae	*Eupithecia longipalpata*	1	0	1
Geometridae	*Eupithecia misturata*	1	2	3
Geometridae	*Eupithecia sabulosata*	1	0	1
Geometridae	*Eupithecia subapicata*	3	1	4
Geometridae	*Eupithecia subcolorata*	3	0	3
Geometridae	*Eupithecia unicolor*	2	0	2
Geometridae	*Eustroma fasciata*	1	3	4
Geometridae	*Eustroma semiatrata*	2	2	4
Geometridae	*Gabriola dyari*	32	27	59
Geometridae	*Hesperumia latipennis*	7	8	15
Geometridae	*Hesperumia sulphuraria*	6	5	11
Geometridae	*Hydria undulata*	3	1	4
Geometridae	*Hydriomena furcata*	8	7	15
Geometridae	*Hydriomena marinata*	91	55	146
Geometridae	*Hydriomena renunciata*	34	41	75
Geometridae	*Hydriomena speciosata*	5	4	9
Geometridae	*Hypagyrtis unipunctata*	12	19	31
Geometridae	*Idaea dimidiata*	4	14	18
Geometridae	*Iridopsis emasculata*	239	426	665
Geometridae	*Itame confederata*	1	0	1
Geometridae	*Lambdina fiscellaria*	2	3	5
Geometridae	*Macaria signaria*	140	175	315
Geometridae	*Macaria ulsterata*	4	7	11
Geometridae	*Melanolophia imitata*	5	2	7
Geometridae	*Mesoleuca ruficillata*	3	1	4
Geometridae	*Mycterophora longipalpata*	7	1	8
Geometridae	*Nematocampa resistaria*	34	98	132
Geometridae	*Nemoria darwiniata*	13	15	28
Geometridae	*Neoalcis californiaria*	32	12	44
Geometridae	*Neoterpes trianguliferata*	2	0	2
Geometridae	*Nepytia umbrosaria*	10	10	20

Family	Species	Coniferous	Deciduous	Total
Geometridae	*Orthonama centrostrigaria*	3	13	16
Geometridae	*Perizoma costiguttata*	3	2	5
Geometridae	*Perizoma curvilinea*	70	72	142
Geometridae	*Perizoma grandis*	272	475	747
Geometridae	*Pero behrensaria*	13	7	20
Geometridae	*Pero mizon*	30	35	65
Geometridae	*Pero morrisonaria*	23	39	62
Geometridae	*Plagodis phlogosaria*	1	8	9
Geometridae	*Plemyria georgii*	12	14	26
Geometridae	*Probole alienaria*	18	46	64
Geometridae	*Probole amicaria*	0	1	1
Geometridae	*Protitame matilda*	0	1	1
Geometridae	*Protoboarmia porcelaria*	8	27	35
Geometridae	*Sabulodes aegrotata*	161	330	491
Geometridae	*Scopula junctaria*	3	8	11
Geometridae	*Selenia alciphearia*	5	19	24
Geometridae	*Sicya crocearia*	2	3	5
Geometridae	*Spargania magnoliata*	4	2	6
Geometridae	*Stamnoctenis pearsalli*	15	4	19
Geometridae	*Stamnodes blackmorei*	10	47	57
Geometridae	*Stenoporpia pulmonaria*	5	1	6
Geometridae	*Thallophaga taylorata*	8	5	13
Geometridae	*Trichodezia albovittata*	1	0	1
Geometridae	*Trichodezia californiaria*	0	1	1
Geometridae	*Triphosa haesitata*	1	0	1
Geometridae	*Venusia cambrica*	159	329	488
Geometridae	*Venusia pearsalli*	4	21	25
Geometridae	*Xanthorhoe defensaria*	17	13	30
Geometridae	*Xanthorhoe ferrugata*	8	13	21
Geometridae	*Xanthorhoe labradorensis*	0	1	1
Geometridae	*Xanthorhoe macdunnoughi*	1	0	1
Geometridae	*Xanthorhoe munitata*	1	0	1
Geometridae	*Xanthorhoe pontiaria*	4	9	13
Hepialidae	*Hepialus matthewi*	1	0	1
Lasiocampidae	*Malacosoma californicum*	1	46	47
Lasiocampidae	*Phyllodesma americana*	16	26	42
Lasiocampidae	*Tolype distincta*	27	9	36
Limacodidae	*Tortricidia testacea*	25	61	86
Lymantriidae	*Dasychira grisefacta*	4	10	14
Lymantriidae	*Dasychira vagans*	3	10	13
Lymantriidae	*Orgyia antiqua*	1	2	3

Family	Species	Coniferous	Deciduous	Total
Noctuidae	*Abagrotis pulchrata*	4	1	5
Noctuidae	*Abagrotis trigona*	1	0	1
Noctuidae	*Abrostola urentis*	2	6	8
Noctuidae	*Achytonix epipaschia*	102	157	259
Noctuidae	*Achytonix praecuta*	1	0	1
Noctuidae	*Acronicta grisea*	0	5	5
Noctuidae	*Acronicta hesperida*	13	54	67
Noctuidae	*Acronicta impleta*	0	2	2
Noctuidae	*Adelphagrotis stellaris*	2	8	10
Noctuidae	*Agroperina dubitans*	3	6	9
Noctuidae	*Agrotis vancouverensis*	3	3	6
Noctuidae	*Aletia oxygala*	1	0	1
Noctuidae	*Amphipoea americana*	2	0	2
Noctuidae	*Amphipyra pyramidoides*	0	2	2
Noctuidae	*Anaplectoides prasina*	3	9	12
Noctuidae	*Andropolia aedon*	9	7	16
Noctuidae	*Apamea alia*	1	0	1
Noctuidae	*Apamea amputatrix*	0	4	4
Noctuidae	*Apamea atriclava*	6	5	11
Noctuidae	*Apamea castanea*	2	2	4
Noctuidae	*Apamea vultuosa*	3	1	4
Noctuidae	*Aseptis adnixa*	27	92	119
Noctuidae	*Aseptis binotata*	30	22	52
Noctuidae	*Aseptis ethnica*	2	1	3
Noctuidae	*Asticta victoriae*	3	5	8
Noctuidae	*Autographa ampla*	2	5	7
Noctuidae	*Autographa californica*	0	1	1
Noctuidae	*Autographa corusca*	0	5	5
Noctuidae	*Bellura obliqua*	0	3	3
Noctuidae	*Bomolocha abalienalis*	8	2	10
Noctuidae	*Bomolocha bijugalis*	0	6	6
Noctuidae	*Bomolocha palparia*	3	31	34
Noctuidae	*Brachylomia rectifascia*	1	0	1
Noctuidae	*Cucullia dentilinea*	2	0	2
Noctuidae	*Dargida procincta*	1	2	3
Noctuidae	*Diarsia esurialis*	61	120	181
Noctuidae	*Diarsia rosaria*	0	2	2
Noctuidae	*Egira crucialis*	1	0	1
Noctuidae	*Euplexia benesimilis*	9	10	19
Noctuidae	*Euxoa obeliscoides*	0	1	1
Noctuidae	*Feltia herilis*	1	1	2

Family	Species	Coniferous	Deciduous	Total
Noctuidae	*Galgula partita*	1	1	2
Noctuidae	*Graphiphora haruspica*	4	9	13
Noctuidae	*Heliothis phloxiphagus*	0	2	2
Noctuidae	*Hemeroplanis finitima*	15	15	30
Noctuidae	*Homorthodes communis*	7	5	12
Noctuidae	*Homorthodes fractura*	2	62	64
Noctuidae	*Homorthodes furfurata*	7	13	20
Noctuidae	*Homorthodes hanhami*	0	1	1
Noctuidae	*Homorthodes irrorata*	1	0	1
Noctuidae	*Hypena californica*	4	11	15
Noctuidae	*Hyppa xylinoides*	1	3	4
Noctuidae	*Idia aemula*	11	7	18
Noctuidae	*Lacanobia lilacina*	1	1	2
Noctuidae	*Lacanobia lutra*	2	4	6
Noctuidae	*Lacinipolia cuneata*	9	16	25
Noctuidae	*Lacinipolia davena*	2	0	2
Noctuidae	*Lacinipolia illaudabilis*	0	1	1
Noctuidae	*Lacinipolia olivacea*	3	1	4
Noctuidae	*Lacinipolia rectilinea*	32	32	64
Noctuidae	*Lacinipolia strigicollis*	3	1	4
Noctuidae	*Leucania farcta*	5	11	16
Noctuidae	*Lithacodia albidula*	16	13	29
Noctuidae	*Melanchra adjuncta*	2	6	8
Noctuidae	*Mycterophora longipalpata*	0	1	1
Noctuidae	*Noctua pronuba*	2	4	6
Noctuidae	*Ochropleura plecta*	3	9	12
Noctuidae	*Oligia illocata*	2	0	2
Noctuidae	*Oligia indirecta*	2	5	7
Noctuidae	*Palthis angulalis*	0	5	5
Noctuidae	*Panthea portlandia*	75	25	100
Noctuidae	*Papaipema insulidens*	0	1	1
Noctuidae	*Parabagrotis cupidissima*	3	1	4
Noctuidae	*Parabagrotis exertistigma*	17	4	21
Noctuidae	*Parabagrotis formalis*	3	1	4
Noctuidae	*Parabagrotis insularis*	0	1	1
Noctuidae	*Parabagrotis sulinaris*	2	2	4
Noctuidae	*Peridroma saucia*	0	1	1
Noctuidae	*Perigonica angulata*	1	0	1
Noctuidae	*Perizoma curvilinea*	2	0	2
Noctuidae	*Phalaenophana pyramusalis*	0	1	1
Noctuidae	*Phlogophora periculosa*	26	19	45

Family	Species	Coniferous	Deciduous	Total
Noctuidae	*Polia discalis*	0	10	10
Noctuidae	*Polia nimbosa*	39	82	121
Noctuidae	*Polychrysia morigera*	0	1	1
Noctuidae	*Properigea albimacula*	7	2	9
Noctuidae	*Pseudorthodes irrorata*	14	44	58
Noctuidae	*Pyrrhia exprimens*	0	1	1
Noctuidae	*Rivula propinqualis*	6	26	32
Noctuidae	*Scoliopteryx libatrix*	1	8	9
Noctuidae	*Spaelotis bicava*	1	0	1
Noctuidae	*Spodoptera praefica*	1	1	2
Noctuidae	*Syngrapha celsa*	7	25	32
Noctuidae	*Syngrapha rectangula*	4	7	11
Noctuidae	*Xestia flavotincta*	5	7	12
Noctuidae	*Xestia mustelina*	2	2	4
Noctuidae	*Xestia plebeia*	0	1	1
Noctuidae	*Xestia smithii*	0	1	1
Noctuidae	*Zale lunata*	0	1	1
Noctuidae	*Zale minerea*	1	3	4
Noctuidae	*Zanglognatha jacchusalis*	0	3	3
Noctuidae	*Zosteropoda hirtipes*	4	4	8
Noctuidae	*Zotheca tranquilla*	1	13	14
Notodontidae	*Nadata gibbosa*	135	230	365
Notodontidae	*Oligocentria pallida*	7	13	20
Notodontidae	*Oligocentria semirufescens*	40	143	183
Notodontidae	*Schizura concinna*	0	1	1
Notodontidae	*Schizura ipomeae*	9	26	35
Notodontidae	*Schizura unicornis*	4	5	9
Saturniidae	*Antheraea polyphemus*	24	54	78
Sphingidae	*Smerinthus cerisyi*	1	4	5
Thyatiridae	*Euthyatira semicircularis*	7	5	12
Thyatiridae	*Habrosyne scripta*	9	29	38
Thyatiridae	*Pseudothyatira cymatophoroides*	6	25	31
Total		3650	5864	9514

Appendix F. Bat echolocation call identification key

I viewed files in Analook (v4.9j). This program has a range of pre-defined filters that differentiate between series of dots that are smoothly connected to one another (those with a high likelihood of being pulses of sound produced by echolocating bats), and dots that are disjunct from adjacent dots (those with a low likelihood of being sounds produced by bats), and makes each of these two types of dots different colors. I viewed files with the least discriminating filter provided by the program (filter 1) on, so that dots with very low likelihood of being sounds produced by bats were filtered out. Analook also has the capacity to measure certain characteristics of calls displayed on the screen. I did not use these measurements, but did view files with the "measurement mode" turned on so that groups of smoothly connected dots were automatically highlighted by the program. With these settings (filter =1, offdots = on, and measurement mode = on), "offdots" (those dots that were filtered out) were one color, maindots (those smoothly connected dots used by Analook to measure call characteristics) were a second color, and the remaining dots were a third color.

I used the following objective criteria to categorize files into one of three groups: (1) noise unlikely to have been produced by bats, (2) fragments of calls made by bats that I could not reliably identify, or (3) call sequences identifiable to one of five bat phonic groups.

1. File contains ≥2 pulses (groups of smoothly connected dots) within the frequency range 18-80 KHz, each separated by <1 sec of silence..........2
   Otherwise.......... conclude that no bat activity occurred within the time period sampled by this file
2. File contains ≥2 pulses having ≥6 dots recognized as "maindots" separated by <1 sec of silence..........4
   Otherwise..........3
3. File contains ≥2 broadband pulses with no knee and with minimum frequency in the range 25-35 KHz..........MYEV/MYTH
   Otherwise..........conclude that this is a call fragment and do not attempt further identification
4. Majority of "maindots" in the majority of pulses are either within 30-35 KHz or within 50-60 KHz: file must contain distinct pulses within both of these ranges..........COTO
   Otherwise..........5
5. Majority of "maindots" in the majority of pulses are within 47-59 KHz..........MYCA/MYYU
   Otherwise..........6
6. Majority of "maindots" in the majority of pulses are within 38-52 KHz..........MYLU/MYVO
   Otherwise..........7
7. Majority of "maindots" in the majority of pulses are within 18-32 KHz..........LANO/EPFU/LACI

Appendix G. Candidate models relating bat activity to number of insects captured of different orders and size classes in riparian areas of the Oregon Coast Range, summers 2002-2004, for MYLU/MYVO (a), MYCA/MYYU (b), MYEV/MYTH (c), COTO (d), and EPFU/LANO/LACI (f). Models were ranked according to Akaike's Information Criteria adjusted for small sample sizes (AIC_c). Sign indicates whether the regression coefficient was positive or negative.

a. Activity of MYYU/MYVO

Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
number of small insects	+	0	0.67	0.47
number of Diptera	+	2.2	0.22	0.42
number of all insects	+	3.6	0.11	0.39
number of Trichoptera	+	10.8	0	0.20
number of medium insects	+	13.5	0	0.11
number of large insects	+	13.6	0	0.11
null		14.0	0	-
number of Lepidoptera	+	16.5	0	0

b. Activity of MYCA/MYYU

Explanatory variable in model	Sign	ΔAIC_c	w_i	Proportion of variance explained
number of small insects	+	0	0.58	0.26
number of Diptera	+	1.9	0.23	0.21
number of all insects	+	3.6	0.09	0.15
null		5.3	0.04	-
number of large insects	+	6.8	0.02	0.04
number of Trichoptera	+	7.3	0.01	0.02
number of Lepidoptera	+	7.5	0.01	0.02
number of medium insects	+	7.7	0.01	0.01

Appendix G (Continued).

c. Activity of MYEV/MYTH

Explanatory variable in model	Sign	ΔAIC$_c$	w_i	Proportion of variance explained
null		0	0.30	-
number of Coleoptera	+	1.2	0.16	0.05
number of medium insects	+	2.0	0.11	0.02
number of Lepidoptera	+	2.1	0.10	0.02
number of small insects	-	2.5	0.09	0
number of all insects	+	2.6	0.08	0
number of Hemiptera	+	2.6	0.08	0
number of large insects	+	2.6	0.08	0

d. Activity of COTO

Explanatory variable in model	Sign	ΔAIC$_c$	w_i	Proportion of variance explained
number of medium insects	-	0	0.39	0.15
number of large insects	-	1.5	0.19	0.10
null		1.7	0.17	-
number of all insects	-	2.3	0.12	0.07
number of small insects	-	3.2	0.08	0.04
number of Lepidoptera	-	3.9	0.05	0.01

e. Activity of EPFU/LANO/LACI

Explanatory variable in model	Sign	ΔAIC$_c$	w_i	Proportion of variance explained
number of Hemiptera	-	0	0.27	0.10
null		0	0.27	-
number of small insects	+	2.4	0.08	0.01
number of Coleoptera	+	2.6	0.08	0
number of large insects	-	2.6	0.08	0
number of medium insects	-	2.6	0.08	0
number of all insects	+	2.6	0.07	0
number of Lepidoptera	-	2.6	0.07	0

Appendix H. Candidate models from step 2 of the model selection procedure, relating bat activity to vegetation characteristics at multiple spatial scales in riparian areas of the Oregon Coast Range, summers 2002-2004. We ranked all models containing one level-1 explanatory variable in combination with one level-2 explanatory variable plus the null model according to $\mathrm{AIC_c}$ for MYCA/MYYU (a), MYLU/MYVO (b), MYEV/MYTH (c), and EPFU/LANO/LACI (d). Models were ranked according to Akaike's Information Criteria adjusted for small sample sizes ($\mathrm{AIC_c}$).

a. Activity of MYCA/MYYU

Level-2 explanatory variables	Level-1 explanatory variables	$\Delta\mathrm{AIC_c}$	w_i
riparian buffer vegetation	% cover of deciduous shrubs	0.0	0.71
watershed vegetation	% cover of deciduous shrubs	2.8	0.17
riparian buffer vegetation	% cover of shrubs	4.3	0.08
watershed vegetation	% cover of shrubs	7.3	0.02
riparian buffer vegetation	activity area vegetation rarity	10.1	0
null	null	10.2	0
riparian buffer vegetation	activity area vegetation composition	12.1	0
watershed vegetation	activity area vegetation rarity	12.2	0
riparian buffer vegetation	species richness of understory trees	12.4	0
watershed vegetation	activity area vegetation composition	12.9	0
riparian buffer vegetation	open air space above stream channel	13.3	0
watershed vegetation	open air space above stream channel	15.9	0
watershed vegetation	species richness of all woody vegetation	16.6	0

b. Activity of MYLU/MYVO

Level-2 explanatory variables	Level-1 explanatory variables	$\Delta\mathrm{AIC_c}$	w_i
watershed vegetation	open air space above stream channel	0.0	0.29
riparian buffer vegetation	open air space above stream channel	0.2	0.26
watershed vegetation	activity area vegetation rarity	2.0	0.11
riparian buffer vegetation	activity area vegetation rarity	2.0	0.11
null	null	2.2	0.10
watershed vegetation	% cover of deciduous canopy trees	4.3	0.03
riparian buffer vegetation	activity area vegetation composition	4.8	0.03
riparian buffer vegetation	% cover of deciduous canopy trees	4.9	0.03
riparian buffer vegetation	species richness of shrubs	6.0	0.01
riparian buffer vegetation	% cover of all vegetation	6.6	0.01
watershed vegetation	species richness of canopy trees	6.8	0.01
watershed vegetation	% cover of all vegetation	6.9	0.01

Appendix H (Continued).

c. Activity of MYEV/MYTH

Level-2 explanatory variables	Level-1 explanatory variables	ΔAIC_c	w_i
riparian buffer vegetation	% cover of canopy trees	0.0	0.39
watershed vegetation	% cover of canopy trees	0.0	0.39
null	null	3.0	0.09
watershed vegetation	species richness of understory trees	4.8	0.04
riparian buffer vegetation	species richness of understory trees	5.6	0.02
watershed vegetation	% cover of all deciduous vegetation	5.6	0.02
riparian buffer vegetation	% cover of deciduous canopy trees	6.4	0.02
watershed vegetation	open air space above stream channel	7.0	0.01
riparian buffer vegetation	open air space above stream channel	7.3	0.01
watershed vegetation	activity area vegetation composition	8.5	0.01
watershed vegetation	activity area vegetation rarity	9.0	0
riparian buffer vegetation	activity area vegetation composition	9.0	0
riparian buffer vegetation	activity area vegetation rarity	9.2	0

d. Activity of EPFU/LANO/LACI

Level-2 explanatory variables	Level-1 explanatory variables	ΔAIC_c	w_i
riparian buffer vegetation	open air space above stream channel	0.0	0.70
watershed vegetation	open air space above stream channel	1.8	0.28
riparian buffer vegetation	% cover of canopy trees	7.4	0.02
watershed vegetation	% cover of canopy trees	10.4	0
riparian buffer vegetation	species richness of shrubs	24.7	0
watershed vegetation	species richness of shrubs	24.8	0
riparian buffer vegetation	% cover of deciduous canopy trees	26.1	0
watershed vegetation	% cover of deciduous canopy trees	26.2	0
null	null	28.4	0
watershed vegetation	activity area vegetation rarity	31.2	0
riparian buffer vegetation	activity area vegetation rarity	31.4	0

Appendix I. Candidate models from step 4 of the model selection procedure, relating bat activity to vegetation characteristics in riparian areas of the Oregon Coast Range, summers 2002-2004 for MYCA/MYYU (a), MYLU/MYVO (b), MYEV/MYTH (c), and EPFU/LANO/LACI (d). All explanatory variables are those dealing with vegetation characteristics at the stream reach or nightly activity area scale. Models were ranked according to Akaike's Information Criteria adjusted for small sample sizes (AIC_c) and Akaike weights(w_i). Sign indicates whether regression coefficients were positive or negative.

a. Activity of MYCA/MYYU

Explanatory variables in model	Sign	ΔAIC_c	w_i
% cover of deciduous shrubs	-	0.0	0.89
% cover of shrubs	-	4.5	0.09
activity area vegetation rarity	+	9.5	0.01
null		9.7	0.01
activity area vegetation composition	-	10.7	0.00
open air space above stream channel	+	13.3	0.00
species richness of all woody vegetation	+	13.9	0.00

b. Activity of MYLU/MYVO

Explanatory variables in model	Sign	ΔAIC_c	w_i
open air space above stream channel	+	0.0	0.55
activity area vegetation rarity	+	2.1	0.19
% cover of deciduous shrubs	-	2.6	0.15
null		4.3	0.06
species richness of shrubs	-	6.1	0.03
% cover of all vegetation	-	6.8	0.02

c. Activity of MYEV/MYTH

Explanatory variables in model	Sign	ΔAIC_c	w_i
% cover of canopy trees	+	0.0	0.84
null		5.2	0.06
species richness of understory trees	-	6.3	0.04
open air space above stream channel	-	7.3	0.02
% cover of deciduous understory trees	-	7.7	0.02
activity area vegetation composition	-	9.0	0.01
activity area vegetation rarity	-	9.2	0.01

Appendix I (Continued).

d. Activity of EPFU/LANO/LACI

Explanatory variables in model	Sign	ΔAIC_c	w_i
% cover of canopy trees	-	0.0	0.54
open air space above stream channel	+	0.4	0.43
% cover of deciduous canopy trees	-	7.4	0.01
species richness of shrubs	+	9.5	0.00
activity area vegetation rarity	-	9.7	0.00
activity area vegetation composition	+	11.5	0.00
null		11.6	0.00