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ARTHROPOD PREY OF WILSON'S WARBLERS IN THE UNDERSTORY OF DOUGLAS-FIR FORESTS

JOAN C. HAGAR,[1,3] KATIE M. DUGGER,[2] AND EDWARD E. STARKEY[1]

ABSTRACT.—Availability of food resources is an important factor in avian habitat selection. Food resources for terrestrial birds often are closely related to vegetation structure and composition. Identification of plant species important in supporting food resources may facilitate vegetation management to achieve objectives for providing bird habitat. We used fecal analysis to describe the diet of adult Wilson's Warblers (*Wilsonia pusilla*) that foraged in the understory of Douglas-fir (*Pseudotsuga menziesii*) forests in western Oregon during the breeding season. We sampled arthropods at the same sites where diet data were collected, and compared abundance and biomass of prey among seven common shrub species. Wilson's Warblers ate more caterpillars (Lepidoptera larvae), flies (Diptera), beetles (Coleoptera), and Homoptera than expected based on availability. Deciduous shrubs supported higher abundances of arthropod taxa and size classes used as prey by Wilson's Warblers than did evergreen shrubs. The development and maintenance of deciduous understory vegetation in conifer forests of the Pacific Northwest may be fundamental for conservation of food webs that support breeding Wilson's Warblers and other shrub-associated, insectivorous songbirds. *Received 28 April 2006. Accepted 23 February 2007.*

Food availability is a basic, critical habitat component that often limits reproductive success and survival of breeding birds (Martin 1987, Rodenhouse and Holmes 1992). Distribution and abundance of food have been correlated with population size of birds and are major factors in habitat selection and use (Wiens 1989, Block and Brennan 1993). The availability of food resources for terrestrial birds often is closely tied to vegetation structure and composition (Robinson and Holmes 1982, Holmes and Schultz 1988, Whelan 1989). Unfortunately, researchers rarely quantify direct linkages between vegetation and food resources (Holmes 1981), relying instead on correlative relationships between vegetation structure and bird density or abundance. These relationships can be obscure and unpredictable because birds do not usually respond directly to variables chosen by human observers to quantify habitat (Morse 1985). Thus, evaluation of habitat on the basis of vegetation structure may be unreliable unless associations between wildlife and vegetation are based on a detailed knowledge of species-specific resource requirements (Van Horne 1983). Direct measurements of resources, such as arthropod biomass available to insectivorous birds, may better predict habitat use than variables that describe vegetation (Brush and Stiles 1986). An understanding of the trophic pathways from vegetation to songbirds would provide an empirical foundation for management of vegetation to achieve objectives for managing bird habitat. The first step in understanding trophic links between birds and vegetation is to identify the composition of birds' diets. Once composition of the diet is known, it should be possible to identify plant species and habitat conditions that are important in supporting those food resources.

The goal of our study was to identify shrub species important in supporting arthropod prey for Wilson's Warblers (*Wilsonia pusilla*). We hypothesized that abundance of arthropod prey would differ among several of the most common plant species occurring in the understory of Douglas-fir (*Pseudotsuga menziesii*) forests. Our specific objectives were to: (1) identify the taxa and size categories of arthropods Wilson's Warblers use as prey, and (2) compare abundance and biomass of prey arthropods among common understory shrubs.

METHODS

Study Area.—Study sites were in forests of the Oregon Coast Range, in the Western Hemlock (*Tsuga heterophylla*) forest vegetation zone (Franklin and Dyrness 1988), between 200 and 500 m elevation. Mild, wet winters

[1] Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, 777 NW 9th St., Ste 400, Corvallis, OR 97330, USA.

[2] Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA.

[3] Corresponding author;
e-mail: joan_hagar@usgs.gov

and dry summers characterize the regional climate. Sites were on lands managed by the Bureau of Land Management and the U.S. Forest Service. We sampled seven stands that were chosen to represent a range of variability in understory structure. All stands were dominated by Douglas-fir, but represented a range of ages and structural conditions. Four stands were relatively young, 55- to 65-years of age, and had regenerated naturally following clearcut harvesting. A single age cohort dominated the overstory of these stands with few (<1/ha) large trees and well-decayed snags persisting from previous stands. Three of these young stands had been thinned to uniform spacing 19–28 years prior to this study; the fourth remained unthinned. The remaining three stands had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). Major understory plant species included sword fern (*Polystichum munitum*), bracken fern (*Pteridium aquilinum*), salal (*Gaultheria shallon*), Oregon-grape (*Berberis nervosa*), vine maple (*Acer circinatum*), and oceanspray (*Holodiscus discolor*).

Diet Sampling.—We addressed our first objective by identifying the taxonomic groups and sizes of arthropods in fecal samples collected from adult Wilson's Warblers and comparing those to arthropods generally available on understory vegetation. We examined 87 fecal samples collected from 77 individual Wilson's Warblers that had been captured in mistnets between mid-May and mid-July, 1996 and 1997. We identified arthropod fragments to the lowest taxonomic level possible using well-illustrated entomology texts and guides (Borror and White 1970, Shattuck 1985, Moldenke et al. 1987, Borror et al. 1989) and consultation with experts (A. R. Moldenke, Oregon State University; G. J. Brenner, Pacific Analytics Inc., Albany, OR). We measured lengths of whole femurs, tibias, and mandibles using an ocular micrometer fitted on the microscope. We estimated the original length of arthropod prey from fragments using regression equations developed from arthropods collected on shrubs in the Oregon Coast Range (Hagar 2004). We applied these regressions to whole tibias, femurs, and mandibles in fecal samples. We averaged predicted body lengths derived from femora and tibiae for spiders because we were frequently unable to distinguish spider femora from tibiae in fecal samples.

Arthopod Sampling.—Arthropods used to estimate available prey for Wilson's Warblers were collected from understory vegetation within 10 days of fecal sample collection in each stand, coinciding temporally and spatially with diet sampling. Arthropods (and fecal samples) were collected twice at each site between 26 May and 26 June, and between 30 June and 30 July. A shrub-beating method (Borror et al. 1989, Cooper and Whitmore 1990) was used to sample sedentary arthropods that are potential prey for Wilson's Warblers. Beating foliage to dislodge arthropods was an adequate method for sampling free-living, sedentary prey items available to birds, but organisms such as miners and borers were inadequately sampled because we did not visually inspect for organisms that may have been attached to vegetation. These organisms likely offer less food value to many species of insectivorous birds because of their relative inaccessibility and the increased effort required to forage on them effectively (Holmes and Schultz 1988).

We were logistically limited to sampling arthropods on vegetation ≤2 m above the forest floor. Wilson's Warblers are known to forage to the maximum height of the available vegetation (Stewart et al. 1977), but 75% of the foraging events observed on our study sites occurred in the layer of vegetation sampled for arthropods (Hagar 2004). However, we were unable to measure all prey available to Wilson's Warblers, and consulted the literature to evaluate the potential abundance of selected prey taxa in the forest canopy before making conclusions regarding prey availability and selection. We use ''selection'' to indicate that an arthropod group was used as prey more than expected based on frequency of occurrence in the environment.

''Shrub'' refers to any woody plant species or fern having foliage within 2 m of the forest floor. Shrubs were selected for sampling at 50- to 75-m intervals along randomly established transects in each stand (Table 1). Species of vegetation sampled varied within and between stands because the two most dominant shrub species (based on percent cover) at each sampling point were selected for beating. Eight to 31 beating samples from each stand were col-

TABLE 1. Common and scientific names, and sample sizes (number of beating samples) of understory shrubs from which arthropod prey was sampled, Oregon Coast Range, 1996–99.

Common name	Scientific name	Acronym	*n*
Vine maple	*Acer circinatum*	ACCI	252
California hazel	*Corylus cornuta*	COCO	47
Salal	*Gaultheria shallon*	GASH	257
Oceanspray	*Holodiscus discolor*	HODI	61
Sword fern	*Polystichum munitum*	POMU	187
Bracken fern	*Pteridium aquilinum*	PTAQ	132
Western hemlock	*Tsuga heterophylla*	TSHE	156
Oregon-grape*	*Berberis nervosa*	BENE	7
Pacific dogwood*	*Cornus nuttalli*	CONU	1
Indian plum*	*Oemleria cerasiformis*	OECE	1
Douglas-fir*	*Pseudotsuga menziesii*	PSME	8
Thimbleberry*	*Rubus parviflora*	RUPA	1
Salmonberry*	*Rubus spectabilis*	RUSP	20
Snowberry*	*Symphoricarpos albus*	SYAL	3
Red huckleberry*	*Vaccinium parvifolium*	VAPA	3

* Sample size insufficient to include in comparison of prey load among plant species.

lected in each sampling period, depending on the size of the stand and the length of transect sampled. A different transect was established in each stand for each sample period within a year. Each shrub sample consisted of a surface area of ~1 m^2, corresponding to the size of the beating sheet. Thus, one sample of a shrub was approximately equal to 100 leaves (vine maple, oceanspray, and salmonberry [*Rubus spectabilis*]), 50 leaves (salal and California hazel [*Corylus cornuta*]), 5 fronds of bracken fern and 8 of sword fern, or a 1-m^2 branch (western hemlock). Arthropods were dislodged from clipped branches and foliage onto a canvas sheet and aspirated into vials. Plant material was dried and weighed.

We used an expanded sample of arthropods, collected over four summer seasons (May–Jul) 1996–1999 to describe differences in prey resources supported among shrub species. The sites represented were those used for collecting Wilson's Warbler diet data, plus six additional, similar stands in the same region of the central Oregon Coast Range (Doolittle 2000). We compared arthropod abundance among shrub species that were sampled in at least five stands and over at least 3 years.

Statistical Analyses.—The frequency of occurrence of each arthropod group in the diet was calculated as the number of fecal samples containing a given arthropod group divided by the total number of fecal samples. The lowest taxonomic levels that could be identified from fragments in fecal samples defined arthropod groups used for analyses. We calculated frequency of occurrence of each arthropod group from all beating samples (all shrub species pooled) collected in both years to derive a measure of available prey. We compared the frequency of occurrence of arthropod groups in the diet of Wilson's Warblers with frequency of occurrence on shrubs, and ranked groups by the ratio of frequency of occurrence in diet to that on shrubs. We used this forage ratio (Krebs 1989) as an index of prey selection by Wilson's Warblers with ratios >1 indicating greater than expected use based on availability in the understory. We focused analyses of prey sizes on arthropod groups that occurred in >60% of Wilson's Warbler diets and had forage ratios >1.

We used the Kolmogorov-Smirnov statistic (Steel and Torrie 1980) to test whether the distribution of arthropod sizes was the same for arthropods consumed by Wilson's Warblers as for arthropods collected from vegetation (PROC NPAR1WAY, SAS Institute 2000). We compared size distributions for larvae (including Lepidoptera [caterpillars] and Symphyta [sawflies]), Diptera (flies), Coleoptera (beetles), Homoptera, and all adult arthropods pooled. We used an *alpha* level of 0.05 for significance.

We compared the abundance (number of individuals/100 g dry plant matter) and biomass (arthropod weight [mg]/100 g dry plant mat-

ter) of arthropod groups identified as being selected as prey, based on the results of the diet analysis, among seven understory shrub species (Table 1). Arthropod weights were calculated from regression models that estimated wet weight based on body length (Hagar 2004). We pooled data across all 4 years to compare the abundance and biomass of five arthropod categories (adult beetles and flies >3 mm, adult Homoptera >2 mm, caterpillars >6 mm in length, and all arthropod prey combined) among plant species. The combined category of arthropod prey included adult flies and beetles >3 mm, caterpillars and sawfly larvae >6 mm, and all other adult arthropods >2 mm in length (except diplopods).

We used a Kruskal-Wallis non-parametric ANOVA with rank transformations (SAS Institute 2000) to test for differences in arthropod abundance and biomass among plant species for all prey groups except the category of combined taxa. We log-transformed response variables to normalize data and stabilize variances for the combined category of arthropod prey. A parametric ANOVA was used to test for differences in overall prey abundance and biomass among plant species (PROC MIXED, SAS Institute 2000). We evaluated overlap of 90% confidence intervals around back-transformed medians (all arthropod prey combined) or mean ranks (all other prey groups) to compare responses between specific plant species (Steidl et al. 1997). Significance was set at *alpha* = 0.05.

RESULTS

Arthropods in Diet.—We identified 15 groups of arthropod taxa in 87 Wilson's Warbler fecal samples from both years (Table 2). Nine families within four Orders also were identified from fragments: Homoptera: Achilidae, Aphididae, and Cercopidae; Neuroptera: Chrysopidae; Coleoptera: Cantharidae and Mordellidae; and Diptera: Empididae, Mycetophillidae, and Sciaridae. Caterpillars (Lepidoptera larvae), Homoptera, flies, and beetles had high frequencies of occurrence in fecal samples (>60%), and had forage ratios >1 (Table 2). Adult Lepidoptera and arthropod eggs had the highest forage ratios, but occurred relatively infrequently in the diet and were not well sampled by shrub-beating. In contrast, spiders occurred frequently, both in the diet and on vegetation.

TABLE 2. Arthropods in diets of Wilson's Warblers (n = 87) and on shrubs (n = 681 samples from beating) in the Oregon Coast Range, 1996–97. The ratio of the frequency of occurrence in diet to that on shrubs (forage ratio) is interpreted as an index of prey selection with ratios >1 indicating greater than expected use based on availability.

Group	Occurrence (%)		Forage ratio
	Diet	Shrubs	
Lepidoptera, adults	18	<1	45.98
Unknown arthropod eggs	14	1	11.49
Lepidoptera, larvae *	63	12	5.06
Homoptera (all taxa) *	86	51	1.69
Diptera *	99	59	1.67
Hymenoptera, wasps	46	28	1.67
Hymenoptera, Symphyta larvae	20	12	1.64
Coleoptera (all taxa) *	84	58	1.45
Homoptera, Cercopidae	23	16	1.44
Araneida (all spiders)	85	90	0.94
Neuroptera	5	7	0.67
Acari (mites)	2	20	0.11
Collembola	5	56	0.08
Psocoptera	2	31	0.07
Hemiptera	1	19	0.06

* Arthropod groups that occurred in > 60% of diets and had forage ratios >1.

Average size of adult arthropods consumed was ~4 mm and ranged from 2 to 10 mm (Fig. 1A). The size distribution of adult arthropods consumed differed (Kolmogorov-Smirnov two-sample test, $P < 0.001$) from the distribution for available adult arthropods indicating that Wilson's Warblers consumed prey that were larger than the most abundant items available. This pattern was consistently significant across the most frequently consumed adult arthropod groups (Kolmogorov-Smirnov two-sample test, $P < 0.001$, Fig. 1B–D). We did not find evidence of the largest available size classes (>12 mm) of adult arthropods, including flies, beetles, and spiders, in the diet.

Larvae, primarily caterpillars and sawflies, were the largest prey items consumed by Wilson's Warblers. Larvae ranged from ~6 to 26 mm in length. The size distribution of larvae consumed also differed (Kolmogorov-Smirnov two-sample test, $P < 0.001$) from that of available larvae because warblers were eating mostly the larger (>6 mm) larvae, which oc-

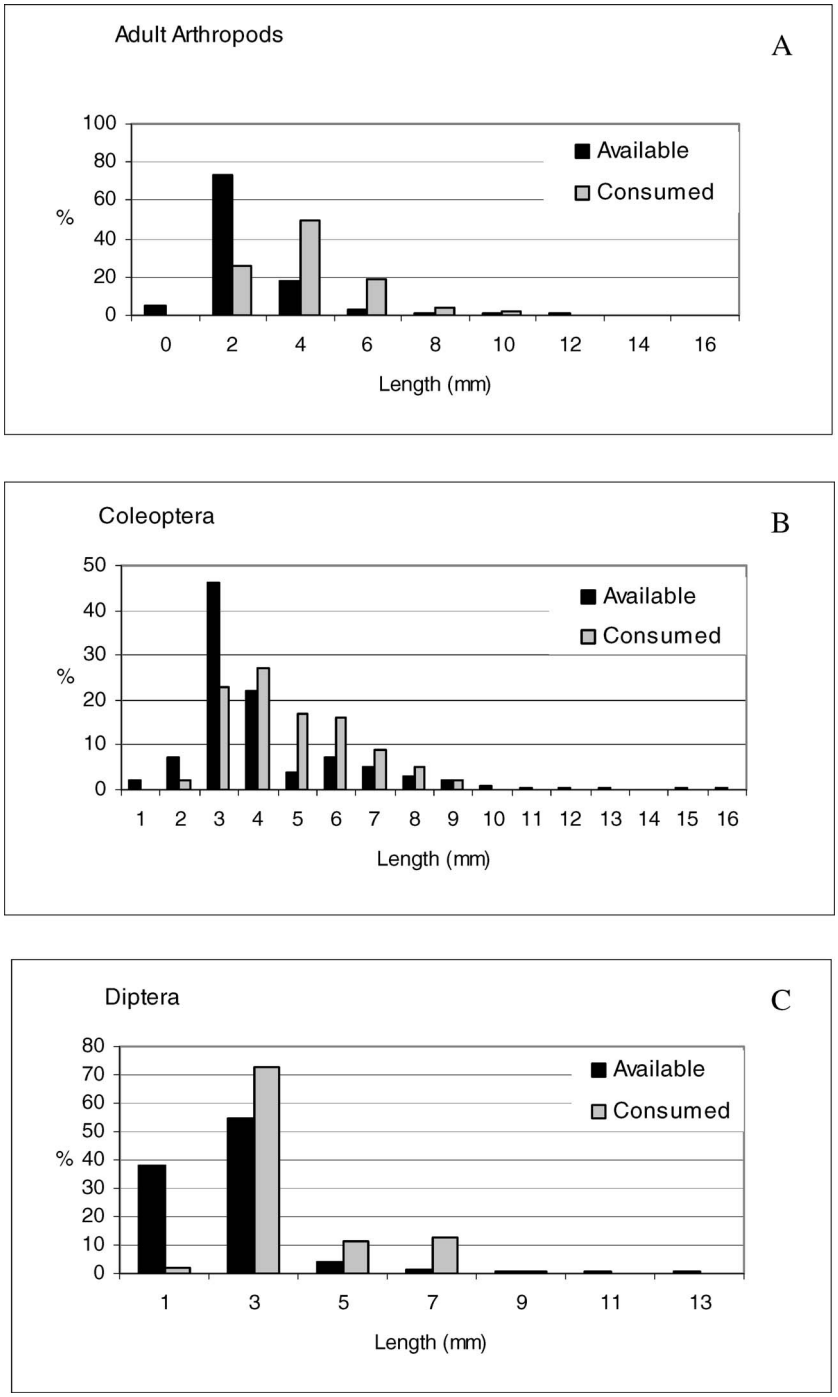
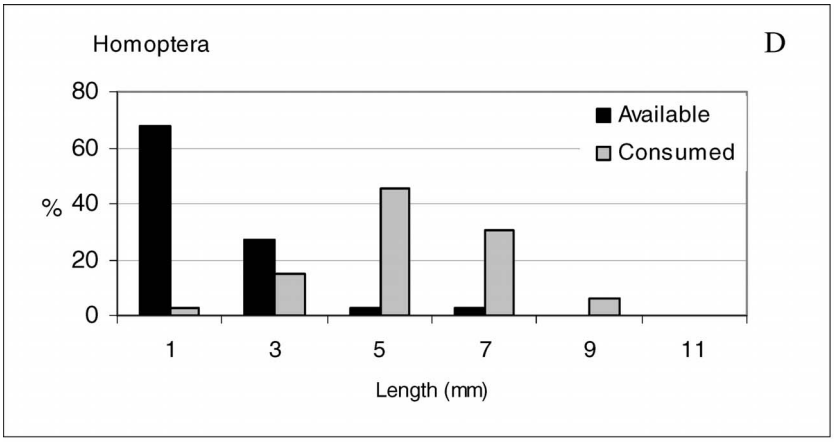


FIG. 1. Distribution among size classes of (A) adult arthropods, (B) Coleoptera, (C) Diptera, (D) Homoptera, and (E) sawfly and Lepidoptera larvae available as prey and those consumed by Wilson's Warblers in the Oregon Coast Range, 1996–1997.



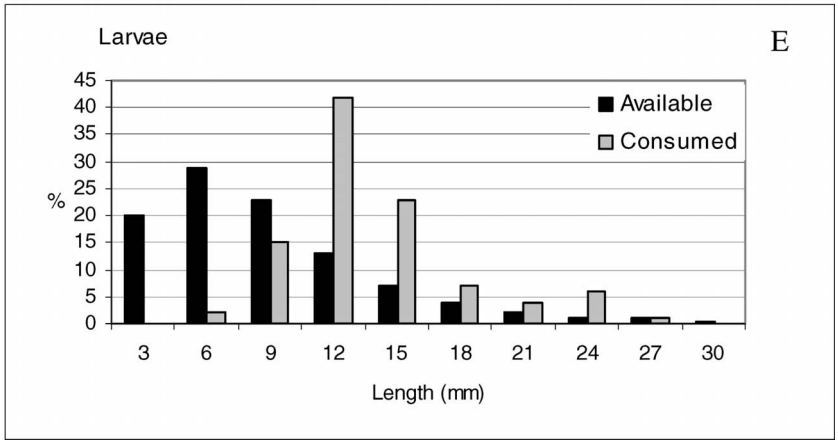


FIG. 1. Continued.

curred less frequently than those in the smaller size classes (Fig. 1E).

Arthropods in Understory Vegetation.— Thirteen insect Orders, seven non-insect arthropod taxa, and two mollusk taxa were identified from 28,438 individuals collected from 15 understory plant species over 4 years. The most abundant taxa overall were aphids and spiders, each accounting for more than 20% of the total number of individuals collected. Linyphiidae and Theridiidae, both web-spinning families, were the most abundant spiders.

Both abundance and biomass of all prey taxa combined varied significantly ($P < 0.001$, ANOVA) among plant species. Median prey abundance on bracken fern was more than 1.5 times greater than on any other species (Fig. 2A). Bracken fern also supported a higher biomass of prey than all plant species except oceanspray (Fig. 2B). Sword fern supported the second highest abundance of arthropod prey after bracken, but prey biomass was relatively low, reflecting the small size of most arthropods on this fern species. Western hemlock supported a lower abundance of prey than all other shrub species sampled, and biomass supported was lower than all except vine maple.

Caterpillars were rare on the vegetation we sampled, occurring in only 14% of the 1,136 beating samples across all shrub species. Abundance and biomass of caterpillars (>6 mm) differed (Kruskall-Wallis; abundance: $\chi^2_6 = 15.9$, $P = 0.01$, biomass: $\chi^2_6 = 12.9$, $P = 0.04$) among plant species. Oceanspray had a greater abundance and biomass of caterpillars

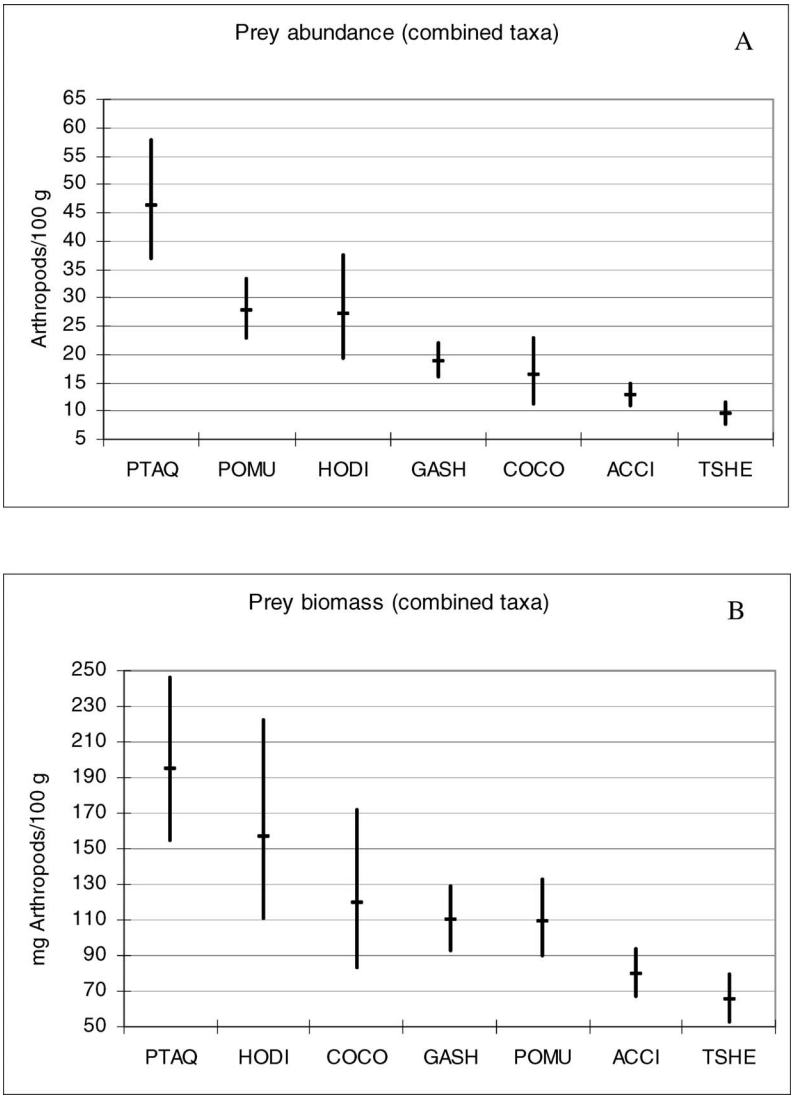


FIG. 2. (A) Median abundance index (individuals/100 g dry plant material) and (B) biomass index (mg/100 g dry plant material) with 90% confidence limits of arthropod prey for Wilson's Warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in abundance or biomass if confidence limits of one do not overlap the median of the other.

than all other understory species except California hazel (Fig. 3). Hazel also had a relatively high rank for caterpillar abundance and biomass, although 90% confidence intervals overlapped mean values for vine maple and western hemlock. The frequency of occurrence of caterpillars also was higher on oceanspray (21%) and California hazel (36%) than on vine maple (16%), western hemlock (18%), bracken fern (11%), salal (9%), and sword fern (7%). Sword fern supported the lowest abundance and biomass of caterpillars of all plant species sampled (Fig. 3).

Abundance and biomass of flies (>3 mm) varied (Kruskall-Wallis: abundance: χ^2_6 = 16.1, P = 0.01, biomass: χ^2_6 = 14.3, P = 0.03) among plant species. Bracken fern and oceanspray ranked highest in abundance and

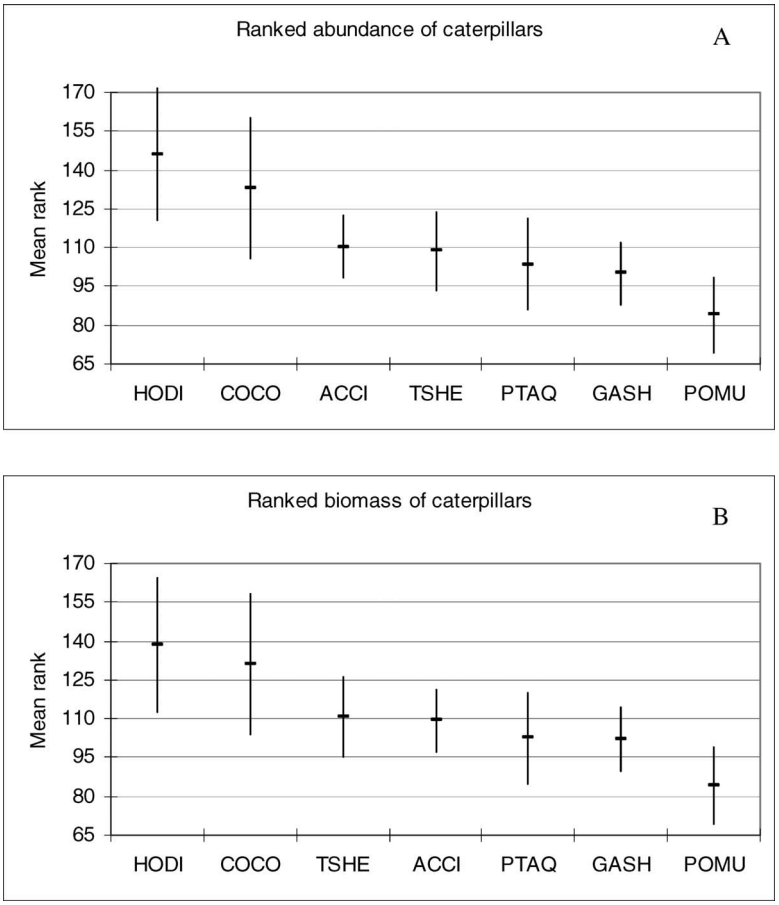


FIG. 3. (A) Ranked abundance and (B) biomass with 90% confidence limits of caterpillar (Lepidoptera larvae) prey for Wilson's Warblers on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

biomass of flies, but overlapping confidence intervals with vine maple, salal, and sword fern provided weak evidence of differences among these five species. Western hemlock and California hazel had the lowest rankings for both abundance and biomass of flies (Fig. 4).

Abundance and biomass of beetles (>3 mm) also differed (Kruskall-Wallis: abundance: $\chi^2_6 = 20.3$, $P < 0.01$, biomass: $\chi^2_6 = 16.1$, $P = 0.01$) among plant species. Western hemlock ranked lower for beetle abundance than all species except salal (Fig. 5), whereas California hazel, vine maple, oceanspray, sword fern, and bracken were all similar. Hazel ranked higher for biomass of beetles than all species except vine maple and oceanspray, whereas western hemlock, salal, sword fern, bracken, and oceanspray did not differ.

Homoptera abundance and biomass were clearly distinguished by plant species (Kruskall-Wallis: abundance: $\chi^2_6 = 49.4$, $P < 0.001$, biomass: $\chi^2_6 = 49.9$, $P < 0.001$) with bracken fern out-ranking all other plant species (Fig. 6). California hazel, salal, and sword fern ranked lower than bracken but higher than vine maple, oceanspray, and western hemlock in abundance and biomass of homopteran prey supported.

DISCUSSION

Wilson's Warbler Diet.—Breeding Wilson's Warblers preyed on a wide range of arthropod taxa, but consumed caterpillars, flies, beetles,

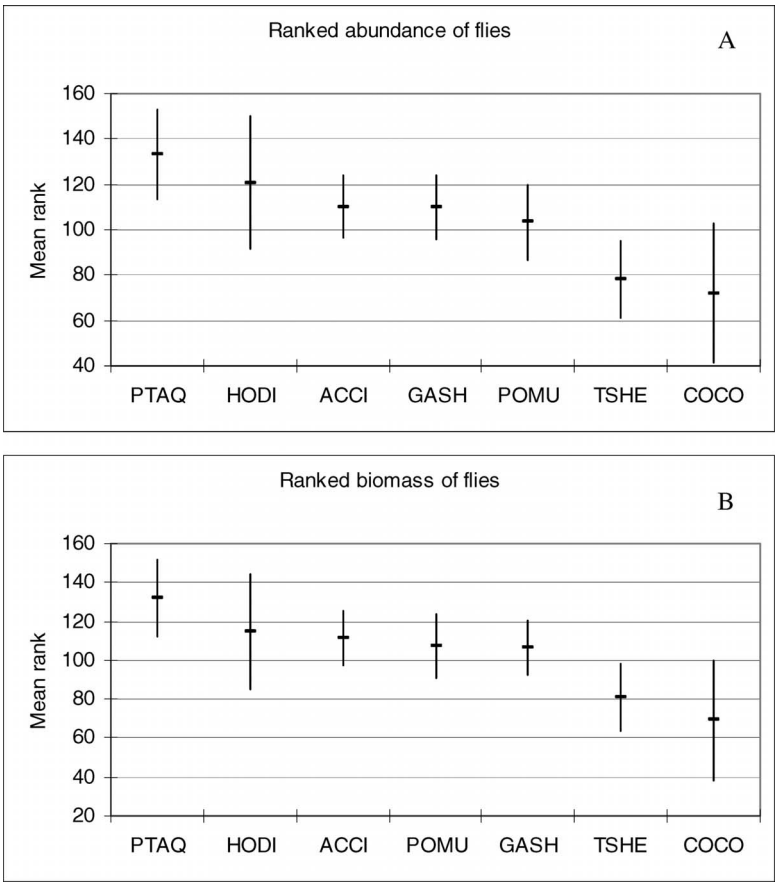


FIG. 4. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult flies (Diptera >3 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

and Homoptera more frequently than expected based on availability. Caterpillars are known to be especially important prey for many neotropical migrant species that breed in temperate forests (Holmes et al. 1979, Graber and Graber 1983, Sample et al. 1993). Raley and Anderson (1990) also reported that caterpillars were an important component of Wilson's Warbler diets in montane willow (*Salix* spp.) habitats. Caterpillars and sawfly larvae have high calcium concentrations relative to many other arthropod groups (Schowalter and Crossley 1983), providing insectivorous birds with an essential resource for egg-laying. Caterpillar abundance and biomass have also been positively correlated with productivity and nestling growth rates of insectivorous birds (Holmes et al. 1992, Naef-Daenzer et al. 2000). Caterpillars probably represented an important source of energy and nutrition for birds on our study sites.

Active, flying insects such as adult flies and wasps likely were under-sampled with the foliage beating method we used to estimate available arthropod prey. Flies may have been more available than estimated in both understory and overstory vegetation, which would have caused an overestimate of the forage ratio. However, a large proportion of flies in the diet is supported by published accounts (Beal 1907, Ammon and Gilbert 1999) and reflects the hover-gleaning and aerial fly-catching foraging strategy frequently used by Wilson's Warblers (Bent 1953, Stewart et al. 1977). The selection of flies that we observed is consistent with the findings of Raley and Anderson

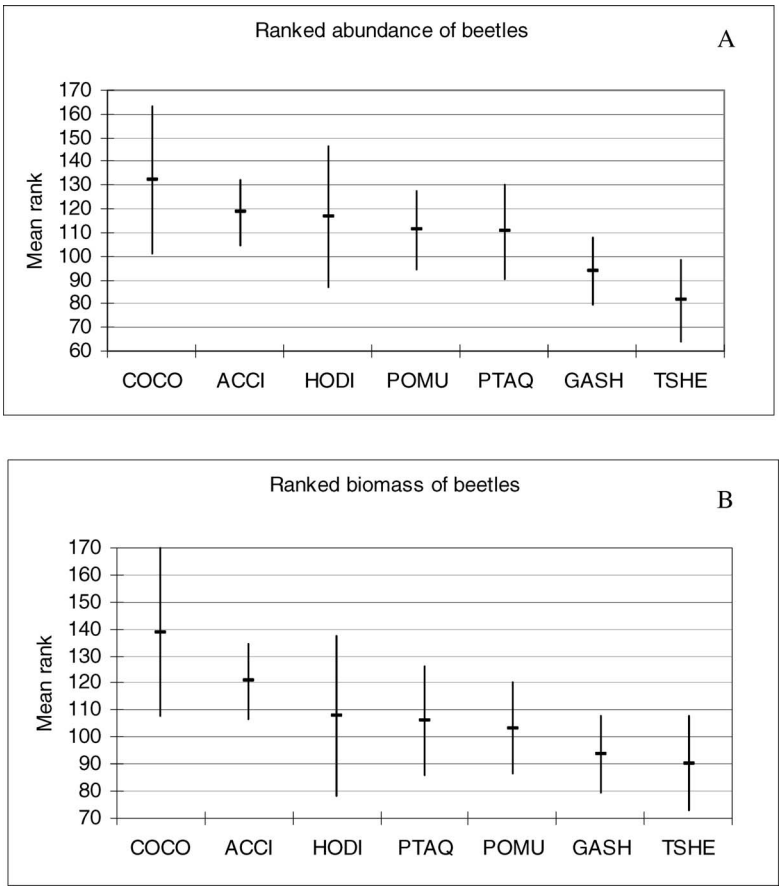


FIG. 5. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult beetles (Coleoptera >3 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

(1990) for Wilson's Warblers foraging in montane willow habitats.

A high frequency of beetles in the diet relative to that on shrubs also is consistent with preferential selection of beetles as prey by Wilson's Warblers reported by Raley and Anderson (1990). We identified cantharid and mordellid beetles in warbler diets. Raley and Anderson (1990) also identified Cantharidae as a large proportion of beetles consumed by Wilson's Warblers. Mordellids are common on foliage but, unlike cantharids, they tend to move rapidly or take flight when alarmed (Borror and White 1970). We identified fragments of mordellids in only two of 87 Wilson's Warbler fecal samples.

Regardless of taxa, arthropods ≤2 mm in length were infrequent in diets of the birds we examined, even though this size class was abundant on understory vegetation. This is consistent with findings of Raley and Anderson (1990), who reported that Wilson's Warblers select prey >3 mm. Adult arthropods >12 mm in length also rarely occurred in the diet of Wilson's Warblers. However, adult arthropods that exceeded the maximum lengths in Wilson's Warbler diets were rare on the vegetation we sampled.

Distribution of Prey on Understory Plant Species.—Common understory plant species on our study sites varied in abundance and biomass of arthropod prey. Herbivorous insect species often are associated with a narrow range of plant taxa, which define characteristic assemblages of arthropods on each plant species (Schowalter 2000). We were not able to

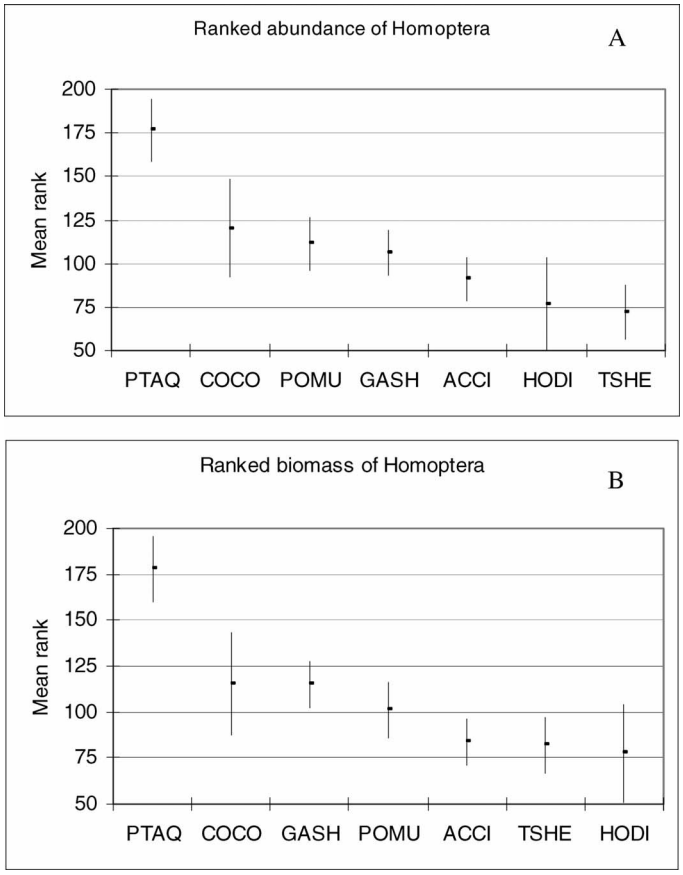


FIG. 6. (A) Ranked abundance and (B) biomass with 90% confidence limits of adult Homoptera (>2 mm) on seven understory plant species in the Oregon Coast Range (Table 1). Two plant species differ significantly in prey abundance or biomass if confidence limits of one do not overlap the mean of the other.

identify most arthropods below the taxonomic level of family, but we found differences among plant species even for the coarser prey categories analyzed.

Plant species that ranked the highest for prey loads of arthropod taxa included oceanspray (caterpillars), California hazel (caterpillars and beetles), and bracken fern (combined prey taxa, flies, and Homoptera). Deciduous shrubs tended to rank higher for prey than evergreen shrubs. Others have noted the importance of deciduous shrubs and trees as foraging substrates (Morrison and Meslow 1983) and as sources of arthropod prey, particularly caterpillars, in conifer forests in the Pacific Northwest (Willson and Comet 1996). A large proportion of the Lepidoptera diversity in western forests is associated with deciduous trees and shrubs (Hammond and Miller 1998). Populations of forest insect species can fluctuate dramatically among generations, but prey diversity provides a stable resource for generalist insectivores over time (Jackson 1979). Oceanspray may be particularly important as a source of prey for birds because it supports both high diversity and high abundance of Lepidoptera (Muir et al. 2002). Western hemlock in the forest understory also was a potential source of caterpillars for birds, but supported low levels of all other prey.

Bracken, a fern that grows new fronds each spring from perennial rhizomes, supported a notably high abundance and biomass of all prey taxa pooled and Homoptera relative to other understory plants. Bracken fern supports a high abundance of herbivores and their associated predators (Lawton 1976), especially where it grows in large, dense patches in sun-

lit areas (Doolittle 2000). In contrast, the evergreen fern species, sword fern, supported a relatively high abundance but low biomass of arthropods, reflecting an arthropod assemblage dominated by small detritivores such as Pscoptera and Collembola (Doolittle 2000) that were not important in bird diets. Few species of caterpillar are found on sword fern (Miller 1995).

CONSERVATION IMPLICATIONS

Insectivorous birds respond to spatial variation in arthropod availability among plant species (Johnson 2000) because foraging efficiency is likely maximized where prey density or biomass is highest (Royama 1970, Zach and Falls 1976, Whelan 1989). Our data indicate that broad-leaved deciduous shrubs and bracken fern provide optimal foraging habitat for breeding Wilson's Warblers because these plant species supported the highest abundance and biomass of foliage-dwelling arthropods ≥2 mm in length, particularly caterpillars, flies, beetles, and Homoptera.

Forest management has important effects on foraging habitat for Wilson's Warblers and other birds by influencing the structure and composition of vegetation communities. Traditionally, understory vegetation, particularly woody shrubs, has not been favored in management directed at timber production in the Pacific Northwest. The goal of standard vegetation management, using herbicides or manual methods, is to reduce cover of understory vegetation to minimize competition with crop trees (Burhill et al. 1989). Forest practice regulations require landowners to control competing vegetation as a means of ensuring successful conifer regeneration after clear-cut harvests (Oregon Department of Forestry 2006). Thus, shrub and hardwood tree cover in the Oregon Coast Range has declined over the past five decades (Kennedy and Spies 2004). Parallel declines in populations of shrub-associated bird species, including Wilson's Warbler, MacGillivray's Warbler (*Oporornis tolmiei*), and Swainson's Thrush (*Catharus ustulatus*) (Sauer et al. 2004) may be related to these regional changes in habitat.

Management goals for much of the federal forestlands in the Pacific Northwest have recently shifted from an emphasis on timber production to maintenance of ecosystems for a broader spectrum of products and services, including biodiversity and restoration of late-seral habitat. Managers plant or otherwise foster the growth of conifer regeneration in the understory, often after thinning or group-selection harvests, to encourage development of multi-layered forest stands (Tappeiner et al. 2002). Our results indicate that understory conifers contribute less to food resources for birds than a diverse assemblage including deciduous shrubs. Thus, a stand with deciduous shrubs in the understory is likely to be more functionally diverse than one with an understory composed of shade-tolerant conifers.

Our results indicate that deciduous vegetation is an important source of arthropod prey, especially caterpillars, which are preferred by Wilson's Warblers and other insectivorous birds. Forest management practices that maintain deciduous shrubs can help meet bird conservation goals. Furthermore, understory shrubs may serve an important function in maintaining the diversity of multiple taxa through associated food webs.

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