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FOOD AVAILABILITY, FORAGING BEHAVIOR, AND DIET OF AUTUMN MIGRANT LANDBIRDS IN THE BOISE FOOTHILLS OF SOUTHWESTERN IDAHO

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Abstract. Food availability and acquisition are critical components of a stopover site's suitability, but we know relatively little about how changes in food availability affect the stopover ecology of migrating landbirds. We examined fruit and arthropod availability in three habitats, studied foraging behavior and diet, and investigated use versus availability for passerines migrating through southwestern Idaho in autumn. Hemiptera dominated foliage-dwelling arthropod communities in all three habitats, whereas Hymenoptera were most numerous among ground-dwelling arthropods. Mountain shrubland had relatively high biomass of both ground-dwelling and foliage-dwelling arthropods, whereas conifer forest had high biomass of foliage-dwelling arthropods only and shrubsteppe had high biomass of ground-dwelling arthropods only. Species' foraging behavior varied, but most species foraged in mountain shrubland more often than expected by chance. Diets of most species included a high proportion of certain Hemiptera and Hymenoptera with smaller proportions of Coleoptera, Diptera, and Heteroptera; Coleoptera and some Hemiptera were consistently preferred by most species. Importantly, all 19 bird species examined consumed some fruit, and this is the first documentation of frugivory for two warbler species. These data point to the importance of several arthropod taxa, especially the Hemiptera and Hymenoptera, and fruits to landbirds migrating in mountain shrubland in autumn. Finally, we found no effect of annual variation of fruit or arthropod abundance on migrants' energetic condition, suggesting that food was sufficient for mass gain in all years of this study and/or that foraging behavior may be plastic enough to allow birds to gain mass despite annual differences in food availability.

Key words: *avian diet, food availability, foraging behavior, migration, resource use, stopover ecology.*

Disponibilidad de Alimento, Comportamiento de Forrajeo y Dieta de Aves Terrestres Migratorias de Otoño en las Estribaciones Boscosas del Sudoeste de Idaho

Resumen. La disponibilidad y la adquisición de alimento son componentes críticos de la calidad de un sitio de parada, pero sabemos relativamente poco sobre cómo los cambios en la disponibilidad de alimento afectan la ecología de parada de las aves terrestres migratorias. Examinamos la disponibilidad de frutos y artrópodos en tres hábitats, estudiamos el comportamiento de forrajeo y la dieta e investigamos el uso versus la disponibilidad para los paserinos que migran en otoño a través del sudoeste de Idaho. Los hemípteros dominaron las comunidades de artrópodos que viven en el follaje en los tres hábitats, mientras que los himenópteros fueron más numerosos entre los artrópodos que viven en el suelo. El arbustal de montaña tuvo una biomasa relativamente alta de artrópodos que viven en el suelo y en el follaje, mientras que el bosque de coníferas tuvo una biomasa alta sólo de artrópodos que viven en el follaje y la estepa arbustiva tuvo una biomasa alta sólo de artrópodos que viven en el suelo. El comportamiento de forrajeo de las especies varió, pero la mayoría de las especies forrajearon más frecuentemente en el arbustal de montaña que lo esperado por azar. La dieta de la mayoría de las especies incluyó una alta proporción de hemípteros e himenópteros con una menor proporción de coleópteros, dípteros y heterópteros; los coleópteros y algunos hemípteros fueron consistentemente preferidos por la mayoría de las especies. De modo destacado, todas las 19 especies de aves examinadas consumieron algo de frutos y este es el primer registro de frugivoría por parte de dos especies de arañeros. Estos datos señalan la importancia en el arbustal de montaña de varios taxones de artrópodos, especialmente de hemípteros e himenópteros, y de los frutos para las aves terrestres migratorias de otoño. Finalmente, no encontramos un efecto de la variación anual de la abundancia de frutos o artrópodos sobre la condición energética de los migrantes, sugiriendo que el alimento fue suficiente para el aumento de la masa en todos los años de este estudio y/o que el comportamiento de forrajeo puede ser lo suficientemente plástico como para permitir que las aves ganen masa a pesar de las diferencias anuales en la disponibilidad de alimento.

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INTRODUCTION

Efficient use of stopover habitat is critical for successful migration because birds must replenish fuel stores, rest, and avoid predators before resuming migration (Moore et al. 1995). Furthermore, a bird's ability to gain mass is the main criterion we use to judge the suitability of a stopover site (Petit 2000, Kelly et al. 2002, Carlisle et al. 2005a, Guglielmo et al. 2005). Thus stopover sites must provide access to suitable food. Not surprisingly, Buler et al. (2007) concluded that food availability is likely the most important variable influencing the distribution of migratory birds during stopover. Though migrants are certainly influenced by spatial and temporal differences in food availability (Rodewald and Brittingham 2007), and such a relationship has been demonstrated for wintering birds (Brown and Sherry 2006), relatively few studies have established a direct connection between food abundance and the energetic condition of actively migrating birds (e.g., Bibby et al. 1976). Additionally, a high density of migrants can negatively affect migrants' ability to gain mass (Hansson and Pettersson 1989, Moore and Wang 1991, Kelly et al. 2002), but whether this pattern is driven by the direct effects of food availability or the indirect effects of competitive interactions is unknown. As we strive to better understand the migratory habits and conservation needs of landbirds in western North America, it is important not only to quantify habitat-use patterns but also to identify the specific habitat attributes that lead to a particular stopover site being suitable.

Theoretically, each species should select habitats that enable time optimization at a stopover site (Alerstam and Lindström 1990, Schaub and Jenni 2000, Erni et al. 2002, Schmaljohann and Dierschke 2005). Moore (1991) showed that migrants are able to both diversify and intensify foraging behavior in order to meet the increased energetic demands of migration. Migrants actively select foods in order to meet their nutritional requirements, and diet composition during migration may differ from that at other seasons (Jordano 1988, Stiles 1993, Bairlein 1998, 2002, Parrish 2000). Likewise, the nutrient composition of arthropods and fruits can vary spatially and temporally (Johnson et al. 1985, Stiles 1993, Papon et al. 2000, Mayntz and Toft 2001), and Bairlein (1998) showed that diets varying in their nutrient components have significant effects on mass gain in captive migrants. Moreover, the nutrient content of diets can affect composition of deposited fat, which can, in turn, affect physiological performance (Pierce et al. 2005). If a bird cannot locate preferred food types, because of being in the "wrong" habitat or because of a lack of suitable habitat, its ability to successfully complete migration in a timely manner may be compromised.

Some species or guilds may be more flexible in microhabitat use than others (Petit 2000), and species' diets can differ in relation to morphology, behavior, and habitat use. Microhabitat and diet data are particularly needed for migrants in western North America given the paucity of data regarding the stopover ecology of these birds generally (Carlisle et al. 2009) and the shrinking availability of the riparian habitats thought to be preferred by many species (Finch and Wang 2000, Petit 2000, Mehlman et al. 2005, Webb et al. 2007).

Continued human development pressure that decreases the amount of suitable stopover habitat and forecasted warmer and drier weather in many areas important for migration stopover (IPCC 2007) could combine to diminish the availability of food for western migrants in the future. For example, degradation and loss of stopover habitat will likely increase competition, decrease access to resources, and, at a minimum, slow the pace of migration (Moore et al. 1995). With the increasing human-induced challenges facing migratory birds (Mehlman et al. 2005, Carlisle et al. 2009) and the fact that the majority of migratory landbirds' annual mortality occurs during migration (Sillett and Holmes 2002, Paxton et al. 2007), there is increasing urgency to understand what makes stopover habitat "suitable" and what factors might affect the success of individuals at stopover sites. In particular, adequate food supplies and sufficient cover from predators are likely the two most important components of suitable stopover habitat. More complete information about the foods important to migrants is needed for suitable habitat to be identified as well as for prediction of how these food sources might be affected by landscape and climate changes. Finally, identifying the relationship between food availability, diet preferences, and performance of migrants during stopover is an important step toward a more complete understanding of their stopover ecology.

Previous research in the Boise Foothills of southwestern Idaho during fall migration has indicated that most migrants that breed in woodland are more numerous in shrubby deciduous habitats (mountain shrubland and shrub-dominated riparian) than in conifer forest or shrubsteppe (Carlisle et al. 2004) and that most migrants captured in the shrubby deciduous habitats are able to gain mass (Carlisle et al. 2005a). In the present study, our main goals were to evaluate food availability and the foraging behavior and diet of autumn migrants and, secondarily, to examine the effect of changes in food availability on migrants' energetic condition. To accomplish this, we sampled food (arthropod and fruit) availability, foraging behavior, and diet in three adjacent habitats and compared results to published data on energetic condition of migrants at the same site (Carlisle et al. 2005a). Specifically, we examined use versus availability by contrasting migrants' diets to the abundance of potential food sources sampled in the microhabitats frequented by birds. We also examined the potential effect of changes in food abundance from year to year on migrants' energetic condition, predicting that yearly food abundance should not vary substantially given their documented mass gain in all years of the study (Carlisle et al. 2005a). Ours

is one of the first studies of food availability for and resource use by migrating landbirds in western North America.

METHODS

STUDY SITE

We conducted this study 12 km east of Boise, Ada County, Idaho (43° 36′ N, 116° 05′ W) on Lucky Peak (1845 m), the southernmost peak of the Boise Foothills. The study area is composed of a mosaic of three major habitats: conifer forest, mountain shrubland, and shrubsteppe (Appendix A, available at http://dx.doi.org/10.1525/cond.2012.100209; additional details on the site in Carlisle et al. 2004). The conifer forest is almost completely dominated by Douglas-fir (*Pseudotsuga menziesii*), the mountain shrubland is composed mostly of bitter cherry (*Prunus emarginata*), and big sagebrush (*Artemisia tridentata*) is the dominant plant species in shrubsteppe.

FOOD AVAILABILITY

Arthropod sampling. To examine annual, intra-seasonal, and habitat differences in food resources for autumn migrants, we used branch-clip and pitfall-trap samples of arthropods in each habitat type (Cooper and Whitmore 1990, Johnson 2000). During autumn of 2000 and 2001, we sampled arthropods at four sites each in conifer forest, mountain shrubland, and shrubsteppe. To examine intra-seasonal changes in the arthropod community, we divided the season into four periods of sampling separated by about 10 days (early-mid August, late August/early September, mid September, and late September/early October). Arthropod sampling consisted of five subsamples (branch-clip and pitfall) from each of four representative areas, such that 20 subsamples of each type were collected from each habitat in each period. In each area, we collected one sample at a central location and the other four 10 m from the center point in each of the four cardinal directions. These five subsamples were pooled to yield four samples per habitat for each interval. All samples were collected during the morning and in similar weather (generally clear and calm days). For each of the three habitats we focused sampling on the dominant plant species mentioned above; hereafter, we refer to branch-clipping results by the habitat type, not vegetation species.

To add a third year of sampling for the mountain shrubland (the habitat that migrants used most in the first two years of the study), in 2002 we sampled branches during sample periods 1 and 2 because arthropod numbers in mountain shrubland dropped off dramatically after early September in both 2000 and 2001 (see Results). To prevent confusion with 2000–01 data for all habitats, we summarize the 2002 data in the Results and present more detail in Appendix B online.

Our branch-clipping method followed Johnson (2000), which he found to be effective in measuring the availability of food for foliage insectivores, which include most migrants we studied. Briefly, we placed a cloth bag around a terminal branch (approximately 0.5 m in length in each case), ranging from near ground level to just over 9 m, and quickly sealed the drawstring to prevent arthropods from escaping before clipping the branch into the bag. We then shook the bag to dislodge arthropods from the branch before removing the branch from the bag and inspecting it for remaining arthropods. We weighed the branch (nearest gram) to correct insect biomass for vegetation mass, then identified, counted, and measured (to the nearest 1 mm) all arthropods on site and estimated the biomass for each category on the basis of published length–weight relationships (Rogers et al. 1977, Calver and Wooller 1982). Arthropods were identified to family whenever possible (otherwise to order or suborder) with reference to specimens collected at the study site by JDC as well as to Borror et al. (1989). Arthropod taxonomy follows Maddison and Schulz (2009). In comparisons with diet data, we categorized arthropods to correspond with the taxonomic levels identified from gut contents and/or feces.

Arthropod biomass was not significantly influenced by branch height in any of the three habitats ($P = 0.6$ for conifer forest; $P = 0.99$ for mountain shrubland; $P = 0.13$ for shrubsteppe; ANOVA). Thus, while our samples did not include the full height range of branches on which migrants forage in conifer forest, we found minimal variation in arthropod biomass over the range sampled so we pooled data from all heights for subsequent analyses. We summarized and analyzed branch-clip data in three ways: (1) Number of arthropods per branch, (2) arthropod biomass per branch, and (3) arthropod biomass per 10 g of branch mass. In general, all three methods gave similar results, and here we report arthropod biomass per branch (for results from the other two methods, see Carlisle 2005; for justification for use of multiple approaches to summarize/analyze arthropod data, see Appendix C online).

Because several common western North American migrants, such as sparrows, forage extensively on the ground and because certain arthropod taxa may not be sampled well via branch clipping, we used pitfall traps to sample ground-dwelling arthropods (Cooper and Whitmore 1990). Not all arthropods captured via this method were "ground-dwelling" taxa per se (e.g., flies and wasps); rather, we use this term to separate arthropods captured in pitfall traps from foliage-dwelling arthropods sampled via branch clipping. We used coffee cans (15.3 cm diameter; 16.7 cm depth) sunken in to the ground and level with the surface with a thin (1–2 cm) layer of soapy water in the bottom to trap arthropods. For one day during each sampling period, we "operated" each can (removing the lid and adding soapy water) for 5 hr starting at sunrise. After 5 hr, we removed, identified, and counted all arthropods, removed remaining water with a turkey baster, and replaced the lid until the next sampling period. We present biomass data here as mg of arthropods per trap; details for the number of arthropods per trap can be found in Carlisle (2005).

Fruit sampling. Because fruits were only found in the mountain shrubland habitat, we limited sampling of fruits to this habitat. To characterize the relative abundance of fruits, we counted unripe, ripe, and overripe fruits for all fruiting species in the

mountain shrubland habitat on 10 transects (12 × 2 m). These transects were aligned with the net lanes for each of the 10 mist nets (for capturing birds) operated at this study site such that the 1 × 12-m strip of natural vegetation on either side of the net lane was counted. We counted fruits of several shrub species, including bitter cherry, chokecherry (*P. virginiana*), serviceberry (*Amelanchier alnifolia*), wild currant (*Ribes* sp.), and rose (*Rosa woodsii*), once during early August and once in early September of 2000, 2001, and 2002. In addition, because fruit abundance in September closely paralleled that in August (fruits differing only in state of ripeness), we counted fruits in early August of 2003 and 2004 to extend the inter-annual comparison.

FORAGING BEHAVIOR

We made at least 10 instantaneous (snapshot) observations of foraging by 25 species of migrant birds over four fall migration seasons (2000–2003) throughout each species' passage. Though birds are known to stop over at the site for 3–6 days (Carlisle et al. 2005a) and it would be difficult to guarantee that we never recorded data on the same individual twice, we attempted to avoid observing an individual repeatedly. We focused snapshot observations on a bird's first attempt to forage after it was initially observed (Hejl et al. 1990). Because one objective of this study was to determine the proportion of species-specific observations in certain habitats, we limited observations of foraging behavior to a core area of the study site that included approximately 33% conifer forest, 33% mountain shrubland, and 33% shrubsteppe (Appendix A online; proportions roughly similar to ridgeline habitats in the surrounding area). Observers (CHR and JDC) walked slowly along one main path about 450 m in length that transected all three habitats while looking and listening for target species. Observers tried to spend approximately equal time in each habitat in order to have a roughly equal chance of observing a foraging bird in each habitat (though we acknowledge that birds' detectability may differ by habitat). The vast majority (97%) of the 1189 observations of foraging were made during the first 5 hr after sunrise.

For each foraging maneuver observed, we recorded habitat and foraging-behavior variables (detailed in Appendix D online) that have previously been shown to be important in niche differentiation in birds (Morse 1968, Holmes et al. 1979, Hutto 1981, Franzreb 1984). We compared foraging behaviors within guilds (e.g., warblers, flycatchers) of similar species (Holmes et al. 1979). We also compared data on foraging to results from mist netting and surveying in Carlisle et al. (2004) to determine if habitat associations found by different methods were consistent.

DIET COMPOSITION

We analyzed fecal and regurgitation samples from 19 species of migrants from which we collected ≥10 diet samples. Fecal samples were collected from 2000 to 2003 before, during, or after processing of captured birds during the first 5 hr after sunrise. As with foraging data, we collected diet samples throughout the entire period of each species' fall passage. Although all three habitats occurred in the immediate area, for optimal capture efficiency, given the height range of the shrubs (similar to the height of the nets) and the higher density of birds in this habitat, we placed nets in the mountain shrubland only (for details of netting, see Carlisle et al. 2005a). However, because of the proximity of the three habitat types, birds could have been foraging in conifer and/or shrubsteppe immediately prior to capture. Although birds observed for foraging behavior may have also been captured for diet sampling, we were not able to identify individuals in the field and are uncertain if any were sampled by both methods. After extracting birds from nets, we placed them in clean bird bags prior to banding and measuring them and/or briefly in a box lined with wax paper prior to release. In addition, during 2000 and 2001 we collected regurgitated samples by administration of a tartar emetic (Poulin and Lefebvre 1995, Carlisle and Holberton 2006). Although regurgitated samples tended to include more individual arthropods, Carlisle and Holberton (2006) found that overall diet composition according to emetic and fecal samples was broadly similar; therefore we use both sample types to describe diets here. Diet-analysis methods are detailed in Appendix E online.

STATISTICAL ANALYSES

We used factorial ANOVA to test for differences in arthropod numbers and biomass by habitat, year, and sample period; we also tested for interactions among these predictor variables. We used χ^2 tests to compare the frequency of different arthropod taxa by year and sample period.

With data on foraging, we examined use vs. availability but limited our analyses to conifer forest and mountain shrubland habitats because the species we studied can be considered woodland migrants, the shrubsteppe had fewer foliage arthropods, and only two (of 1189) individuals in this study, one Ruby-crowned Kinglet (*Regulus calendula*) and one Yellow-rumped Warbler (*Setophaga coronata*), were observed foraging in shrubsteppe. Thus, since mountain shrubland and conifer forest occur in the study area in equal proportions, we used χ^2 tests to compare the number of observed attempts at foraging in these habitats against the null hypothesis of a 50:50 ratio between the two habitats for each species. For intra-guild comparisons, we compared data on species' foraging behavior in two ways: variables with continuous data (absolute and relative foraging height) via *t*-tests or ANOVA, variables with categorical data (horizontal foraging position, vegetation density, proportionate use of aerial foraging maneuvers) via χ^2 tests (Zar 1996).

We used data on foraging behavior to compare dietary use versus measured food availability for 13 bird species with ≥10 diet samples collected during 2000 and 2001 (same seasons that arthropods were sampled). For species that targeted ≥75% of

their foraging attempts in one habitat, we compared arthropod composition of the diet to the arthropod community sampled in that habitat. For example, 87% of foraging attempts by the Golden-crowned Kinglet (*Regulus satrapa*) were in conifer forest, so we compared its diet to conifer-forest arthropods only. Conversely, seven species focused >75% of foraging attempts in mountain shrubland, and we compared their diet to mountain-shrubland arthropods. The remaining species foraged in both habitats to some degree (but <75% in either), and we compared diets of these species to a combined total of arthropods sampled in conifer forest and mountain shrubland.

To test diet composition vs. arthropod availability, we used a simple index of percent use minus percent availability (Strong 2000). For each bird species, we subtracted the percentage of arthropod biomass available (combined sum of branch clippings and pitfall traps) from that in the diet (all samples combined) for each arthropod order, suborder, or family that contributed at least 1% of biomass for diet or availability and/or was a taxon unique to a particular habitat. Positive values indicate preference for a certain food type, whereas negative values suggest avoidance of that food type (Strong 2000). We used the sign test to determine whether most species consumed or avoided certain arthropod taxa (more positive or negative values than expected by chance).

When making multiple comparisons among groups within the same data set, we used a sequential Bonferroni method to hold the overall α error rate at $P = 0.05$ (Rice 1989, Zar 1996).

RESULTS

FOOD AVAILABILITY

Foliage-dwelling arthropods. Arthropod biomass (mg) per branch differed significantly by habitat, year, sample period, and the interaction of habitat × sample period variables (Table 1; Fig. 1). The habitat-by-sample-period interaction was significant because in conifer forest and mountain shrubland arthropod biomass declined significantly through the season whereas in shrubsteppe it remained relatively stable at a low level through the season (Table 1; Fig. 1). Arthropod biomass per branch was highest in conifer forest (36.12 ± 2.25 mg branch^{-1}), intermediate in mountain shrubland (25.15 ± 2.36 mg branch^{-1}), and lowest in shrubsteppe (7.47 ± 1.77 mg branch^{-1}; Table 1). Biomass per branch (all habitats pooled) was significantly higher in 2000 (30.93 ± 2.34 mg branch^{-1}) than in 2001 (14.78 ± 1.15 mg branch^{-1}; Table 1), and arthropod biomass decreased progressively from sample period 1 through 4 (Table 1; Fig. 1). Continued sampling showed that in 2002 arthropod data for mountain shrubland were comparable to those for 2001 and significantly lower than those for 2000 (Appendix B online). Results for numerical and corrected biomass data from branch clipping were very similar (Carlisle 2005).

Several arthropod taxa occurred solely or primarily in one habitat (Appendix F online) and thus might be considered indicator taxa for a particular habitat, especially in comparisons of food availability to diet data. For example, of 3888 psyllids sampled, >99% were collected in mountain shrubland. More than 92% of all aphids were sampled in shrubsteppe. Ants made up a fairly small proportion of foliage-dwelling arthropods in each habitat but most (71%) were sampled in shrubsteppe. Insects found exclusively or primarily in conifer forest included scale insects, pine and spruce aphids (Hemiptera: Sternorrhyncha: Adelgidae), stilt bugs, and leafhoppers (Hemiptera: Auchenorrhyncha: Cicadellidae). Among less frequently captured insects, spittle bugs (Hemiptera: Auchenorrhyncha: Cercopidae) and soft-winged flower beetles (Coleoptera: Melyridae) were found most often in conifer forest. In contrast, ladybird beetles (Coleoptera: Coccinellidae) and leaf bugs (Hemiptera: Heteroptera: Miridae) were the only taxa with adequate sample sizes whose distributions among habitats were relatively equal.

Ground-dwelling arthropods. Biomass per trap of ground-dwelling arthropods varied by habitat, year, and sample period, and there was a significant interaction between habitat and year (Table 1; Fig. 2). In all three habitats, arthropod biomass was lower in 2001 than in 2000; however, this difference was not significant for conifer forest, which explains the significant habitat-by-year interaction (Table 1). Arthropod biomass was significantly higher early in the migration season (sample period 1) than later in the season (sample periods 3 and 4) and was intermediate in mid-season (sample period 2; Table 1). The biomass of ground-dwelling arthropods was significantly higher in mountain shrubland and shrubsteppe (29.55 ± 4.34 and 30.51 ± 4.50 mg trap^{-1}, respectively) than in conifer forest (5.35 ± 1.19 mg trap^{-1}; Table 1; Fig. 2). Across all habitats, it

TABLE 1. Results of ANOVA on biomass (mg) of arthropods sampled by branch clipping and in pitfall traps from three habitats throughout the autumn at Lucky Peak, Idaho, 2000–2001. Only significant interactions are shown.

Source	df	Sum of squares	*F*	*P*
Biomass per branch				
Habitat	2	13658.69	28.31	<0.001
Year	1	6982.93	28.95	<0.001
Sample period	3	6650.27	9.19	<0.001
Habitat by sample period	6	3676.68	2.54	<0.03
Error	68	16404.41	—	—
Biomass per pitfall trap				
Habitat	2	13814.93	12.56	<0.001
Sample period	3	8270.71	5.06	<0.003
Year	1	14403.61	26.20	<0.001
Habitat by year	2	5457.47	4.96	0.01
Error	67	36835.64	—	—

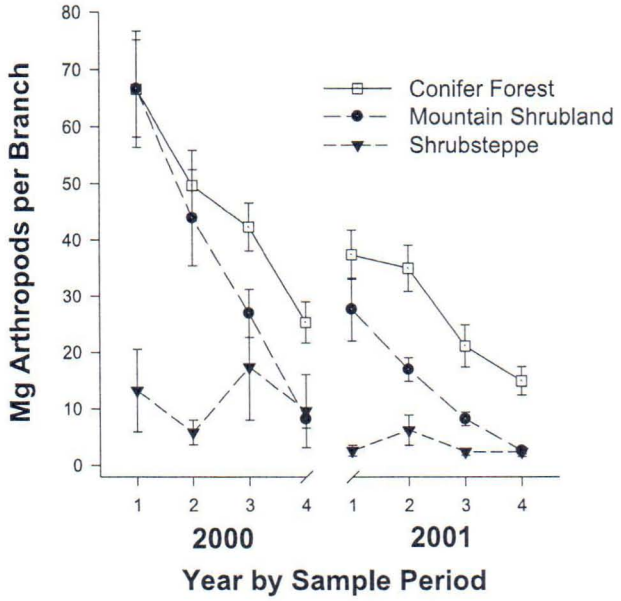

FIGURE 1. Annual and seasonal variation in biomass of foliage-dwelling arthropods (mg per branch) in three habitats during 2000 and 2001 at Lucky Peak, Idaho. Data are from samples of clipped branches and are presented as means ± SE. Periods sampled are (1) mid August, (2) late August/early September, (3) mid September, and (4) late September/early October.

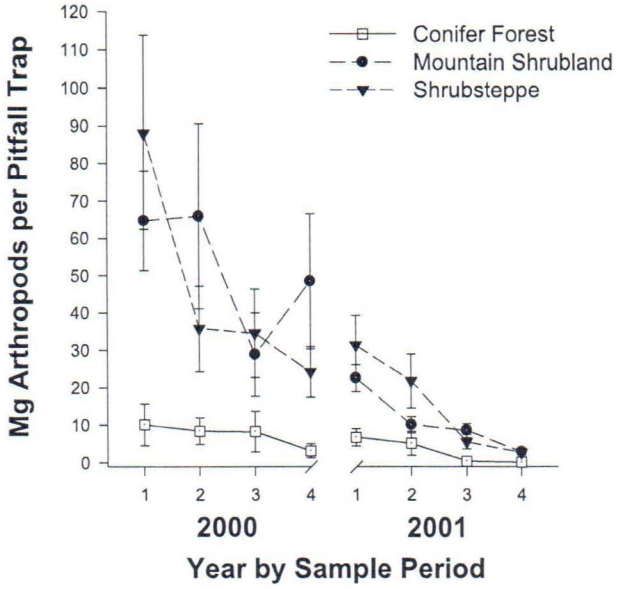

FIGURE 2. Annual and seasonal variation in biomass of ground-dwelling arthropods (mg per pitfall trap) in three habitats during 2000 and 2001 at Lucky Peak, Idaho. Data are from pitfall traps and are presented as means ± SE. Periods sampled are (1) mid August, (2) late August/early September, (3) mid September, and (4) late September/early October.

was over 3 times higher in 2000 (33.62 ± 4.12 mg trap^{-1}) than in 2001 (10.05 ± 1.22 mg trap^{-1}; Table 1).

Fruit abundance. In the mountain shrubland, the only habitat in which fruit was available, we documented annual differences in fruit abundance as well as seasonal differences in fruits' stage of ripeness (Fig. 3). In 2003, the year of most prolific fruiting, the number of fruits was more than an order of magnitude greater than in 2002 and 2004, the two years of lowest fruit abundance (Fig. 3). In both 2000 and 2001 fruit production was relatively high compared to 2002 and 2004. Despite this annual variation in the number of fruits produced, fruits ripened by early August of each year, and most were overripe by the middle of September (Fig. 3).

From 2000 through 2004 combined, 95% of fruits counted in mountain shrubland habitat were bitter cherry, although wild currant (4%), chokecherry (1%), serviceberry (0.3%), and rose (0.2%) also produced fruit in most years. The proportion of fruits contributed by each species varied by year such that in years of low bitter cherry production, currants (which fruited more steadily from year to year) accounted for proportionally higher fruit output (Appendix G online). Although not present in our sampling plots, the fruiting plants thimbleberry (*Rubus parviflorus*) and elderberry (*Sambucus sp.*) were found in the surrounding area (JDC, pers. obs.).

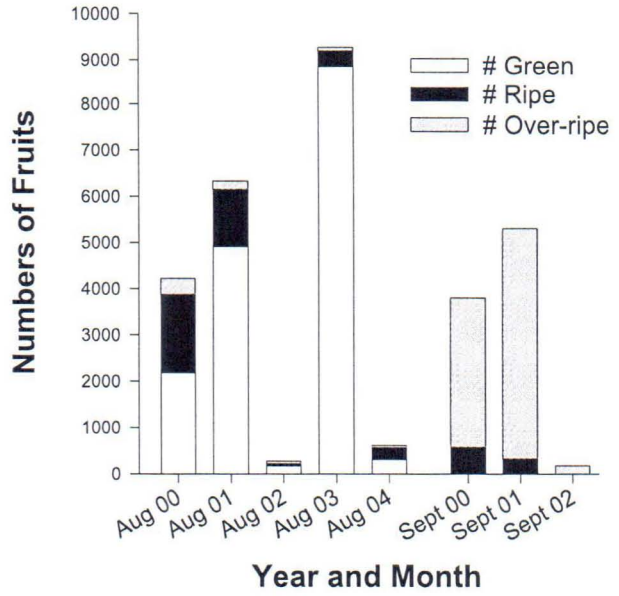

FIGURE 3. Numbers of fruits by stage of ripeness counted during early August 2000–2004 and early September 2000–2002 at Lucky Peak, Idaho.

FORAGING BEHAVIOR

Most species focused the majority of their foraging in the mountain shrubland (bitter cherry and other deciduous shrubs), and this concentration was significant for 13 of the 25 species (see Appendix D online for species-specific details). In contrast, for only seven species were >40% of attempts in conifer forest, and four of these foraged in conifers significantly more than expected on the basis of habitat availability (Appendix D online).

DIET COMPOSITION

Each species' diet generally matched its pattern of foraging behavior in that birds observed foraging in a particular habitat consumed arthropod taxa unique to that habitat (see Appendix E online for species-specific details). Pooled across 660 diet samples from 19 bird species analyzed, the Auchenorrhyncha (e.g., Cercopidae, Cicadellidae) and Sternorrhyncha (Psyllidae) were migrants' predominant dietary items and together made up 59% of all arthropods consumed (Appendix E online). Other arthropods constituting sizable portions of migrants' diets included the Hymenoptera (16%), Coleoptera (9%), Heteroptera (6%), Diptera (4%), Araneae (2%), and Lepidoptera (1%). Important families represented in the diets included psyllids (Psyllidae, 50% of total), ants (Formicidae, 10%), leafhoppers (Cicadellidae, 7%), spittlebugs (Cercopidae, 2%), yellowjackets and hornets (Vespidae, 1%), and ground beetles (Carabidae, 1%). All species ate fruit to some degree during migration, and fruit occurred in at least 30% of diet samples from each species (Appendix E online).

USE VERSUS AVAILABILITY

Foraging behavior (by habitat). Generally, the woodland migrants we studied did not forage in habitats in proportion to their availability (Appendix D online). For example, birds made very few foraging attempts (<0.2 %) in shrubsteppe, which occupied about 33% of the sampled area. Even when comparisons are limited to conifer forest vs. mountain shrubland, few species used these habitats in the same (equal) proportions as they occurred. Only the Yellow-rumped and Townsend's (*Setophaga townsendi*) warblers used these habitats in relatively equal proportions (Appendix D online). Of the 18 other species with at least 19 observations, 13 preferred mountain shrubland and five used conifer forest most often (Appendix D online).

Diet (consumption vs. availability). Beetles (Coleoptera) and spittle bugs (Cercopidae) were routinely preferred across the set of migrants studied (both $P < 0.05$; Table 2). In contrast, most species ate spiders, flies, and adult moths less than expected from their availability (all $P < 0.05$; Table 2). For other taxa, patterns were more complex and often differed depending on the specific bird species. For instance, vespid wasps were generally not eaten by most migrants but were highly preferred by Western Tanagers (*Piranga ludoviciana*). Stilt bugs, which were restricted to conifer forest, were consumed by six of the 15 migratory bird species examined but less than expected overall. Ants were heavily consumed by sparrows and flycatchers but eaten less than expected by most other birds. Stink bugs (Hemiptera: Heteroptera: Pentatomidae) occurred in diets of about half the species and were especially favored by Warbling Vireos (*Vireo gilvus*). For several prey taxa, notably certain Heteroptera, leafhoppers, and psyllids, the apparent preference or avoidance of the item depended on the habitat to which the bird's diet was compared. For instance, psyllids were consumed to some degree by all species, but generally less than expected by those that divided time between conifer forest and mountain shrubland. Meanwhile, all species occurring primarily in mountain shrubland consumed psyllids as much as or more than expected, except for the White-crowned Sparrow (*Zonotrichia leucophrys*), which consumed more seed and fruit than arthropods (Table 2; Appendix E online). Heteroptera accounted for a higher proportion of arthropods in conifer forest than in mountain shrubland, and birds foraging primarily in conifer forest appeared to eat less Heteroptera than expected whereas those foraging primarily in mountain shrubland consumed more Heteroptera than expected.

RELATIONSHIP OF FOOD AVAILABILITY AND ENERGETIC CONDITION OF MIGRANT BIRDS

We found significant differences by year in the availability of arthropods and fruits, with relatively high availability of arthropods and moderate numbers of fruits in 2000, lower availability of arthropods (approximately half the 2000 level) and relatively high abundance of fruit in 2001, and lower availability of arthropods (similar to that of 2001) but extremely low abundance of fruit in 2002 (Fig. 4). To test for possible effects of differing food availability on the condition of migrants, we examined

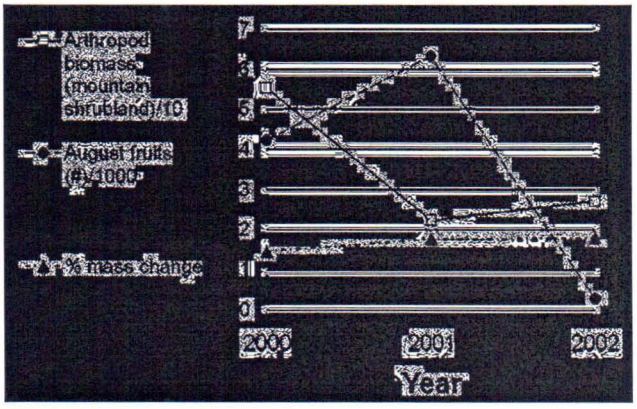

FIGURE 4. Biomass of arthropods and numbers of fruits in mountain shrubland relative to average percent mass change (from first to last capture) in each year for migratory birds (all species averaged) from 2000 to 2002 at Lucky Peak, Idaho. For convenience of scale on this figure, data on food availability were transformed as follows: arthropod biomass/10 and number of fruits (counted during August)/1000.

TABLE 2. Use by (diet) vs. availability to (arthropod samples) passerines migrating in autumn at Lucky Peak, Idaho, 2000–2001. Data shown are percent use minus percent available (both based on proportion of arthropod biomass); negative values indicate avoidance (or lack of use) of a category of prey, whereas positive values indicate use greater than availability. "Availability" for each bird species (shown in bold) drawn from habitat preferences for foraging (see text) such that one species' diet is compared directly to arthropods sampled in conifer forest, seven species' diets are compared to arthropods sampled in mountain shrubland, and seven species' diets are compared to the combined total of arthropods samped in both habitats. Categories consumed significantly more than expected denoted by **; those consumed less than expected denoted by * (sign test).[a]

	n	Araneae *	Heteroptera	Berytidae *	Pentatomidae	Cercopidae**	Cicadellidae	Psyllidae	Coleoptera**	Hymenoptera	Formicidae	Wasp	Vespidae *	Lepidoptera	Larvae	Moth *	Diptera *
Conifer forest		**22.9**	**23.3**	**19.1**	**2.9**	**1.0**	**18.3**	**0.3**	**2.4**	**7.4**	**1.4**	**1.2**	**4.8**	**1.4**	**0.1**	**1.3**	**2.7**
Golden-crowned Kinglet	11	–15.9	8.7	–9.4	-2.9	5.2	-6.1	2.0	17.7	–5.0	–1.4	1.3	–4.8	1.4	–0.1	–1.3	–2.7
Conifer and mountain shrubland		**12.2**	**21.1**	**8.4**	**1.6**	**0.5**	**8.6**	**26.1**	**2.4**	**14.9**	**5.8**	**2.1**	**7.0**	**0.6**	**0.1**	**0.6**	**7.2**
Dusky Flycatcher	20	–12.1	–5.6	–8.4	8.4	1.0	8.4	–17.9	14.1	31.6	32.4	6.3	–7.0	8.7	8.5	0.2	–1.0
Hammond's Flycatcher	21	–9.1	–8.9	–8.4	–0.7	–0.5	–7.8	1.1	21.2	8.4	9.9	5/5	–7.0	1.8	2.4	–0.6	–0.7
Warbling Vireo	27	–10.1	7.3	–8.4	25.5	19.5	–7.4	–6.9	3.7	–12.8	–4.9	–0.9	–7.0	18.7	19.3	–0.6	–6.5
Yellow-rumped Warbler	22	–11.2	–17.2	–6.4	–1.6	8.3	4.2	–6.3	44.4	–6.1	–0.3	0.6	–7.0	0.6	0.8	–0.3	–1.8
Townsend's Warbler	20	–9.8	–12.0	–0.8	–1.6	14.5	–3.1	24.2	5.6	–10.0	–4.2	1.2	–7.0	–0.2	–0.1	–0.1	–3.1
Western Tanager	21	–12.2	–12.2	–8.4	5.7	1.1	–8.4	–26.0	6.6	62.2	–2.6	6.9	57.9	0.8	1.4	–0.6	–6.2
Dark-eyed Junco[b]	26	–12.2	–16.3	–8.4	–1.6	–0.5	1.6	–20.4	20.5	6.9	15.8	–1.8	–7.0	–0.6	–0.1	–0.6	–1.7
Mountain shrubland		**3.8**	**1.4**	**0.03**	**0.6**	**0.02**	**1.0**	**46.5**	**2.4**	**20.7**	**9.2**	**2.8**	**8.8**	**0.03**	**0.0**	**0.03**	**10.7**
Ruby-crowned Kinglet	34	2.4	4.5	2.0	–0.6	0.5	3.2	19.8	7.8	–19.4	–8.8	–1.8	–8.8	–0.03	—	–0.03	–6.8
Nashville Warbler[c]	26	–0.6	4.9	0.6	0.7	0.9	0.4	30.6	2.6	–15.0	–8.6	–1.0	–5.4	0.2	—	0.2	–10.6
Orange-crowned Warbler[d]	20	2.8	6.9	–0.03	2.8	2.1	0.9	12.0	13.0	–18.5	–7.8	–2.0	–8.8	3.7	3.8	–0.03	–10.7
MacGillivray's Warbler	18	2.0	7.1	1.9	1.1	3.3	1.7	4.2	2.4	–9.5	0.03	–0.8	–8.8	8.7	8.8	–0.03	–8.8
White-crowned Sparrow	29	–3.8	3.6	–0.03	–0.6	4.2	1.7	–43.4	6.0	44.9	55.1	–1.5	–8.8	4.4	4.4	–0.03	–7.8

[a]Three arthropod taxa were not included in this table as they were never identified in samples of the diet of these species. However, their availability was as follows: Archaeaognatha accounted for 0.3% of biomass in conifer forest, 6.3% in mountain shrubland, and 3.6% in the combined sample; Coccoidea (scale insects) made up 15.9% in conifer forest, 0% in mountain shrubland, and 7.0% of the combined total; and Orthoptera (which were eaten by at least one Black-headed Grosbeak) accounted for 1.6% in conifer forest, 5.8% in mountain shrubland, and 4.0% of the combined total.

[b]*Junco hyemalis.*

[c]*Oreothlypis ruficapilla.*

[d]*Oreothlypis celata.*

stopover-ecology data from the same study site and years (Carlisle et al. 2005a), predicting that years of lower food availability (2001–2002, especially 2002) should result in poorer energetic condition of migrant birds. However, data on mass change, proportions of birds recaptured, and stopover duration from recaptured birds (seven species) from 2000 to 2002 revealed that although a few species fared slightly better in one or two of these years, no annual differences were significant. Regression data showed similar results (Carlisle et al. 2005a). Recaptured Yellow Warblers (*Setophaga petechia*) gained less mass in 2001 than in other years, but this pattern was not observed in other warblers, and only the Dusky Flycatcher (*Empidonax oberholseri*) showed similar, lower gains in 2001. Samples of the principal frugivores at the site, Townsend's Solitaire (*Myadestes townsendi*), Western Tanager, and Black-headed Grosbeak (*Pheucticus melanocephalus*) were too small to be tested for differences in energetic condition by year. White-crowned Sparrows consumed a moderate amount of fruit and, while the increase was not significant, they appeared to gain mass more effectively in 2001 (a year of particularly high fruit abundance). However, these sparrows ate proportionately more seed matter (the availability of which we did not measure) than fruit, and this reliance on other food sources may have allowed them to perform well even in years of low fruit abundance. Overall, in terms of weight gain, there were no years

in which most species of migrants fared better than in others (Carlisle et al. 2005a) despite annual variation in the availability of arthropods and fruit (Fig. 4).

DISCUSSION

Habitats differ in their relative availability of food, and migrants can track these resource differences during stopover (Graber and Graber 1983, Hutto 1985, Blake and Hoppes 1986, Martin and Karr 1986, Suthers et al. 2000, Rodewald and Brittingham 2002). While in their study of migrating Sedge Warblers (*Acrocephalus schoenobaenus*) in Britain Bibby et al. (1976) established a direct correlation between measured food levels and migrants' condition in different years, few other studies have directly examined the connection between food availability and mass gain of migrating birds. This is particularly true in western North America (but see Kelly et al. 2002), where relatively little is known about stopover ecology in general (Carlisle et al. 2009) and about food availability in particular.

FOOD AVAILABILITY

We found that the two arthropod-sampling methods complemented each other in that the branch clipping detected foliage-dwelling arthropods whereas the pitfall traps sampled more ground-dwelling taxa and also better sampled flies (Diptera) and yellowjackets and hornets (Vespidae)—taxa that may avoid capture via branch clipping because of their mobility and visual ability but might be attracted to the soapy water we used in pitfall traps.

Data on the availability of arthropods to migrants in the western United States are limited. McGrath et al. (2009) documented highest availability of Thysanoptera, Hemiptera, and Diptera during spring migration along the Colorado River, and Kelly et al. (2002) sampled high densities of Coleoptera, Diptera, Hymenoptera, and "Homoptera" (Auchenorrhyncha and Sternorrhyncha) in their study of food availability for Wilson's Warbler (*Cardellina pusilla*) in fall in New Mexico. Our data contrast with studies during spring migration and the breeding season, mostly from the eastern United States, that have found Lepidoptera larvae as significantly preferred prey (Graber and Graber 1983, Holmes and Schultz 1988, Moore and Wang 1991). Although we found lepidopteran larvae consumed in greater proportion than their abundance, and they are likely preferred as diet items, our data suggest that these insects were not abundant enough during autumn to be an important component of most migrants' diet. During spring migration this pattern may be different. The arthropod communities we observed are broadly similar to those used by migrants wintering in forests of Jamaica (Johnson 2000), with the Hemiptera and Araneae being dominant, but the proportion of Coleoptera, Hymenoptera, and Diptera was higher in Jamaica than in Idaho. Similarly, Poulin and Lefebvre (1997) documented high numbers of these taxa in Panama, including higher abundances of Diptera and Coleoptera than we found in Idaho.

FORAGING BEHAVIOR

Results for foraging by habitat are consistent with count data from the same study area (Carlisle et al. 2004), the abundance and richness of migrants being higher in shrubby deciduous habitats than in conifer forest or shrubsteppe. As reported by other studies of foraging during migration (Hutto 1981, Parrish 2000, Petit 2000), we found evidence that some species of woodland migrants broadened their repertoire of behaviors during migration stopover beyond that at other times of the year, in terms of both habitat type and maneuvers used. Species varied greatly in foraging behaviors, and some differences were apparent even within guilds of related species. For instance, the seven warblers we studied differed in each variable examined. Relationships among species were quite complex, but some general trends emerged. Especially notable was the MacGillivray's Warbler (*Geothlypis tolmiei*), which foraged lower and more to the inside of dense shrubby deciduous vegetation than did other warblers. Townsend's and Yellow-rumped warblers differed from the other warblers in using conifer forest and mountain shrubland in roughly equal proportions, foraging higher (in absolute but not relative terms), and foraging farther toward branch tips. Overall, MacGillivray's and Townsend's and Yellow-rumped warblers occupied opposite ends of the spectrum of warblers' foraging behavior. These data are consistent with previous observations of these warblers' foraging behavior (see Morse 1989 for review) and also suggest that there is some niche separation among these species at stopover sites in addition to during the breeding season.

Results for the kinglets broadly match those of Franzreb (1984, data from breeding season in Arizona) and Keast and Saunders (1991, data from spring migration in Ontario) especially in that the Ruby-crowned hovered in a much higher proportion of foraging attempts than did the Golden-crowned, which more often forages from a perch. The division of deciduous (Ruby-crowned) and coniferous (Golden-crowned) habitats closely matches the findings of Keast and Saunders (1991), whereas less deciduous habitat was available in Franzreb's (1984) study area. Thus, while Ruby-crowned Kinglets breed mostly in areas dominated by conifers, they tend to use deciduous trees or shrubs much more during migration (Swanson et al. 2008).

Foraging behaviors of the two *Empidonax* flycatchers were strikingly similar. Though these species tend to segregate during the breeding season, with Hammond's (*E. hammondii*) occurring in denser forest (coniferous and sometimes aspen) and the Dusky occurring in forest edge areas with more deciduous shrubs—a pattern observed at Lucky Peak during June (JDC, pers. obs.)—it appears that, like Ruby-crowned

Kinglets, Hammond's Flycatchers shift to using more deciduous habitat during autumn migration.

DIET COMPOSITION

The diets of the autumn migrants we studied were composed of a mix of arthropods dominated by the Auchenorrhyncha, Sternorrhyncha, Coleoptera, Hymenoptera, Heteroptera, and Diptera, although it varied by species. The relatively high consumption of Coleoptera is similar to that found among spring migrants in Arizona (McGrath et al. 2009) and could be biased by the indigestibility of the elytra and the relative ease of locating the elytra in diet samples. In some ways, the arthropod components of autumn migrants' diets in Idaho are similar to those of migrants wintering in the tropics in the birds' use of beetles and ants (Poulin and Lefebvre 1995, 1997, Strong 2000). However, the high importance of Hemiptera (especially Auchenorrhyncha and Sternorrhyncha) in Idaho is a departure from these results and from studies of spring migrants, for which Lepidoptera are more important (Graber and Graber 1983, Moore and Wang 1991). These differences may simply reflect the arthropods available in different places and at different times of year. Diets of spring migrants in Arizona (McGrath et al. 2009) are similar to autumn migrant diets we observed in that Auchenorrhyncha, Sternorrhyncha, Heteroptera, and Coleoptera were all important dietary components and Lepidoptera were not common in either study.

THE IMPORTANCE OF FRUITS IN MIGRANTS' DIETS

The extent of frugivory we observed adds to building evidence that fruits are important dietary components during the nonbreeding season for many species that we think of as primarily insectivorous (Jordano 1988, Blake and Loiselle 1992, Parrish 1997, 2000, Smith et al. 2007, Smith and McWilliams 2010). Jordano (1988) and Parrish (1997) both found that diets combining fruit and arthropods (omnivory) led to migrants gaining weight more rapidly than did diets of strict frugivory or insectivory. Thus the frugivory of migrants at Lucky Peak may also suggest that many of the primarily insectivorous birds we studied were expanding their feeding repertoire for migratory fattening, as found by Parrish (1997, 2000). Kelly and Hutto (2005) reported little to no frugivory among western warblers, especially those endemic to western North America, but also pointed out how little work had been done in this arena. All species of warblers we studied ate fruit, and this is the first report of frugivory for Townsend's and MacGillivray's warblers (Pitochelli 1995, Wright et al. 1998). In fact, although for no species of warbler did fruits make up more than 17% of the diet volume, at least 50% of diet samples of every one of these species contained some fruit. It is possible that documenting this extent of frugivory among western migrants was simply a matter of sampling in a place with abundant fruit—in this case, a montane shrubland. Most studies of migration in the West to date have been done in riparian areas, and few have examined migrants' diets. Given the widespread distribution and summer ripening of numerous species of fruiting shrubs in western mountains, we expect that frugivory of landbirds migrating in autumn might be relatively common in similar habitats in western North America.

To summarize the diet and foraging data, we found that (1) most autumn migrants foraged in shrubby deciduous habitats, (2) most species differed in foraging repertoires and diet composition, and (3) all species consumed a variable combination of arthropods and fruit. Whereas foraging-behavior data for many species broadly matched those of previous studies, diet composition differed (from the relatively few studies to date; cited above) both in terms of proportions of arthropod groups as well as the inclusion of fruit as an important dietary component. We think it likely that migrating birds are flexible enough to adjust their behavior at a stopover site by foraging where prey/fruit is abundant and by consuming the most readily available food types that still allow them to gain mass. At Lucky Peak, arthropods were most abundant in the mountain shrubland and Douglas-fir forest, the order Hemiptera was the most abundant type of arthropod, and fruits were only available in the mountain shrubland. Thus, taken together, diet and foraging data suggest that food availability is likely one factor that drove habitat occupancy toward shrubby deciduous habitats. In particular, the combination of arthropods and the only fruit available at the study site may have led to a high proportion of birds (both species and individuals) feeding in mountain shrubland. Other possible explanations for a preference for mountain shrubland could include provision of better cover and/or fruit use to meet water needs in the relatively arid western environment.

DIET COMPOSITION VERSUS ARTHROPOD AND FRUIT AVAILABILITY

Together, the 19 bird species studied consumed most types of arthropods detected by our sampling methods; exceptions were scale insects (abundant in conifers, but not documented in the diet), Archaeaognatha (bristletails—common ground-dwelling hexapods in both mountain shrubland and shrubsteppe), and Orthoptera (eaten only in two observations). Whereas each bird species differed somewhat in its arthropod consumption, there were several invertebrate taxa that were eaten preferentially, including spittle bugs, stink bugs (especially by vireos), and beetles. Other taxa were consumed frequently but in proportions relatively equal to or less than their availability, and these included psyllids, leafhoppers, flies, and Hymenoptera. All species consumed fruit to varying degrees, and we found fruits from all fruit-producing shrub species at the study site in diet samples across the bird community. While some preference for and avoidance of certain items was evident, the diets of most migrants reflected

the availability of food in the habitats in which they foraged, including the prevalence of fruit in the diets of many species.

IMPLICATIONS OF FOOD AVAILABILITY ON ENERGETIC CONDITION OF MIGRANTS

Our data demonstrate that although the availability of both arthropods and fruit differed markedly by year, variation in food availability did not have a detectable effect on migrants' energetic condition. Several plausible explanations exist for the absence of a correlation between food availability and migrants' energetic condition. These include (1) our measures of "food availability" did not adequately measure food as it is perceived/used by migrants; (2) our measures of birds' condition did not adequately detect significant differences; and/or (3) the "lower" levels of arthropods measured in 2001 and 2002 (as compared to 2000) and very low numbers of fruit in 2002 were not low enough to have a measurable effect on migrants' condition.

Items in the diet of migrants were encountered frequently in our sampling of arthropods (as found by Johnson 2000), and we often observed migrants foraging on these items (JDC, pers. obs.). Thus, though sampling food availability as the bird perceives it is certainly a challenge, our measures of food availability were sampling the vast majority of what the migrants consumed. We recognized the need to tailor food-availability studies to particular bird species (Holmes and Schultz 1988) and with the birds' perspective in mind (Wolda 1990). Thus our sampling of arthropod prey on branches and in pitfall traps was focused on areas where migrants were observed foraging and turned up all of the major components of the prey the migrants we studied consumed. Therefore, we suggest that our measures of food availability can, at a minimum, be viewed as an index to food abundance and that the measured differences among years (observed in both branch-clipping and pitfall-trap sampling) indicated actual differences in availability of food for migrant birds.

While some authors have argued that recaptured migrants are not necessarily representative of the entire population of migrants (e.g., Winker et al. 1992), the variables analyzed by Carlisle et al. (2005a) are standard and are likely reliable indicators of migrants' stopover ecology at this site. This conclusion is strengthened by the general correspondence of data from recaptured birds with regressions of mass vs. time of day (based on data from all captured birds) from the same site (Carlisle et al. 2005a). Future investigations of this sort might be enhanced by the coupling of standard stopover data with measures of plasma metabolites indicating energetic condition and migrants' fattening (Guglielmo et al. 2005).

Finally, we considered the possibility that food availability, despite measured differences among years, was not low enough to affect migrants. It is possible that in all years in which we measured arthropod availability, arthropod and/or fruit numbers/biomass were above a threshold required for mass gain. It is interesting to consider that insectivorous birds (primarily the Ruby-crowned Kinglet) are most abundant at Lucky Peak at a time (late September into early October; Carlisle et al. 2005b) when arthropod availability is lower than in August. The fact that very large numbers of kinglets (and smaller numbers of other migrants) are succeeding at stopover (Carlisle et al. 2005a) when arthropod numbers are depressed relative to earlier in the season suggests that, if a threshold exists below which arthropod availability affects migrants, it is lower than the levels we measured during this study.

Interference competition can negatively affect migrants' condition even though arthropod numbers are high relative to bird density. For example, Kelly et al. (2002) found that migrants did not perform as well when the density of birds was high, even when arthropods were abundant. Whether or not competition among migrants is an important factor shaping their success at our study site, it appears that migrants were relatively unaffected by changes in arthropod and fruit availability—at least during the years we studied. Thus we might ask, Under what conditions might food limitation during migration occur? Contributing factors likely include season, geography, resource abundance and quality, and migrants' abundance (Hansson and Pettersson 1989, Kelly et al. 2002). It's possible that at some sites we might expect to see food limitation only during years of extremely low production of preferred arthropods or fruits (for example, during severe droughts). To better understand factors underlying the suitability of stopover sites for migratory birds and the potential for changes in food abundance to affect the energetic condition of migrants, we recommend continued study of food availability and avian energetic condition over many years under varying climatic conditions and in a variety of habitat types. Such an effort would be especially timely in the face of a changing climate that could bring warmer and drier weather to many areas important for migration stopover in the West (IPCC 2007).

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