

5-1-2005

Stopover Ecology of Autumn Landbird Migrants in the Boise Foothills of Southwestern Idaho

Jay D. Carlisle
Boise State University

Gregory S. Kaltenecker
Boise State University

David L. Swanson
University of South Dakota

STOPOVER ECOLOGY OF AUTUMN LANDBIRD MIGRANTS IN THE BOISE FOOTHILLS OF SOUTHWESTERN IDAHO

JAY D. CARLISLE^{1,2,3}, GREGORY S. KALTENECKER¹, and DAVID L. SWANSON²

¹*Idaho Bird Observatory, Department of Biology, Boise State University,
1910 University Dr., Boise, ID 83725*

²*Department of Biology, University of South Dakota, 414 E. Clark St., Vermillion, SD 57069*

Abstract. The topography of western North America provides a complex landscape for landbird migrants, and stopover patterns in this region are poorly understood. We examined seven years of stopover data (1997–2003) from a montane area in southwestern Idaho to determine whether this area provides suitable stopover habitat. We compared the proportion of birds recaptured, stopover duration, and changes in energetic condition within and among species and between two mist-netting sites located in different habitats. The proportion of birds recaptured ranged from zero to over 20%, and fewer than 5% of individuals were recaptured in most species. Mean minimum stopover durations from recapture data ranged from 1 to 10 days; most species averaged less than 6 days. Stopover duration estimates from open-population models were comparable but generally greater than estimates from recapture data. As found in stopover studies from other regions, stopover metrics varied within and among species in Idaho. However, most migrants in this study exhibited an ability to gain mass, evidenced both by recapture data and by regression of energetic condition against time since sunrise. These data imply that montane habitats in Idaho are suitable stopover sites. It follows that these habitats might serve an important role for many landbird migrants during the period of late summer molt and autumn migration, a time when many lowland areas of the West, including some riparian systems, are especially arid. We suggest that including montane nonriparian habitats in future stopover ecology studies will allow for a more complete understanding of migrant habitat needs in the West.

Key words: habitat suitability, Idaho, Intermountain West, landbird migration, stopover ecology.

Ecología de Aves Migrantes de Otoño Durante Períodos de Escala en el Piedemonte de Boise, Suroeste de Idaho

Resumen. La topografía del oeste de Norte América representa un paisaje complejo para las aves terrestres migratorias, y los patrones de escala migratoria en esta región son poco conocidos. En este estudio examinamos datos de escalas migratorias colectados a través de siete años (1997–2003) en un área montana del suroeste de Idaho para determinar si esta área provee hábitats de escala adecuados. Comparamos la proporción de aves recapturadas, la duración del período de escala y los cambios en la condición energética por especie y entre especies y entre dos sitios de captura con redes de niebla ubicados en hábitats diferentes. La proporción de aves recapturadas varió entre cero y más del 20%, y en la mayoría de las especies menos del 5% de los individuos fueron recapturados. La duración mínima promedio de los períodos de escala estimada a partir de datos de recapturas estuvo entre uno y 10 días, y la estancia promedio de la mayoría de las especies fue menor de seis días. Los estimados de la duración de los períodos de escala calculados con modelos de población abierta fueron comparables (pero generalmente mayores) a los estimados basados en datos de recaptura. Tal como se ha encontrado en estudios sobre escalas migratorias realizados en otras regiones, en Idaho las mediciones tomadas durante el período de escala variaron dentro de cada especie y entre especies. Sin embargo, la mayoría de las especies migrantes que estudiamos tuvieron la habilidad de incrementar su peso, lo que se evidenció por medio de los datos de recaptura y de análisis de regresión entre la condición energética y el tiempo transcurrido desde la salida del sol. Estos datos implican que los ambientes montanos de Idaho son lugares de escala migratoria adecuados. Por lo tanto, estos hábitats pueden ser importantes para muchas aves terrestres durante el período de la muda del final del verano y la migración de otoño, un momento durante el cual muchas áreas de tierras bajas del

Manuscript received 25 August 2004; accepted 2 February 2005.

³ E-mail: jcarlisl@usd.edu

oeste, incluyendo sistemas riparios, son especialmente secas. Sugerimos que incluir ambientes montanos no riparios en estudios futuros de la ecología de los períodos de escala migratoria permitirá tener un entendimiento más completo de los requerimientos de hábitat de las aves migratorias en el oeste.

INTRODUCTION

Migration is an energetically expensive time period for birds. Locating stopover habitat that is suitable for rest and fuel deposition is critical to the successful completion of migration and to the overall fitness of *en route* migrants (Moore and Wang 1991, Moore et al. 1995). Mortality during migration may serve as a factor limiting landbird populations (Sillett and Holmes 2002) and may be especially high during fall migration because of the large proportion of inexperienced juvenile birds. To implement effective conservation strategies, it is imperative to know which stopover sites support high abundances of migrants, and also which habitats provide opportunities for mass gain for the majority of migrants.

The ability of migrant birds to gain mass during stopover is an important determinant of site suitability, and different sites may be more or less suitable for different species or guilds (Dunn 2001). Variable suitability of stopover sites can be attributed to habitat features, as well as the density of migrants (potential competitors) encountered at the site (Hansson and Peterson 1989, Kelly and Finch 2002). Additionally, different species and individuals within species vary in their ability to meet the energetic demands of migration (Moore and Kerlinger 1987, Kuenzi et al. 1991, Wang et al. 1998). Meeting the energetic demands of migration may be especially difficult for relatively inexperienced, immature birds or females excluded from foraging sites by dominant males (Ketterson and Nolan 1985, Wang et al. 1998). Considering these factors, assessing stopover site suitability across the entire migrant assemblage is important for research and conservation.

Few data exist on the stopover ecology of landbird migrants in western North America and the existing studies focus mainly on riparian habitats (Otahal 1995, Wang et al. 1998, Finch and Wang 2000). While riparian areas are clearly important for many migrants, several studies suggest that montane habitats also support high numbers of migrants during fall migration (Austin 1970, Greenberg et al. 1974, Blake 1984, Hutto 1985, Carlisle et al. 2004). In this study,

we examined stopover patterns and mass trends over a seven-year period for the autumn landbird migrant assemblage in a montane area of southwestern Idaho. We used several metrics to examine the stopover ecology of migrants, including the proportion of birds recaptured, stopover duration, and changes in energetic condition. We compared age and sex related patterns, and tested for differences among years. In addition, for two years of the study (1998–1999), we compared stopover data between two habitats, the main mist-netting site located in upland shrubs and a nearby station in a riparian draw.

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 Boise foothills, comprised of north-south trending peaks and hills in the Boise Mountains, form the northern boundary of the Snake River Plain and the southernmost extension of the central Idaho mountains. The study site is located at the boundary between two major vegetation types: the mostly forested mountains to the north and the shrubsteppe dominated Great Basin to the south. Four distinct habitat types occur in a mosaic at Lucky Peak and throughout the Boise Mountains: conifer forest, mountain shrubland, shrubsteppe, and willow-dominated riparian shrub (willow riparian; see Carlisle et al. 2004).

MIST NET CAPTURES

We captured birds using mist-nets in mountain shrubland and willow riparian habitats (Carlisle et al. 2004). We operated mist nets daily for 5 hours beginning at sunrise, except in the case of extreme temperatures ($>32^{\circ}\text{C}$ or $<0^{\circ}\text{C}$), high winds, or continuous precipitation. The mountain-shrubland site was the main mist-netting site and it was operated from 12 August–21 October 1997, 5 August–15 October 1998, 31 July–15 October 1999, 18 July–16 October 2000, and 16 July–15 October 2001, 2002, and 2003. For two years, we operated a willow-riparian site to draw comparisons against the mountain-shrub-

land site and the riparian site was operated from 21 August–14 October 1998 and 2 August–29 September 1999. We identified captured birds to species, age (after hatch-year [AHY] or hatch-year [HY]), and sex (Pyle 1997) and fitted each with individually numbered, U.S. Geological Survey aluminum leg bands. We did not band hummingbirds but individually marked tail feathers to prevent double-counting of individuals. We also recorded date, time, natural wing chord (to the nearest mm), body mass to the nearest 0.1 g (with an electronic scale [after 1997]), and fat stores for each bird (Pyle 1997, DeSante et al. 2003). Subcutaneous fat stores were estimated visually, based largely on furcular and abdominal fat stores, according to an 8-point scale used in the MAPS program (DeSante et al. 2003)—a scale generally comparable to Helms and Drury (1960) but with two additional categories (fat scores 6 and 7) for exceptionally fat migrants. We re-examined body mass and fat stores of birds that were recaptured at least one day after initial capture.

STUDY SPECIES

We assigned species to one of three discrete categories for comparisons: Neotropical migrants (generally long-distance migrants), temperate migrants (generally short-distance migrants), and irregular migrants (species that do not migrate every year). We classified Neotropical migrants according to DeGraaf and Rappole (1995), but applied more stringent criteria such that \geq half of the geographical winter distribution must be south of the United States (see Carlisle et al. 2004). Based on MAPS (Monitoring Avian Productivity and Survivorship) data from the same study site, we also assigned each migrant species to one of four breeding status codes (Rimmer and McFarland 2000, DeSante et al. 2003). Regular breeders (B) were defined as birds within their normal breeding range that bred at the study site in most or all years, sporadic breeders (S) were defined as birds within the normal breeding range but which bred less regularly at the site, passage migrants (P) were birds outside of the breeding range that occurred only as migrants at the site, and altitudinal migrants (A) were birds within their normal breeding range, but which only used the site during migration.

Distinguishing migrants from local breeders. A number of species bred at the study site or

nearby in addition to migrating through the study site. Individual birds that were known to be local breeders (banded at the site, birds in juvenile molt, adults captured with dependent juveniles, or birds in heavy symmetric molt) were excluded from analyses. Nonetheless, a number of birds likely dispersing from the nearby area were captured during this study, particularly in late July. While capture totals for local birds were generally very small relative to numbers encountered during migration, the possibility exists that data on stopover ecology may be biased if non migrants were included. To separate migrants from breeding or locally dispersing individuals, we plotted numbers of new captures against date for each species to examine early season capture patterns in both age classes. Once these plots were examined, a cut-off date was chosen before which all captures were considered nonmigrants. For example, Hammond's Flycatchers (*Empidonax hammondi*) exhibited a pattern of very few early season captures consisting of recently-fledged but fully-feathered juveniles and molting adults followed by a lull and then a much greater abundance of birds in mid-August; thus, the cut-off date for this species occurred just prior to the second wave of captures. In most cases, the number of excluded early-season birds was negligible when compared to the total number of migrants.

STATISTICAL ANALYSES

Stopover behavior and energetics. Because of the greater sampling effort and the larger sample sizes involved, all analyses were based on data from the mountain-shrubland site except when we made direct comparisons of stopover parameters with the willow-riparian site (see separate section below). To evaluate inter- and intraspecific differences in the behavior exhibited during stopover, we compared the proportion of birds recaptured, stopover duration, and changes in energetic condition. We defined energetic condition as the residuals from individuals' mass controlling for body size (wing chord). The proportions of birds recaptured were compared by frequency analysis (χ^2 ; Brower et al. 1990). When the proportion of birds recaptured differed significantly among years, we ran pairwise single degree-of-freedom tests to determine which year(s) had significantly different recapture proportions from others (Zar 1996, Carlisle et al. 2004). We compared stopover duration with

nonparametric Kruskal-Wallis or Mann-Whitney *U*-tests and differing means (of Kruskal-Wallis tests) by Dunn's test (Zar 1996). We used *t*-tests to compare initial energetic condition within species and between sites (Zar 1996). We also used *t*-tests to compare initial energetic condition of birds captured only once to birds later recaptured to evaluate whether recaptured birds were in different energetic condition upon initial capture. For species with adequate sample sizes ($n \geq 10$), we computed rates of daily mass change for recaptured birds by subtracting mass at initial capture from mass at final recapture, dividing by stopover duration, and correcting for time of day (Cherry 1982).

We estimated minimum stopover duration by subtracting the initial capture date from the final recapture date (Cherry 1982), a conservative but widely used estimate of the time migrants spend at stopover sites. Additionally, we estimated stopover duration using open-population models that were developed with all captures for each species in each year (Viallefont et al. 1998). Goodness-of-fit tests were used to determine whether the parameters in each model could be estimated. Due to small sample sizes or uneven distribution of captures, we were unable to estimate some species by year combinations; however, the estimates provided offer a different approximation of stopover durations by considering the time before and after first and last captures (Schaub et al. 2001). We then compared stopover duration estimates between recapture data and open-population model estimates.

Because mass change of recaptured birds may not be representative of the entire migrant population (Winker et al. 1992) and adequate sample sizes were available for relatively few species, we also used a regression of energetic condition on time since sunrise for all birds captured to include more species in the analysis. We generated equations for rates of diurnal change in energetic condition from a regression of mass on wing chord for all species with at least 40 individuals captured, excluding recaptures (Winker 1995). Regression equations were based only on the first 5 hr after sunrise. Due to concerns regarding the applicability of this method and, specifically, how the relationship between mass and wing chord might affect results, we also used an alternate analysis relying on residuals in order to confirm the results. First, we generated residuals from a regression of mass on wing

chord for each species and we then regressed these residuals against time since sunrise. Data from both analysis techniques were remarkably similar. Due to the similarity of the results, we only present data from the regressions of residuals on time since sunrise. We compared mass gain estimates from recapture data and regression models to determine if the two methods were consistent in assessing whether migrants were gaining or losing mass (Winker et al. 1992).

To examine possible differences among years, we compared annual variation in stopover duration and mass changes among recaptured birds for species with at least 10 recaptures in each year. Among-year differences in sampling effort were small, so this should have little effect on estimates of stopover duration and mass change among years. We used ANCOVA to test for annual variation in energetic condition in 18 migrant species with at least 50 individual captures in three or more autumn seasons. We then used least squares means to separate years differing in *y*-intercepts (Zar 1996).

Comparing between mist-netting sites. The two major habitats used by migrants at Lucky Peak were mountain shrubland and willow riparian (Carlisle et al. 2004). The vegetation height and structure at both sites were similar but the species composition differed; willows (*Salix* sp.) were more prevalent at the riparian site, and cherries (*Prunus* sp.) dominated in the mountain shrubland (Carlisle et al. 2004). Also, the willow-riparian site, located in a draw, was smaller in area and more linear than the mountain-shrubland site along the ridge. To examine potential differences in stopover parameters between sites, we compared recapture proportions, stopover duration, and changes in energetic condition between the mountain shrubland and willow riparian mist-netting sites using data from common banding days during 1998–1999. During this time period, we recaptured 10 or more individuals at each site for only five species (Ruby-crowned Kinglet [*Regulus calendula*], Spotted Towhee [*Pipilo maculatus*], Dark-eyed Junco [*Junco hyemalis*], White-crowned Sparrow [*Zonotrichia leucophrys*], and Lazuli Bunting [*Passerina amoena*]); therefore, we restricted intraspecific comparisons of stopover energetics among recaptured birds to these species. However, we combined data for all species with at least 20 individual captures at each site to

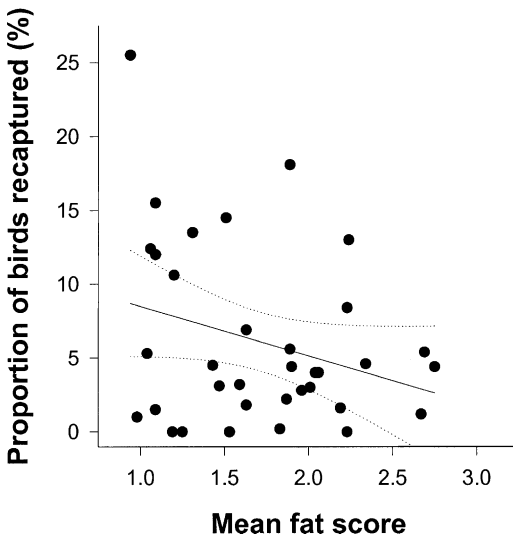


FIGURE 1. Proportion of birds recaptured (%) plotted against mean fat score for 35 autumn migrant species in Idaho; $r^2 = 0.08$, $P = 0.09$. Fat scores range from 0 to 7 and are drawn from DeSante et al. (2003). Circles are data points for each species, solid line is the predicted relationship between fat score and recapture proportion, and dotted lines are the 95% confidence intervals.

compare other stopover parameters between sites. Thus, we compared recapture proportions and stopover duration between sites for Neotropical migrants (12 species), temperate migrants combined (6 species), and all migrants (19 species; includes 1 irregular migrant). Lastly, we compared mass gain rates from regression equations between sites using ANCOVA (Zar 1996).

We considered results statistically significant when $P \leq 0.05$. When making multiple comparisons using the same data set (i.e., by species or migrant strategy), we used sequential Bonferroni to control against making Type II errors (Rice 1989).

RESULTS

STOPOVER PATTERNS IN THE MOUNTAIN-SHRUBLAND HABITAT

Recapture proportions. The proportion of migrants recaptured at least one day after original capture ranged from 0% to over 25% for the 35 species with at least 40 captures (Table 1). Only nine species had recapture proportions over 10% and 21 species (60% of species) had recapture proportions under 5%. Only the Black-capped

Chickadee (*Poecile atricapilla*) showed recapture proportions over 20%. The highest recapture proportion for a true passage migrant was 18% for the White-crowned Sparrow. The only species with no recaptures were those with relatively small numbers ($n < 100$); thus, all migrant species with higher sample sizes showed at least some stopover tendency (Table 1). There was a trend ($P = 0.09$) for species with lower average fat scores upon initial capture to be recaptured in higher proportions (Fig. 1).

Energetic condition and stopover duration among recaptured birds. We examined age-related patterns of stopover duration and mass changes in recaptured birds from 11 species (Table 2). Mean minimum stopover duration for individual species ranged from 1–10 days (Table 2). While immature birds tended to stopover longer than adults in most species, there was no significant age difference for any of the 11 species (Table 2). Stopover duration estimates from open-population models (calculated from all individuals, including recapture frequencies, of a species in a given year) were generally greater than those from recaptured birds, although in a few cases estimates from the two methods were very similar. Estimates from open-population models averaged 1.9 times longer than minimum estimates from recapture data but ranged from 0.6 to 5.0 times longer.

Mean mass change among recaptured individuals was positive for most species (Table 2); however, the percent of individuals losing mass ranged from 25% to 67% for each species (Table 1). Thus, while most species seemed to gain mass, there was much variability among individuals. Mass changes were generally similar among age groups for most species but in Yellow Warblers (*Dendroica petechia*), the only species with significant age-related differences, adults showed significantly greater mass gain (Table 2).

After sequential Bonferroni corrections, none of the 10 species with ≥ 5 recaptures for each sex showed significant intersexual differences in mass change during stopover (all $P > 0.05$) or in stopover duration (all $P > 0.05$).

We analyzed 13 migrant species with ≥ 10 recaptures (9 Neotropical and 4 temperate) for differences in mass gain rates between birds recaptured one day after original capture and those recaptured at least two days later. After Bonferroni corrections, three of these species, Spotted

Towhee, Dark-eyed Junco, and White-crowned Sparrow, showed significant differences in mass gain rates (all $P < 0.01$ after corrections) such that birds with longer stopover durations gained mass at a higher rate than birds staying only one day. Four other species (Dusky Flycatcher [*Empidonax oberholseri*] and Nashville [*Vermivora ruficapilla*], MacGillivray's [*Oporornis tolmiei*], and Wilson's warblers [*Wilsonia pusilla*]) exhibited similar patterns of birds with longer stopover durations showing better rates of mass change but these were not significant after Bonferroni corrections.

Diurnal changes in energetic condition. Seventeen of 36 species examined (those with ≥ 40 captures) exhibited significant changes in energetic condition during the first 5 hours of the day (Table 3). Only one of these species, the Calliope Hummingbird, lost mass through the morning hours; the remaining species showed significant mass gains (Table 3).

Arrival condition vs. stopover propensity. Of 14 species (those with ≥ 10 recaptures), only Black-headed Grosbeak (*Pheucticus melanocephalus*) and Spotted Towhee showed significantly higher energetic condition upon arrival for birds captured only once than for those later recaptured (both $P < 0.01$ after Bonferroni corrections). Both Ruby-crowned Kinglets and White-crowned Sparrows exhibited similar patterns (of single capture birds showing higher energetic condition) but were not significant after Bonferroni corrections. However, the remaining 10 species showed broad overlap between groups.

Interannual comparisons. Nine species had sufficient recaptures in multiple years of the study to allow for interannual comparisons of stopover duration and mass change. Stopover duration appeared to vary somewhat among years but only Ruby-crowned Kinglet showed significant differences (Table 4; the apparent difference for White-crowned Sparrow was no longer significant after Bonferroni corrections). Four species analyzed appeared to show significant differences in mass change among recaptured birds among years (Table 5; but none were significant after Bonferroni corrections). No year was shown to be universally better for all (or most) species analyzed. Recapture proportions showed the most variation among years; six of 10 species showed significant differences (Table 6; differences for Orange-crowned War-

bler were no longer significant after Bonferroni corrections). As with mass change differences among years, recapture proportion variation among years appeared to vary independently among species (Table 6).

Of 18 species examined for interannual differences in energetic condition (those with at least 50 individuals captured in each year), only Ruby-crowned Kinglet and Dark-eyed Junco showed significant differences in condition gain rates during the morning hours among years (Ruby-crowned Kinglet: slower mass gain in 1997 than all other years, $P < 0.0001$; Dark-eyed Junco: faster mass gain in 1997, 1998, and 2001, $P = 0.01$). Conversely, 14 species exhibited significantly different initial energetic condition (y-intercepts) among years (all $P < 0.05$; all species examined except Warbling Vireo, Wilson's Warbler, and Chipping Sparrow). As with mass change data from recaptured birds, no year was universally more suitable across species. In fact, the years in which particular species attained better energetic condition varied considerably across species.

COMPARING BETWEEN NETTING SITES 1998–1999

Recapture proportions were significantly higher at the willow-riparian site than the mountain-shrubland site for all species combined and for temperate migrants, but did not differ for Neotropical migrants (Table 7). Recapture proportions differed significantly for only one of the 19 species examined (Dark-eyed Junco; Table 7) whereas mean minimum stopover duration was greater at the willow-riparian site for two of the five species and both migrant groups (Table 7). Dark-eyed Juncos showed significant differences in mass change between sites; recaptured juncos gained significantly more mass at the willow-riparian site than at the mountain-shrubland site, where they actually lost mass (Table 7). Thus, while not universal, there was a tendency for migrants to be recaptured more often, stay longer, and, at least in one species, gain more mass at the willow-riparian site.

In addition to comparing data from recaptured birds, we also compared rates of mass gain (slopes of regression equations of energetic condition against time since sunrise for all new captures) between sites by ANCOVA for the five species compared using recapture data (see Table 7). We found no significant differences be-

TABLE 1. Breeding status, sample size (n), proportion of birds recaptured, percent of recaptured individuals losing mass, and morphological measurements (mean \pm SD) for Idaho migrants with $n \geq 40$. All data come from initial captures at the mountain-shrubland site.

Species	Status ^a	n	Percent recaptured	Percent losing mass ^b	Mass (g)	Fat score ^c	Wing (mm)
NEOTROPICAL MIGRANTS							
Calliope Hummingbird (<i>Stellula calliope</i>)	B	165	–	–	2.6 \pm 0.2	1.3 \pm 1.0	42.9 \pm 1.5
Rufous Hummingbird (<i>Selasphorus rufus</i>)	P	74	–	–	3.5 \pm 0.4	2.5 \pm 1.2	44.8 \pm 1.5
Western Wood-pewee (<i>Contopus sordidulus</i>)	A	67	0.0	–	12.9 \pm 0.9	1.3 \pm 0.8	82.1 \pm 2.4
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	B	1735	5.3	55.7	11.0 \pm 0.7	1.0 \pm 1.0	66.2 \pm 2.5
Hammond's Flycatcher (<i>Empidonax hammondi</i>)	S	520	0.2	0.0	10.4 \pm 0.7	1.8 \pm 1.1	68.1 \pm 2.5
Western Flycatcher (<i>Empidonax difficilis</i>) ^d	P	75	0.0	–	11.6 \pm 1.0	2.2 \pm 1.0	65.8 \pm 2.7
Cassin's Vireo (<i>Vireo cassinii</i>)	B	414	4.0	62.5	15.0 \pm 1.0	2.1 \pm 1.5	72.7 \pm 1.8
Warbling Vireo (<i>Vireo gilvus</i>)	B	884	1.6	53.8	11.8 \pm 0.9	2.2 \pm 1.4	65.8 \pm 1.7
House Wren (<i>Troglodytes aedon</i>)	B	47	13.0	0.0	10.5 \pm 0.8	2.2 \pm 1.4	51.1 \pm 1.6
Swainson's Thrush (<i>Catharus ustulatus</i>)	S	81	0.0	–	30.4 \pm 1.9	1.2 \pm 0.9	96.5 \pm 2.9
Nashville Warbler (<i>Vermivora ruficapilla</i>)	B	915	6.9	33.3	8.3 \pm 0.6	1.6 \pm 1.5	58.7 \pm 2.3
Orange-crowned Warbler (<i>Vermivora celata</i>)	B	1193	4.0	25.5	8.8 \pm 0.6	2.0 \pm 1.3	60.2 \pm 2.3
Yellow Warbler (<i>Dendroica petechia</i>)	B	727	13.5	42.3	9.1 \pm 0.7	1.3 \pm 1.4	59.6 \pm 2.1
Townsend's Warbler (<i>Dendroica townsendi</i>)	P	428	1.2	20.0	9.6 \pm 0.8	2.7 \pm 1.3	64.1 \pm 2.1
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	B	1665	15.5	46.6	11.0 \pm 0.8	1.1 \pm 1.3	58.6 \pm 2.1
Wilson's Warbler (<i>Wilsonia pusilla</i>)	P	384	5.4	27.8	7.7 \pm 0.6	2.7 \pm 1.2	56.1 \pm 1.7
Western Tanager (<i>Piranga ludoviciana</i>)	B	910	1.8	71.4	30.2 \pm 2.6	1.6 \pm 1.3	91.6 \pm 2.3
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	B	241	8.4	31.6	47.7 \pm 6.1	2.2 \pm 1.9	99.5 \pm 2.2
Lazuli Bunting (<i>Passerina amoena</i>)	B	248	12.0	35.7	14.5 \pm 1.2	1.1 \pm 1.2	69.0 \pm 2.3
Brewer's Sparrow (<i>Spizella breweri</i>)	B	105	12.4	30.8	10.6 \pm 0.8	1.1 \pm 1.1	60.9 \pm 1.9
Chipping Sparrow (<i>Spizella passerina</i>)	B	603	5.6	70.4	12.3 \pm 0.9	1.9 \pm 1.3	70.1 \pm 2.3
TEMPERATE MIGRANTS							
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	B	7376	4.6	30.2	6.2 \pm 0.4	2.3 \pm 1.3	57.7 \pm 2.0
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	S	461	2.8	50.0	5.7 \pm 0.4	2.0 \pm 1.3	54.1 \pm 1.9
Townsend's Solitaire (<i>Myadestes townsendi</i>)	P	290	3.2	25.0	34.0 \pm 2.0	1.6 \pm 1.0	113.0 \pm 3.0
Hermit Thrush (<i>Catharus guttatus</i>)	B	202	3.0	40.0	26.5 \pm 2.8	2.0 \pm 1.2	91.6 \pm 5.3
American Robin (<i>Turdus migratorius</i>)	B	133	1.5	0.0	81.0 \pm 5.3	1.1 \pm 1.1	132.5 \pm 4.4
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	B	1124	1.0	50.0	11.6 \pm 0.7	1.0 \pm 1.0	74.0 \pm 2.6
Spotted Towhee (<i>Pipilo maculatus</i>)	B	915	14.5	37.5	38.1 \pm 2.5	1.5 \pm 1.4	83.8 \pm 2.7
Fox Sparrow (<i>Passerella iliaca</i>)	P	68	4.5	0.0	27.3 \pm 2.0	1.4 \pm 1.2	78.4 \pm 2.8
Dark-eyed Junco (<i>Junco hyemalis</i>)	B	3219	4.4	55.8	17.6 \pm 1.1	1.9 \pm 1.1	75.9 \pm 2.9
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	P	2181	18.1	33.1	23.8 \pm 2.0	1.9 \pm 1.3	74.8 \pm 2.6
IRREGULAR MIGRANTS							
Black-capped Chickadee (<i>Poecile atricapilla</i>)	A	141	25.5	58.8	10.6 \pm 0.7	0.9 \pm 0.7	64.0 \pm 2.3
Mountain Chickadee (<i>Poecile gambeli</i>)	B	502	10.6	38.1	10.6 \pm 0.7	1.2 \pm 0.9	65.8 \pm 2.1
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	B	459	4.4	30.0	10.4 \pm 0.7	2.8 \pm 1.4	66.4 \pm 1.9
Brown Creeper (<i>Certhia americana</i>)	B	45	2.2	0.0	7.8 \pm 0.6	1.9 \pm 1.1	63.7 \pm 2.2
Pine Siskin (<i>Carduelis pinus</i>)	S	388	3.1	50.0	12.0 \pm 0.9	1.5 \pm 1.1	71.5 \pm 2.0
Cassin's Finch (<i>Carpodacus cassinii</i>)	B	45	0.0	–	26.7 \pm 2.1	1.5 \pm 1.1	89.8 \pm 2.1

TABLE 2. Age comparison of stopover data for commonly recaptured migrants in Idaho mountain shrubland, 1997–2003 (data not analyzed if $n < 5$ for either age class). Minimum stopover duration is the number of days elapsed between first and last capture, and mass change reflects the total change in mass of this time interval. Values are mean \pm SE with sample size (n) in parentheses. Scientific names for all species are provided in Table 1.

Species	Minimum stopover duration (days)			Mass change (g)		
	AHY	HY	P	AHY	HY	P
NEOTROPICAL MIGRANTS						
Dusky Flycatcher	4.6 \pm 0.7 (21)	3.7 \pm 0.3 (66)	0.34	0.11 \pm 0.08 (21)	-0.08 \pm 0.06 (64)	0.03 ^a
Nashville Warbler	2.6 \pm 0.5 (28)	2.9 \pm 0.4 (34)	0.23	0.27 \pm 0.13 (26)	0.24 \pm 0.07 (33)	0.68
Orange-crowned Warbler	1.8 \pm 0.3 (9)	2.2 \pm 0.2 (39)	0.50	0.35 \pm 0.13 (9)	0.41 \pm 0.08 (38)	0.79
Yellow Warbler	3.3 \pm 1.0 (8)	4.5 \pm 0.4 (91)	0.44	0.61 \pm 0.07 (7)	0.13 \pm 0.06 (89)	0.003
MacGillivray's Warbler	6.0 \pm 0.8 (32)	5.1 \pm 0.3 (218)	0.33	0.08 \pm 0.19 (30)	0.11 \pm 0.04 (216)	0.67
Wilson's Warbler	1.3 \pm 0.2 (6)	1.7 \pm 0.3 (14)	0.77	0.17 \pm 0.22 (5)	0.27 \pm 0.12 (13)	0.52
Western Tanager	7.5 \pm 2.5 (2)	2.8 \pm 1.0 (13)	–	0.41 \pm 2.39 (2)	-0.67 \pm 0.53 (12)	–
Black-headed Grosbeak	–	3.2 \pm 0.6 (18)	–	–	0.63 \pm 0.34 (18)	–
Lazuli Bunting	10.0 \pm 2.9 (8)	6.1 \pm 1.1 (22)	0.19	0.33 \pm 0.13 (8)	0.18 \pm 0.29 (19)	0.35
Chipping Sparrow	3.8 \pm 1.6 (6)	4.1 \pm 0.9 (23)	0.89	-0.10 \pm 0.20 (5)	-0.28 \pm 0.13 (23)	0.54
TEMPERATE MIGRANTS						
Ruby-crowned Kinglet	1.7 \pm 0.2 (79)	2.0 \pm 0.2 (127)	0.14	0.08 \pm 0.02 (62)	0.11 \pm 0.03 (113)	0.12
Townsend's Solitaire	–	6.2 \pm 2.0 (9)	–	–	0.60 \pm 0.65 (8)	–
Yellow-rumped Warbler	4.0 \pm 0.0 (1)	2.8 \pm 0.6 (10)	–	–	0.13 \pm 0.18 (10)	–
Spotted Towhee	6.3 \pm 1.7 (4)	10.2 \pm 0.6 (133)	–	-1.78 \pm 0.64 (4)	0.83 \pm 0.22 (79)	–
Dark-eyed Junco	4.3 \pm 0.7 (39)	5.2 \pm 0.4 (92)	0.24	-0.11 \pm 0.15 (36)	-0.09 \pm 0.09 (79)	0.90
White-crowned Sparrow	6.2 \pm 0.6 (69)	6.8 \pm 0.3 (306)	0.34	0.74 \pm 0.23 (64)	0.77 \pm 0.12 (257)	0.90

^a Not significant after Bonferroni corrections.

tween sites in mass gain rates during the morning hours for any of these species.

DISCUSSION

STOPOVER PATTERNS IN THE MOUNTAIN-SHRUBLAND HABITAT

Recapture proportions, stopover duration, and mass change among recaptured birds. Recapture proportions in this study varied widely among species and these differences may reflect differences in migratory strategies. Ten species in this study were recaptured in proportions $< 2\%$ whereas nine species had recapture proportions $> 10\%$. While not consistent across all species,

there was a tendency for species with lower mean fat scores at initial capture to have a higher likelihood of recapture, suggesting that energetic condition upon arrival or the migratory strategy of each species may affect stopover propensity.

Generally, recapture proportions observed here are comparable to those of other stopover studies (Kuenzi et al. 1991, Morris et al. 1996, Carlisle 1998) but were substantially higher than those at a montane site in Vermont that was deemed relatively unsuitable for migrants (Rimmer and McFarland 2000). Several factors may affect the amount of time that a migrant spends

←

^a Breeding status: B = regular breeder, S = sporadic breeder, P = passage migrant, A = altitudinal migrant.

^b Percent of recaptured individuals showing mass loss between first and last capture.

^c Fat scores from DeSante et al. (2003).

^d Likely both Pacific-slope (*Empidonax difficilis*) and Cordilleran (*E. occidentalis*) Flycatchers based on Pyle (1997).

TABLE 3. Summary of linear models for change in residuals of energetic condition (mass regressed against wing chord) against time since sunrise for migrants in Idaho mountain shrubland with $n \geq 40$; 1997 to 2003. Variables: b = y-intercept, F indicates how well the linear model fits the data, and r^2 measures what proportion of the change in energetic condition can be attributed to elapsed time. Asterisks indicate the level of significance such that * = $P < 0.05$, ** = $P < 0.001$.

Species	n	b	F	r^2	Mass change ^a
NEOTROPICAL MIGRANTS					
Calliope Hummingbird (<i>Stellula calliope</i>)	130	0.11	4.3*	0.03	-0.191
Rufous Hummingbird (<i>Selasphorus rufus</i>)	57	0.12	0.6	0.01	-0.065
Western Wood-pewee (<i>Contopus sordidulus</i>)	66	-0.21	1.5	0.02	0.478
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	1674	-0.06	5.4*	<0.01	0.128
Hammond's Flycatcher (<i>Empidonax hammondi</i>)	486	-0.20	22.2**	0.04	0.469
Western Flycatcher (<i>Empidonax difficilis</i>) ^b	72	-0.04	0.1	<0.01	0.051
Cassin's Vireo (<i>Vireo cassinii</i>)	379	-0.15	2.1	<0.01	0.308
Warbling Vireo (<i>Vireo gilvus</i>)	845	-0.08	1.5	<0.01	0.163
House Wren (<i>Troglodytes aedon</i>)	42	-0.26	1.3	0.03	0.687
Swainson's Thrush (<i>Catharus ustulatus</i>)	78	-0.14	0.3	<0.01	0.587
Nashville Warbler (<i>Vermivora ruficapilla</i>)	875	-0.17	26.6**	0.03	0.411
Orange-crowned Warbler (<i>Vermivora celata</i>)	1124	-0.08	6.8**	<0.01	0.183
Yellow Warbler (<i>Dendroica petechia</i>)	698	-0.04	0.7	<0.01	0.073
Townsend's Warbler (<i>Dendroica townsendi</i>)	398	-0.20	10.9*	0.03	0.486
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	1612	-0.14	20.2**	0.01	0.310
Wilson's Warbler (<i>Wilsonia pusilla</i>)	367	-0.10	4.4*	0.01	0.218
Western Tanager (<i>Piranga ludoviciana</i>)	871	-0.18	1.3	<0.01	0.323
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	231	-1.03	1.7	<0.01	2.610
Lazuli Bunting (<i>Passerina amoena</i>)	234	-0.12	0.7	<0.01	0.358
Brewer's Sparrow (<i>Spizella breweri</i>)	102	-0.05	0.1	<0.01	0.102
Chipping Sparrow (<i>Spizella passerina</i>)	558	-0.31	14.7**	0.03	0.559
TEMPERATE MIGRANTS					
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	6422	-0.12	253.9**	0.04	0.276
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	397	-0.12	18.7**	0.05	0.334
Townsend's Solitaire (<i>Myadestes townsendi</i>)	242	-0.81	18.7**	0.07	1.766
Hermit Thrush (<i>Catharus guttatus</i>)	185	-0.26	1.3	<0.01	0.572
American Robin (<i>Turdus migratorius</i>)	95	0.39	0.2	<0.01	-1.013
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	1052	-0.25	44.6**	0.04	0.431
Spotted Towhee (<i>Pipilo maculatus</i>)	901	0.14	1.1	<0.01	-0.326
Fox Sparrow (<i>Passerella iliaca</i>)	58	-0.02	0.0	<0.01	0.111
Dark-eyed Junco (<i>Junco hyemalis</i>)	2433	-0.26	48.8**	0.02	0.526
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	1875	-0.20	6.9*	<0.01	0.383
IRREGULAR MIGRANTS					
Black-capped Chickadee (<i>Poecile atricapilla</i>)	131	0.01	0.0	<0.01	-0.005
Mountain Chickadee (<i>Poecile gambeli</i>)	464	-0.21	16.7**	0.03	0.402
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	451	-0.13	5.4*	0.01	0.295
Brown Creeper (<i>Certhia americana</i>)	44	-0.11	0.8	0.02	0.330
Pine Siskin (<i>Carduelis pinus</i>)	321	-0.04	0.1	<0.01	0.094

^a Projected change in mass (in grams) during 5-hour banding session; calculated by multiplying 5-hour change in energetic condition by average wing chord for each species (metrics based on regression of condition index on time since sunrise).

^b Likely both Pacific-slope (*Empidonax difficilis*) and Cordilleran (*E. occidentalis*) Flycatchers based on Pyle (1997).

at a stopover site (and, therefore, recapture proportions) including habitat suitability, degree of isolation of the stopover site, competition, weather, and the bird's condition upon arrival (Richardson 1978, Graber and Graber 1983, Moore and Wang 1991, Kelly et al. 2002). Due

to the need to rebuild fat loads, lean (fat-depleted) birds often stopover longer than fat birds (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990, Morris 1996). It seems plausible that sites with more suitable habitat would retain more migrants and thus have higher re-

TABLE 4. Annual variation (mean ± SE) in minimum stopover duration (days) for migrants in Idaho mountain shrubland with at least 10 recaptures in each year. Sample sizes (*n*) are given in parentheses. Dashes indicate species by year combinations with fewer than 10 recaptures (not included in interannual comparisons). We used nonparametric tests to examine differences among years; Mann-Whitney U tests when comparing two years and Kruskal-Wallis tests for three or more years. Superscript letters are used to indicate years considered significantly different by Dunn's test. An asterisk indicates that data were not significant after bonferroni corrections.

Species	1997	1998	1999	2000	2001	2002	2003	<i>P</i>
Dusky Flycatcher	—	3.7 ± 0.7 (13)	3.2 ± 0.5 (17)	2.9 ± 0.5 (16)	4.4 ± 1.0 (10)	4.4 ± 0.6 (25)	—	0.43
Nashville Warbler	—	—	—	2.5 ± 0.4 (19)	2.6 ± 0.5 (16)	2.8 ± 0.4 (13)	—	0.58
Orange-crowned Warbler	—	—	—	2.3 ± 0.4 (19)	1.8 ± 0.2 (19)	—	—	0.43
Yellow Warbler	—	—	—	4.0 ± 0.6 (25)	4.6 ± 1.0 (17)	3.6 ± 0.6 (35)	6.3 ± 1.1 (12)	0.12
MacGillivray's Warbler	—	4.7 ± 0.7 (23)	4.7 ± 0.9 (23)	5.6 ± 0.7 (43)	4.7 ± 0.4 (63)	5.6 ± 0.5 (69)	6.4 ± 0.8 (27)	0.18
Ruby-crowned Kinglet	2.4 ± 0.2 (50) ^A	1.4 ± 0.1 (51) ^B	1.1 ± 0.1 (12) ^B	1.6 ± 0.1 (92) ^{AB}	1.5 ± 0.2 (46) ^{AB}	2.1 ± 0.3 (61) ^{AB}	2.2 ± 0.3 (22) ^{AB}	0.001
Spotted Towhee	10.2 ± 1.3 (27)	11.5 ± 1.1 (47)	8.6 ± 1.4 (18)	—	7.6 ± 1.2 (14)	—	11.9 ± 2.1 (19)	0.39
Dark-eyed Junco	4.3 ± 1.1 (18)	5.6 ± 0.5 (77)	—	4.3 ± 0.8 (25)	—	—	—	0.14
White-crowned Sparrow	7.5 ± 1.0 (42) ^{AB}	4.4 ± 0.8 (27) ^B	7.7 ± 0.5 (105) ^A	3.8 ± 0.6 (12) ^{AB}	6.2 ± 0.6 (62) ^{AB}	5.5 ± 1.5 (11) ^{AB}	6.8 ± 0.5 (117) ^{AB}	0.02*

capture proportions. For instance, in this study and in Maine (Morris et al. 1996) and South Dakota (Carlisle 1998), recaptured birds generally showed positive mass changes whereas among spring migrants in Mississippi and autumn migrants in Vermont, recaptured birds did not fare as well (Kuenzi et al. 1991, Rimmer and McFarland 2000). In the case of the Mississippi birds, this pattern might be explained by a reduced digestive capacity in birds that had just completed the long flight over the Gulf of Mexico (Gannes 2002, Karasov et al. 2004). Further study is needed to determine if a consistent pattern of higher recapture rates and higher mass gains exists at more suitable sites.

Another possible explanation for differences in recapture proportions among sites is that smaller sites or those with greater isolation (i.e., islands of suitable habitat surrounded by a less, or unsuitable, matrix) experience higher recapture proportions. In this study, recapture proportions were higher in our relatively isolated riparian site than in mountain shrubland. The relatively higher recapture rates on Appledore Island, Maine (Morris et al. 1996) and in South Dakota woodlots (Carlisle 1998) might also be, at least partially, explained by isolation.

Adult birds are generally more efficient foragers than immature birds (Wunderle 1991). It follows that less efficient foraging should lead to a slower rate of fat and mass gain resulting in longer stopover and higher recapture rates for hatching year birds. Evidence for such a difference has been found for some species in several studies of age-specific stopover duration (Morris et al. 1994, Woodrey and Moore 1997, Wang et al. 1998). In Idaho, we found broad overlap in both stopover duration and mass change between adults and immatures. While there was a tendency for immature birds to stay longer than adults, this was not the case in all species and in only one of 11 species did adults gain more mass than immature birds. Thus, we found little evidence for adults stopping over more efficiently than immatures at our study site.

Intersexual competition within species may also affect stopover patterns. The dominant sex might gain fat and mass faster and stopover for shorter periods than the subordinate sex (Lindstrom et al. 1990). However, we found no significant differences in stopover behavior between sexes. Intersexual competition does not appear to be an important factor affecting stop-

TABLE 5. Annual variation (mean \pm SE) in mass change (g) between first and last capture for Idaho migrants with at least 10 recaptures in each year. Sample sizes (n) are given in parentheses. Dashes are placed in species by year combinations with less than 10 recaptures. We used nonparametric tests to examine differences among years; Mann-Whitney U tests when comparing two years and Kruskal-Wallis tests when comparing more than two years. Superscript letters are used to indicate years considered significantly different by Dunn's test. An asterisk indicates that data were not significant after bonferroni corrections.

Species	1998	1999	2000	2001	2002	2003	P
Dusky Flycatcher	-0.20 \pm 0.1 (12)	-0.05 \pm 0.1 (17)	-0.002 \pm 0.1 (14)	-0.13 \pm 0.1 (10)	-0.009 \pm 0.1 (25)	-	0.48
Nashville Warbler	-	-	0.14 \pm 0.1 (18)	0.36 \pm 0.1 (24)	0.28 \pm 0.1 (13)	-	0.36
Orange-crowned Warbler	-	-	0.42 \pm 0.1 (16)	0.44 \pm 0.1 (18)	-	-	0.89
Yellow Warbler	-	-	0.24 \pm 0.1 (24) ^A	0.002 \pm 0.1 (17) ^{AB}	0.28 \pm 0.1 (34) ^A	-0.17 \pm 0.1 (12) ^B	0.01*
MacGillivray's Warbler	-0.04 \pm 0.1 (22)	-0.14 \pm 0.2 (23)	0.15 \pm 0.1 (43)	0.12 \pm 0.1 (63)	-0.26 \pm 0.1 (69)	-0.08 \pm 0.1 (27)	0.16
Ruby-crowned Kinglet	0.25 \pm 0.0 (49) ^A	0.0 \pm 0.0 (12) ^B	0.10 \pm 0.0 (91) ^B	0.14 \pm 0.0 (46) ^{AB}	0.07 \pm 0.0 (60) ^B	0.17 \pm 0.1 (22) ^{AB}	0.007*
Spotted Towhee	1.61 \pm 0.3 (42) ^A	0.42 \pm 0.5 (18) ^{AB}	-	0.07 \pm 0.5 (14) ^B	-	0.42 \pm 0.5 (19) ^{AB}	0.05*
Dark-eyed Junco	-0.08 \pm 0.1 (77)	-	-0.16 \pm 0.2 (25)	-	-	-	0.43
White-crowned Sparrow	0.31 \pm 0.2 (27) ^{AB}	1.38 \pm 0.2 (101) ^A	0.55 \pm 0.3 (12) ^{AB}	0.69 \pm 0.2 (58) ^{AB}	0.29 \pm 0.6 (10) ^{AB}	0.43 \pm 0.2 (113) ^B	0.007*

TABLE 6. Annual variation in recapture proportions for the ten most commonly recaptured migrants; expressed as percent of new captures (total n given parenthetically). We used chi-squared (χ^2) tests to examine differences among years. Superscript letters are used to indicate years that were significantly different from each other. An asterisk indicates that differences were not significant after Bonferroni corrections.

Species	1997	1998	1999	2000	2001	2002	2003	P
Dusky Flycatcher	0.0 (82)	5.9 (187)	6.4 (264)	5.4 (294)	4.8 (209)	8.0 (314)	2.9 (307)	0.06
Warbling Vireo	4.3 (47)	2.3 (128)	1.2 (67)	0.0 (160)	0.8 (120)	1.5 (130)	3.7 (108)	0.19
Nashville Warbler	2.0 (51) ^B	2.1 (93) ^B	0.0 (143) ^B	9.2 (207) ^A	11.9 (202) ^A	10.0 (130) ^A	4.0 (76) ^B	<0.001
Orange-crowned Warbler	0.0 (94) ^C	0.8 (123) ^C	0.9 (107) ^{BC}	6.2 (258) ^A	11.9 (202) ^A	10.0 (130) ^A	4.0 (76) ^B	<0.001
Yellow Warbler	14.3 (7)	5.4 (37)	11.5 (61)	13.7 (183)	5.9 (323) ^A	3.5 (171) ^{AB}	4.3 (116) ^{AB}	0.01*
MacGillivray's Warbler	5.4 (56) ^D	12.3 (186) ^{BC}	10.7 (224) ^C	15.8 (272) ^B	18.1 (348) ^A	21.0 (315) ^A	13.3 (211) ^{BC}	0.003
Ruby-crowned Kinglet	4.9 (1009) ^A	4.9 (1042) ^A	1.8 (674) ^B	5.7 (1611) ^A	4.8 (962) ^A	5.0 (1219) ^A	2.8 (777) ^B	<0.001
Spotted Towhee	15.5 (168) ^B	28.8 (163) ^A	11.2 (161) ^{BC}	6.9 (101) ^C	11.4 (123) ^{BC}	7.7 (65) ^C	12.1 (157) ^{BC}	<0.001
Dark-eyed Junco	2.5 (771) ^C	9.9 (777) ^A	1.1 (283) ^D	4.8 (518) ^B	1.6 (316) ^{CD}	1.6 (251) ^{CD}	1.7 (233) ^{CD}	<0.001
White-crowned Sparrow	20.0 (215) ^{BC}	12.3 (253) ^D	28.2 (383) ^A	7.7 (156) ^E	15.0 (439) ^{CD}	5.7 (193) ^E	23.2 (514) ^B	<0.001

TABLE 7. Comparison of 1998–1999 stopover data (mean ± SE) from recaptured birds at the mountain shrubland (MS) and willow riparian (WR) mist-netting sites for five species with at least 10 recaptures at each site, and for Neotropical and temperate migrants combined. Recapture proportions were compared with chi-squared (χ^2) tests, stopover durations were compared with Mann-Whitney U tests, and changes in mass were compared with student's *t* tests. An asterisk indicates the level of significance (* = $P < 0.05$, ** = $P < 0.01$) and is placed by the site with the higher value.

Species	Proportion recaptured		Stopover duration (days)		Total mass change (g)		Rate of mass change (g per 24 hours)	
	MS	WR	MS	WR	MS	WR	MS	WR
Ruby-crowned Kinglet	30/913	12/198	1.3 ± 0.2	3.3 ± 1.1*	0.19 ± 0.04	0.29 ± 0.13	0.15 ± 0.03	0.11 ± 0.06
Spotted Towhee	36/253	19/90	8.6 ± 1.6	8.6 ± 0.9	0.83 ± 0.29	0.22 ± 0.28	0.08 ± 0.10	0.0 ± 0.04
Dark-eyed Junco	39/585	91/457**	5.9 ± 0.6	5.3 ± 0.4	-0.15 ± 0.13	0.25 ± 0.12*	-0.03 ± 0.04	0.04 ± 0.05
White-crowned Sparrow	83/512	82/508	5.0 ± 0.5	6.7 ± 0.6*	0.71 ± 0.20	0.82 ± 0.20	0.08 ± 0.06	0.14 ± 0.04
Lazuli Bunting	14/77	14/77	6.5 ± 1.6	9.2 ± 1.5	0.42 ± 0.37	0.26 ± 0.29	0.01 ± 0.05	0.11 ± 0.10
All temperate migrants	193/2421	204/1364**	5.4 ± 0.3	6.2 ± 0.3*				
All Neotropical migrants	95/1954	51/877	4.2 ± 0.4	5.9 ± 0.7*				
All migrants combined	289/4413	255/2352**	5.1 ± 0.3	6.1 ± 0.3**				

over behavior at our study site and this is consistent with data from another western stopover study (Wang et al. 1998).

Some birds lose weight upon arrival and only begin to accrue sizable mass gains after a few days of stopover (Rappole and Warner 1976, Hansson and Pettersson 1989), while other studies have found that birds are able to gain mass immediately (Cherry 1982, Moore and Kerlinger 1987). In Idaho, we found that birds staying longer tended to gain more mass than birds staying only one day. Some species showed mass gains for both short and longer stopovers, whereas others averaged mass losses during single day stopovers and mass gain during longer stopovers. This finding suggests that an adjustment time is involved for some birds early in stopover before they are able to add mass in an efficient manner. Whether this adjustment is due to digestive limitations or other factors such as site unfamiliarity or competition with previously settled migrants is not known. However, it is unlikely that digestive limitations constrains migrants arriving at Lucky Peak, since these birds have not yet faced a major geographical barrier such as the Gulf of Mexico (Kuenzi et al. 1991) or deserts of the Old World (Gannes 2002, Karasov et al. 2004). This pattern of mass loss among migrants with one day stopovers may also reflect stress associated with capture and handling (i.e., loss of foraging time or physical damage); however, many individuals do maintain or gain mass during single day stopovers suggesting that all captured birds are not adversely affected.

Diurnal changes in energetic condition. A number of studies have used changes in energetic condition among recaptured individuals to examine the suitability of a site, but recaptured individuals may not be representative of the migrant population as a whole (Winker et al. 1992). In particular, birds with less fat are more likely to remain at a stopover site than fatter birds (Moore and Kerlinger 1987, Loria and Moore 1990, Morris 1996), potentially biasing recapture data toward leaner birds. Winker et al. (1992) pioneered the application of linear regression of mass on time since sunrise for all first-time captures to examine whether the population as a whole (not just recaptured birds) is able to gain mass at a particular site. Dunn (2001) also applied this method to migrants at Long Point, Ontario, Canada and found that

most species were meeting or exceeding energetic demands of migration. Here, we used a variation on this method and, while there was some variation among species in rates of condition gain, we found that most Idaho migrants were gaining mass through the morning hours, suggesting that Lucky Peak serves as a suitable stopover site. Conversely, the two common hummingbirds at the site showed negative slopes which may have been caused either by the diurnal migratory behavior of hummingbirds (i.e., hummingbirds captured later in the morning had traveled farther that day, therefore using up more energy stores) or that nectar resources at our site are not sufficient for hummingbirds to meet their energetic needs during migration.

Correspondence between recapture and regression results. Winker et al. (1992) found that recapture data indicated mass losses for many species whereas regression data indicated that many of these species were gaining mass. In contrast, we found general agreement between regression data and mass change among recaptured birds. Twelve of 15 species showed consistent patterns between the two methods; seven species showed significant mass gains across both measuring techniques. Species that did not fit this pattern included Dark-eyed Junco, a late-season migrant with a locally wintering population; thus, sampled birds likely included both migrants and arriving winter residents. The positive mass gains for most species strongly suggest that our study site serves as suitable stopover habitat for a wide range of migrants.

Arrival condition vs. stopover propensity. For two species, the Black-headed Grosbeak and the Spotted Towhee, birds captured only once exhibited higher energetic condition at initial capture than those later recaptured. This finding supports previous research that stopover duration is related to energetic condition and that birds in poorer condition have longer stopovers (Moore and Kerlinger 1987, Morris 1996). However, this was not a widespread pattern and several frequently recaptured species (Nashville and MacGillivray's warblers and Lazuli Bunting) had patterns suggesting that recaptured birds were in better initial condition than individuals captured only once. Thus, we found no clear pattern between arrival condition and stopover duration.

Interannual comparisons. We found ample evidence for year-to-year variation in stopover

parameters among recaptured birds. Recapture proportions varied significantly among years for most species whereas fewer species had significant interannual differences in stopover duration and mass change. Based on ANCOVA analyses, we also found interannual variation in initial energetic condition for most species. Morris et al. (1996) had similar findings of annual variation in recapture proportions, stopover duration, and mass changes for some, but not all, species among the migrant assemblage in Maine. However, Kuenzi et al. (1991) found evidence for variation in recapture proportions but not stopover duration or mass changes among spring migrants in Mississippi. Interannual variation in weather, migrant density, or food availability could drive such differences in stopover parameters among years. The fact that interannual stopover patterns for most species in this study varied independently relative to other species suggests that the causes for this variability differed among species.

COMPARING BETWEEN MIST-NETTING SITES

We found several striking differences between the willow-riparian and mountain-shrubland sites. There was a tendency for higher recapture proportions and longer stopover duration at the willow-riparian site. For example, Dark-eyed Juncos were about three times as likely to be recaptured at the willow-riparian site and Ruby-crowned Kinglets stayed more than twice as long at the willow-riparian site than at the mountain-shrubland site. We may have been more likely to recapture a higher proportion of migrants at the willow-riparian netting site due to its smaller size and more isolated nature. Also, recaptured Dark-eyed Juncos gained more mass in willow riparian than at the mountain-shrubland site. However, recaptured birds of all species except juncos were able to gain mass at both sites. Regression data also showed similar, positive rates of energetic condition gain at both sites. Thus, these data suggest that both sites serve well as stopover habitats.

CONCLUSIONS

The deciduous habitats at Lucky Peak, Idaho appear to provide suitable stopover habitat for landbird migrants because most species showed mass gains. Montane deciduous habitats (including riparian draws and mountain shrublands) are patchily distributed throughout much of the In-

termountain West (Barbour and Billings 1988). Previous studies have documented that migrants use montane habitats especially during autumn (Blake 1984, Hutto 1985, Carlisle et al. 2004). This is the first study to investigate stopover patterns in western montane habitats and, by documenting positive energetic changes among most migrants at our site, we provide further evidence that these habitats deserve further research and conservation attention as autumn stopover habitats.

ACKNOWLEDGMENTS

This study was funded by the many contributors to the Idaho Bird Observatory, including Boise State University, USDA Forest Service, Idaho Department of Fish and Game (IDFG), USDI Bureau of Land Management, the National Forest Foundation, Boise Cascade Corporation, USGS Snake River Field Station, and countless private donations; we are very thankful for their support. This material is based upon work supported under a National Science Foundation Graduate Research Fellowship and University of South Dakota Graduate Research Grants to JDC. We thank the many field workers at Lucky Peak for their skilled and valuable assistance. Many other community volunteers from Idaho Department of Fish and Game, coordinated by Mary Dudley, gave valuable assistance. Jerry Scholten of IDFG has been a tremendous asset for all years of the study. We thank Melissa Mustillo, Kristen Covino, Sara Morris, and H. David Sheets for running the open-population models in estimating stopover duration. We thank Jeff Kelly and Yong Wang for their very helpful and insightful comments on an earlier version of this manuscript. Thanks also to Pat Heglund and Susan Skagen for organizing this symposium and special section. Last but not least, we are very grateful to Karen Olmstead for statistical assistance.

LITERATURE CITED

- AUSTIN, G. T. 1970. Migration of warblers in southern Nevada. *Southwestern Naturalist* 15:231–237.
- BARBOUR, M. G., AND W. D. BILLINGS [EDS.]. 1988. North American terrestrial vegetation. Cambridge University Press, Cambridge, UK.
- BLAKE, J. G. 1984. A seasonal analysis of bird communities in southern Nevada. *Southwestern Naturalist* 29:463–474.
- BROWER, J. E., J. H. ZAR, AND C. N. VON ELDE. 1990. Field and laboratory methods for general ecology. 4th ed. McGraw Hill, Boston, MA.
- CARLISLE, H. A. 1998. Abundance, diversity, and energetic condition of Neotropical woodland migrants during stopover in a geographically isolated farmstead woodlot in southeastern South Dakota. M.A. thesis, University of South Dakota, Vermillion, SD.
- CARLISLE, J. D., S. L. STOCK, G. S. KALTENECKER, AND D. L. SWANSON. 2004. Habitat associations, relative abundance, and species richness of autumn landbird migrants in southwestern Idaho. *Condor* 106:549–566.
- CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. *Auk* 99:725–732.
- DEGRAAF, R. M., AND J. H. RAPPOLE. 1995. Neotropical migratory birds: natural history, distribution, and population change. Cornell University Press, Ithaca, NY.
- DESANTE, D. F., K. M. BURTON, P. VELEZ, AND D. FROEHLICH. 2003. MAPS manual: instructions for the establishment and operation of constant-effort bird-banding stations as part of the Monitoring Avian Productivity and Survivorship (MAPS) Program. Unpubl. Doc., Institute for Bird Populations, Point Reyes Station, CA.
- DUNN, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. *Journal of Field Ornithology* 72:419–432.
- FINCH, D. M., AND Y. WANG. 2000. Landbird migration in riparian habitats of the middle Rio Grande: a case study. *Studies in Avian Biology* 20:88–98.
- GANNES, L. Z. 2002. Mass change pattern of Blackcaps refueling during spring migration: evidence for physiological limitations to food assimilation. *Condor* 104:231–239.
- GRABER, J. W., AND R. R. GRABER. 1983. Feeding rates of warblers in spring. *Condor* 85:139–150.
- GREENBERG, R., T. KEELER-WOLF, AND V. KEELER-WOLF. 1974. Wood warbler populations in the Yolla Bolly Mountains of California. *Western Birds* 5:81–90.
- HANSSON, M., AND J. PETTERSSON. 1989. Competition and fat deposition in Goldcrests (*Regulus regulus*) at a migration stop-over site. *Die Vogelwarte* 35: 21–31.
- HELMS, C. W., AND W. H. DRURY. 1960. Winter and migratory weight and fat: field studies on some North American buntings. *Bird-Banding* 31:1–40.
- HUTTO, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120–132.
- KARASOV, W. H., B. PINSHOW, J. M. STARCK, AND D. AFIK. 2004. Anatomical and histological changes in the alimentary tract of migrating Blackcaps (*Sylvia atricapilla*): a comparison among fed, fasted, food-restricted, and refed birds. *Physiological and Biochemical Zoology* 77:149–160.
- KELLY, J. F., L. S. DELAY, AND D. M. FINCH. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. *Auk* 119:210–213.
- KETTERSON, E. D., AND V. NOLAN JR. 1985. Intraspecific variation in avian migration: evolutionary and regulatory aspects, p. 553–579. *In* M. A. Rankin [ED.], Migration: mechanisms and adaptive significance. University of Texas Contributions in Marine Science Supplement No. 27.
- KUENZI, A. J., F. R. MOORE, AND T. R. SIMONS. 1991. Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93:869–883.
- LINDSTROM, A., D. HASSELQUIST, S. BENCH, AND M. GRAHN. 1990. Asymmetric contests over resources

- for survival and migration: a field experiment with Bluethroats. *Animal Behaviour* 40:453–461.
- LORIA, D. E., AND F. R. MOORE. 1990. Energy demands of migration on Red-eyed Vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24–35.
- MOORE, F. R., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MOORE, F. R., AND Y. WANG. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85–90.
- MOORE, F. R., S. A. GAUTHREAUX JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: important link in conservation, p. 121–144. *In* T. E. Martin and D. M. Finch [EDS.], *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York.
- MORRIS, S. R. 1996. Mass loss and probability of stopover by migrant warblers during spring and fall migration. *Journal of Field Ornithology* 67:456–462.
- MORRIS, S. R., M. E. RICHMOND, AND D. W. HOLMES. 1994. Patterns of stopover by warblers during spring and fall migration on Appledore Island, Maine. *Wilson Bulletin* 106:703–718.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- OTAHAL, C. D. 1995. Sexual differences in Wilson's Warbler migration. *Journal of Field Ornithology* 66:60–69.
- PYLE, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA.
- RAPPOLE, J. H., AND D. W. WARNER. 1976. Relationships between behavior, physiology, and weather in avian transients at a migration stopover site. *Oecologia* 26:193–212.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30:224–272.
- RIMMER, C. C., AND K. P. MCFARLAND. 2000. Migrant stopover and postfledgling dispersal at a montane forest site in Vermont. *Wilson Bulletin* 112:124–136.
- SCHAUB, M., R. PRADEL, L. JENNI, AND J. D. LEBRETON. 2001. Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. *Ecology* 82:852–859.
- SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71: 296–308.
- VIALLEFONT, A., J. D. LEBRETON, A. M. REBOULET, AND G. GORY. 1998. Parameter identifiability and model selection in capture-recapture models: a numerical approach. *Biometrical Journal* 40:313–325.
- WANG, Y., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropical migrants. *Auk* 112:690–700.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109:853–862.
- WOODREY, M. S., AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.
- WUNDERLE, J. M., JR. 1991. Age-specific foraging proficiency in birds. *Current Ornithology* 8:273–324.
- ZAR, J. H. 1996. *Biostatistical analysis*. Prentice Hall, NJ.