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ELEVATIONAL DIFFERENCES IN ESTIMATED FATTENING RATES SUGGEST THAT HIGH-ELEVATION SITES ARE HIGH-QUALITY HABITATS FOR FALL MIGRANTS

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ABSTRACT.—Many migrant songbird species use high-elevation habitats for stopovers in fall throughout North America, but whether these are good migration habitats as indicated by high fueling rates or other measures has not been previously quantified. At high-quality stopover sites, birds can refuel while maintaining their optimal or preferred migration schedules. We used plasma metabolite analysis to estimate fueling rates of four songbird species during the fall migration period over 3 years at two high-elevation (1,200 m above sea level) and two low-elevation (<25 m above sea level) sites in southwestern British Columbia. For three species with more frugivorous diets during fall—the Fox Sparrow (*Passerella iliaca*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), and Hermit Thrush (*Catharus guttatus*)—estimated fattening rates (defined as residual plasma triglyceride levels) were 37–65% higher at high-elevation sites than at low-elevation sites. By contrast, the largely insectivorous and smaller-bodied Orange-crowned Warbler (*Oreothlypis celata*) had higher estimated fattening rates at low-elevation sites. We found no elevational differences in plasma beta-hydroxybutyrate or glycerol levels except in Hermit Thrushes, which had lower glycerol levels at high elevation. Estimated fattening rates did not differ among the two sparrows and the Hermit Thrush at high-elevation sites, and all three had higher fattening rates than Orange-crowned Warblers. Our data showing strong elevational differences in residual plasma triglyceride levels support the hypothesis that high elevations can be high-quality stopover habitats and, thus, should be considered for protection in songbird management and conservation plans. Received 7 October 2011, accepted 30 August 2012.

Key words: alpine and subalpine habitats, fall migration, high-elevation habitats, migratory body-condition measures, migratory stopover habitats, plasma metabolites, songbird migration.

Diferencias entre Elevaciones en las Tasas Estimadas de Engorde Sugieren que los Sitios de Alta Elevación son Hábitats de Alta Calidad para los Migrantes de Otoño

RESUMEN.—Muchas especies de aves canoras migrantes usan hábitats de grandes elevaciones como sitios de parada en el otoño a través de todo Norte América, pero no se ha cuantificado si tales sitios son buenos hábitats con base en indicadores como altas tasas de abastecimiento y otras medidas. En sitios de parada de alta calidad, las aves pueden reabastecerse mientras mantienen sus ritmos migratorios óptimos o preferidos. Usamos análisis de metabolitos del plasma para estimar las tasas de reabastecimiento de cuatro especies de aves canoras durante la migración de otoño por un periodo de tres años, en dos sitios de alta elevación (1200 m sobre el nivel del mar) y dos sitios de baja elevación (<25 m) en el suroriente de Columbia Británica. Para tres especies con dietas más frugívoras durante el otoño (*Passerella iliaca*, *Zonotrichia atricapilla* y *Catharus guttatus*) las tasas estimadas de engorde, definidas como los niveles residuales de triglicéridos en el plasma, fueron 37 a 65% mayores en los sitios de altas elevaciones que en los de bajas elevaciones. En contraste, la especie principalmente insectívora y de menor tamaño *Oreothlypis celata* tuvo tasas estimadas de engorde mayores en los sitios de baja elevación. No encontramos diferencias con respecto a la elevación en los niveles plasmáticos de beta-hidroxibutirato o de glicerol excepto en *C. guttatus*, que presentó niveles menores de glicerol en altas elevaciones. Las tasas estimadas de engorde no difirieron entre *P. iliaca*, *Z. atricapilla* y *C. guttatus* en los sitios de alta elevación, y estas especies presentaron tasas de engorde mayores que las de *O. celata*. Nuestros datos demuestran diferencias pronunciadas con respecto a la elevación en los niveles residuales de triglicéridos en plasma y sustentan la hipótesis de que los sitios de alta elevación pueden ser hábitats de parada migratoria de alta calidad. Por lo tanto, estos ambientes deben ser considerados para su protección en los planes de manejo y conservación.

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EFFECTIVE CONSERVATION OF migratory birds requires research across the entire avian annual cycle to inform potential management and habitat conservation (Faaborg et al. 2010a). Most research and management has focused on the breeding season, but recent technologies and approaches have facilitated studies of migrants on their wintering grounds (Marra et al. 1998, Norris and Marra 2007) and at stopover sites (Guglielmo et al. 2005, Williams et al. 2007, Smith and McWilliams 2010, Seewagen et al. 2011). Nevertheless, our understanding of the year-round ecology and evolution of migratory birds, including nonbreeding and migration phases, remains patchy, and studying “en route” ecology at stopover sites continues to be particularly challenging (Petit 2000, Carlisle et al. 2009, Faaborg et al. 2010b).

Depending on their migration route and strategy, avian migrants may encounter sufficient and continuous stopover habitat that allows them to refuel without deviating far from their “optimal” migration schedule and route (Faaborg et al. 2010a). However, many species are constrained to specialized and discontinuous habitats for their stopovers, such that body condition and survival for some or all cohorts are compromised (Baker et al. 2004). For migratory songbirds, lowland riparian habitats are considered to be especially important for stopovers, particularly in the western United States and Canada (Skagen et al. 1998, Wiebe and Martin 1998, Finch and Yong 2000). Riparian habitat makes up a small fraction (~1%) of the western U.S. landscape (Knopf et al. 1988), and the overall availability of this low-elevation stopover habitat type is declining with agricultural intensification and urban development. This habitat loss may contribute to future population declines of western songbirds (Ohmart 1994, Carlisle et al. 2009). Fortunately, migratory songbirds can and do use other stopover areas, such as high-elevation habitats (Wilson and Martin 2005). Thus, it is important to determine whether these alternative and less-studied habitats can provide high-quality stopover sites capable of supporting high fueling rates (Seewagen et al. 2011).

Several studies have documented seasonal migration of birds to high-elevation habitats (Pattie and Verbeek 1966, Hutto 1985, Morton 1991, Rimmer and McFarland 2000, Jenni and Kéry 2003, DeLong et al. 2005). More than 200 bird species have been documented using alpine or subalpine zones in North America (Martin 2001). Within British Columbia, high-elevation habitats represent ~50% of the land base, and surveys in montane, subalpine, and alpine areas of Vancouver Island and southern British Columbia indicate that migrants use high-elevation sites as stopover and foraging habitat during postbreeding dispersal and migration periods from August through October (Martin and Ogle 1998, Wilson and Martin 2005). Use of such habitats during fall migration coincides with a period of high resource availability at high elevations due to delayed seasonality compared with lower elevations, where resources have already declined (Körner 1999, Carlisle et al. 2009). This later pulse of food, especially fruits and insects, likely creates a stopover habitat advantageous for birds undergoing migratory fattening (Martin 2001, Smith et al. 2007, Smith and McWilliams 2010).

We used plasma metabolite analysis (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005, Williams et al. 2007, Smith and McWilliams 2010, Seewagen et al. 2011) to investigate stopover site quality and differences in estimated fattening rates in songbirds during fall migration at two low-elevation (<25 m

above sea level) and two high-elevation (1,200 m above sea level) sites in southwestern British Columbia, Canada. Plasma metabolite analysis uses residual plasma triglyceride levels (controlling for body mass and other covariates) to estimate rates of fattening or refueling. High levels of plasma triglyceride represent high fattening rates, and its measurement provides a more informative method than using “static” measures of body condition (e.g., mass or fat score) at the time of capture (see below). Studies have typically also measured other metabolites associated with fasting or mass loss (glycerol, beta-hydroxybutyrate), as we do here, but residual plasma triglyceride level is more informative for estimation of fattening rate, and for detecting site differences, than is variation in glycerol and beta-hydroxybutyrate (e.g., Guglielmo et al. 2002, Acevado Seaman et al. 2006, Williams et al. 2007; see below). Plasma metabolite analysis has been validated for the estimation of relative fattening rates, both in captive (Seaman et al. 2005, Cerasale and Guglielmo 2006) and free-living birds (Schaub and Jenni 2001, Guglielmo et al. 2005, Anteau and Afton 2008). Because plasma triglyceride levels measure the “direction” of fueling or fasting conditions, they tend to vary with time of day, body mass, and diet type, but conveniently do not vary widely with avian age class, intervals between capture and bleed time, seasonal date, or intensity of prebasic molting period (Jenni-Eiermann and Jenni 1994, Guglielmo et al. 2005). Thus, plasma triglyceride tends to be the single most useful lipid metabolite for assessing fattening and fuel deposition in free-living migratory birds (Smith and McWilliams 2010). Here, we present data for four migratory songbirds—the Fox Sparrow (*Passerella iliaca*), Golden-crowned Sparrow (*Zonotrichia atricapilla*), Hermit Thrush (*Catharus guttatus*), and Orange-crowned Warbler (*Oreothlypis celata*)—that differ in diet (insectivorous, omnivorous, frugivorous) and migration strategy (short, intermediate, long-distance; see below) to test the hypothesis that high-elevation sites can provide high-quality stopover sites capable of supporting high fueling rates for migrant birds.

METHODS

Study sites and species.—We conducted field work during fall migration in 2003, 2004, and 2005 at two high-elevation and two low-elevation sites in southwestern British Columbia. The high-elevation sites were (1) Mt. Seymour Provincial Park (MTSY: 49°23′N, 122°56′W, 1,200 m; 7 August–15 October 2003, 30 August–14 October 2004, 15 August–12 October 2005) and (2) Cypress Provincial Park, Hollyburn Mountain (CYPR: 49°24′N, 123°10′W, 1,200 m; 31 August–15 October 2004, 19 August–18 October 2005). The low-elevation sites were (1) Maplewood Flats Conservation Area (MPLW: 49°18′N, 123°0′W, 5 m; 19 September–4 October 2004, 18 August–20 October 2005) and (2) Rocky Point Bird Observatory (RPBO: 48°20′N, 123°30′W, 24 m; 26 September–2 October 2004, 23 September–2 October 2005). The range of capture and bleed dates for each species in our study was more restricted than the above total periods, which represent regional dates of migration (see below for details). The two high-elevation sites had a southeast aspect and were located in the subalpine Mountain Hemlock (*Tsuga mertensiana*) biogeoclimatic zone (Pojar et al. 1991), characterized at these sites by trees showing Krumholtz formation (mainly small Mountain Hemlock, wet sedge meadow, and ephemeral ponds). The MPLW site was

characterized by a mixture of young hardwoods, grassy meadow, and blackberry (*Rubus* spp.), and RPBO by a mix of tall grass meadow, hardwoods, and shrubs such as wild rose (*Rosa* spp.). In this region, the Coastal Western Hemlock zone has a mean annual temperature of $\sim 8^{\circ}\text{C}$, with summer temperatures typically $>10^{\circ}\text{C}$ (Pojar et al. 1991). The mean annual temperature for the Mountain Hemlock zone is $\sim 0^{\circ}\text{C}$, with temperatures exceeding 10°C only from mid-June through August.

Fox Sparrows are short- to intermediate-distance migrants that eat insects, seeds, and fruit during fall migration (Weckstein et al. 2002). Median capture date at low elevation was 21 September for both hatch-year (HY) and after-hatch-year (AHY) birds, with captures ranging from 25 August to 26 October ($n = 668$ individuals). The Golden-crowned Sparrow, an intermediate-distance migrant, eats mainly seeds and fruit in fall (Norment et al. 1998). Its median capture date at low elevation was 22 September for HY and 25 September for AHY, with captures ranging from 1 September to 20 October ($n = 467$). The Hermit Thrush is a short-distance migrant. Locally nesting birds in British Columbia depart by late August and are replaced by smaller numbers of northern birds in September and October. Hermit Thrushes are largely frugivorous in fall (Dellinger et al. 2012), with a median capture date at low elevation of 26 September for HY and 28 September for AHY birds (range: 31 August–20 October; $n = 409$). The Orange-crowned Warbler is a long-distance, Neotropical migrant that is largely insectivorous in fall (Gilbert et al. 2010). Its median capture date was 26 August for HY and 12 September for AHY birds, but capture date ranged from 27 July to 15 October ($n = 626$; data for all species from RPBP provided by Wendy Easton, 2003–2005).

Field methods.—At RPBO, birds were blood-sampled opportunistically in coordination with the normal migration-monitoring and capture activities at this site. At all other sites, mist nets were opened for 5 h starting at dawn, and a continuous-loop song playback of 10 passerine species was played adjacent to the nets. Nets were checked every 10 min, and time of capture was recorded as the time when a bird was first observed in the net. Birds were removed from the nets, placed in a light cloth bag, and carried to a tent for bleeding and processing. Bleed time was calculated as the interval (minutes) from capture time to the time the blood sample was taken. Birds were weighed in the capture bag using a Pesola scale (± 1 g) and measured (flattened wing length measured to ± 0.2 mm, tarsus to ± 0.1 mm, and culmen to ± 0.3 mm). Furcular fat deposits were visualized to estimate fat scores on an ordinal scale from zero to 5 following Helms and Drury (1960), where zero represented no visible fat and a fat score of 5 described a greatly distended mound (no fat scores of 5 observed). Sex could only be reliably determined for the Orange-crowned Warbler using fall plumage, but birds were aged (HY or AHY) in all species, where possible, on the basis of plumage (Pyle 1997).

Blood samples (always $<10\%$ of estimated blood volume) were taken by brachial venipuncture using a 26-gauge needle and heparinized capillary tubes. Samples were stored above ice until centrifuged, and plasma was stored at -20°C until metabolite assays were performed.

Plasma metabolite assays.—All assays were run in 400- μL , flat-bottom 96-well microplates (NUNC, Denmark) and read with a microplate spectrophotometer (Biotec 340EL or Power-wave X 340), as previously described (e.g., Acevado Seaman et

al. 2006, Williams et al. 2007). Not all metabolites could be determined for all individuals, because of small plasma volumes; on the basis of previous studies, we prioritized triglyceride and glycerol assays. Free glycerol and total glycerol were assayed via sequential color endpoint assay (Sigma-Aldrich Canada, Oakville, Ontario), using 5 μL of plasma with 240 and 60 μL of glycerol reagent (A) and triglyceride reagent (B), respectively, with a reading taken at 540 nm after 10 min of incubation at 37°C after the addition of each reagent. Plasma triglyceride concentration (mmol L^{-1}) was calculated by subtracting free glycerol from total glycerol. Inter-assay coefficients of variation were 10.8% for glycerol and 6.9% for triglyceride ($n = 64$ assays over 3 years), based on chicken (hen) plasma pools included in each assay.

Beta-hydroxybutyrate (B-OH) was measured by kinetic endpoint assay (E0907979, R-7 Biopharm, Marshall, Michigan) in the first year, following Guglielmo et al. (2005). In subsequent years, we used a Megazyme kit and standards (Megazyme International, Bray, Ireland) with a slight modification of the method of Guglielmo et al. (2005); background absorbance for each plate was taken at 1 min 30 s, prior to rapid addition of the diaphorase solution, and final absorbances were read at 15 min. We assayed 34 samples using both Biopharm and Megazyme kits to determine a conversion factor between the two methods (Megazyme values = Biopharm values $\times 0.44$) and used the adjusted values for 2003 data. The inter-assay coefficient of variation for B-OH was 11.6% ($n = 29$ assays), based on chicken (hen) plasma pools included in each assay.

Statistical analysis.—All statistical analyses were carried out using SAS software, version 9.2 (SAS Institute 2008). The metabolite distributions approximated normality, and log transformation decreased normality (based on a lower value for the Shapiro-Wilks W statistic), so we analyzed the raw, nontransformed data. We first analyzed age distributions (HY and AHY) by species and elevation, and then effects of sex (Orange-crowned Warbler only) and age on “estimated fattening rate,” defined as residual plasma triglyceride level, after controlling for significant covariates (see below). We then focused on the effect of elevation per se, using general linear models (GLM procedure), initially running a full model with plasma metabolite concentration, body mass, or fat score as the dependent variable, elevation as the main factor, and body mass, bleed time, time of day (in relation to sunrise), and Julian date as covariates where appropriate. We then removed any nonsignificant terms ($P > 0.05$), and we present results of the reduced model only, including significant covariates. In these analyses we pooled data by year and locations within elevation classes, because of the unbalanced nature of sampling (see Table 1), but in subsequent analyses we explicitly tested for effects of sampling location and year at each elevation where sample sizes allowed (see below). Values are presented as least-square means \pm SE throughout, unless otherwise stated.

RESULTS

Age–Sex Distribution and Residual Plasma Triglyceride Levels

In Orange-crowned Warblers, the proportion of males and females captured at high- and low-elevation sites did not differ ($\chi^2 = 0.30, P > 0.5$), and residual plasma triglyceride levels between sexes

TABLE 1. Sample sizes of four songbird species captured and sampled in southwestern British Columbia for plasma metabolites to estimate fattening rates, by year, elevation (high: 1,200 m; low: <25 m), and site (abbreviations are defined in the text).

Species	2003				2004				2005				Total		
	High		Low		High		Low		High		Low		All	High	Low
	MTSY	CYPR	MPLW	RPBO	MTSY	CYPR	MPLW	RPBO	MTSY	CYPR	MPLW	RPBO			
Fox Sparrow					4	7		24	12	4		21	72	27	45
Golden-crowned Sparrow					7	1		19	10	2		25	63	20	43
Hermit Thrush	169				125	90	3	23	185	168	1	25	779	727	52
Orange-crowned Warbler					26	14	2	10	41	14	43	1	151	95	56

at either low or high elevation did not differ ($P > 0.40$ in both cases, controlling for mass and time of day). Overall, HY birds predominated in our sample of captured birds at both low-elevation (149/184 = 81.0%) and high-elevation sites (672/860 = 78.1%; age class was not available for 9 birds captured at low elevation and 12 at high elevation). Hatch-year birds predominated (>75%) at both elevations in Golden-crowned Sparrows and Hermit Thrushes, and at low elevation in Fox Sparrows, whereas age distributions were more even in Orange-crowned Warblers and in Fox Sparrows at high-elevation sites (Fig. 1). Overall, there was no difference in residual plasma triglyceride levels between HY and AHY birds for any species at either elevation ($P \geq 0.20$ in all cases).

Residual Plasma Triglyceride Levels, Body Mass, and Fat Score in Relation to Elevation

Fox Sparrow.—Mean date of capture was earlier at high-elevation (16 September \pm 2.4 days) than at low-elevation sites (28 September \pm 0.4 days; $P < 0.001$). However, birds were captured earlier and for a longer period at high-elevation sites (range: 31 August–18

October) such that dates of captures bracketed those at low-elevation sites (range: 23 September–8 October). Average time between capture and blood sampling did not differ between high-elevation (26.5 \pm 3.4 min, range: 5–67, $n = 26$) and low-elevation sites (26.0 \pm 2.0 min, range: 7–60, $n = 45$; $P > 0.8$).

Residual plasma triglyceride levels were dependent on elevation (controlling for time of day, $P < 0.001$; no other covariates were significant in the full model, $P > 0.75$): birds at high-elevation sites had ~65% higher fattening rates (1.17 \pm 0.077 mmol L⁻¹) than birds at low-elevation sites (0.71 \pm 0.062 mmol L⁻¹; $F = 21.6$, $df = 1$ and 65, $P < 0.001$; Fig. 2). Residual plasma triglyceride increased with time of day at both high ($F = 3.38$, $df = 1$ and 25, $P < 0.01$) and low elevation ($F = 4.01$, $df = 1$ and 39, $P < 0.01$), but this increase was greater at high-elevation sites (elevation \times time interaction, $F = 3.95$, $df = 1$ and 65, $P = 0.05$; Fig. 3). Plasma B-OH and glycerol levels did not vary with elevation ($P > 0.15$ in both cases, either including all covariates or for reduced models).

Body mass did not vary with elevation ($F = 0.34$, $df = 1$, 70, $P > 0.5$; Fig. 4A), and there was no relationship between body mass

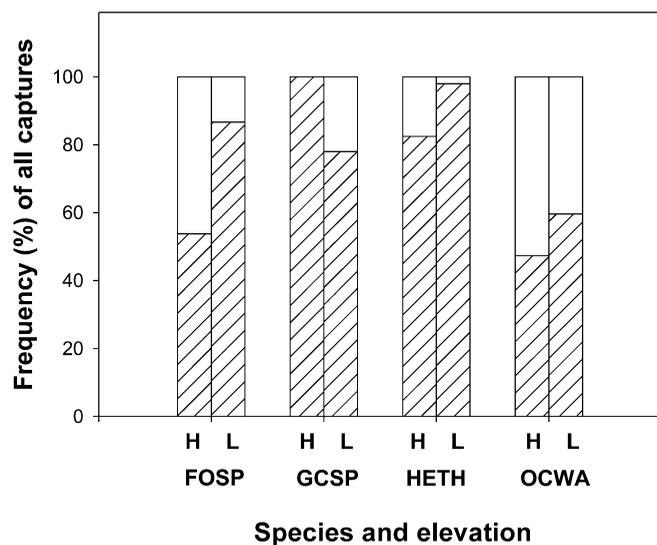


FIG. 1. Age distribution of captured birds by species and elevation (H = high, L = low; shaded bars = hatch-year, open bars = after-hatch-year; FOSP = Fox Sparrow, GCSP = Golden-crowned Sparrow, HETH = Hermit Thrush, and OCWA = Orange-crowned Warbler).

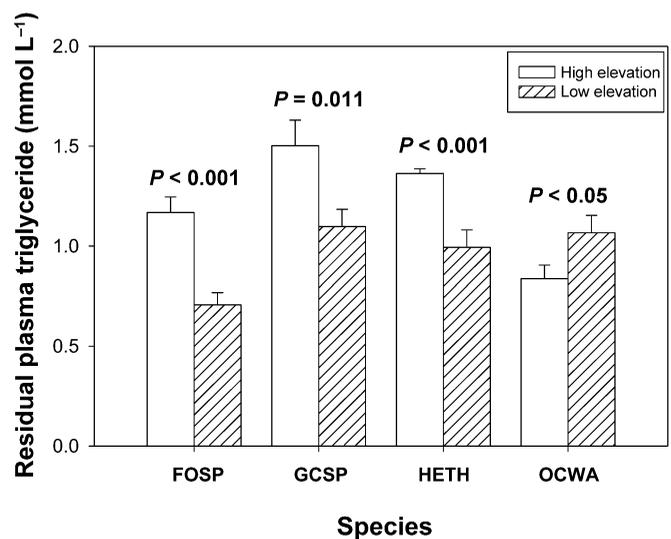


FIG. 2. Residual plasma triglyceride (controlling for covariates) in relation to high and low elevations in four migratory songbird species (FOSP = Fox Sparrow, GCSP = Golden-crowned Sparrow, HETH = Hermit Thrush, and OCWA = Orange-crowned Warbler). Values are least-square means \pm SE.

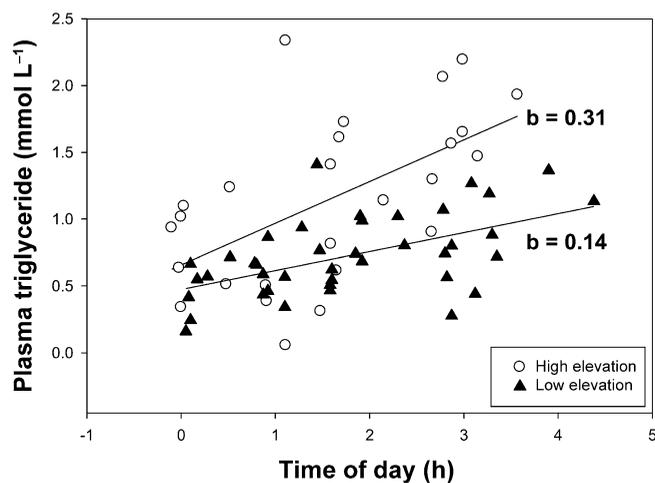


FIG. 3. Plasma triglyceride in relation to time of day (hours after sunrise) at high and low elevations in Fox Sparrows.

and time of day ($P > 0.20$) or with Julian date ($P > 0.35$) at either elevation. Fox Sparrows captured at high-elevation sites had greater fat scores than those at low-elevation sites ($F = 11.40$, $df = 1$ and 70 , $P < 0.01$; Fig. 4B). However, fat score did not vary with time of day ($P > 0.05$) or with Julian date ($P > 0.20$) at either elevation. Fat scores ranged from 1 to 4 at high-elevation sites and from zero to 3 at low-elevation sites.

Golden-crowned Sparrow.—Mean date of capture was earlier at high-elevation (20 September \pm 2.2 days) than at low-elevation sites (28 September \pm 0.3 days; $P < 0.001$), but birds were captured earlier and for a longer period at high-elevation sites (range: 6 September–18 October) and again bracketed capture dates at low-elevation sites (range: 23 September–2 October). Average time between capture and blood sampling did not differ between high-elevation (27.4 ± 5.2 min, range: 8–85, $n = 18$) and low-elevation sites (26.9 ± 2.5 min, range: 5–60, $n = 43$; $P > 0.9$).

Residual plasma triglyceride levels were dependent on elevation (no other variable was significant in the full model; $P > 0.10$): birds at high-elevation sites had 37.8% higher residual plasma triglyceride levels (1.50 ± 0.128 mmol L⁻¹) than birds at low-elevation sites (1.10 ± 0.087 mmol L⁻¹; $F = 6.84$, $df = 1$ and 59 , $P = 0.011$; Fig. 2). Residual plasma triglyceride levels did not change with time of day while controlling for elevation ($F = 1.00$, $df = 1$ and 57 , $P > 0.30$). Plasma B-OH and glycerol levels did not vary with elevation ($P > 0.05$ in both cases, either including all covariates or for reduced models).

Golden-crowned Sparrows were significantly heavier at low-elevation sites than at high-elevation sites ($F = 8.20$, $df = 1$ and 60 , $P < 0.01$; Fig. 4A), but there was no relationship between body mass and time of day ($P > 0.10$) or with Julian date ($P > 0.6$) at either elevation. Fat score also varied with elevation but, in contrast to mass, birds at higher elevation had higher fat scores ($F = 4.41$, $df = 1$ and 60 , $P < 0.05$; Fig. 4B). However, fat score did not vary with time of day ($P > 0.05$) or with Julian date ($P > 0.05$) at either elevation. Fat scores ranged from 1 to 3 at high-elevation sites and from zero to 3 at low-elevation sites.

Hermit Thrush.—Mean date of capture was earlier at high-elevation (18 September \pm 0.6 days; range: 7 August–18 October) than at low-elevation sites (28 September \pm 0.6 days; range: 19 September–20 October; $P < 0.001$). Average time between capture and

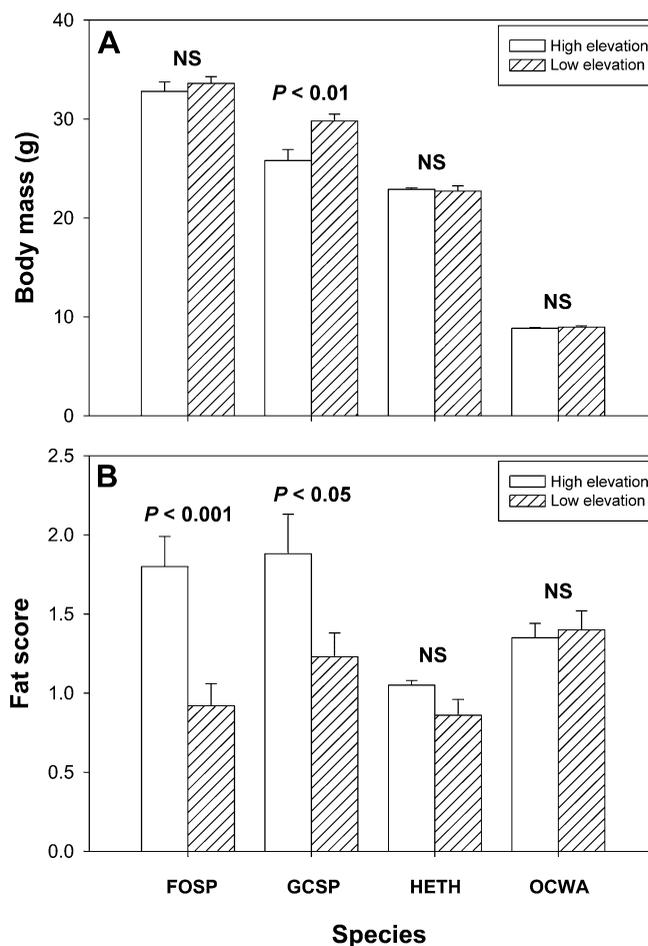


FIG. 4. Variation in (A) body mass and (B) fat score in relation to high and low elevations in four migratory songbird species (FOSP = Fox Sparrow, GCSP = Golden-crowned Sparrow, HETH = Hermit Thrush, and OCWA = Orange-crowned Warbler). Values are least-square means \pm SE.

blood sampling did not differ between high-elevation (21.9 ± 0.6 min, range: 1–78, $n = 712$) and low-elevation sites (23.6 ± 1.9 min, range: 7–60, $n = 52$; $P > 0.4$).

Residual plasma triglyceride levels were dependent on elevation, pooling all data (controlling for time of day, $P < 0.001$; no other covariate significant in the full model): birds at high-elevation sites had 37.3% higher fattening rates (1.36 ± 0.023 mmol L⁻¹) than birds at low-elevation sites (0.99 ± 0.088 mmol L⁻¹; $F = 16.7$, $df = 1$ and 676 , $P < 0.001$; Fig. 2). The result was the same when data were restricted to 2004 and 2005, when birds were sampled at both elevations in each year (high-elevation rates = 1.40 ± 0.028 mmol L⁻¹; low-elevation = 1.08 ± 0.095 mmol L⁻¹; $F = 10.28$, $df = 1$ and 523 , $P < 0.01$; time of day, $P < 0.001$, Julian date, $P < 0.05$).

In a model including elevation and year, there was no effect of year ($P > 0.5$) and no elevation \times year interaction ($P > 0.05$), only a significant effect of elevation ($F = 13.9$, $df = 1$ and 523 , $P < 0.001$; controlling for time of day, $P < 0.001$). Similarly, there was no difference in residual plasma triglyceride among years when the three sites sampled in more than one year were analyzed separately (RPBO, CYPR, or MTSY, $P \geq 0.10$ in all cases). Finally, there was

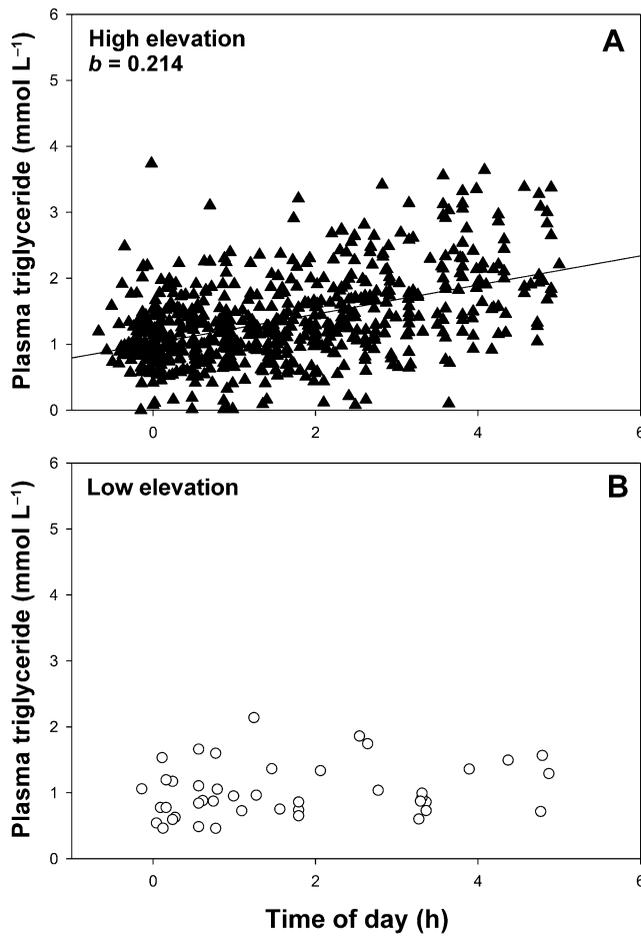


FIG. 5. Plasma triglyceride in relation to time of day (hours after sunrise) at high and low elevations in Hermit Thrushes.

no difference in residual plasma triglyceride levels of birds sampled at the two different high-elevation sites in either 2004 or 2005 ($P > 0.10$), or of birds sampled at the two low-elevation sites in 2004 ($P > 0.70$). The slope of the relationship between residual plasma triglyceride levels and time of day differed with elevation in Hermit Thrushes (elevation \times time interaction, $P < 0.01$). Plasma triglyceride increased with time of day at high-elevation sites ($F = 169.3$, $df = 1$ and 633 , $P < 0.001$), but not at low-elevation sites ($P > 0.2$; Fig. 5).

After pooling all data, plasma glycerol was also dependent on elevation in Hermit Thrushes (controlling for body mass, $P < 0.05$, and time of day, $P < 0.001$): birds at high-elevation sites had lower glycerol levels (0.84 ± 0.014 mmol L⁻¹) than birds at low-elevation sites (1.20 ± 0.056 mmol L⁻¹; $F = 36.9$, $df = 1$ and 629 , $P < 0.001$). Plasma B-OH did not vary with elevation ($P > 0.09$, either including all covariates or for reduced models).

Neither body mass ($P > 0.7$) nor fat score ($P > 0.05$) varied with elevation in Hermit Thrushes (Fig. 4A, B). Similarly, both body mass and fat score were independent of time of day and Julian date at both elevations ($P > 0.10$ in all cases). Fat scores ranged from zero to 4 at high- and low-elevation sites, with most birds having fat scores of 1 (48% and 67% at low and high elevations, respectively).

Orange-crowned Warbler.—Mean date of capture was earlier at high-elevation sites (31 August \pm 1.1 days, range: 15 August–28 September) compared with low-elevation sites (11 September \pm 1.8

days, range: 18 August–20 October; $P < 0.001$). Average time between capture and blood sampling did not differ between high-elevation (24.2 ± 1.8 min, range: 4–73, $n = 90$) and low-elevation sites (25.7 ± 2.0 min, range: 3–60, $n = 55$; $P > 0.5$).

On the basis of the pooled data, residual plasma triglyceride levels were dependent on elevation (controlling for body mass, $P < 0.05$, and time of day, $P < 0.01$; no other covariate significant in the full model). However, in contrast to the other species, birds at high-elevation sites had lower residual triglyceride (0.84 ± 0.068 mmol L⁻¹) than birds at low-elevation sites (1.07 ± 0.088 mmol L⁻¹; $F = 4.08$, $df = 1$ and 97 , $P < 0.05$; Fig. 2). Plasma triglyceride levels increased with time of day ($F = 9.63$, $df = 1$ and 97 , $P < 0.001$), but there was no effect of elevation ($P > 0.4$) nor a time \times elevation interaction ($P > 0.8$). Plasma glycerol and B-OH were independent of elevation ($P > 0.40$ in both cases, either including all covariates or for reduced models).

Neither body mass ($P > 0.4$) nor fat score ($P > 0.7$) varied with elevation in Orange-crowned Warblers (Fig. 4A, B). Similarly, both body mass and fat score were independent of time of day and Julian date at either elevation ($P > 0.10$ in all cases). Fat scores ranged from zero to 3 at high- and low-elevation sites, with the greatest proportion of birds having fat scores of 1 (40% and 70% at low and high elevations, respectively).

Comparison of Residual Plasma Triglyceride Levels among Species

There was a highly significant species \times elevation interaction for residual plasma triglyceride levels ($F = 7.04$, $df = 3$ and 898 , $P < 0.001$; Fig. 2). At high-elevation sites, there was no difference in residual plasma triglyceride for Fox Sparrows, Golden-crowned Sparrows, or Hermit Thrushes ($P \geq 0.8$ in all cases), but all three species had higher residual triglyceride levels than Orange-crowned Warblers ($P \leq 0.015$ in all cases). Conversely, at low-elevation sites, Fox Sparrows had lower residual triglyceride than Golden-crowned Sparrows and Hermit Thrushes ($P < 0.025$ in both cases), but no other species contrasts were significant.

DISCUSSION

Triglyceride levels of birds that are gaining fat are generally high, and we predicted high residual triglyceride levels at high-elevation sites during fall migration because of the delayed timing of seasonal food availability (fruits, seeds, and insects) at higher elevations. Our analyses supported this prediction for three of four species (Fox Sparrow, Golden-crowned Sparrow, and Hermit Thrush), all of which consume large quantities of fruit during fall migration (Norment et al. 1998, Weckstein et al. 2002, Dellinger et al. 2012). Blueberries appeared to be an important food source for Hermit Thrushes, Fox Sparrows, and Golden-crowned Sparrows at our subalpine sites, based on incidental examination of feces while birds were being handled and processed and periodic counts of marked blueberry bushes at high-elevation sites. By contrast, the smaller-bodied Orange-crowned Warbler, which is largely insectivorous during fall migration (Gilbert et al. 2010), showed the opposite pattern, with higher residual plasma triglyceride levels at low-elevation sites. Furthermore, at high-elevation sites there was no difference in residual plasma triglyceride levels among the three more frugivorous species, and all had higher triglyceride levels than Orange-crowned Warblers. At low elevation,

Fox Sparrows had lower residual plasma triglyceride levels than Golden-crowned Sparrows and Hermit Thrushes. Fox Sparrows eat a mixture of insects, seeds, and fruit during fall migration (Weckstein et al. 2002), whereas Golden-crowned Sparrows and Hermit Thrushes are more strictly fruit- or seed-eaters (Norment et al. 1998, Dellinger et al. 2012). Our results therefore support the novel idea that high-elevation sites can represent high-quality fall stopover habitat where migrants are able to replenish fat reserves.

Our study illustrates the utility of estimating fattening rate from residual, mass-corrected plasma triglyceride levels and confirms the results and conclusions of many similar studies (Guglielmo et al. 2002, 2005; Williams et al. 2007) in that body mass, fat scores, and other metabolites (glycerol, beta-hydroxybutyrate) do not provide meaningful information on fattening rates. Body mass and fat scores provide static measures of putative body “condition” at the time of capture; however, two individuals could have the same mass or fat score, but have opposite trajectories of mass change, one gaining and the other losing mass (Williams et al. 1999, Schaub and Jenni 2001, Guglielmo et al. 2005). Plasma triglyceride analysis captures this dynamic nature of refueling. In the present study, body mass did not differ among birds captured in high- versus low-elevation sites for three of our four focal species, and in Hermit Thrushes body mass was actually higher at low-elevation sites, the opposite of the pattern we found for estimated fattening rate. Our result would be consistent with lighter birds preferentially using high-elevation sites to benefit from the potential to achieve high fattening rates.

We note that using traditional body-condition measures of fat scores, all species at high elevation generally had a fat score between 1 and 2, whereas the birds captured at low elevation had fat scores close to or below 1. Using a much larger data set for the same capture period during the same two years at RPBO, average fat scores were 0.95 for Fox Sparrows, 0.67 for Golden-crowned Sparrows, 0.58 for Hermit Thrushes, and 0.89 for Orange-crowned Warblers, values generally a bit lower than in our low-elevation data set (W. Easton unpubl. data; see above and Fig 4B). These relatively low fat scores for low elevation are to be expected, perhaps because many of the coastal migrants in British Columbia are short- or medium-distance migrants, or migrate via short hops over land without crossing large geographic barriers and, thus, do not need to put on large fat reserves. Thus, plasma triglyceride analysis appears to provide a more informative method of measuring body-condition dynamics for migrants in more northerly locations.

We also found no relationship between body mass at the time of capture and either time of day or date, consistent with other studies that suggest that plotting mass by unit time (either daily or seasonally) cannot reliably predict fattening rate or trajectories (e.g., Williams et al. 2007). Fat scores also did not vary consistently with elevation across species: in Hermit Thrushes and Orange-crowned Warblers, fat scores were independent of elevation. Fox Sparrows and Golden-crowned Sparrows had higher fat scores at higher elevations, consistent with the hypothesis of higher fattening rates at high-elevation sites, but this could also be explained by fatter birds preferentially occupying high-elevation sites independent of fattening rates per se. However, as with body mass, fat score did not vary systematically with either time of day or date, which confirms that plotting fat score by unit time cannot reliably estimate fattening rate. In some cases, these analyses are confounded by short length-of-stay and rapid turnover of migratory birds at stopover sites. If

birds arrive, fatten rapidly, depart, and then are replaced by newly arriving birds of lower body mass or fat score, then average mass or fat score will not change with time at the population level, even though individual birds are fattening (Guglielmo et al. 2002, Williams et al. 2007). Our results also confirm that variation in (residual) plasma triglyceride levels is more informative for estimation of fattening rate, and for detecting site differences, than is variation in glycerol and beta-hydroxybutyrate, as observed in other studies (Guglielmo et al. 2002, Acevado Seaman et al. 2006, Smith and McWilliams 2010). Glycerol and beta-hydroxybutyrate provide metabolic signals of fasting or mass loss (but for problems with interpretations of plasma glycerol levels, see Guglielmo et al. 2005), and we would not expect these metabolites to be as informative during migration, when most individuals tend to be actively fattening during the day rather than losing mass.

Although plasma metabolites can provide useful information about fuel deposition and resource use by birds at migration stopover sites, it is important to issue several cautionary points. First, our data are correlative and do not establish a causal relationship between fattening rates and habitat quality (here defined as food availability and/or quality). Some of the elevational differences in fueling rates may be linked to species differences in diet preferences (amount of fruit compared with insects or seeds, or nutritional quality of fruits at stopover sites; Smith et al. 2007, Smith and McWilliams 2010). Low- and high-elevation sampling sites probably differ with respect to several other factors (temperature, food availability, ground cover, predators, etc.; Martin 2001) that could contribute to the elevational differences we observed in residual plasma triglyceride levels.

In addition, we did not determine the status or the origin of the birds we blood-sampled, and it is possible that we sampled a mix of postbreeding residents, elevational migrants, or stopover migrants. However, our study suggests that any bird (regardless of origin) would benefit by utilizing high-elevation habitats in fall where they could achieve high fattening rates. This could allow for a rapid recovery of “condition” in nonmigratory residents following breeding, or for more rapid migration in true migrants, but both would clearly benefit. In addition, our results suggest that there might be an advantage for locally breeding, low-elevation birds to become “altitudinal migrants” (e.g., Morton 1991, Boyle 2008) in fall, moving up to higher elevations to benefit from the delayed seasonality of food at these sites. Possibly, some of the benefits of high estimated fattening rates might be offset by costs associated with increased metabolic rate at high elevations as a response to generally colder nighttime temperatures at higher elevations. However, high-elevation migrants might also be able to save energy by reducing the cost of descending and later ascending again to resume migration compared with birds stopping at low-elevation sites. They may also compensate for such increased metabolic costs, and still benefit from high fueling rates during the day, through use of heterothermy, nocturnal torpor, or behavioral adaptations such as moving to lower elevations for nighttime (e.g., Wojciechowski et al. 2011). These are questions for future research.

In Fox Sparrows and Hermit Thrushes, we found evidence of an increase in estimated fattening rate with time lapsed since dawn (although we did not detect this fasting signal for glycerol or beta-hydroxybutyrate). This has been reported in previous studies and is consistent with an overnight fast and resumption of feeding at dawn (Guglielmo et al. 2002, 2005; Williams et al. 2007). However, in our

study the increase in estimated fattening rate with time was steeper at high elevation (i.e., birds at high elevation had higher residual plasma triglyceride levels at any time during the day than those at low elevation). This may represent an additional advantage of high-elevation stopover sites; if birds can replenish reserves more quickly after the onset of foraging at dawn, they might be able to continue migration more quickly, with shorter stopover periods.

Our data suggest that high-elevation sites are high-quality habitats for some migrating birds in fall. In support of this idea, we attempted to sample at a third low-elevation site (Seymour Demonstration Forest) but had very low capture numbers despite equivalent mist-netting effort between this and our other low-elevation sites. We found no evidence that experienced AHY birds used high-elevation sites more or that inexperienced HY birds were excluded from high-elevation sites. As expected, the majority of birds sampled were HY, and there was no difference in estimated fattening rates of HY and AHY birds for any species at either elevation. Similarly, we found no evidence of differences in residual plasma triglyceride levels between sexes at either low or high elevation. This lack of an age or sex effect on estimated fattening rates has also been reported in several previous studies (Guglielmo et al. 2002, 2005; Williams et al. 2007) and suggests that, regardless of species, high-elevation sites provide good stopover habitat for all ages and both sexes.

Much of western North America is composed of montane, subalpine, and alpine habitats. In British Columbia, high-elevation habitats comprise ~50% of the landbase (A. Banner et al. unpubl. data), yet the importance of these habitats for songbirds outside the breeding season is poorly known (Martin 2001). In earlier studies, we found extensive use of high-elevation habitats for a period of up to 3 months (mid-August to mid-October) for ~200 species, including tundra-breeding birds during fall migration and local forest-breeding resident birds (Martin and Ogle 1998, Martin 2001, Wilson and Martin 2005). Here, we have shown that there are advantages to making these elevational movements for several species because high-elevation habitats function as high-quality fall stopover sites. These high-elevation sites are also characterized by higher estimated fattening rates earlier in the day than low-elevation habitat in the same geographic area. Although our data are correlative and we need to determine the key mechanisms driving differences in refueling rates with elevation, we recommend that high-elevation (mountain) habitats in other geographic regions be investigated for their potential importance as avian fall migration stopover habitats. With known high-quality stopover sites such as riparian habitats declining in quantity and quality (Finch and Yong 2000), a greater understanding of the relative importance of high-elevation habitats as stopover sites will facilitate more effective and targeted conservation strategies for migratory birds.

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