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Reservoir water levels do not influence daily mass gain of warblers at a riparian stopover site

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ABSTRACT. Hydroelectric dam operations that lead to fluctuations in the water levels of reservoirs can influence the amount of riparian habitat available for migrating songbirds and may impact the use and quality of remaining habitat. Our objective was to determine if use of riparian habitats and mass gain by five warbler species at the Columbia River-Revelstoke Migration Monitoring Station in British Columbia, Canada, were influenced by water levels in the surrounding Arrow Lakes Reservoir. We analyzed fall migration data collected from 1998 to 2006. Capture rates of American Redstarts (*Setophaga ruticilla*), Common Yellowthroats (*Geothlypis trichas*), Orange-crowned Warblers (*Vermivora celata*), Wilson's Warblers (*Wilsonia pusilla*), and Yellow Warblers (*Dendroica petechia*) varied between years and weeks of the migration period, but were not affected by annual or weekly variation in water levels. Annual variation in capture rates was driven by hatch-year birds (>80% of individuals captured were juveniles) and could reflect conditions on the breeding grounds that influence productivity. We found that mass gain by the five species of warblers varied between 0.32% and 0.98% of lean body mass/hour. Mass gain did not vary between years or across weeks of the migration period and was not influenced by annual or weekly variation in reservoir water levels. Although the amount of available riparian habitat was reduced when reservoir water levels were high, we found no evidence that this loss of habitat influenced either the number of warblers or the mass gain of warblers using the riparian habitat that remained. Body mass at the time of first capture varied between years and across weeks for all five species. For American Redstarts and Orange-crowned Warblers, body mass declined as average weekly water levels increased, a pattern that could arise if water levels influenced either their settlement decisions or length of stay.

RESUMEN. **Los niveles del agua en un embalse no influyen en el incremento del peso diario de parulidos en un sitio de parada migratorio ripario**

Las operaciones de las represas hidroeléctricas que resultan en fluctuaciones en los niveles del agua de los embalses pueden influenciar la cantidad de hábitat ripario disponible para las aves migratorias y podrían tener impacto en el uso y la calidad del hábitat remanente. Nuestro objetivo fue determinar si el uso de los hábitats riparios y el incremento en el peso de cinco especies de parulidos en la estación de monitoreo migratorio del Rio Columbia-Revelstoke en British Columbia, Canada fueron influenciados por los niveles del agua en el embalse de Arrow Lakes. Analizamos datos de la migración de otoño colectados desde 1998 hasta 2006. Las tasas de captura de *Setophaga ruticilla*, *Geothlypis trichas*, *Vermivora celata*, *Wilsonia pusilla*, y *Dendroica petechia* variaron entre años y semanas durante el periodo migratorio pero no fueron afectados por la variación anual o semanal en el nivel del agua. La variación anual en las tasas de captura fue influenciada por aves de primer año (>80% de los individuos capturados fueron juveniles) y podrían reflejar condiciones en las áreas de reproducción que influyen en la productividad. Encontramos que el incremento en el peso de cinco especies de parulidos varió entre 0.32–0.98% de la masa corporal magra/hr. El incremento en el peso no varió entre años o a través de semanas durante el periodo migratorio y no fue influenciado por la variación anual o semanal en los niveles del agua del embalse. Aunque la cantidad de hábitat ripario disponible fue reducido cuando los niveles del agua del embalse fueron altos, no encontramos evidencia de que ésta perdida de hábitat influenciaba el numero de parulidos o el incremento del peso de los parulidos usando el hábitat ripario que permanecia. El peso corporal en el momento de la primera captura varió entre años y a través de semanas para las cinco especies. Para *S. ruticilla* y *V. celata*, el peso corporal disminuyó a menudo que el promedio semanal de los niveles del agua incrementaban, cual es un patrón que podría existir si los niveles del agua influyen en su decisión de parar o no en el sitio, o cuánto tiempo permanecer en el sitio.

Key words: Dendroica petechia, Geothlypis trichas, migration, Parulidae, refuelling rates, Setophaga ruticilla, Vermivora celata, Wilsonia pusilla

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Songbirds face numerous challenges as they migrate between temperate and tropical areas. The high energetic cost of long-distance travel (Wikelski et al. 2003, McWilliams et al. 2004) forces individuals to stop frequently and compete with other migrants and residents in unfamiliar habitat for food to fuel the next stage of migration. Mortality rates on migration, although difficult to measure, are consequently likely to be high. Sillett and Holmes (2002) estimated that monthly mortality rates of Black-throated Blue Warblers (*Dendroica caerulescens*) were at least 15 times higher during migration than on the breeding or wintering grounds. Biologists have therefore emphasized the importance of conserving high-quality stopover habitat, where birds can rapidly accumulate energy stores, when developing conservation strategies for migratory songbirds (Moore 2000, Skagen et al. 2005, Carlisle et al. 2009).

Migratory songbirds stop and refuel in a variety of habitats during migration and many species show geographic variation in habitat use (Petit 2000). Resources in riparian habitats may, however, be critical for many migrants, particularly in the western United States and Canada (Wiebe and Martin 1998, Finch and Yong 2000, Kelly and Hutto 2005). Unfortunately, riparian habitat makes up a small fraction (about 1%) of the western landscape (Knopf et al. 1988) and this fraction continues to decline as natural flow regimes are modified, floodplains are developed, and land is cleared for agriculture or urban development (Fleischner 1994, Poff et al. 1997). The continued loss and degradation of this apparently critical stopover habitat may contribute to future population declines of western songbirds (Ohmart 1994, Moore et al. 1995). Conversely, protection, preservation, and restoration of riparian habitat may be required as part of an effective conservation plan for migratory songbirds (Skagen et al. 2005).

Hydroelectric development has contributed to the loss of riparian habitat in the Pacific Northwest; 16 major dams have created a reservoir system that has led to the loss of more than 87% of the riparian habitat within the Canadian portion of the Columbia River Basin (Moody et al. 2007). Hydroelectric dam operations that lead to fluctuations in the water levels of the reservoirs continue to flood remnant riparian habitat in the summer and fall, and may increase competition among migratory birds in the habitat that remains, reducing stopover habitat quality. Identifying and reducing the impacts of operational decisions on the quantity and quality of riparian habitat available for migratory birds may help reduce competition, allowing birds to replenish energy stores more rapidly and reducing mortality during migration.

Our objective was to determine if hydroelectric dam operations that influence water levels in the Arrow Lakes Reservoir, Revelstoke, British Columbia, influence the use and quality of remnant riparian habitat used by migratory wood warblers during fall migration. We assessed use of riparian habitat use using capture rates at the Columba River-Revelstoke Migration Monitoring Station, located in riparian habitat that is surrounded by water when Arrow Lakes Reservoir is at full pool. We assessed stopover habitat quality by measuring the rate of mass gain of warblers during stopover. Several investigators have used daily mass gain by migratory songbirds to assess and compare stopover habitat quality (e.g., Dunn 2000, 2002, Ktitorov et al. 2008).

We predicted that warblers would use the stopover site more in years when water levels in the reservoir were high because alternative riparian habitat located within the drawdown zone of the reservoir is flooded and unavailable. We also predicted that mass gain would be lower during years of high water levels in the reservoir because flooding reduces the amount of available foraging habitat around the stopover site, increases competition among migrants for food, or both.

METHODS

We examined the fall migration and stopover ecology of warblers in British Columbia, Canada, using data collected at the Columba River-Revelstoke Migration Monitoring Station on Machete Island in the Arrow Lakes Reservoir (49.088 N, 115.678 W). The migration station is located in willow/cottonwood habitat (438.5–441 m asl) surrounded by wet grassland and sedge wetland. Water levels and the amount of vegetated habitat surrounding the migration station vary seasonally and between years (Fig. 1, Table 1) as a result of hydroelectric dam operations within the Columbia River system. Some areas of the migration station are subject to flooding when water levels approach full pool (440 m).

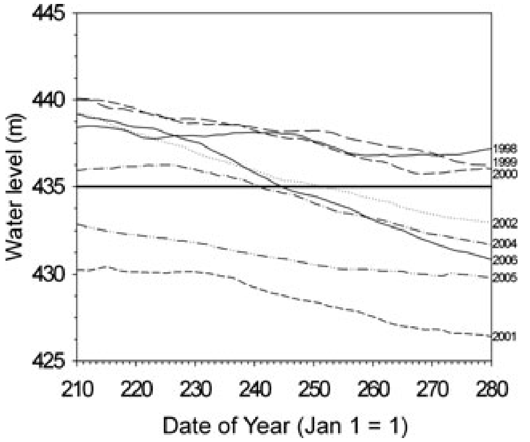

Fig. 1. Seasonal variation in the water levels in Arrow Lakes Reservoir during fall migration from 1998 to 2002 and from 2004 to 2006. Data are shown for the period from 29 July (date of year = 210) to 3 October (date of year = 280). The horizontal line shows the lowest elevation that willow habitat is found within the drawdown zone. For analyses, we classified 1998, 1999, and 2000 as high-water years, 2002, 2004, and 2006 as intermediate years, and 2001 and 2005 as low-water years.

Study species. We studied five species of warblers that were among the most common species captured at our migration monitoring station, including American Redstarts (*Setophaga ruticilla*), Common Yellowthroats (*Geothlypis trichas*), Orange-crowned Warblers (*Vermivora celata*), Wilson's Warblers (*Wilsonia pusilla*), and Yellow Warblers (*Dendroica petechia*). All five species feed primarily on insects and other arthropods, but Common Yellowthroats tend to forage on the ground and in low vegetation (Guzy and Ritchison 1999), Wilson's Warblers and Yellow Warblers forage predominantly in shrubs and understory trees (Ammon and Gilbert 1999, Lowther et al. 1999), and Orange-crowned Warblers and American Redstarts forage in shrubs, understory trees, and the tree canopy (Sherry and Holmes 1999, Gilbert et al. 2010). The former three species may therefore be more impacted by rising water levels that inundate grass and shrub habitat. Population trends for the five species in British Columbia differ; Wilson's Warblers and Yellow Warblers have exhibited long-term population declines over the last 40 yr (−5.7% and −1.8% per year, respectively), whereas American Redstart, Common Yellowthroat, and Orange-crowned Warbler populations are relatively stable (Collins and Downes 2009).

Data sampling, classification, and selection. We used data collected during fall migration from 1998 to 2002 and from 2004 to 2006. The station did not operate in 2003. The station was operated following a standardized protocol, with migration monitored using standard-effort mist-netting. Mist-nets (2.6 m × 12 m; 30-mm mesh) at permanent locations were opened at sunrise for 6 hr on each day of the fall

Table 1. Reservoir water level impacts on the amount of tree, shrub, grass, unvegetated, and wetland habitat within the drawdown zone of the Arrow Lakes Reservoir between Revelstoke (the northern limit of the reservoir and site of the migration monitoring station) and Shelter Bay, 50 km to the south. The drawdown zone is defined as the footprint of the reservoir when the water level is the maximum allowed (440 m). Habitat types were assigned within 50 m × 50 m plots from aerial photos. Plots were categorized as tree habitat if they contained trees >5 m in height and shrub habitat if they contained small or large patches of shrubs, but no trees. Plots were defined as wetland habitat if they contained permanent water in the drawdown zone that was isolated from the main body of the reservoir (Gill and van Oort, unpubl. data).

Water level (m)	Tree (ha)	Shrub (ha)	Grass (ha)	Unvegetated (ha)	Wetland (ha)
430	281	439	2220	711	286
431	281	439	2219	709	286
432	281	435	2055	242	286
433	281	424	1746	82	284
434	281	420	1334	40	283
435	281	401	831	21	205
436	281	333	431	13	145
437	281	250	215	2	118
438	281	116	99	0.5	111
439	214	34	34	0	13
440	103	8	5	0	5

Table 2. Mist-netting effort at the Columbia River-Revelstoke Migration Monitoring station from 1998 to 2006. The station did not operate in 2003. Nets were always opened at sunrise and remained open for 6 hr.

Year	Period	Max. no. nets	Total net hours
1998	8 Aug–30 Sept	12	2206
1999	3 Aug–29 Sept	11	1933
2000	1 Aug–27 Sept	13	2250
2001	1 Aug–30 Sept	15	3469
2002	1 Aug–30 Sept	12	3341
2004	1 Aug–30 Sept	12	3129
2005	1 Aug–30 Sept	12	2681
2006	1 Aug–30 Sept	12	3299

migration season, weather permitting. Specific operational details for each year are provided in Table 2. Nets were checked every 30 min and all birds were banded with USGS aluminum bands.

Data collected on the focal species included the date and time of capture, body mass, wing chord (closed wing length), and, where possible, age and sex. Body mass was measured using a digital scale (±0.1 g). Wing chord was measured (±0.5 mm) using a stainless-steel wing rule. Age and sex were determined using skull ossification and plumage characteristics (Pyle 1997). For analyses, we assigned birds into three classes: after-hatch-year (AHY) females, AHY males, and hatch-year (HY) birds. We did not distinguish between HY females and males because many cannot be sexed by plumage characteristics.

For analyses examining body mass gain, we included data from birds captured for the first time in any given year where we had complete information on date and time of capture, body mass and wing chord, and sex and age class. We deleted records of individuals with mass or wing chord values falling below the 1st percentile or above the 99th percentile of all measurements to exclude possible errors in measurement or recording. We also excluded HY birds identified as local juveniles based on feather development and plumage (Pyle 1997). Our data set is nevertheless likely to include resident AHY and local HY birds as well as migrants because American Redstarts, Common Yellowthroats, and Yellow Warblers all breed in riparian habitat within the drawdown zone of Arrow Lakes Reservoir.

Reservoir water levels. Water levels in the Arrow Lakes Reservoir, a 240-km long reservoir system in the upper Columbia River valley, fluctuate due to changes in inflow that are impacted by winter snow-pack, the timing of snowmelt, precipitation, and water release decisions at the downstream Hugh Keenleyside Dam. Willow/cottonwood habitat in the drawdown zone is found almost exclusively at elevations above 435 m so there is a marked difference in the impact of hydroelectric dam operations on potential foraging habitat for migratory songbirds in years when water levels reach full pool (440 m, the maximum allowed) and years when water levels do not exceed 435 m. For our analyses, we distinguish between high-water years when the reservoir approached full pool (>438.5 m) and water levels were above 435 m for the entire fall migration season (1998, 1999, and 2000), low-water years when water levels did not exceed 435 m during the fall migration season (2001 and 2005), and intermediate years when water levels exceeded 435 m for only part of the season (2002, 2004, and 2006; Fig. 1).

Statistical analyses. We used regression models to determine if differences in water levels of the Arrow Lakes Reservoir among years or across the season influenced capture rates and daily mass gain of five warbler species. Capture rate for each sex/age class of each species was calculated for each week of the migration season as the number of birds caught per 100 net hours. Weekly, rather than daily, rates were calculated to reduce the number of zeros in the data set (Week 1 began on 29 July). Even with grouping weekly data together, we still needed to use generalized linear models with a negative binomial distribution and log link to examine variation in weekly capture rates of each species. We initially examined how capture rates varied by sex/age class, week, and year. We subsequently examined how capture rates varied with the type of year (high-, intermediate-, or low-water) and the average water level in each week. In both cases, we initially fitted full models that included all main effects and interactions between sex/age class and temporal or water-level variables, and sequentially removed nonsignificant interaction terms ($P > 0.05$) and then nonsignificant main effects until only significant terms remained. Significance was assessed using the change in deviance associated with dropping the term from the more complete model. Model residuals were examined for normality and heterogeneity of variances.

We estimated daily mass gain using a regression of body mass of first-capture birds and time of capture in relation to sunrise (Dunn 2000, 2002). We included wing chord as a covariate to account for size differences among individuals, age/sex class to account for mass differences due to age or sex, and week to account for any mass differences associated with stage of the migration. We used interaction terms to determine if mass gain varied with the size or age/sex of an individual, week of the season, or year. This method assumes that birds arrive at the site at or before dawn, that the time of capture is independent of the birds mass at dawn, and that the gain in average mass of birds captured during the 6 h after sunrise represents the average mass gain of individuals of that size or age/sex class in the area. This method was preferred over using recapture data because many birds were captured only once, and handling birds may lead to a decline in body mass (Winker et al. 1992, Schwilch and Jenni 2001). We initially fitted a full model including wing chord, sex/age class, week, year, and their interaction with time and sequentially removed nonsignificant interaction terms and then nonsignificant main effects until only significant terms remained. We then fitted models that examined how mass or mass gain varied with the type of year (high-, intermediate-, or low-water) and the average weekly water level. These models controlled for any differences in mass associated with body size (wing chord), sex/age class, or week by including them as terms along with the type of year and average weekly water level. Significance was assessed using the change in the variance ratio associated with dropping the term from a more complete model. We back-checked all main effects and their interaction with time against the final model to ensure that order effects did not influence our results. Residuals were examined for normality and heterogeneity of variances. All analyses were conducted using Genstat Version 12 (VSN International, Rothamsted, UK).

RESULTS

Temporal variation in capture rates. Capture rates varied with age/sex class and week of the migration season for all five species of wood warblers (Fig. 2, Table 3). Capture rates of HY birds were about 10 times higher than those of adults for all species. Seasonal variation in capture rates of two species that breed within the drawdown zone of the Arrow Lakes Reservoir (Common Yellowthroats and Yellow Warblers) differed from the other species. Capture rates of Yellow Warblers were highest in week 1 and declined as the migration season progressed. Capture rates of Common Yellowthroats were high during week 1, declined, and then peaked during week 5. In contrast, capture rates of American Redstarts, Orange-crowned Warblers, and Wilson's Warblers had a single peak (Fig. 2). For Common Yellowthroats, differences in weekly capture rates varied with sex and age classes, with capture rates of HY birds peaking before those of adults (Fig. 2, Table 3). Capture rates of all species varied across years (Table 3).

We found no consistent effect of reservoir water levels on capture rates of wood warblers during fall migration. Year-to-year variation in water levels had a significant, but different effect on capture rates of three species (Table 3). Capture rates of Common Yellowthroats were highest during high-water years, capture rates of Wilson's Warblers were highest during intermediate years, and capture rates of Orange-crowned Warblers were highest during low- and intermediate- water years (Table 4). We found no significant effect of water levels on the capture rates of American Redstarts and Yellow Warblers. Average weekly water levels had no effect on capture rates of any species after controlling for seasonal variation in capture rates (Table 3).

Temporal variation in mass and mass gain. Body mass of all five species increased with the amount of time between sunrise and capture (Table 5). Mean mass gain varied from 0.025 g/h for American Redstarts to 0.073 g/h for Wilson's Warblers, corresponding to increases of 0.32% and 0.98% of lean body mass/hour, respectively (Table 6). Rates of change in mass did not vary with body size (wing chord), age/sex class, the week of the migration period, or across years for any of the five species (all interactions with time $P > 0.05$, Table 5). However, we found weekly and interannual variation in body mass for all species (Table 5). Body mass peaked during the final 2–3 weeks of the migration season for American Redstarts, Orange-crowned Warblers, Wilson's Warblers,

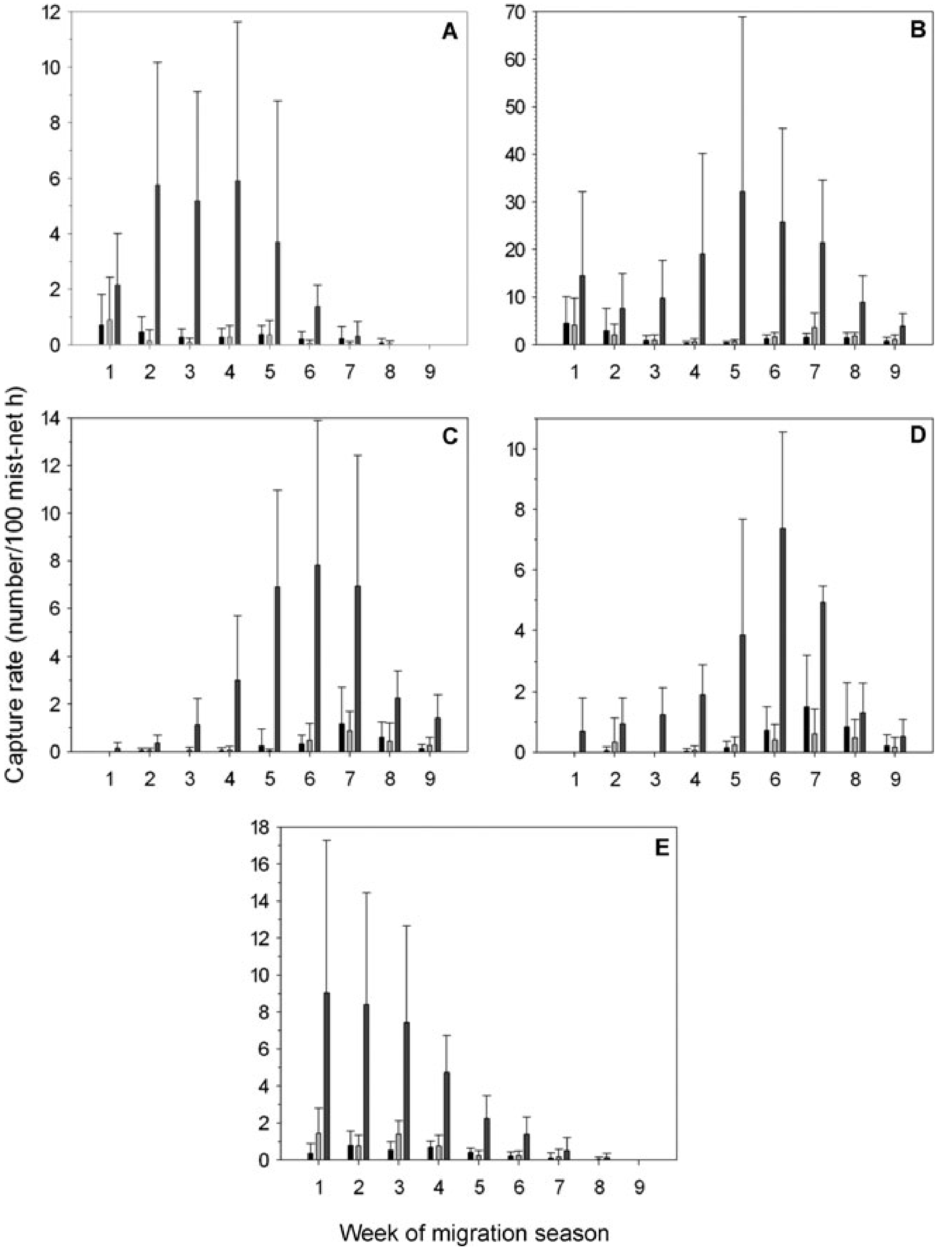

Fig. 2. Capture rates of (A) American Redstarts, (B) Common Yellowthroats, (C) Orange-crowned Warblers, (D) Wilson's Warblers, and (E) Yellow Warblers at the Columbia River-Revelstoke Migration Monitoring Station during fall migration. Capture rates (number/100 mist-net hours ± SD) are averaged across the 8 yr of the study. Week 1 begins on 29 July. Bars denote AHY females (black), AHY males (light gray), and HY birds (dark gray).

Table 3. Results from generalized linear models examining variation in capture rates of five species of warblers at the Columbia River-Revelstoke Migration Monitoring Station from 1998 to 2006.

		Species[a]									
		AMRE		COYE		OCWA		WIWA		YWAR	
	df	Δ Dev[b]	*P*	Δ Dev	*P*	Δ Dev	*P*	Δ Dev	*P*	Δ Dev	*P*
Temporal and age/sex class model											
Year	7	15.8	0.03	54.7	<0.001	43.4	<0.001	54.1	<0.001	14.9	0.04
Week[c]	8	46.9	<0.001	–	–	109.6	<0.001	96.0	<0.001	99.1	<0.001
Class[d]	2	137.5	<0.001	–	–	192.8	<0.001	131.2	<0.001	177.1	<0.001
Week*Class[e]	16	20.8	0.19	65.1	<0.001	10.2	0.85	22.6	0.13	7.8	0.96
Reservoir water level model											
Year type[f]	2	4.0	0.13	25.1	<0.001	30.2	<0.001	21.8	<0.001	0.7	0.71
Water level[g]	1	1.2	0.28	0.1	0.72	2.6	0.11	3.2	0.08	0.2	0.66
Year type*Class	4	3.7	0.46	1.9	0.76	2.9	0.47	6.5	0.17	3.5	0.48
Water level*Week	8	1.9	0.98	11.2	0.19	5.7	0.65	10.8	0.26	4.7	0.79

[a] AMRE = American Redstart, COYE = Common Yellowthroat, OCWA = Orange-crowned Warbler, WIWA = Wilson's Warbler, and YWAR = Yellow Warbler.
[b] Change in deviance associated with dropping a term.
[c] Weeks were ordered beginning with the start of week 1 that began on 29 July.
[d] Birds were classified as AHY females, AHY males, and HY individuals.
[e] * Denotes interaction between terms.
[f] Years were classified as being high-water years, intermediate years, or low-water years based on variation in water levels in the Arrow Lakes Reservoir.
[g] Water levels were averaged daily maximum water levels associated with each week of the migration period.

Table 4. Model predictions ± SE from generalized linear models examining variation in the capture rates (numbers per 100 mist-net hours) of warblers at the Columbia River-Revelstoke Migration Monitoring Station from 1998 to 2006. Abbreviations, variable definitions, and significance of effects in models are presented in Tables 3.

		Species				
		AMRE	COYE	OCWA	WIWA	YWAR
Temporal and age/sex class model[a]						
Class	AHY F	0.29 ± 0.07	1.56 ± 0.21	0.29 ± 0.07	0.40 ± 0.08	0.35 ± 0.07
	AHY M	0.20 ± 0.05	1.86 ± 0.22	0.25 ± 0.06	0.26 ± 0.06	0.56 ± 0.09
	HY	2.63 ± 0.27	15.2 ± 1.25	3.40 ± 0.27	2.55 ± 0.24	3.60 ± 0.30
Reservoir water level model[b]						
Year type	Low	1.09 ± 0.28	4.68 ± 0.63	1.49 ± 0.21	0.87 ± 0.16	1.58 ± 0.24
	Intermed	1.27 ± 0.26	5.00 ± 0.56	1.83 ± 0.20	1.60 ± 0.20	1.58 ± 0.20
	High	0.71 ± 0.16	9.07 ± 0.97	0.66 ± 1.1	0.63 ± 0.10	1.38 ± 0.19

[a]Predictions from the temporal and age/sex class models control for week to week variation in capture rate.
[b]Predictions from the reservoir water level models control for week and age/sex class effects.

and Yellow Warblers (Table 7). In contrast, body mass of Common Yellowthroats was highest during the first 2 weeks of migration (Table 7). Differences in mean body mass across years were not consistent across species, with mean body mass highest in 1998 for Common Yellowthroats and Yellow Warblers, 2004 for American Redstarts, and 2006 for Orange-crowned Warblers and Wilson's Warblers. Mean body mass was lowest in 1999 for Yellow Warblers, 2000 for Orange-crowned Warblers and Wilson's Warblers, 2001 for Common Yellowthroats, and 2002 for American Redstarts. Mass also increased with body size (estimated using wing chord) for all species (Table 5). After controlling for differences in wing chord, mass also differed among age/sex classes for Common Yellowthroats and Yellow Warblers (Tables 5 and 7).

Warbler abundance at the migration station, estimated using the total capture rate of the five species for a given week, had no effect on rates of mass gain for any species (Table 5). Warbler abundance did have a significant effect on the body mass of two species, with the mean body mass of American Redstarts (AMRE) and Yellow Warblers (YWAR) declining as the weekly capture rate of warblers increased (Table 5; model effect size ± SE, AMRE = -0.003 ± 0.001, YWAR = -0.004 ± 0.002).

Reservoir water levels had no effect on the rate at which warblers gained mass. Year-to-year variation in water levels during migration and average weekly water levels had no effect on mass gain (all interactions with time $P > 0.05$; Table 5). The type of year did have an effect on the body mass of Wilson's and Yellow warblers captured. However, mean body mass was as high or higher during high-water years as low-water years, and lowest during intermediate years. Weekly water levels influenced the body mass of two species, with American Redstarts averaging 0.2 g lighter and Orange-crowned Warblers (OCWA) 0.1 g lighter when the reservoir water level was at 440 m than when it was at 430 m (Table 5; model effect size ± SE, AMRE = -0.016 ± 0.006, OCWA = -0.012 ± 0.006).

DISCUSSION

Although the amount of available shrub habitat in the drawdown zone of the Arrow Lakes Reservoir is considerably lower when water levels are high, we found no consistent relationship between interannual or seasonal variation in water levels and capture rates of five species of warblers. We also found no evidence that daily mass gain of any species was reduced in years when water levels were high or varied across the season in relation to average weekly water levels in the reservoir. This contrasts with work at 22 sites in Europe where body mass gain of Eurasian Redstarts (*Phoenicurus phoenicurus*) and Willow Warblers (*Phylloscopus trochilus*) was related to the amount of suitable stopover habitat (shrub or forest cover) within 3 or 5 km, respectively (Ktitorov et al. 2008). Our results suggest that factors other than availability of riparian habitat at a local scale influence use of riparian habitat

Table 5. Results from generalized linear models examining variation in mass of warblers captured at the Columbia River-Revelstoke Migration Monitoring Station from 1998 to 2006. Abbreviations and variables not defined as footnotes are consistent with Table 3.

		Species									
		AMRE		COYE		OCWA		WIWA		YWAR	
	df	Δ v.r.[a]	*P*	Δ v.r.	*P*	Δ v.r.	*P*	Δ v.r.	*P*	Δ v.r.	*P*
Temporal and class model[b]											
Time[c]	1	4.2	0.03	66.5	<0.001	23.9	<0.001	51.9	<0.001	12.8	<0.001
Time*Year	7	0.7	1.0	0.0	1.0	2.4	0.94	6.5	0.48	0.7	1.0
Time*Week	8	0.4	1.0	0.2	1.0	0.03	1.0	0.4	1.0	4.9	0.68
Time*Class	2	1.1	0.58	0.0	1.0	0.5	0.80	0.0	1.0	0.1	0.96
Time*Body size	1	2.5	0.12	0.6	0.32	0.04	0.84	0.01	0.93	3.2	0.07
Time*Abundance	1	1.9	0.17	0.4	0.51	1.1	0.29	0.01	0.91	0.1	0.76
Year	7	22.9	0.002	28.1	0.002	21.4	0.004	27.3	<0.001	76.8	<0.001
Week	8	45.1	<0.001	182	<0.001	114	<0.001	69.7	<0.001	47.9	<0.001
Class	2	3.1	0.22	13.3	0.001	1.6	0.38	2.7	0.26	17.4	<0.001
Body size[d]	1	80.3	<0.001	780	<0.001	146	<0.001	126	<0.001	130	<0.001
Abundance[e]	1	5.4	0.02	3.6	0.06	0.6	0.45	0.02	0.88	5.2	0.02
Reservoir water level model[f]											
Time*Year type	2	0.03	0.99	0.02	0.99	1.4	0.50	0.0	1.0	0.0	1.0
Time*Water level	1	0.9	0.35	0.1	0.90	0.3	0.58	0.7	0.68	0.5	0.50
Year type	2	5.1	0.08	5.5	0.06	1.5	0.23	7.5	0.02	54.6	<0.001
Water level	1	6.6	0.01	0.9	0.35	4.1	0.04	0.01	0.93	0.2	0.67

[a]Change in variance ratio associated with dropping a term.
[b]Sample sizes were: AMRE, AHY-f = 57, AHY-m = 27, HY = 570; COYE, AHY-f = 234, AHY-m = 306, HY = 2899; OCWA, AHY-f = 60, AHY-m = 60, HY = 789; WIWA, AHY-f = 94, AHY-m = 52, HY = 625; YWAR, AHY-f = 64, AHY-m = 108, HY = 788.
[c]Time was measured in hours since sunrise.
[d]Body size was incorporated into models using wing chord.
[e]Warbler abundance at the migration station was estimated for each week using the combined capture rate of individuals from each sex/age class of each species.
[f]Reservoir water level models control for any variation in body mass associated with the week of the migration period, size and class of individuals, and abundance of wood warblers at the migration station by including these terms in the models.

Table 6. Mass change of five species of warblers at the Columbia River Revelstoke Migration Monitoring Station during fall migration expressed as grams/hour and percent of lean body mass/hour.

Species	Mass gain ± SE (grams/hour)[a]	Mass gain (% lean body mass/hour)[b]
American Redstart	0.025 ± 0.012	0.32
Common Yellowthroat	0.057 ± 0.007	0.57
Orange-crowned Warbler	0.051 ± 0.011	0.59
Wilson's Warbler	0.073 ± 0.002	0.98
Yellow Warbler	0.041 ± 0.011	0.45

[a]Mass gain (grams/hour) values presented are effect sizes ± SE for the variable time since sunrise in general linear models examining variation in body mass, and controlling for any effects of year, week of migration, warbler abundance, sex/age class, and body size (see Table 5).

[b]Mass gain expressed as percent lean body mass/hour is calculated using model-estimated body mass at sunrise as an estimate of lean body mass.

by migrants along the Columbia River in British Columbia.

Most warblers captured in our study were HY birds, with capture rates of HY birds about five times greater than those of adults for all five species of warblers. This pattern is consistent with data from other migration stations (Dunn et al. 2006, Hobson et al. 2007), and indicates that capture rates at migration stations will be impacted by conditions on breeding grounds that lead to interannual variation in productivity. The observed differences among species in years with high and low capture rates could be due to differences in productivity that arise because the five species breed in different areas or because events on breeding grounds impact some species and not others.

Riparian habitat in the upper Columbia River Basin apparently provides sufficient resources for migrants during fall migration. Mean rates of mass gain at our migration monitoring station ranged from 0.32% of lean body mass/hour for American Redstarts to 0.98% of lean body mass/hour for Wilson's Warblers. These rates are similar to those reported at 15 other sites across Canada (average mass gain = 0.53%, range = 0.10–0.80%, N = 14 species; Dunn 2002) and well above the threshold levels required to cover overnight energy use and accumulate fuel for migration (estimated as 0.24% and 0.26% for American Redstarts and Wilson's Warblers, respectively; Dunn 2002). Hydroelectric dam

Table 7. Model predictions ± SE from generalized linear models examining variation in the mass (grams) of warblers at the Columbia River-Revelstoke Migration Monitoring Station from 1998 to 2006. Abbreviations and variables are defined in Tables 3 and 5. Sample sizes and significance of effects in models are presented in Table 5.

		Species				
		AMRE	COYE	OCWA	WIWA	YWAR
Temporal and age/sex class model[a]						
Week	1	8.0 ± 0.07	10.3 ± 0.04	8.6 ± 0.04	7.3 ± 0.14	9.0 ± 0.05
	2	7.8 ± 0.04	10.4 ± 0.04	8.5 ± 0.17	7.4 ± 0.09	9.0 ± 0.04
	3	7.8 ± 0.04	10.2 ± 0.04	8.6 ± 0.09	7.4 ± 0.08	9.0 ± 0.04
	4	7.8 ± 0.04	10.0 ± 0.03	8.4 ± 0.06	7.4 ± 0.06	9.0 ± 0.05
	5	8.0 ± 0.05	9.9 ± 0.02	8.5 ± 0.04	7.5 ± 0.04	9.0 ± 0.07
	6	8.1 ± 0.07	10.0 ± 0.02	8.7 ± 0.03	7.5 ± 0.03	9.0 ± 0.08
	7	8.6 ± 0.13	10.0 ± 0.02	8.8 ± 0.04	7.7 ± 0.03	9.5 ± 0.13
	8	8.3 ± 0.25	10.1 ± 0.03	9.0 ± 0.05	7.8 ± 0.05	10.3 ± 0.26
	9		10.2 ± 0.05	9.0 ± 0.07	7.9 ± 0.09	
Class	AHY-f	8.0 ± 0.07	9.9 ± 0.04	8.6 ± 0.07	7.5 ± 0.05	9.2 ± 0.09
	AHY-m	7.9 ± 0.09	10.1 ± 0 04	8.7 ± 0.07	7.6 ± 0.07	9.2 ± 0.06
	HY	7.9 ± 0.02	10.1 ± 0.01	8.7 ± 0.02	7.6 ± 0.02	9.0 ± 0.02
Reservoir operation model[b]						
Year type	Low	8.0 ± 0.03	10.0 ± 0.02	8.7 ± 0.05	7.6 ± 0.04	9.0 ± 0.03
	Intermed	7.9 ± 0.02	10.1 ± 0.02	8.7 ± 0.02	7.5 ± 0.02	8.9 ± 0.03
	High	7.9 ± 0.05	10.1 ± 0.02	8.7 ± 0.03	7.6 ± 0.04	9.2 ± 0.04

[a]Predictions for temporal and age/sex class model control for year and body size effects.

[b]Predictions for reservoir operations control for week, class, and body size effects.

operations influenced water levels in the Arrows Lake Reservoir, but did not affect mass gain in warblers from 1998 to 2006. This may change if the addition of extra turbines at the Revelstoke and Mica Dam upstream of the Arrow Lakes Reservoir, due to be completed in 2010 and 2014, extend the period when the reservoir is at full pool and prolonged flooding adversely impacts vegetation and leads to further loss of willow habitat.

The rate at which migratory songbirds gain mass during stopover might be expected to vary with age if young birds are less efficient foragers (Wunderle 1991) or are excluded from more nutritious food sources by older birds. However, we found no evidence that rates of mass gain varied with age for any warbler species. This may be due to the relatively small number of older birds we captured (13–18% of individuals captured). However, Jones et al. (2002) also found that rates of mass gain of adults and immatures did not differ for most species captured during fall migration at Long Point, Ontario, including American Redstarts, Common Yellowthroats, Wilson's Warblers, and Yellow Warblers. Thus, our results and those of Jones et al. (2002) suggest that the foraging skills of young birds are comparable to those of adults by the time they migrate and that young birds are not disadvantaged, either because there is little competition for food or there is little need to accumulate reserves rapidly during this stage of migration.

We also found no evidence that rates of mass gain varied with the number of warblers at our study site. Previous studies have provided some evidence that competition leads to density-dependent mass gain in migratory songbirds. For example, Kelly et al. (2002) found that mass gain of migratory Wilson's Warblers was negatively related to their abundance at a stopover site in New Mexico, and Moore and Yong (1991) found that most (8 of 9) species passing through Louisiana gained more mass when abundance of migrants was low than when abundance was high. The absence of any detectable effect of age or competition on mass gain in our study suggests that there are sufficient resources in riparian habitat at our study site for migrants to accumulate the reserves needed at this relatively early stage of migration. However, the numbers of migratory warblers did have negative effects on the body mass of American Redstarts, Yellow Warblers, and, perhaps, Common Yellowthroats, suggesting that competition may affect other aspects of stopover behavior, such as settlement decisions, transience, and departure probability (Dierschke and Delingat 2001, Whalen and Watts 2002).

The body mass of warblers captured in our study varied across the season. For most species, body mass increased during the final stages of migration monitoring. Because daily mass gain did not vary seasonally, this pattern may arise because migrants captured later in our study either arrived with more reserves (e.g., Wichmann et al. 2004) or stayed longer and built up more reserves prior to departing. To our knowledge, the latter has not been documented (but see Polak and Szewczyk 2007). Multistate mark-recapture models (e.g., Calvert et al. 2009) could be used to test these alternatives and would further our understanding of seasonal variation in use of stopover sites.

For all five species of warblers in our study, mean body mass was higher in some years than others. However, we found no consistency across species for years associated with the capture of either heavier or lighter birds. Fuel loads can be affected by migratory strategies and weather conditions (e.g., head winds, temperature, and precipitation) that influence energy expenditure prior to arrival, and by local weather conditions that influence departure decisions from stopover sites (Richardson 1990, Schaub et al. 2004, Robson and Barriocanal 2008, Calvert et al. 2009). The former is a more plausible explanation for our results because differences among species in natal origin and weather conditions along different migration routes could lead to species-specific variation in body mass, whereas weather conditions that influence departure decisions would be expected to result in consistent patterns across the five species.

Body mass of two of the five species of wood warblers in our study was negatively related to the average weekly water levels in the Arrow Lakes Reservoir. American Redstarts and Orange-crowned Warblers captured during weeks when the reservoir was at full pool were, on average, 0.2 and 0.1 g lighter than birds captured when water levels were low and did not impact willow habitat in the drawdown zone of the reservoir. Birds may be lighter when captured because water levels influence the settlement decisions of "lean" and "fat" birds with lighter birds being forced to settle at the stopover site, whereas heavier birds continue to migrate in search of better habitat. Fat scores are reported to influence the habitat selection decisions and transience of migratory birds (Tietz and Johnson 2007, Ktitorov et al. 2010). Alternatively, birds may not remain at sites as long when less foraging habitat and fewer resources are available (e.g., Lourenco et al. 2010). Consequently, hydroelectric dam operations that influence reservoir water levels and the amount of riparian habitat at stopover sites may influence the settlement decisions and length of stay of American Redstarts and Orange-crowned Warblers.

In sum, our results indicate that remnant riparian habitat along the Columbia River in British Columbia currently provides warblers with stopover habitat that allows them to gain body mass and fuel southward migration. Hydroelectric dam operations that influenced water levels in the Arrow Lakes Reservoir and the amount of riparian habitat surrounding our study site had no detectable impact on capture rates and daily mass gain of warblers. Higher water levels in the reservoir were, however, associated with reduced body mass at capture for two of the five species studied. Given the potential importance of riparian habitat for migratory songbirds, the level of riparian habitat loss over the last century, and the possibility that future hydroelectric development will lead to further habitat loss, additional studies are needed before concluding that hydroelectric dam operations have no impact on migratory songbirds. Future studies should evaluate how hydroelectric dam operations might affect the stress levels and physiological state of migrants during stopover and their stopover behavior (e.g., transience, departure probabilities, and use of alternative habitat) because these factors may also influence mortality during migration.

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