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Tracing salmon nutrients in riparian food webs: isotopic evidence in a ground-foraging passerine

Katie S. Christie, Morgan D. Hocking, and Thomas E. Reimchen

Abstract: The predictable annual spawning of anadromous salmon (genus *Oncorhynchus* Suckley, 1861) provides an important marine resource subsidy to terrestrial species throughout the North Pacific. Using isotopic ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), we examine pathways of salmon nutrient uptake by a ground-foraging passerine, the winter wren (*Troglodytes troglodytes* (L., 1758)), captured above and below waterfall barriers to salmon migration from two rivers on the central coast of British Columbia. Wren feathers exhibited substantial variation in $\delta^{15}N$ (range = 18.6‰) and $\delta^{13}C$ (range =7.9‰), approximating the isotopic range of invertebrates sampled at our study sites. Mean $\delta^{15}N$ values of feathers and feces representing the fall diet of winter wrens were enriched by 4.8‰ and 8.0‰, respectively, below versus above the waterfall barriers. We observed positive relationships between $\delta^{15}N$ and $\delta^{13}C$ in fall-grown feathers and fecal samples below the falls but not above the falls, and large positive shifts (as high as 14.3‰) in ^{15}N from summer to fall within individual birds. The large isotopic variation observed in this system likely can be explained by the mobility of wrens, isotopic variation in their prey, and individual variation in the consumption of fly larvae from salmon carcasses. Our results identify both direct and indirect pathways by which salmon-derived nutrients are cycled into top-level consumers.

Résumé : La fraie annuelle prévisible des saumons anadromes (le genre *Oncorhynchus* Suckley, 1861) représente un apport marin important de ressources aux espèces terrestres dans toute la région du Pacifique Nord. Les rapports isotopiques d'azote ($\delta^{15}N$) et de carbone ($\delta^{13}C$) nous ont servi à examiner les voies d'introduction des nutriments provenant des saumons chez des passereaux qui se nourrissent au sol, des troglodytes mignons (*Troglodytes troglodytes* (L., 1758)), capturés en amont et en aval de chutes formant des barrières à la migration des saumons dans deux rivières de la côte centrale de la Colombie-Britannique. Les plumes des troglodytes affichent des variations importantes de $\delta^{15}N$ (étendue = 18,6 ‰) et de $\delta^{13}C$ (étendue = 7,9 ‰) qui s'approchent de l'étendue des variations isotopiques des invertébrés échantillonnés sur nos sites d'étude. Les valeurs moyennes de $\delta^{15}N$ des plumes et des fèces représentant le régime alimentaire des troglodytes mignons en automne en aval des chutes se sont enrichies respectivement de 4,8 ‰ et de 8,0 ‰ par comparaison aux valeurs en amont des barrières formées par les chutes. Il existe des relations positives entre $\delta^{15}N$ et $\delta^{13}C$ dans les plumes élaborées à l'automne et dans les fèces en aval, mais non en amont des chutes; il se produit aussi de forts accroissements des valeurs de ^{15}N (pouvant atteindre 14,3 ‰) de l'été à l'automne chez un même oiseau. L'importante variation isotopique observée dans ce système peut vraisemblablement s'expliquer par la mobilité des troglodytes, par la variation isotopique de leurs proies et la variation individuelle de consommation de larves de mouches provenant de carcasses de saumons. Nos résultats identifient à la fois des voies directes et indirectes par lesquelles les nutriments dérivés des saumons sont recyclés vers les consommateurs de niveau supérieur.

[Traduit par la Rédaction]

Introduction

In the Pacific Northwest where streams and forest soils are nutrient-limited, the flow of marine nutrients via spawning salmon (genus *Oncorhynchus* Suckley, 1861) to terrestrial and aquatic systems may be intrinsic to ecosystem functioning (Willson and Halupka 1995; Gende et al. 2002; Zhang et al. 2003). This marine subsidy to terrestrial habitats predicts the occurrence of aggregations of vertebrate predators (Cederholm et al. 2000; Reimchen 2000), while the input of nitrogen and phosphorus can initiate bottom–up ecosystem effects such as increased primary productivity and invertebrate biomass (Wipfli et al. 1998; Helfield and Naiman 2001; Stockner 2003).

Links between salmon and higher trophic levels, such as passerines, in terrestrial systems have only recently been

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recognized. In the fall, passerines have been observed feeding on fly larvae from salmon carcasses from multiple coastal watersheds (Willson and Halupka 1995; Cederholm et al. 2000; Hocking and Reimchen 2006). During the spring, the increased productivity of salmon streams is thought to result in higher breeding densities of passerines (Gende and Willson 2001; Christie and Reimchen 2008). However, the pathways through which passerines obtain and benefit from salmon nutrients have not been documented.

Subsidies of nutrients and prey across habitat boundaries can be measured using stable isotope analysis (e.g., Anderson and Polis 1998), and this has been particularly useful in tracing salmon-derived nutrients into terrestrial ecosystems (Bilby et al. 1996; Ben-David et al. 1998; Hilderbrand et al. 1999). High $\delta^{15}N$ and $\delta^{13}C$ signatures in terrestrial consumers predict a diet of salmon (e.g., Darimont and Reimchen 2002), whereas elevated $\delta^{15}N$ but not $\delta^{13}C$ signatures predict an indirect pathway in which marine nitrogen (but not carbon) is taken up by terrestrial vegetation and soil N pools (Ben-David et al. 1998; Hocking and Reimchen 2002).

In this study, we use stable isotope methods to trace salmon nutrients in the feathers and feces of the winter wren (*Troglodytes troglodytes* (L., 1758)), a representative of higher vertebrate consumers in the terrestrial food web. Winter wrens are generalist insectivores that primarily forage on substrates that include the forest floor, coarse woody debris, and understory vegetation. In the Pacific Northwest, this species is a year-round resident, and during the breeding season, pairs maintain a mean territory size of 1.38 ha. After the breeding period, females and young tend to disperse from the breeding territory (Hejl et al. 2002).

This study builds upon previous isotopic investigations from two salmon-bearing watersheds on the central coast of British Columbia, Canada (Hocking and Reimchen 2002; Mathewson et al. 2003; Wilkinson et al. 2005). These watersheds, supporting between 20 000 and 50 000 spawning salmon annually, have waterfalls 1–2 km from the estuary that prevent farther upstream migration of salmon, and thus delineate the influence of salmon-derived nutrients. We compare the isotopic signatures of winter wrens captured above and below the waterfall barriers and relate their isotopic signatures to those of their potential invertebrate prey (litter invertebrates). We further examine isotopic signatures over time by sampling feathers and feces representing different seasons (summer and fall) and examine dietary shifts within individuals. We predict that the isotopic variability in winter wrens will reflect that of the soil invertebrate prey base, which is known to vary spatially (above and below falls) and in species composition over time (Hocking and Reimchen 2002, 2006).

Materials and methods

Study sites and sampling

This study occurred north of Bella Bella, on the Clatse (52°20′N, 127°50.3′W) and Neekas (52°28′N, 128°8.0′W) rivers, British Columbia. Both rivers have large runs (over 20 000) of chum (*Oncorhynchus keta* (Walbaum, 1792)) and pink (*Oncorhynchus gorbuscha* (Walbaum, 1792)) salmon that spawn from late August until early November. Five to 10 m waterfalls act as complete barriers to upstream migration of salmon 0.9 and 1.7 km from the mouth of the Clatse and Neekas rivers, respectively. Both rivers occur in the Coastal Western Hemlock Biogeoclimatic Zone characterized by small-scale disturbance (such as windfall and debris slides), high annual precipitation, and nutrient-poor soils (Meidinger and Pojar 1991).

We collected invertebrates to represent the isotopic range of prey available to winter wrens. These included Collembola, millipedes, and spiders inhabiting the litter layer, as well as fly larvae collected directly from salmon carcasses. Litter fauna were collected in summer of 2000 (millipedes and spiders) and spring and fall of 2001 (Collembola and spiders) using pitfall traps established in 10 m × 10 m plots located near mist-net stations above and below the waterfalls and within 20 m of the stream. Composite Collembola samples (*Ptenothrix maculosa* (Schött, 1891) (Dicyrtomidae) and *Tomocerus flavescens* Tullberg, 1871 (Tomoceridae)) representing 44–298 individuals were used as the $\delta^{15}N$ and $\delta^{13}C$ isotopic baselines for the litter community on each watershed. *Cybaeus* Koch, 1868 spiders are an apex predator within the litter food chain (Hocking and Reimchen 2002).

We used mist nets to capture winter wrens in September and October of 2001–2002, and from late June through mid-October of 2003. In 2001–2002, three mist nets were used alternatively above and below the falls. In 2003, mist nets were open simultaneously in clusters 200–300 m above and below the falls (7 below, 8 above). These locations were chosen because of their proximity to invertebrate sample plots, and because they were sufficiently distant from the waterfalls to minimize capture of wrens with territories that encompassed both salmon-influenced and noninfluenced areas (mean territory size of a winter wren = 1.38 ha; Hejl et al. 2002). Nets were placed within 50 m of the river and were open only on days without significant rainfall or wind.

Captured wrens were aged as young (hatching year) or adult (after-hatching year) by degree of skull ossification, plumage, and presence of a yellow commissure (gape) (Pyle 1997). Each bird was banded with a USFWS aluminum leg band and two tail feathers were plucked. If the bird was moulting, new body feathers (still partially sheathed) were plucked. If a bird was recaptured, newly replaced tail feathers were sampled. We were aware of the possibility of young birds dispersing from non-salmon natal territories into salmon-influenced areas. To address this, we collected fecal samples, which were likely to represent the more recent diet of wrens in the vicinity of capture in September and October of 2003. Fecal samples were collected when wrens defecated in the hand or capture bag while being processed, or onto a known substrate while under observation.

Stable isotope analysis

Feather and fecal samples were stored with silica gel to maintain dryness. Feathers were rinsed and soaked in a 2:1 chloroform and methanol solution for 24 h to remove lipids and then dried at 60° for at least 24 h. Feathers were then chopped into small (<2 mm) fragments and both vane and rachis were used. A total of 1 mg of feather fragments was loaded into tin capsules. Fecal samples and whole invertebrate specimens were dried at 60 °C for at least 48 h and ground into a fine powder by hand (fecal samples) or

with a Wig-L-Bug grinder (Crescent Dental Co., Chicago, Illinois) (invertebrates). All samples were analyzed by continuous flow – isotope ratio mass spectrometry (CF–IRMS) of nitrogen and carbon using a Robo prep elemental analyzer interfaced with a Europa 20:20 isotope ratio mass spectrometer. Samples were processed at the University of Saskatchewan Stable Isotope Facility, Saskatoon. Isotopic ratios (heavy isotope/light isotope) were expressed in δ notation and reflect deviation in parts per mil (‰) from international standards (PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen). Isotopic ratios were calculated according to $\delta^{15}N$ or $\delta^{13}C$ (‰) = $[R_{sample}/(R_{standard} - 1)] \times 1000$, where R is the ratio of the heavy isotope (^{15}N or ^{13}C) to the light isotope (^{14}N or ^{12}C). Measurement error was approximately ±0.1‰ for ^{13}C and ±0.3‰ for ^{15}N.

Statistical analysis

We used a single fixed factor analysis of variance (ANOVA) (SPSS version 15.0; SPSS Inc., Chicago, Illinois) to test for the effect of location (salmon present below falls, but not above falls) on $\delta^{15}N$ and $\delta^{13}C$ of invertebrate groups, feathers, and fecal samples. For invertebrate groups, a separate analysis was conducted for each group and watershed. For feathers and fecal samples, we pooled data from both watersheds (Clatse or Neekas) and included watershed as a predictor variable in the ANOVAs. Depending on the age and moult status of each bird, feathers could be classified as summer grown (in the case of hatch-year birds prior to their first prebasic moult) or fall grown (all other cases). Summer-grown and fall-grown feathers were analyzed separately.

We assessed the relationship between the two isotopes using linear regression, where $\delta^{13}C$ was used as a predictor of $\delta^{15}N$ for feathers and fecal samples. We also examined seasonal shifts within individual wrens by testing whether isotopic values of feathers grown in the summer differed from those grown in the fall (paired t tests). To account for potential seasonal effects of wren prey, we examined seasonal isotopic variation ($\delta^{15}N$ and $\delta^{13}C$) in *Cybaeus* spiders, apex litter predators, collected in June, August, and September (ANOVA).

Results

Invertebrate groups of Collembola (Clatse: $n = 8$; Neekas: $n = 8$), millipedes (Clatse: $n = 9$; Neekas: $n = 15$), spiders (Clatse: $n = 59$; Neekas: $n = 57$), and fly larvae (Clatse: $n = 4$; Neekas: $n = 24$) collected above and below the waterfall barrier represented a wide isotopic range of prey available to winter wrens. Enrichment of $\delta^{15}N$ but not $\delta^{13}C$ was observed in spiders, millipedes, and Collembola collected below the falls (access to salmon) compared with above the falls (no access to salmon) (ANOVA — $\delta^{15}N$: all $F \geq 47.97$, all df > 4, $P < 0.001$; $\delta^{13}C$: all $F \leq 2.60$, all df > 4, $P \geq 0.13$). Fly larvae had the highest $\delta^{15}N$ and $\delta^{13}C$ signatures of all species owing to their diet of salmon (Table 1, Fig. 1). Spiders, millipedes, and Collembola had higher $\delta^{15}N$ signatures at Neekas River than at Clatse River (Table 1; ANOVA, all $F \geq 12.58$, all df > 4, $P \leq 0.002$) and $\delta^{13}C$ of Collembola, but not other groups, was greater at Neekas River than Clatse River (ANOVA, $F_{[3,12]} = 87.63$, $P < 0.001$). Apex spider predators, *Cybaeus* spp., captured in June, August, and September showed consistent isotope signatures across all seasons (ANOVA — $\delta^{15}N$: $F_{[2,111]} = 0.72$, $P = 0.49$; $\delta^{13}C$: $F_{[2,111]} = 2.66$, $P = 0.07$).

In total, we captured 5 winter wrens in 2001 (Clatse: $n = 3$; Neekas: $n = 2$), 12 wrens in 2002 (Clatse: $n = 5$; Neekas: $n = 7$), and 40 wrens in 2003 (Clatse: $n = 19$; Neekas: $n = 21$) for a total of 57. Six individuals were recaptured, and all but one were recaptured in the same location. This individual was initially captured above the falls, and subsequently (24 days later) recaptured below the falls.

Feathers from winter wrens exhibited substantial variation in $\delta^{15}N$ and $\delta^{13}C$, approximating the range of isotopic values represented by all invertebrate groups sampled (Fig. 1). $\delta^{15}N$ values for wren feathers ranged from –0.8‰ to 17.8‰ at the Clatse River and –0.02‰ to 15.8‰ at the Neekas River, while $\delta^{13}C$ values ranged from –26.0‰ to –18.1‰ at the Clatse River and –25.6‰ to –21.0‰ at the Neekas River. Similar isotopic patterns were observed across the waterfall barrier at both watersheds, where mean $\delta^{15}N$ values of feathers were higher below the falls than above the falls, and mean $\delta^{13}C$ values did not vary substantially over the waterfall barrier (Table 1).

Fall-grown feathers sampled from winter wrens below the falls had significantly higher $\delta^{15}N$ values compared with wrens captured above the falls (mean difference of 4.8‰; ANOVA: $F_{[3,25]} = 5.61$, $P = 0.03$) (Fig. 2*a*). This difference was not observed in summer-grown feathers ($F_{[3,36]} = 0.88$, $P = 0.35$). $\delta^{13}C$ did not differ across the falls for feathers grown in the summer or fall (both $P > 0.18$). We observed a strong positive relationship between $\delta^{15}N$ and $\delta^{13}C$ in fall-grown feathers below the falls (linear regression: $F_{[1,20]} = 12.19$, $P < 0.01$, $r^2 = 0.39$) but not above the falls ($F_{[1,6]} = 0.40$, $P = 0.56$, $r^2 = 0.07$). This relationship was not observed in summer-grown feathers.

Fecal samples from winter wrens collected in the fall showed higher mean $\delta^{15}N$ and $\delta^{13}C$ values (by 8.0‰ and 2.6‰, respectively) below the falls compared with above the falls (ANOVA — $\delta^{15}N$: $F_{[3,22]} = 42.17$, $P < 0.001$; $\delta^{13}C$: $F_{[3,22]} = 14.26$, $P = 0.001$) (Fig. 2*b*). A positive relationship between $\delta^{15}N$ and $\delta^{13}C$ was observed below the falls (linear regression: $F_{[1,15]} = 7.28$, $P = 0.02$, $r^2 = 0.34$) but not above the falls ($F_{[1,8]} = 0.02$, $P = 0.88$, $r^2 = 0.003$). Mean fecal percent C and percent N values were lower and more heterogeneous than those from feather samples (Table 1). To determine whether this heterogeneity was linked to isotopic signatures of feces, we tested for possible relationships between C/N ratios and fecal $\delta^{15}N$ or $\delta^{13}C$. We found no significant relationship between either isotope and fecal C/N ratios ($r^2 < 0.14$, df = 24, $P > 0.05$). C/N ratios and fecal percent N did not differ across the waterfall barrier (Mann Whitney U test: $P > 0.05$). However, fecal percent C was, on average, lower and more variable below the falls compared with above the falls (Mann–Whitney U test: $U = 31.00$, $P = 0.02$, df = 23; Levene's test for equality of variance: $F_{[1,23]} = 8.19$, $P = 0.01$).

Large positive isotopic shifts (as high as 14.3‰) between feathers grown in the summer and fall were observed in birds for which multiple feather generations were sampled (Fig. 3). We observed significant differences in $\delta^{15}N$ but not $\delta^{13}C$ between summer-grown and fall-grown feathers

Table 1. Feather and fecal $\delta^{15}N$, $\delta^{13}C$, percent N, and percent C values of winter wren (*Troglodytes troglodytes*) and invertebrate groups at Clatse and Neekas rivers, British Columbia.

Species or group	River	Tissue	Season	Location	$\delta^{15}N$ (mean ± SE)	$\delta^{13}C$ (mean ± SE)	Percent N (mean ± SE)	Percent C (mean ± SE)	*n*
Winter wren	Clatse	Feather	Summer	Below falls	6.6±1.5	–23.4±0.5	14.2±0.1	47.0±0.4	9
				Above falls	6.1±0.8	–24.1±0.3	14.3±0.1	47.2±0.5	8
			Fall	Below falls	10.0±1.8	–23.0±1.0	14.1±0.3	47.2±0.7	6
				Above falls	5.0±0.9	–24.0±0.3	13.9±0.2	46.2±0.5	5
		Feces	Fall	Below falls	8.8±0.9	–24.9±0.5	10.0±1.5	38.8±1.6	9
				Above falls	1.7±1.9	–27.7±0.7	8.4±0.3	43.4±1.4	3
	Neekas	Feather	Summer	Below falls	5.8±1.1	–23.5±0.9	14.1±0.1	46.8±0.2	16
				Above falls	4.0±0.9	–23.2±0.4	14.2±0.2	47.2±0.4	6
			Fall	Below falls	9.6±1.3	–23.6±0.4	14.1±0.2	47.9±0.5	15
				Above falls	5.2±1.4	–24.7±0.9	13.5±0.4	46.6±0.1	2
		Feces	Fall	Below falls	10.2±1.5	–24.9±0.8	9.3±0.7	41.5±1.1	7
				Above falls	1.6±0.6	–27.3±0.5	11.4±0.6	43.8±0.6	6
Fly larvae	Clatse		Fall	Below falls	14.8±0.2	–19.0±0.2	9.5±0.2	55.9±1.1	4
	Neekas		Fall	Below falls	15.1±0.1	–18.7±0.1	11.6±0.8	51.9±1.6	24
Spiders	Clatse		Spring–Summer–Fall	Below falls	9.6±0.3	–24.9±0.1	13.8±0.1	48.5±0.4	28
				Above falls	5.3±0.2	–24.9±0.1	13.5±0.2	48.2±0.6	31
	Neekas		Spring–Summer–Fall	Below falls	13.3±0.4	–25.1±0.2	13.4±0.2	48.3±0.5	26
				Above falls	5.6±0.2	–25.2±0.1	13.5±0.1	48.0±0.4	31
Millipedes	Clatse		Summer	Below falls	3.9±0.4	–23.5±0.6	6.0±0.2	31.7±1.5	6
				Above falls	1.3±0.2	–22.5±0.5	5.9±0.2	30.2±2.7	3
	Neekas		Summer	Below falls	9.1±0.7	–24.0±0.4	6.0±0.1	32.2±0.6	10
				Above falls	0.5±0.6	–23.8±0.3	5.9±0.3	32.0±0.9	5
Collembola	Clatse		Spring–Fall	Below falls	4.0±0.6	–26.2±0.2	12.6±0.1	45.5±0.1	4
				Above falls	–1.4±0.2	–26.1±0.1	12.2±0.1	45.2±0.3	4
	Neekas		Spring–Fall	Below falls	7.3±0.5	–27.0±0.2	12.1±0.3	46.1±0.6	4
				Above falls	–0.7±0.2	–26.9±0.1	11.4±0.2	46.6±1.0	4

Note: Tissue type, location above or below the waterfalls, and season represented by tissue are indicated.

for individuals captured below the falls (paired *t* test — $\delta^{15}N$: $t_{[1,9]} = -4.98$, $P = 0.001$; $\delta^{13}C$: $t_{[1,9]} = -1.17$, $P = 0.27$). The individual that was initially captured above the falls and later recaptured below the falls showed an increase in feather $\delta^{15}N$ by 5.3‰ and a decrease in $\delta^{13}C$ by 1.0‰. Individual birds for which multiple generations of feathers were sampled above the falls did not appear to undergo such dramatic shifts as those captured below the falls (Fig. 3); however, our sample size ($n = 2$) was small.

Discussion

We observed substantial isotopic variation in the feathers of winter wrens captured from two salmon-bearing watersheds in coastal British Columbia. Other studies of wild birds in a variety of ecosystems show considerably less within-population variation in feather $\delta^{15}N$ (e.g., Thompson et al. 1995; Schmutz and Hobson 1998; Herrera et al. 2003). We suggest that the large isotopic variation observed in winter wrens is due to the isotopic variability of their prey, diet switches to seasonally available fly larvae reared on salmon carcasses, and the ability of wrens to disperse and forage across the gradient of salmon influence.

Despite the mobility of winter wrens, we detected differences in $\delta^{15}N$ of fall-grown feathers and feces of birds separated by only a few hundred metres above and below the waterfall barriers. This pattern of enrichment in $\delta^{15}N$ is mirrored in the litter invertebrates at our study sites, which are thought to acquire marine-derived nitrogen through an indirect pathway of salmon nutrient uptake (Hocking and Reimchen 2002). These watersheds represent a dramatic example of how adjacent food webs can differ substantially in baseline isotopic values, causing subsequent isotopic variability in consumer tissues (Anderson and Polis 1998; Hebert and Wassenaar 2001).

We observed slightly higher $\delta^{15}N$ values in spiders, millipedes, and Collembola captured below the falls at Neekas River compared with Clatse River. This is consistent with previous isotopic studies of plants and soil invertebrates on these watersheds, and can be attributed to the greater salmon biomass in the Neekas River (Hocking and Reimchen 2006). The fact that this pattern was not reflected in the isotopic signatures of winter wrens (ie, no difference was observed between watersheds) is likely due to the combined effects of high isotopic variance and relatively small sample size.

The enrichment in $\delta^{15}N$ of fall-grown feathers but not summer-grown feathers below the falls, in conjunction with large isotopic shifts from summer to fall observed in individual birds, suggests that there is a strong seasonal component to the acquisition of salmon nutrients by winter wrens. Summer-grown feathers of hatch-year birds may have grown at other sites, prior to movement of wrens into salmon-influenced habitats, as exhibited by one individual in our study. Furthermore, salmon-derived nutrients are more directly accessible (in the form of fly larvae hatched from salmon carcasses) to winter wrens in the fall than in the summer.

The seasonal isotopic shifts in $\delta^{15}N$ observed in this study were substantially higher than those recorded for other vertebrates in the wild (e.g., Thompson et al. 1995; Darimont and Reimchen 2002; Cerling et al. 2004) and

Fig. 1. $\delta^{15}N$ and $\delta^{13}C$ signatures in (*a*, *b*) feathers from individual winter wrens (*Troglodytes troglodytes*) and (*c*, *d*) litter invertebrates (mean ± SE) collected from the (*a*, *c*) Clatse and (*b*, *d*) Neekas rivers, British Columbia. Season of growth (feathers) and location above or below the falls are shown. In *c* and *d*, fly larvae were collected from salmon carcasses and represent alternate prey available in fall below the falls.

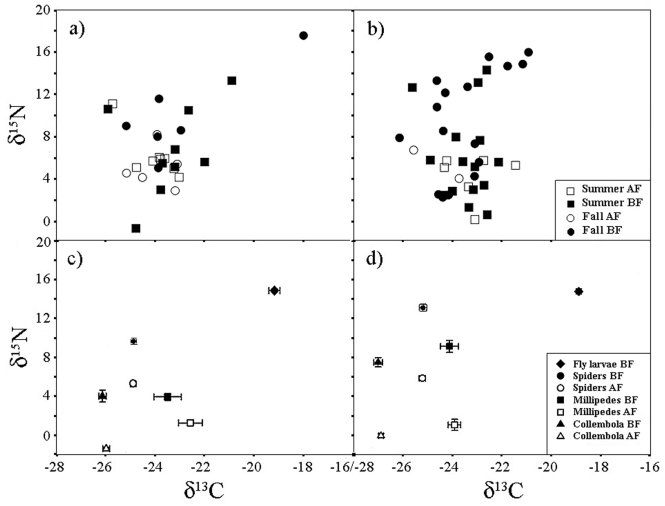
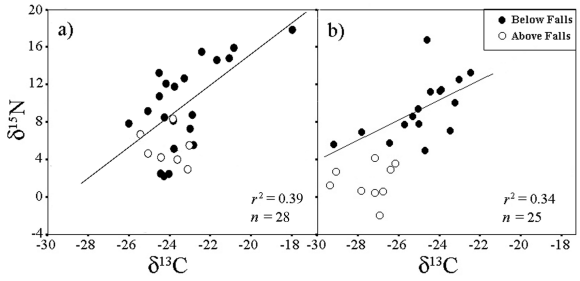


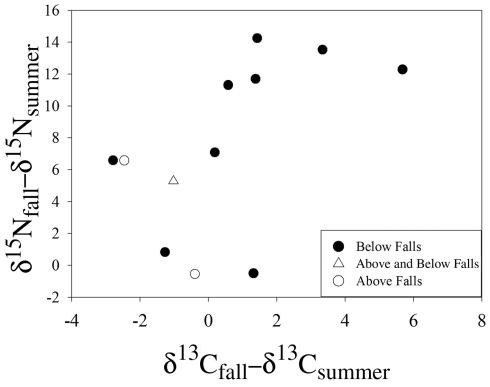
Fig. 2. $\delta^{15}N$ and $\delta^{13}C$ values of (*a*) feathers from winter wrens (*Troglodytes troglodytes*) representing a fall diet and (*b*) feces from winter wrens collected in the fall from above (open symbols) and below (solid symbols) a waterfall barrier to salmon at the Clatse and Neekas rivers, British Columbia, Data are pooled across the two watersheds. Linear regression for fall-grown feathers and feces is significant below the falls (feathers: $F_{[1,20]} = 12.19$, $P < 0.01$, $r^2 = 0.39$; feces: $F_{[1,15]} = 7.28$ $P = 0.02$, $r^2 = 0.34$) but not above the falls (feathers: $F_{[1,6]} = 0.40$, $P = 0.56$, $r^2 = 0.07$; feces: $F_{[1,8]} = 0.02$, $P = 0.88$, $r^2 = 0.003$).



reflect the dietary flexibility of this generalist insectivore. Sample size was small ($n = 2$) for birds collected above the falls for which multiple generations of feathers were obtained, making comparisons between birds caught above and below the falls difficult. However, the large isotopic shifts in feathers of birds captured below the falls were strongly suggestive of a diet influenced by salmon in the fall.

Fecal samples were collected in this study because they represented the diet of birds immediately prior to capture, and as a result were likely to reflect foraging activities in the surrounding area. Isotopic signatures of feces have been used successfully in studies of wild birds (Podlesak et al. 2005; Fujita and Koike 2007; Varo and Amat 2008) and other vertebrates (Sponheimer et al. 2003; Stewart et al. 2003; Codron et al. 2005) to obtain information about the recent diet in a noninvasive manner. There are certain caveats involved in the use of feces in stable isotope studies, such as uncertainties about fractionation associated with the production of nitrogenous waste and the over-representation of coarse, undigested materials in the feces (Sponheimer et al. 2003; Codron et al. 2005; Hwang et al. 2007). In our study, we were not interested in absolute isotope values, but rather in comparing them across localities (above vs. below the falls). We found no significant relationships between $\delta^{15}N$ and $\delta^{13}C$ and fecal C/N ratios despite increased elemental heterogeneity of the fecal samples relative to feather tissues. Our observation of more variable but lower overall percent C below the falls suggests a more diverse, protein-rich diet in the presence of salmon.

Fig. 3. Shift in $\delta^{15}N$ and $\delta^{13}C$ signatures for individual winter wrens (*Troglodytes troglodytes*) collected below a waterfall barrier to salmon at Clatse and Neekas rivers, British Columbia. Shifts were calculated by subtracting isotopic signatures of summer-grown feathers from fall-grown feathers of hatch-year birds. Of a total of 12 birds sampled, 9 were captured below the falls, 2 were captured above the falls, and 1 was initially captured above the falls and recaptured below the falls.



Positive correlations between $\delta^{15}N$ and $\delta^{13}C$ in feces and fall-grown feathers collected below the falls support field observations of winter wrens consuming fly larvae reared from salmon carcasses. Fly larvae on salmon carcasses are highly abundant along the Clatse and Neekas rivers and have been observed as a food source for numerous invertebrate and vertebrate species, including winter wrens (Cederholm et al. 2000; Meehan et al. 2005; Hocking and Reimchen 2006). Such flies have high $\delta^{15}N$ and $\delta^{13}C$ signatures and represent an extension of the marine food chain (4th–5th trophic level) not available to consumers above the falls.

It is likely that winter wrens consumed prey items, such as shrub-associated herbivores and aquatic invertebrates, not sampled in this study (Hejl et al. 2002). It was unrealistic to sample every possible prey item, and we therefore used four groups of common litter invertebrates to exemplify the trophic structure and isotopic range of prey available to winter wrens, within which most terrestrial invertebrate prey groups would be expected to fall. Aquatic invertebrates would likely fall within the range of $\delta^{15}N$ values reported in this study; however, this group may be slightly depleted in ^{13}C relative to terrestrial invertebrates (Chaloner et al. 2002; Hicks et al. 2005).

Previous studies of salmon–bird interactions throughout

the North Pacific have highlighted the importance of salmon (live adults, juveniles, and carcasses) to the life histories of over 100 bird species (Willson and Halupka 1995; Cederholm et al. 2000; Christie and Reimchen 2005). Watersheds supporting salmon are characterized by high densities of carcass-consuming insects in the stream itself and in the surrounding forest (Wipfli et al. 1998; Hocking and Reimchen 2006), and data indicates that the breeding density of passerines is higher along salmon streams than non-salmon-bearing streams and reaches (Gende and Willson 2001; Christie and Reimchen 2008). The annual spawning events of salmon in the North Pacific constitute a large-scale process intrinsic to the terrestrial ecology of this region, and the consequences of widespread declines in salmon populations over the past century (Gresh et al. 2000) are poorly understood and may be substantial.

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