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Carry-over effects of winter habitat vary with age and sex in yellow warblers *Setophaga petechia*

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We use stable isotope data to investigate the role of winter habitat use in altering the breeding phenology of yellow warblers *Setophaga petechia*. We first confirm that $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures vary with winter habitat use in this species. We then examine the relationship between winter habitat use, breeding phenology and productivity within four age-sex-classes, since life history theory would predict that carry-over effects should vary with age and gender. The $\delta^{13}C$ signatures of yellow warblers using riparian habitats over winter were more depleted than the signatures of those using agricultural or scrub habitat. Individuals on the Pacific coast of Mexico were also more $\delta^{15}N$ enriched than those on the southern Gulf of Mexico. $\delta^{13}C$ and $\delta^{15}N$ signatures were only correlated with earlier clutch initiation and subsequent higher productivity in first-breeding-season females. We estimate that shifts in $\delta^{13}C$ equivalent to a shift from scrub to riparian winter habitat would be associated with the production of 0.8 more fledglings by yearling females. Pre-breeding events that influence the timing of breeding could also influence the reproductive performance of older males and females, but we found little evidence that winter habitat use influenced breeding season phenology in these birds.

Carry-over effects are defined as events and/or processes that occur in one period of the annual cycle and affect an individual's fitness in a subsequent period due to the individual making the transition between periods in a different state (Harrison et al. 2011). Carry-over effects in migratory birds, particularly those driven by winter habitat use and affecting subsequent breeding productivity, have received considerable attention over the past decade (Runge and Marra 2005, Webster and Marra 2005, Norris and Marra 2007). To date, such effects have been documented in four migratory bird species and indicated in a fifth: black-tailed godwits *Limosa limosa islandica* (Gill et al. 2001, Gunnarsson et al. 2005, 2006) and barn swallows *Hirundo rustica* (Saino et al. 2004) from populations breeding in Europe, and American redstarts *Setophaga ruticilla* (Marra et al. 1998, Norris et al. 2004, Reudink et al. 2009, Tonra et al. 2011), Kirkland's warblers *Setophaga kirtlandii* (Rockwell et al. 2012), and potentially black-throated blue warblers *Setophaga caerulescens* (Bearhop et al. 2004) from populations breeding in eastern North America. These studies indicate that loss, degradation, or climate-driven variation in the quality of winter habitat could influence migratory populations beyond simply impacting over-winter survival. However, few of these studies included age as a factor in their models: three limited their data to older individuals (Norris et al. 2004, Reudink et al. 2009, Tonra et al. 2011) and five combined age-classes in their analysis (Marra et al. 1998, Gill et al. 2001, Norris et al. 2004, Gunnarsson et al. 2005, 2006).

Life history theory would suggest that the strength of carry-over effects should vary with both age- and sex-class. This is because the ultimate effect of state on an individual's seasonal fitness will differ depending on the costs and constraints faced by that individual (as seen in staging brent geese *Branta bernicla bernicla*; Ebbinge and Spaans 1995). As different age- and sex-classes are likely to vary predictably in the costs and constraints they face (Brown and Roth 2002), it follows that the presence and magnitude of carry-over effects may also vary predictably between classes within a population.

Habitat-driven carry-over effects act through non-fatal differences in the physical condition of individuals. Such differences may have a direct impact on fitness or they may result in variance in biologically relevant events such as onset of migration, the date at which individuals arrive on the breeding grounds and establish a territory, the timing of breeding, and/or the timing of moult. In the latter case, it is the variance in these events that ultimately impact fitness and can be considered the mechanism through which carry-over effects act. In this paper we use the term 'time-mediated' carry-over effect, to distinguish this mechanism from where physical condition directly impacts fitness.

Theoretically, time-mediated carry-over effects resulting from winter habitat use should be more evident in males than in females. The timing of arrival on the breeding grounds typically has a stronger impact on male breeding success: arrival-date-dependent changes in within-pair and extra-pair paternity, polygyny, and greater odds of failing to acquire a territory or mate (and any reproductive success) mean that males may experience a greater range in productivity than females (Lozano et al. 1996, Marra and Holmes 1997, Hasselquist 1998, Langefors et al. 1998, Reudink et al. 2009). In contrast, females are likely to experience less dramatic fitness declines with later arrival dates, driven by decreasing territory and mate quality, mate-sharing, and later clutch initiation dates (Alatalo et al. 1986, Bensch and Hasselquist 1992, Rowe et al. 1994, Brown and Roth 2002, Smith and Moore 2005, Huk and Winkel 2006). Additionally, if female migration is influenced by other factors under stronger selection (such as improving body condition at stop-over sites prior to arrival (Lavee et al. 1991, Yong et al. 1998)), winter-habitat quality may show no relationship to arrival date. Empirical data offers support for this concept: winter habitat quality affected male but not female arrival dates in both American redstarts (Marra et al. 1998, Norris et al. 2004), and black-tailed godwits (Gunnarsson et al. 2006).

Time-mediated carry-over effects may also be more evident in older birds for several reasons. First, familiarity with breeding sites may allow early-arriving, experienced males to select high-quality territories before leaf emergence; lack of prior knowledge may reduce the advantages of early arrival for yearling males (Lozano et al. 1996). Secondly, older individuals may reduce or forgo reproductive investment late in the breeding season in favor of improving the odds of over-winter survival and future reproduction (Brown and Roth 2002). This behavior should produce a strong negative relationship between clutch initiation date and fledge number. Yearling birds, with poorer over-winter survival, may continue to invest in current reproduction and thus show a weaker negative relationship between clutch initiation date and fledge number (Brown and Roth 2002). Finally, younger, inexperienced birds generally have lower reproductive success than older individuals (reviewed by Forslund and Pärt 1995, Fowler 1995) and poor overall performance may simply overwhelm carry-over effects.

It is also possible that greater experience enables older birds to compensate for some of the negative effects of late arrival. For example, late-arriving older females may be able to initiate and complete nest-building more rapidly than late-arriving yearling birds. Such compensation would result in weaker carry-over effects for older birds and could be differentiated from other age differences by weaker effect-slopes for older birds for events occurring after arrival.

Understanding whether the strength of carry-over effects vary among age- and sex-classes is necessary for accurate population modeling. For example, breeding populations of many migratory songbirds contain a large proportion of yearling individuals (e.g. *Setophaga caerulescens*: 38% of males (Graves 1997); *Seiurus aurocapilla*: 39% of males (Porneluzi and Faaborg 1999); *Hylocichla mustelina*: 48% of males and 54% of females (Brown and Roth 2002)). These individuals tend not to be evenly distributed throughout the species range (Graves 1997, Rohwer 2004). Differences in carry-over effect strength between age classes could therefore create regional variation in how a species responds to shifts in winter habitat quality.

In this study we examine whether the quality of winter habitat used by yellow warblers in Mexico/Central America, influences their breeding performance in western Canada and whether the strength of time-mediated carry-over effects varies between sex- and age-classes. Specifically we ask whether winter habitat type, measured indirectly through $\delta^{13}C$ and $\delta^{15}N$ isotope ratios in tissue samples, influences when males establish territories, when females initiate clutches, and whether the timing of these events impact breeding performance. We expect the relationship between breeding season phenology and performance to be negative: late territory establishment and clutch initiation will result in fewer fledged young. We predict that the strength of time-mediated carry-over will vary with age and sex; specifically, that 1) both winter habitat to territory establishment/territory arrival date and habitat to total productivity effects will be stronger in males, and that 2) carry-over effects will be weaker in yearling individuals.

Methods

Study species and location

Yellow warblers are small, insectivorous, nearctic–neotropical migrants that commonly breed in wet deciduous and riparian habitat. Their breeding range covers the majority of the North American continent, and extends as far north as the arctic tree-line (Lowther et al. 1999). Recent genetic and isotopic work suggest that eastern and western populations undergo parallel migration with western populations wintering in Mexico and Central America and eastern populations wintering in Central and South America (Boulet et al. 2006).

Yellow warblers are found in a diversity of natural winter habitats ranging from mangrove, swamp and riparian forests to dry coastal scrub and are also found in a variety of human modified habitats such as pasture, sun/semi-shade coffee plantations, and other cropland (Binford 1989, Greenberg et al. 1996, Garrett and Dunn 1997). The species undergoes a pre-alternate moult prior to spring migration, replacing a variable number of greater covert, body, and crown feathers (Pyle 1997, Quinlan and Green 2010). As yellow warblers are territorial and exhibit winter site fidelity (Morton 1976, Greenberg and Ortiz 1994, Greenberg and Salewski 2005) these feathers are expected to incorporate local isotopic signatures that reflect habitat use (Hobson 1999).

We have studied a banded population of yellow warblers near Revelstoke, British Columbia (50.97°N, 118.20°W) since 2004. Birds are monitored at three, 30–39 ha study plots in riparian habitat bordering the northern section of the Upper Arrow Lakes Reservoir (elevation 435–441 m). These sites consist of seasonally flooded grassland, grading into isolated willow thickets (*Salix* sp.) and ultimately mature black cottonwood *Populus trichocarpa* forest at elevations above the high-water level ($>$ 438 m). The average breeding density of yellow warblers within the study sites is 0.7 pairs ha^{-1}. In the years encompassed by this study, yearling (first-breeding season or 'SY') females accounted for 43.8% of the breeding females at our study sites (annual range 25–57%, $n = 5$ yr) and yearling (SY) males accounted for 30.0% of the breeding males (annual range 13–48%, n = 5 yr).

Monitoring and breeding

Study sites were monitored from early-May until late-July. Territory establishment dates were determined during surveys of the three study plots conducted every 1–2 d. Males were easily detected and captured, as they would begin to sing once on territory and were highly aggressive toward song-playback. Males of both age-classes were typically caught within three days of their appearance using targeted mist-netting. Females were more difficult to detect and capture as they were less conspicuous and less responsive to playback. Females were either caught with their mates or later in the season by placing mist-nets across flight paths used during nest-building, incubation, or while provisioning young. Upon capture, all previously unmarked individuals were fitted with a Canadian Wildlife Service-issued aluminum band and a unique combination of three colour bands (AC Hughes, UK).

Pairs were monitored from early May to late July in 2005–2006, and 2008–2010 in order to determine the onset of breeding and the fate of all nesting attempts. Only pairs that initiated clutches were included in the data that were analysed. Nests were located through close observation of females during nest building and checked every 3 d to determine clutch initiation dates, clutch size, brood size and fledging success. Clutch initiation date was defined as the laying date of the first egg in a female's first nesting attempt of the season. Nestlings were banded seven days after hatching. We assumed that all nestlings present on day 7 successfully fledged unless signs of predation were found in or around the nest after fledging. Fledging was confirmed, in most cases, by observing parents feeding or defending fledglings. Annual productivity for an individual bird was defined as the number of fledglings produced over all nesting attempts. Although rare, some males (3.9%, 7/178 males over 6 yr) obtained two social mates, and it was possible for their seasonal productivity to be higher than that of females.

Sexing and aging

Birds were sexed using plumage (brightness/degree of rufous streaking), behaviour and breeding characteristics (brood patch/cloacal protuberance). Birds were classified as yearling or older birds based on plumage characteristics. Yearling (SY) birds have narrow, tapered primary coverts, tapered retrices with less yellow colouration on the inner webs of the outer tail, and worn prebasic plumage; older (ASY) birds have broad, truncate primary coverts with narrow yellow-olive edging, and truncate retrices with more extensive yellow colouration on the inner webs (Pyle 1997).

Feather samples and stable isotope analysis

We collected three new inner greater covert feathers from all individuals captured on the breeding grounds in 2008–2010. These feathers are easily identifiable because of their brighter pigmentation and lack of wear and carry isotopic signatures from habitat used during pre-alternate molt prior to spring migration (Pyle 1997, Quinlan and Green 2010).

Feathers were washed in 2:1 chloroform:methanol solution for 24 h, drained, and then air-dried in a fume hood for an additional 24 h to remove excess solvent. One mg (± 0.2) of tissue was placed in 9×5 mm smooth-walled tin capsules (Elemental Microanalysis, UK). Tissue samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, UK) at the Univ. of California Davis Stable Isotope Facility in California, USA. Delta values are expressed relative to international standards: V-PDB (Vienna PeeDee Belemnite) for carbon and air for nitrogen; estimated measurement precision was 0.2‰ for δ^{13}C and 0.3‰ for δ^{15}N.

Winter habitat use and δ^{13}C and δ^{15}N

In February and March 2011, we took tissue samples (n = 89) from territorial yellow warblers wintering on the Pacific slope (Chamela, Jalisco; 19.52°N, 105.08°W), and the southern Gulf coast (Los Tuxtlas,Veracruz; 18.57°N, 95.05°W) of Mexico. As birds had not undergone pre-alternate moult we collected red blood cell (RBC) samples to obtain local habitat signatures. Samples were collected from replicate habitat-types across the range of habitat used to determine associated δ^{13}C and δ^{15}N signatures. Within each habitat-replicate we collected 30 µl of blood from the brachial vein of 7–10 birds captured using targeted mist-netting. Blood was held in a hepranized microcapillary tube and cooled on ice for a maximum of 5 1/2 h (average of 3 h) before being spun down for 5 min at 11 000 rpm in a ZIPocrit centrifuge (LW Scientific, USA). Red blood cells were separated and frozen. Once in the lab (Burnaby, Canada) samples were thawed, transferred to eppendorf tubes and placed in a drying oven at 60°C for 3 d. Dried RBCs then weighed and analyzed in the same fashion as feather tissue described in the preceding section.

δ^{13}C patterns are largely driven by plant photosynthetic pathways that differ with water availability (Hobson 2005). Use of cooler, mesic winter habitats is expected to result in depleted δ^{13}C signatures. δ^{15}N in terrestrial animals can show complex variation related the trophic level of dominant prey items and to local environmental factors (e.g. marine inputs, waste, cultivation, and artificial fertilizer) (Kelly 2000, Amundson et al. 2003). However, δ^{15}N also varies more predictably with factors such as climate, temperature, and water and/or nutritional stress (van der Merwe et al. 1990, Hobson et al. 1993, Cormie and Schwarcz 1996, Kelly 2000, Amundson et al. 2003) and enriched δ^{15}N may suggest xeric and/or poor habitats.

Mesic (δ^{13}C depleted) habitats have been shown to be better over-wintering sites for American redstarts (Studds and Marra 2005), Cape May warblers *Setophaga tigrina* (Latta and Faaborg 2002), and northern waterthrushes *Parkesia noveboracensis* (Smith et al. 2010, 2011). Such habitat has greater insect biomass than drier habitat (Studds and Marra 2005, Smith et al. 2010, 2011), resulting in less mass-loss and higher muscle mass for warblers during the dry season (Marra and Holberton 1998, Latta and Faaborg 2002, Smith et al. 2010), earlier fat deposition prior to spring migration (Smith et al. 2010) and earlier spring migration dates (Marra et al. 1998). Mesic riparian habitats in Chiapas, and Jalisco, Mexico contain a greater proportion of older male yellow

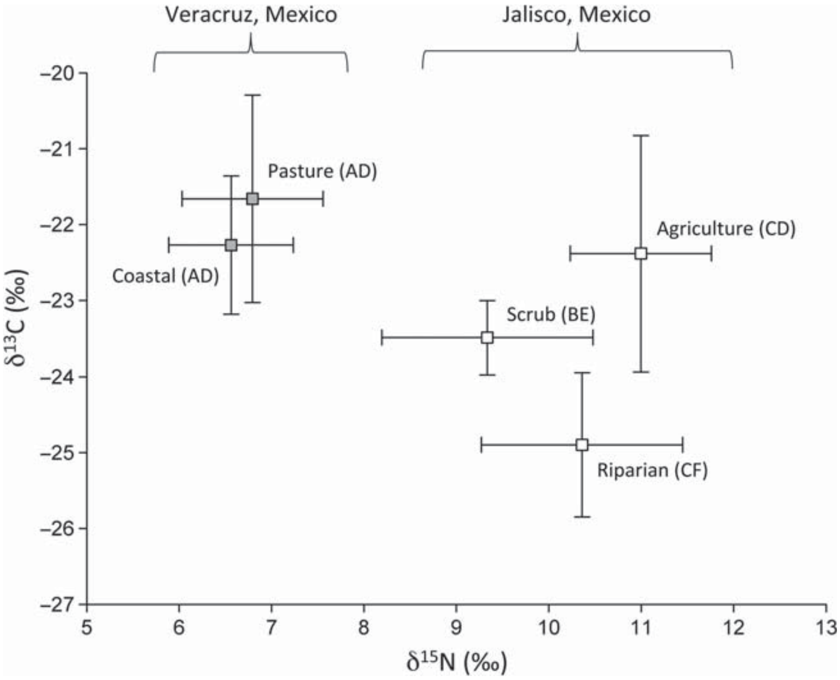

Figure 1. Biplot of the mean (± SD) $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) values of red blood cells from yellow warblers over-wintering in different habitat-types on the southern Gulf coast (Veracruz) and the Pacific slope (Jalisco) of Mexico. Bracketed letters indicate signature overlap: birds from habitats with shared letters were not significantly different from each other in terms of tissue $\delta^{15}N$ (A–C) and/or $\delta^{13}C$ (D–F).

warblers than drier habitat-types, suggesting that riparian habitat is of higher quality (Greenberg et al. 1997, Drake unpubl.). We therefore expected that depleted $\delta^{13}C$ would be associated with earlier territory establishment and clutch initiation in our breeding population (Marra et al. 1998, Norris et al. 2004). We predicted that yellow warblers from poor wintering habitat might have enriched $\delta^{15}N$ signatures if the use of such habitat results in nutritional deficiencies by the end of the wintering period (Hobson et al. 1993). If poor habitats are also dry habitats, then feather samples should be further $\delta^{15}N$ enriched and we would predict high $\delta^{15}N$ values to be associated with high $\delta^{13}C$ values and later territory establishment and clutch initiation dates.

Data analysis

We first assessed whether $\delta^{15}N$ and $\delta^{13}C$ signatures in blood samples collected from birds in Mexico differed across winter habitat-types using analysis of variance and Tukey–Kramer HSD post-hoc tests for each element (Fig. 1). We then evaluated whether $\delta^{13}C$ or $\delta^{15}N$ of winter-grown feathers collected from birds in Revelstoke varied by sex or age-within-sex-classes (Table 1). Revelstoke signatures were non-normally distributed and we therefore used Wilcoxon tests for comparisons between classes. We subsequently used general linear models to evaluate whether winter habitat use influences the territory establishment dates, onset of breeding, and productivity of male and female yellow warblers within different age classes.

The proposed pathways for carry-over effects in male and female warblers are illustrated in Fig. 2. For males we hypothesized that winter habitat could influence territory establishment dates, because occupation of high quality habitat would allow individuals to initiate spring migration earlier and/or in better condition, allowing them to arrive on the breeding grounds earlier. We also tested whether winter habitat use could directly affect clutch initiation, based on the hypothesis that males in high quality habitat might have greater access to resources during winter moult and birds with superior plumage might acquire a mate more rapidly (Studd and Robertson 1985a, b). We used a simpler pathway for females because female arrivals on territories were more difficult to detect than males and later capture and banding made female identity prior to clutch initiation less certain (Fig. 2). Since the female model connects winter habitat use directly to clutch initiation, it may incorporate

Table 1. Summary of stable isotope signatures (n, mean ± SD and range) from winter-grown feathers collected from yellow warblers breeding in Revelstoke, British Columbia. Yearling individuals are in their first breeding season; older birds are at least 2 yr old.

		$\delta^{13}C$ (‰)					$\delta^{15}N$ (‰)				
Age-sex class	n	min	Q1	med	Q3	max	min	Q1	med	Q3	max
Yearling females	42	−24.6	−22.3	−21.5	−20.9	−18.1	5.1	7.6	8.2	9.6	13.3
Older females	41	−23.6	−22.3	−21.7	−21.1	−18.8	5.3	7.6	8.4	9.6	11.4
Yearling males	21	−23.7	−22.5	−21.8	−21.1	−17.4	6.4	7.2	8.5	10.9	12.5
Older males	64	−24.8	−22.3	−21.5	−21.0	−16.8	5.2	7.6	8.9	10.2	15.5
Pooled	168	−24.8	−22.3	−21.6	−21.0	−16.9	5.1	7.6	8.5	9.9	15.5

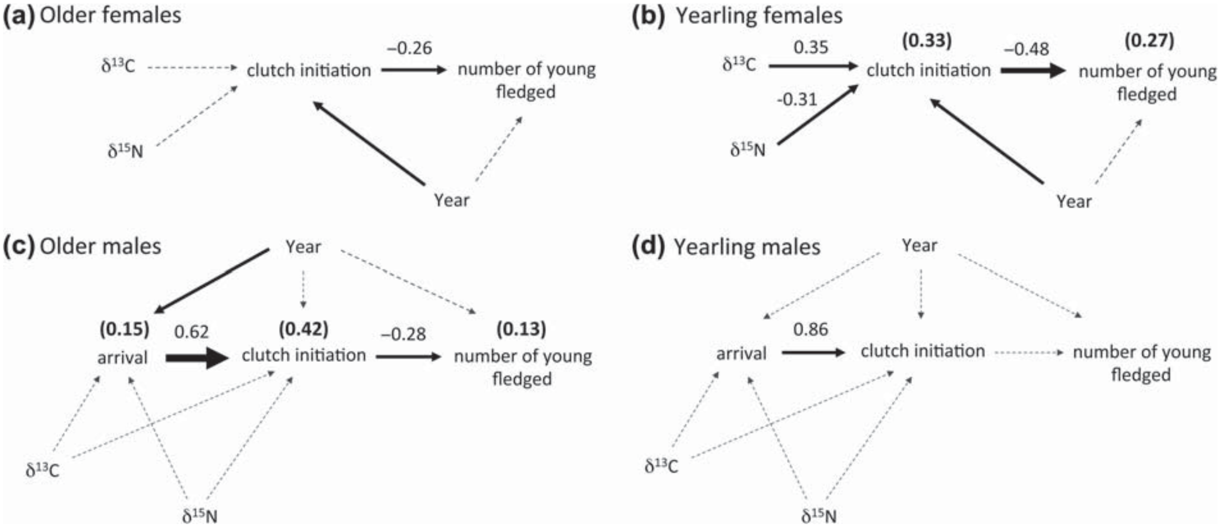

Figure 2. Model pathways for yellow warbler males and females by age class. Black solid lines indicate significant relationships between variables (thickest line $p < 0.0001$, mid-thickness $p < 0.001$, thin line $p < 0.05$). Grey solid lines indicate suggested relationships ($p < 0.1$); dashed lines indicate no statistically-detectable relationship between variables. Standardized beta coefficients for significant continuous variables are shown above each arrow. Whole-model r^2 values are reported in parentheses above the dependent variables for significant relationships only.

winter-habitat effects on bird condition in addition to those acting through arrival-on-territory date (Discussion).

Data for yearling and older birds were analyzed separately because age influences all aspects of breeding (Results). Year was included as a potential explanatory variable in all models. Sample sizes for the different steps in the proposed pathways differ as tissue samples were not obtained from all individuals in all years.

Where winter habitat quality carried-over and impacted breeding productivity, we used standardized partial regression coefficients (βs) for each step in the pathway in order to calculate the total effect of $\delta^{13}C$ and $\delta^{15}N$ on fledgling number. We then used the shift in mean $\delta^{13}C$ and $\delta^{15}N$ values between wintering habitat-types with the greatest isotopic difference to estimate the expected total shift in offspring number associated with variation in winter habitat use (Bart and Earnst 1999, Norris et al. 2004).

Results

Age differences in phenology and breeding performance

We collected data on male territory establishment dates, female nest initiation dates and annual productivity for 132 males and 121 females over five years (2005–2006; 2008–2010). Older males established territories an average of 8.1 d before yearling males (partial $F_{1,131} = 31.4$, $p < 0.0001$) and their social mates initiated nesting an average 8.4 d before those of yearling males (partial $F_{1,123} = 39.4$, $p < 0.001$). Older males fledged twice as many young as yearling males (2.4 ± 1.9 vs 1.1 ± 1.6 (partial $F_{1,129} = 11.7$, $p < 0.001$)). Older females initiated nests an average of 5.3 d before yearling females (partial $F_{1,115} = 18.0$, $p < 0.001$) and produced significantly more fledglings (2.4 ± 0.22 vs 1.4 ± 0.27 (partial $F_{1,120} = 7.7$, $p = 0.006$)).

Winter habitat use and $\delta^{13}C$ and $\delta^{15}N$

Yellow warblers on the Pacific slope of Mexico wintered in riparian forest corridors, agricultural field margins and coastal scrub habitat. Those on the southern Gulf coast wintered within cattle pasture and along coastal habitat. Red blood cell $\delta^{13}C$ and $\delta^{15}N$ signatures differed significantly among these habitats ($\delta^{13}C$: $F_{4,78} = 22.16$, $p < 0.0001$; $\delta^{15}N$: $F_{4,78} = 81.49$, $p < 0.0001$, Fig. 1). Tukey HSD tests showed that $\delta^{15}N$ signatures were significantly more depleted on the southern Gulf coast than on the Pacific slope ($p < 0.0001$). $\delta^{13}C$ signatures on the Pacific slope varied with habitat use ($p = 0.05$), being most depleted in riparian habitats. $\delta^{13}C$ signatures in pasture and coastal habitat on the Gulf of Mexico did not differ ($p = 0.52$).

Within our Revelstoke breeding population, $\delta^{13}C$ and $\delta^{15}N$ signatures were only weakly correlated ($r = 0.13$, $p = 0.09$, $n = 171$) indicating that these signatures were reflecting different aspects of wintering habitat use. $\delta^{13}C$ and $\delta^{15}N$ values did not differ significantly between sex- and age-within-sex-classes (Table 1; $\delta^{13}C$: gender, $Z = 0.09$, $p = 0.93$; age-class females, $Z = -0.36$, $p = 0.72$; age-class males, $Z = -0.84$, $p = 0.40$; $\delta^{15}N$: gender, $Z = -1.51$, $p = 0.13$; age-class females, $Z = 0.30$, $p = 0.76$; age-class males, $Z = -0.05$, $p = 0.96$).

Carry-over effects

Winter habitat use only had a carry-over effect on the productivity of yearling females (Table 2, Fig. 2). More depleted $\delta^{13}C$ signatures and more enriched $\delta^{15}N$ signatures were correlated with earlier clutch initiation dates in this group (Table 2, Fig. 3). Earlier clutch initiation dates were, in turn, associated with the production of more fledglings by yearling females (Fig. 2). Using the isotopic values obtained from wintering birds of known habitat origin in Mexico, this result suggests that birds originating in mesic habitat

Table 2. Results of general linear model analyses for each stage of the proposed pathway from winter habitat use to fledgling productivity. Relationships for yearling and older yellow warbler are reported separately for (A) males and (B) females. Standardized beta coefficients for significant continuous variables are reported in Fig. 2.

	Yearling (SY)					Older (ASY)				
	r^2	n	p	F ratio	Prob > F	r^2	n	p	F ratio	Prob > F
(A) Males										
Arrival	0.18	19	0.55			0.15	63	0.05		
Year				0.12	0.89				4.70	0.01
$\delta^{13}C$				0.00	0.97				1.82	0.18
$\delta^{15}N$				2.28	0.15				0.42	0.52
Clutch initiation	0.61	15	0.09			0.42	58	< 0.0001		
Year				0.18	0.83				1.86	0.17
Arrival				13.23	0.005				29.21	< 0.0001
$\delta^{13}C$				0.24	0.64				2.48	0.79
$\delta^{15}N$				1.02	0.34				0.07	0.12
Fledge number	0.14	39	0.55			0.13	114	0.02		
Year				0.84	0.53				1.76	0.13
Clutch initiation				1.09	0.3				8.89	0.004
(B) Female										
Clutch initiation	0.33	38	0.009			0.10	39	0.47		
Year				3.37	0.05				1.54	0.23
$\delta^{13}C$				5.45	0.03				0.52	0.48
$\delta^{15}N$				4.35	0.04				0.37	0.55
Fledge number	0.27	61	0.007			0.13	84	0.08		
Year				1.48	0.21				1.71	0.14
Clutch initiation				14.93	< 0.001				5.65	0.02

within a dry/seasonal climate region performed better than those with $\delta^{13}C$ and $\delta^{15}N$ signatures consistent with wetter climate regions.

The total effect of $\delta^{13}C$ on the productivity of yearling females was -0.17. Thus, a shift in one standard deviation of $\delta^{13}C$ would be expected to result in a shift of (-0.17) standard deviations in fledglings. Using our wintering isotope data, our model would predict that yearling females occupying habitat at the mesic end of the $\delta^{13}C$ gradient (i.e. $\delta^{13}C$ depleted Pacific riparian forest) would be able to produce 0.8 more fledglings the following summer than counterparts in $\delta^{13}C$ enriched coastal or pasture habitat in the southern Gulf of Mexico. Similarly, the total effect of $\delta^{15}N$ on the productivity of yearling females was 0.15. Our model would thus predict that females with $\delta^{15}N$ signatures equivalent to the average of our Pacific slope site would produce 0.6 more fledglings than birds with signatures equivalent to the southern Gulf coast.

Although we found no evidence of winter habitat effects in our other age-sex classes, early territory establishment was associated with early onset of reproduction and greater annual productivity in older males (Table 2). Similarly, early onset of reproduction in older females was associated with greater annual productivity (Table 2). Although territory establishment dates were related to the onset of reproduction in yearling males, clutch initiation date had no impact on reproductive success (Table 2, Fig. 2).

Annual differences ('year') had significant direct effects on older male territory establishment dates and on yearling female clutch initiation dates (Fig. 2).

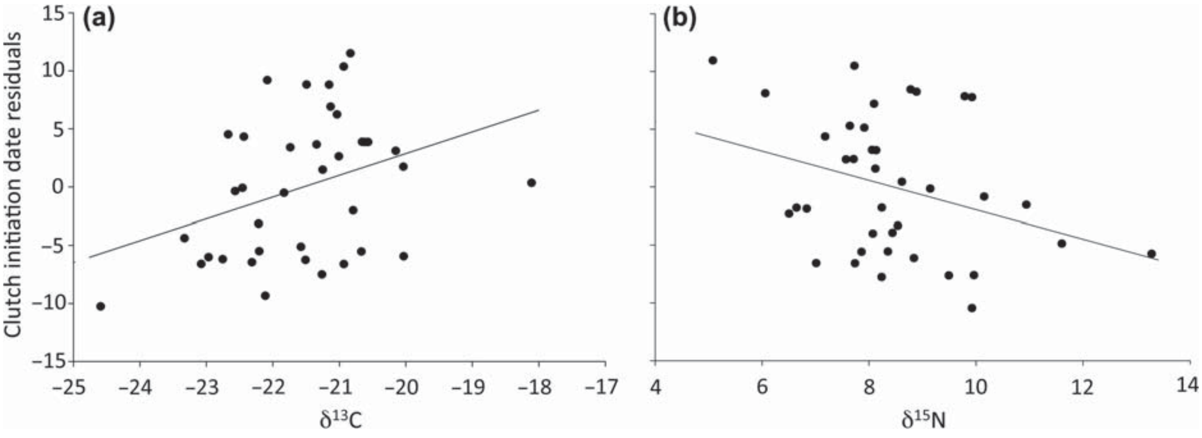

Figure 3. Relationship between winter isotope signatures and clutch initiation date in yearling female yellow warblers. Initiation dates are presented as residuals from a model controlling for year and $\delta^{15}N$ (a) or for year and $\delta^{13}C$ (b).

Discussion

Carry-over effects have generated considerable attention because of their ability to explain some of the observed variation in individual fitness within populations and in population processes between years (Webster and Marra 2005). Our study offers additional support for the concept that events occurring in one season can affect important biological processes in a subsequent season. We expand upon previous work (Marra et al. 1998, Gill et al. 2001, Norris et al. 2004, Gunnarsson et al. 2005, 2006, Reudink et al. 2009, Tonra et al. 2011) by investigating age- and sex-class effects. We predicted that males would experience stronger time-mediated carry-over effects due to the importance of arrival date with regards to territory acquisition and the greater range in productivity experienced by this sex on the breeding grounds. Similarly, we predicted that age-dependent differences in experience and performance would make time-mediated carry-over effects weaker in yearling birds. Contrary to our predictions, there was no evidence that winter habitat, inferred using $\delta^{13}C$ and $\delta^{15}N$, influenced the territory establishment date of yellow warbler males or the clutch initiation dates of their social mate. This differs from research on American redstarts (Marra et al. 1998, Norris et al. 2004) but is consistent with other yellow warbler work in Ohio that found no relationship between male winter $\delta^{13}C$ signatures and the clutch initiation dates of their social mates (Lindsay 2008).

Time-mediated carry-over effects did act on yearling female yellow warblers. For this age-sex class, depleted $\delta^{13}C$ and enriched $\delta^{15}N$ wintering signatures were associated with earlier clutch initiation dates and higher subsequent productivity. Our $\delta^{13}C$ results indicate the yearling females originating from mesic winter habitats have higher fitness than those with signatures suggesting drier habitat use. This finding is consistent with previous migration phenology and carry-over work (Marra et al. 1998, Norris et al. 2004, Smith et al. 2010 (departure delay inferred from body condition)).

The relationship between breeding season phenology and wintering $\delta^{15}N$ signatures has not been previously investigated in landbirds. Our blood $\delta^{15}N$ signatures of yellow warblers sampled on the wintering grounds align with predicted soil $\delta^{15}N$ enrichment patterns produced by regional temperature and precipitation gradients (Handley et al. 1999, Amundson et al. 2003). Coastal Jalisco falls within the As/Aw climate zones (Köppen-Geiger climate designation; Kottek et al. 2006) where high temperatures and low rainfall would produce $\delta^{15}N$ enriched soil. Southern Veracruz (Am climate zone) receives 3 times more precipitation and its soil $\delta^{15}N$ should be correspondingly depleted. As/Aw climate zones cover the northern portion of the yellow warbler wintering range and follow the Pacific slope of Central America as far south as Panama. Wetter climate regions first arise at the southern-most portion of the Gulf of Mexico and then continue southward on the Caribbean coast of Central America. If $\delta^{15}N$ signatures in our yellow warblers reflect regional soil $\delta^{15}N$ signatures, we would expect birds using the northern portion of the wintering range to be uniformly $\delta^{15}N$ enriched, while birds wintering further south would have mixed signatures. Delayed breeding associated with depleted $\delta^{15}N$ may therefore be related to wintering latitude, with yearling females wintering further south arriving later than counterparts from the northern portion of the wintering range.

Tissue $\delta^{13}C$ values in our study population showed a similar range to those reported for American redstarts (Marra et al. 1998, Norris et al. 2005, Reudink et al. 2009) (Table 1). This, when coupled with our wintering data, would suggest that there is sufficient among-individual variation in winter habitat use to produce detectable carry-over effects in other age-sex classes within our population. It is possible that similar habitat variation does not influence spring migration phenology in western songbirds as strongly as it does in eastern populations of American redstarts. Such differences could be driven by regional differences in habitat tolerance or by flyway geography.

Western migrants make greater use of seasonal tropical environments that are mostly avoided by their eastern counterparts (Terborgh 1989). It has been suggested that this pattern is driven by eastern populations becoming specialized with regards to the mesic forests that dominate eastern North America (Terborgh 1989, Rotenberry et al. 1995). Yellow warblers occupy a much broader breeding range than American redstarts, which might suggest that they are less specialized in the tropics as well. An additional feature of western systems is the absence of large geographical barriers. Birds wintering on Caribbean islands, or those crossing the Gulf of Mexico must obtain a threshold mass before initiating migration across open water (Schaub et al. 2008). This could produce a close relationship between the rate of mass gain on wintering territories and departure dates in eastern populations, a pattern which may not be present in the west.

Lack of support for winter habitat-driven carry-over effects in males was not due to the absence of timing effects on the breeding grounds. Territory establishment dates had a large effect on the date by which male yellow warblers had attracted a mate and that mate had initiated reproduction. For older males, the timing of clutch initiation ultimately influenced productivity; for yearling males, it did not, principally because of the low overall reproductive success in this age class. Because breeding season phenology did influence the reproductive success of older males, it is possible that seasonal interactions mediated through migration phenology could be operating in this older age-sex class. Factors such as inter-annual variation in climate (Nott et al. 2002, Vähätalo et al. 2004) deserve exploration, as ‘year’ had a significant effect on the territory establishment dates of older males in this study.

We predicted that time-mediated carry-over effects would be weaker in female yellow warblers. In American redstarts $\delta^{13}C$ had no effect on female arrival dates but instead had a direct effect on the fledging date of those females that successfully reared a clutch (Norris et al. 2004). Fledge date subsequently influenced the productivity of those females. Although female condition would be the most likely mechanism through which winter habitat could influence fledge date, no such correlation was found (Norris et al. 2004) and this relationship may instead be linked to intrinsic quality. As in the merged female age classes assessed in Norris et al. (2004) and Lindsay (2008), we found no evidence of a winter habitat effect on the clutch initiation dates of older yellow warbler females. Contrary to our expectations, we did find evidence of carry-over effects operating via clutch initiation date in yearling females. Genders did not differ significantly in terms of their $\delta^{13}C$ and $\delta^{15}N$ values and yearling females did not differ from older females, making it unlikely that the presence of carry-over effects in this class is due to these individuals occupying a wider range of habitats or relatively worse habitat than other classes (Table 1). It possible that carry-over effects are not seen in older, experienced, females because they are better able to compensate for late arrival on territories by initiating clutches more rapidly. However, our female arrival data does not support this, with lag times to clutch initiation not differing significantly by age. Older females may also differ from yearling females in their migration behavior (with differing departure schedules or stop-over timing) in a way that reduces their spread in arrival dates and subsequent clutch initiation dates. Again, such a hypothesis was not supported by the available data: older females showed a wider absolute range of dates as a product of earlier clutch initiations than yearling females.

That time-mediated carry-over effects vary by age and by sex in yellow warblers has population-level implications. In the 5 yr encompassed by this study, 43.8% of breeding females were yearling birds. As a result, changes in mean winter habitat quality (Norris and Taylor 2006) could be expected to have productivity repercussions for roughly half of the pairs at our study site. The total effect score of $\delta^{13}C$ and $\delta^{15}N$ on the productivity of yearling females was -0.17 and 0.15 respectively, independently corresponding to an estimated shift of 0.8 and 0.6 fledged young across the range of mean isotope values presented in Fig. 1. This response is less than that reported for female American redstarts, where a comparable shift in $\delta^{13}C$ resulted in an estimated shift of 2 fledged young. However, like American redstarts, yellow warblers generally rear a single brood per season and have an average first clutch size of four offspring. Thus, even small shifts in fledgling number represent a large shift in total productivity for an individual. An additional implication of age-specific carry-over effects is geographic. If a greater proportion of yearling birds are found at the periphery of a species breeding range (Graves 1997, Rohwer 2004) and carry-over effects are present in yearling but not older individuals, winter habitat degradation may lead to reduced productivity at the edges of the breeding range but have little effect on productivity within higher-quality breeding areas.

As with all among-individual assessments of carry-over effects, our results have a caveat. In this type of correlational study it is not possible to isolate winter habitat effects from the potential effect of the intrinsic quality of individuals (Harrison et al. 2011). It is possible that intrinsic quality may be driving both winter habitat occupancy and reproductive success, leaving these factors confounded. Within-individual differences in breeding season phenology and winter signatures across years, or studies that incorporate winter habitat alteration (such as food supplementation) and record migration date would be needed to confirm a causal link. Our data are consistent with other work that has shown sex differences in carry-over effect presence or strength (Marra et al. 1998, Norris et al. 2004, Gunnarsson et al. 2005, 2006). However, these previous studies found arrival-mediated carry-over in males and not in females. Our study also indicates that carry-over effects can vary between age classes. Saino et al. (2004) found differences in between-year carry-over effects by age; to our knowledge this is the first paper to show within-year differences.

The wintering ecology of many neotropical warblers is poorly understood. The majority of our current knowledge is based on research conducted on eastern populations wintering in the Caribbean. Carry-over effects and age-sex class variation in carry-over effects may be more evident (and more important from a conservation standpoint (Norris et al. 2004)) among migratory bird species that prefer mesic winter habitat. Such habitats buffer the impact of the late-winter dry season experienced in many regions of the neotropics (Rotenberry et al. 1995) and marked fitness differences may exist between individuals with access to it and those occupying drier habitat. Additional work is needed within the wintering range of western populations and with western warbler species. These populations face different winter climate regimes, and possibly possess a greater tolerance for drier winter habitat types than their eastern counterparts. We advocate incorporating biologically relevant differences such as age-class and sex into carry-over analyses and population models that include carry-over effects in order to better understand how these effects act on individuals within a population and to better predict population effects associated with habitat loss.

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