

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. *Spizella socialis*: 38% of males (Graves 1997); *Spizella monticola*: 39% of males (Porneluzi and Faaborg 1999); *Spizella monticola*: 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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

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 di

warblers than drier habitat-types, suggesting that riparian habitat is of higher quality (Greenberg et al. 1997, Drake unpubl.). We therefore expected that depleted $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ enriched and we would predict high $\delta^{15}\text{N}$ values to be associated with high $\delta^{13}\text{C}$ values and later territory establishment and clutch initiation dates.

Data analysis

We first assessed whether $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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. 21).

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 winter habitat type (Fig. 2). We did not detect that males and females captured in the same winter habitat type were more likely to be paired together (Fig. 2). Since the female model connects winter habitat use directly to clutch initiation, it may incorporate

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 (β s) for each step in the pathway in order to calculate the total effect of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on fledgling number. We then used the shift in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between 3.04 327.6122 Tm 0 Tc (13)Tj 10 0 0 10 219.54 signatures in pasture and coastal habitat on the Gulf of Mexico did not differ ($p = 0.52$).

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

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures differed significantly among these habitats ($\delta^{13}\text{C}$: $F_{4,78} = 22.16$, $p < 0.0001$; $\delta^{15}\text{N}$: $F_{4,78} = 81.49$, $p < 0.0001$, Fig. 1). Tukey HSD tests showed that $\delta^{15}\text{N}$ signatures were significantly more depleted on the southern Gulf coast than on the Pacific slope ($p < 0.0001$). $\delta^{13}\text{C}$ signatures on the Pacific slope varied with habitat use ($p = 0.05$), being most depleted in riparian habitats. $\delta^{13}\text{C}$ signatures in pasture and coastal habitat on the Gulf of Mexico did not differ ($p = 0.52$).

Within our Revelstoke breeding population, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ significantly between sex- and age-within-sex-classes (Table 1; $\delta^{13}\text{C}$: gender, $Z = 0.09$, $p = 0.93$; age-class females, $Z = -0.36$, $p = 0.72$; age-class males, $Z = -0.84$, $p = 0.40$; $\delta^{15}\text{N}$: 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 $\delta^{13}\text{C}$ signatures and more enriched $\delta^{15}\text{N}$ 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 |
| $\delta^{13}\text{C}$ | | | | 0.00 | 0.97 | | | | 1.82 | 0.18 |
| $\delta^{15}\text{N}$ | | | | 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 |
| $\delta^{13}\text{C}$ | | | | 0.24 | 0.64 | | | | 2.48 | 0.79 |
| $\delta^{15}\text{N}$ | | | | 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 |
| $\delta^{13}\text{C}$ | | | | 5.45 | 0.03 | | | | 0.52 | 0.48 |
| $\delta^{15}\text{N}$ | | | | 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures consistent with wetter climate regions.

The total effect of $\delta^{13}\text{C}$ on the productivity of yearling females was -0.17 . Thus, a shift in one standard deviation of $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ gradient (i.e. $\delta^{13}\text{C}$ depleted Pacific riparian forest) would be able to produce 0.8 more fledglings the following summer than counterparts in $\delta^{13}\text{C}$ enriched coastal or pasture habitat in the southern Gulf of Mexico. Similarly, the total effect of $\delta^{15}\text{N}$ on the productivity of yearling females was 0.15. Our model would thus predict that females with $\delta^{15}\text{N}$ 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).

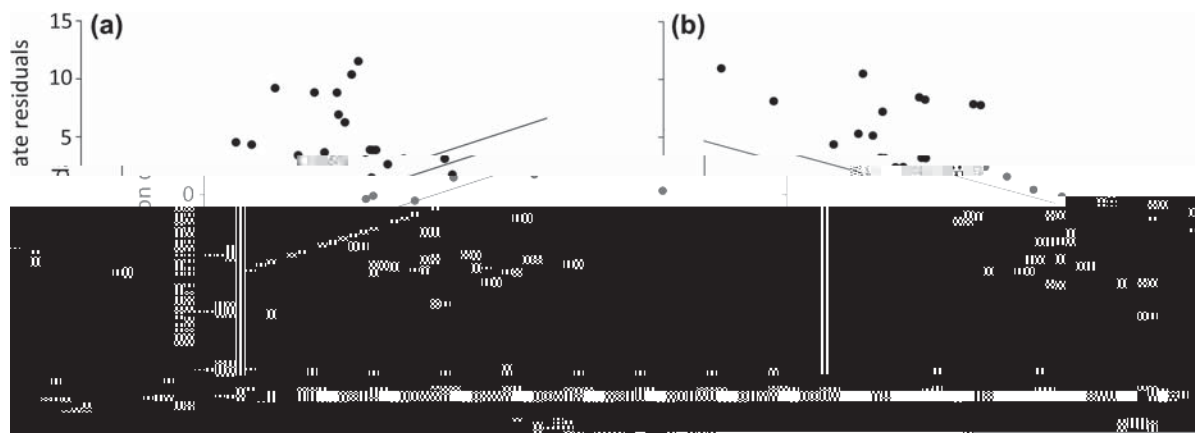


Figure 3. Relationship between winter isotope signatures and clutch initiation date in yearling female yellow warblers. Initiation dates are presented as residuals from a model controlling for year and $\delta^{15}\text{N}$ (a) or for year and $\delta^{13}\text{C}$ (b).

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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