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Winter habitat use does not influence spring arrival dates or the reproductive success of Yellow Warblers breeding in the arctic

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Abstract Winter habitat use can influence the breeding success of migratory songbirds in temperate regions due to its impact on bird condition and breeding phenology. How such carry-over effects vary with latitude is unknown. To address this question, we examined how winter habitat use, inferred from $\delta^{13}C$ and $\delta^{15}N$ signatures in winter-grown feathers, influenced the breeding phenology and productivity of Yellow Warblers (*Setophaga petechia*) at the extreme north of their range in the Canadian arctic (68°N) and compared this population with midlatitude Yellow Warbler (51°N) and American Redstart (*Setophaga ruticilla*; 44°N) populations reported in previous studies. In the arctic, we examined male arrival dates, female clutch initiation dates and the relationship between these timing variables and the number and quality of offspring produced within the season. In contrast to warblers breeding at midlatitudes, we find no support for an impact of winter habitat use on breeding phenology or productivity. Male arrival dates and female clutch initiation dates in both young and older individuals were not correlated with isotopic signatures acquired on the wintering grounds. Males with enriched $\delta^{15}N$ signatures paired more rapidly after arrival, indicating a possible relationship between winter habitat use and condition. This relationship did not enhance annual productivity for these individuals, however, as the negative relationship between breeding phenology and reproductive success in our arctic population was significantly weaker than among Yellow Warblers breeding further south. This reduction or absence of timing effects on productivity in the north effectively removes one pathway through which carry-over effects can act.

Keywords Latitudinal variation · carry-over effects · Productivity · Yellow Warbler · *Setophaga petechia*

Introduction

Studies have shown that the quality of winter habitat occupied by migrant passerines can influence bird condition (Sherry and Holmes 1996; Studds and Marra 2005; Smith et al. 2011). As poor winter conditions can slow premigratory fattening, winter habitat use can delay spring migration and ultimately the timing of events on the breeding grounds (e.g., Marra et al. 1998; Saino et al. 2004). Birds arriving on territories and breeding later in the season may produce fewer offspring, a chain of events that represent a cross-seasonal or "carry-over" effect (Norris et al. 2004). To date, timing-to-productivity effects are the only carry-over effects that have been demonstrated in small migrants; however, wintering habitat use might also carry over to influence productivity via the physical condition of individuals when they arrive on breeding territories (Bearhop et al. 2004).

The influence of wintering-ground events on individual breeding performance might be expected to vary with latitude for several reasons. First, the role of breeding phenology in individual productivity may vary with latitude. Suitable conditions for rearing young exist for a progressively smaller window of time as latitude increases (Newton 2008). A shorter food pulse at northern breeding sites may provide less leeway in the timing of clutch initiation and fewer opportunities to renest, increasing the reproductive costs associated with delayed arrival (Tulp

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and Schekkerman 2008). Secondly, conditions at the start of the breeding period are harsher at more northern latitudes, and body condition and energy reserves may become more important with increasing latitude (Sandberg 1996). Thirdly, for birds wintering in the same region, the energetic costs of migration will be greater with increasing breeding latitude (Wikelski et al. 2003). We might therefore predict that the importance of bird condition at the onset of migration would increase with breeding latitude (Marra 2012) and that time- and condition-mediated carry-over effects will be more pronounced in northern populations. However, it is also possible that with increasing migration distance, events occurring during migration increase in their relative contribution to individual arrival date and condition. For example, the quality of stopover habitat has been linked to subsequent productivity in arctic breeding waterfowl (Ebbinge and Spaans 1995; Mainguy et al. 2002). Migration events may therefore dampen the impact of winter events on breeding processes and make winter to breeding-ground carry-over effects weaker in northern populations.

While carry-over effects have been investigated in songbird populations breeding at midlatitudes (e.g., Saino et al. 2004; Norris et al. 2004; Rockwell et al. 2012; Drake et al. 2013), nothing is known about how winter habitat use might impact passerines breeding in the boreal. All high-latitude studies on carry-over effects to date have been conducted with waterfowl or waders (e.g., Ebbinge and Spaans 1995; Gunnarsson et al. 2005; Legagneux et al. 2011) where differences in breeding biology limit our ability to make inferences about smaller-bodied species. To examine how carry-over effects in passerines may vary with latitude, within-group work is needed. Yellow Warblers have one of the largest breeding ranges of all wood warblers (Parulidae), making them an ideal species with which to examine carry-over effects over a latitudinal gradient. We have previously demonstrated that stable $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures in winter-grown tissue are related to habitat use among Yellow Warblers wintering in Mexico and that winter habitat quality influences the breeding performance of young females, but not older females or males, within a midlatitude population (51°N, Revelstoke, British Columbia) (Drake et al. 2013). In Revelstoke, young females with isotopic signatures consistent with the use of dry winter habitat (enriched $\delta^{13}C$) experienced breeding delays and lower productivity (ca. 0.8 fewer fledglings/year) than those with signatures suggestive of more mesic winter habitat use (Drake et al. 2013). Birds breeding in northwestern regions of North America (such as Revelstoke) share their wintering range with birds that breed at higher latitudes (Boulet et al. 2006). We therefore asked whether carry-over effects in Yellow Warblers breeding at the extreme north of the species range, above the arctic circle in Inuvik, Northwest Territories, Canada (68°N; Fig. 1), were stronger or weaker than those indicated in their conspecifics further south. We anticipated that increased migratory distance, a shorter breeding period, and harsher environmental conditions upon arrival would result in more pronounced carry-over effects in Inuvik relative to midlatitude warbler populations.

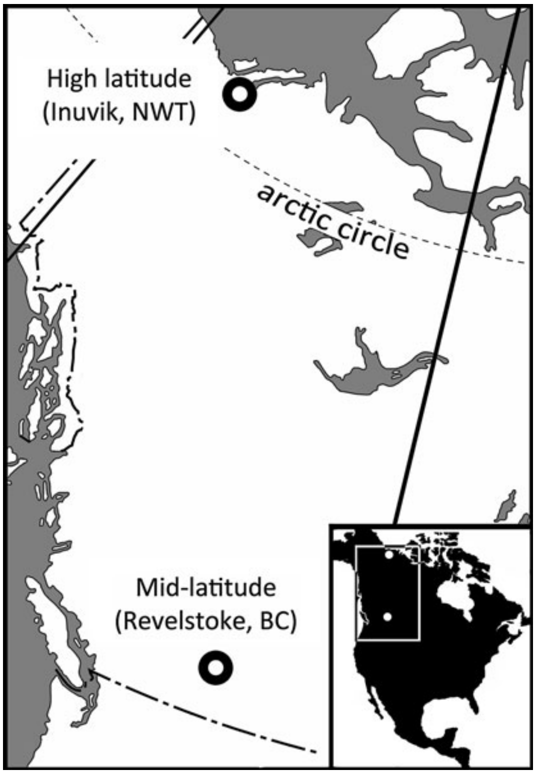

Fig. 1 Study locations of Yellow Warbler (*Setophaga petechia*) populations breeding in western Canada. Our high-latitude, arctic site in Inuvik, NWT (68°21′N, 133°45′W), is located 2,000 km further north than our midlatitude site in Revelstoke, BC (50°57′N, 118°10′W)

We hypothesized that winter habitat quality could carry over to impact breeding success in our arctic breeding birds through two non-exclusive mechanisms: individual timing (time-mediated) and individual condition (condition-mediated) (Fig. 2). In the first scenario, individuals occupying high-quality winter habitat are able to fatten more rapidly and depart the wintering grounds earlier in the spring (Marra et al. 1998; Smith et al. 2010 (departure inferred)). This allows them to arrive at the breeding grounds earlier (Marra et al. 1998; Norris et al. 2004; Reudink et al. 2009) and obtain the productivity advantages that are associated with advanced breeding phenology (Lozano et al. 1996; Smith and Moore 2005; Reudink et al. 2009). In the second scenario, individuals occupying high-quality winter habitat are in better physical condition than their counterparts when they reach the breeding grounds. For males, larger energy reserves, more muscle mass, or higher-quality

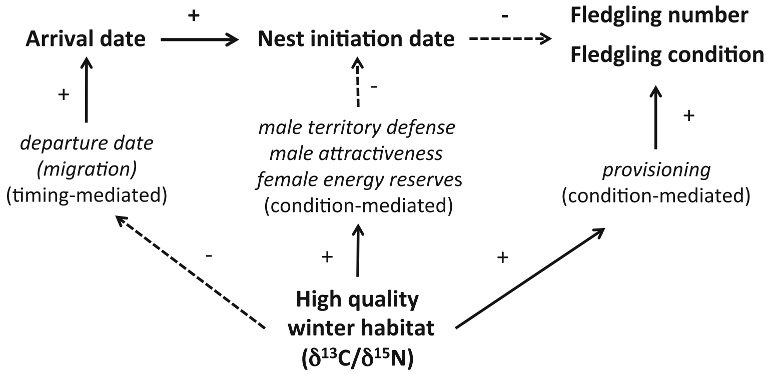

Fig. 2 Suggested pathways through which winter-habitat-driven carry-over effects could act. For females in our study population, clutch initiation date was used as a proxy for arrival date (see text) and therefore condition and timing pathways to clutch initiation are not separate. Depleted δ^{13}C and enriched δ^{15}N tissue signatures are expected to be associated with high-quality winter habitat use

plumage could offer an advantage in territory acquisition/defense and influence female choice, both of which should result in more rapid pairing (Studd and Robertson 1985; Gottlander 1987; Yezerinac and Weatherhead 1997). For females, larger energy reserves might result in more rapid egg-laying (Sandberg and Moore 1996 but see Smith and Moore 2003). Both of these factors could advance breeding phenology in both sexes from the point of clutch initiation rather than from arrival. In addition, habitat-based variation in parental condition could have a direct influence on fledging state and number because females in good condition may produce larger, higher-quality clutches (Smith and Moore 2003) and parents in good condition may provision at a higher rate. We evaluated evidence for time- and condition-mediated carry-over effects in Yellow Warblers breeding in Inuvik using information on winter habitat use inferred from δ^{13}C and δ^{15}N signatures in winter-grown feathers, the dates of male arrival on territories, the timing of breeding and the number and condition of offspring produced by breeding pairs. We subsequently evaluated whether our results differed from those reported in the carry-over effect literature for Yellow Warblers and American Redstarts breeding in British Columbia and Ontario (Drake et al. 2013; Norris et al. 2004).

Materials and methods

Study species

Yellow Warblers are insectivorous Nearctic-Neotropical migrants in the family Parulidae. During the summer, they are found in riparian and wet deciduous habitat throughout North America and, in the west, as far north as the Beaufort Sea (Lowther et al. 1999). Genetic and isotopic work suggests 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). Substantial wintering overlap is seen in mid- and high-latitude populations in the west (Boulet et al. 2006), indicating that northern populations migrate further to reach their breeding grounds than midlatitude populations.

Over winter, Yellow Warblers occupy native habitat ranging from mangrove, swamp and riparian forests to dry coastal scrub as well as a diversity of human-modified habitat such as pasture and cropland (Dunn and Garrett 1997; Greenberg et al. 1996; Binford 1989). The species undergoes pre-alternate molt prior to spring migration, replacing a variable number of greater covert, body and crown feathers (Pyle 1997; Quinlan and Green 2010). Yellow Warblers are territorial on the wintering grounds (Greenberg and Ortiz 1994, Valdez-Juarez, unpublished data), and the habitat used by an individual influences the δ^{13}C and δ^{15}N signatures in their blood (Drake et al. 2013) and ultimately the feathers they grow during this period (Hobson 1999a).

Depleted δ^{13}C is indicative of more mesic habitat use (Hobson et al. 2010). Previous work suggests that this type of habitat is of higher quality for many wintering warblers (Studds and Marra 2005; Latta and Faaborg 2002; Smith et al. 2011) including Yellow Warblers (Drake et al. 2013). δ^{15}N ratios are influenced by regional temperature and precipitation (Amundson et al. 2003) and, at the local level, by factors such as soil cultivation, and marine and artificial fertilizer inputs (Hobson 1999b; Amundson et al. 2003; Croll et al. 2005). δ^{15}N in animal tissue may become further enriched with water and/or nutritional stress (Hobson et al. 1993; Kelly 2000) and with trophic level (Post 2002). Among Yellow Warblers overwintering in Mexico, the greatest variation in tissue δ^{15}N is regional and depleted δ^{15}N may be indicative of wintering origins in higher rainfall regions such as eastern Mexico and southern Central America, while enriched δ^{15}N may suggest wintering origins in the drier northern and Pacific coastal regions of the wintering range (Drake et al. 2013).

We predicted that the direction of the relationship between δ^{13}C, δ^{15}N, and breeding phenology and performance in Inuvik would be the same as in midlatitude warbler populations: winter habitat use conferring more depleted δ^{13}C and more enriched δ^{15}N signatures would be associated with earlier arrival and clutch initiation dates and better breeding performance by individual birds (Norris et al. 2004; Drake et al. 2013).

Study site and population monitoring

Between 2009 and 2011, we monitored a banded population of Yellow Warblers in the taiga plains ecozone near Inuvik, Northwest Territories (68°21′N, 133°45′W; Fig. 1; hereafter Inuvik). Our study site covered 20.0 ha of riparian habitat bordering the Mackenzie River (3–6 m elevation). Low-lying portions of this habitat are dominated by several species of willow shrubs (*Salix* spp.) and by Green Alder (*Alnus crispa*), all of which experience seasonal flooding during spring icebreak. These species are intermixed with White Spruce (*Picea glauca*) at higher elevations (Gill 1973). Yellow Warblers in Inuvik experience an average of 23 h of daylight per day during the breeding period and, in the years of our study, mean daily temperatures of 11.5 ± 0.4 °C, range −2.2–25.5 °C (Environment Canada 2012).

Dates of male arrival on breeding territories were determined during surveys conducted every 1–2 days beginning in mid-May. Male Yellow Warblers sing when establishing territorial boundaries, making them easy to detect. Males are also highly aggressive toward song-playback and were typically caught within 1–2 days of arrival using targeted mist-netting. Females were more difficult to detect, but 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 color bands (AC Hughes, UK).

Breeding pairs were monitored through the entire season (mid-May to late July). Nests were located by following females during the building period and then checked every 3 days to determine clutch initiation dates, clutch size, brood size, and fledgling number. 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, weighed and had tarsus measures taken 7 days after hatching. We calculated the average condition of nestlings within a clutch by calculating the mean tarsus length (mm) and mass (g) for all individuals in the nest. We then regressed mean mass against mean tarsus for the population and used the residuals (i.e., body-size-controlled mass) as a unit-less metric of average clutch "condition." We assumed that all nestlings present on day 7 successfully fledged unless signs of predation were found in or around the nest after fledging. Successful fledging was usually confirmed by observing parents feeding or defending young out of the nest. Annual productivity for an individual bird was defined as the number of fledglings produced over all nesting attempts. Although rare, some males (4 %, $n = 5/128$ males over 3 years) 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 breeding characteristics (brood patch/cloacal protuberance), plumage (brightness/degree of rufous streaking) and behavior. They were then classified as yearling or older birds based on plumage. Yearlings ("second year" or SY birds) have narrow, tapered primary coverts, tapered retrices with less yellow coloration on the inner webs of the outer tail and worn pre-basic plumage; older ("after-second year" or ASY) birds have broad, truncate primary coverts with narrow yellow-olive edging, and truncate retrices with more extensive yellow coloration on the inner webs (Pyle 1997).

Tissue samples and stable isotopic analysis

To obtain winter habitat δ^{13}C and δ^{15}N signatures, we collected three newly grown greater covert feathers (identifiable by their brighter pigment and lack of wear) from all individuals captured. 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 milligram (±0.2) of tissue was placed in 9 mm × 5 mm smooth-walled tin capsules (Elemental Microanalysis, UK), and samples were then analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility in California, USA. Delta values are expressed relative to international standards: Vienna PeeDee Belemnite (V-PDB) for carbon and Air for nitrogen; estimated measurement precision was 0.2 ‰ for δ^{13}C and 0.3 ‰ for δ^{15}N.

Carry-over effects

We used general linear models (JMP 9.0.2, SAS Institute Inc.) to evaluate the effect of winter habitat use on male arrival date, the onset of breeding in males and females, and productivity and offspring condition for both genders. Predicted habitat effects follow the pathway illustrated in Fig. 2. We did not examine the relationship between winter habitat and female arrival as lower detection probabilities and later banding dates made female arrival dates less certain and female identity unreliable until nest construction had begun. Clutch initiation is therefore used as proxy for arrival date in females. Connecting winter habitat use directly to clutch initiation merges condition- versus timing-mediated effects in the female pathway.

All models included "Age" and "Year" effects as covariates as we predicted that timing effects could vary between age classes and between years. We also predicted that the relationships between timing variables could vary with age and year and included "Arrival × Age" and "Arrival × Year" in models predicting male clutch initiation dates, and "Clutch Initiation × Age" and "Clutch Initiation × Year" in models predicting fledgling number and condition. The strength of carry-over effects has been shown to vary by age class (Drake et al. 2013) and by year (Norris et al. 2004). We therefore included "δ^{13}C/δ^{15}N × Age" and "δ^{13}C/δ^{15}N × Year" interaction terms in all models.

Contributing variables for each step in the path analysis were selected using a stepwise procedure where the probability to enter and to leave the model was ≤ 0.05 and ≥ 0.1, respectively. Interaction terms were restricted such that they could only enter the model with their precedent terms. We determined the contribution of δ^{13}C and δ^{15}N to model fit by independently reintroducing them to the final model if they were dropped during the stepwise procedure.

Power to detect carry-over effects observed at midlatitude sites

We used the linear multiple regression test in G*Power 3.1 (Faul et al. 2007) to calculate the power of our Inuvik data to detect isotope effect sizes equivalent to those found in warbler populations breeding at midlatitude sites. First, we calculated our power to detect a δ^{13}C and δ^{15}N effect equivalent to that found in young female Yellow Warblers breeding in Revelstoke, British Columbia (51°N; Drake et al. 2013). Here, variation in δ^{13}C and δ^{15}N values independently explained 11.1 and 8.9 % of the variation in young female clutch initiation dates, and jointly, these isotopes explained 17.1 % of this variation ($n = 38$; for detailed study description see Drake et al. 2013). We used these values and the residual variance described by reduced Inuvik models that included only young females ("Year + δ^{13}C or δ^{15}N" and "Year") to calculate the predicted effect size (f^2) of δ^{13}C and δ^{15}N in Inuvik if these isotopes explained an equivalent amount of variance as documented in Revelstoke. We then used f^2 and the sample size of young females in Inuvik to calculate power ($1 - \beta$). We additionally calculated our power to detect a δ^{13}C effect equivalent to that shown in older American Redstart males at Chaffey's Lock, Ontario (44°N; Norris et al. 2004). Here, variation in δ^{13}C explained 32 % of the variation in arrival dates ($n = 57$; for further detail see Norris et al. 2004). We used this value and the residual variance in arrival date described by a reduced Inuvik model ("Year") for older males to calculate f^2. We then used the sample size of older males in Inuvik to calculate power ($1 - \beta$).

We additionally compared the strength of the relationship between clutch initiation date and productivity for male and female Yellow Warblers in Inuvik to that within a conspecific midlatitude population located in Revelstoke, British Columbia (50°57′N, 118°10′W; Fig. 1; hereafter Revelstoke). In Revelstoke, breeding Yellow Warblers were monitored within three, 30-39-ha blocks of riparian habitat (predominantly *Salix* spp. and *Populus trichocarpa*) along the northern section of the Upper Arrows Lake Reservoir (435–441 m elevation; see also Drake et al. 2013). Breeding data for this population were collected in the same manner as in Inuvik, over the same time period (2009–2011; $n = 69$ females and 76 males). We used a multiple linear regression analysis to test for a "Location × Clutch Initiation" interaction in models predicting fledgling number after accounting for "Year" and "Year × Location" effects.

Results

Population traits

Breeding density in Inuvik was 3.8 pairs/ha. This was higher than in our comparison population in Revelstoke (0.7 pairs/ha; Drake et al. 2013), but lower than that reported for some other midlatitude populations (e.g., 10 pairs/ha; Mazerolle et al. 2005). First breeding season (SY) individuals accounted for 41 % of the female breeding population (range 38–47 %, $n = 3$ years) and 10 % of the male breeding population (range 9–12 %, $n = 3$ years). Breeding pairs fledged an average of 3.3 ± 2.1 offspring per year ($n = 130$ pairs over 3 years).

Male and female Yellow Warblers in Inuvik did not differ significantly in their winter δ^{13}C signatures (δ^{13}C (±SD): -23.3 ± 2.0 vs. -23.1 ± 2.3, $t\,(229) = -0.81$, p (two-tailed) $= 0.42$; Fig. 3). Males, however, had more enriched winter δ^{15}N signatures than females (δ^{15}N (±SD): 8.9 ± 1.5 vs. 8.4 ± 1.4, $t\,(230) = 2.64$, p (two-tailed) $= 0.009$). Wintering signatures of young and older birds did not differ (δ^{13}C: "Age," $p = 0.52$, "Age × Sex," $p = 0.60$; δ^{15}N: "Age," $p = 0.40$, "Age × Sex," $p = 0.92$). Winter δ^{13}C and δ^{15}N signatures were not correlated (Spearman's $\rho = 0.10, p = 0.12, n = 231$).

Carry-over effects

δ^{13}C and δ^{15}N signatures in winter-grown tissue showed no relationship to either male arrival or female clutch

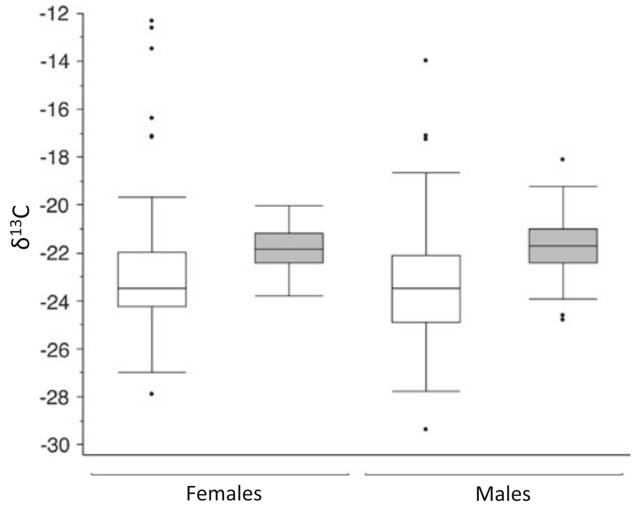

Fig. 3 Summary of δ^{13}C signatures obtained from the winter-grown plumage of Yellow Warblers breeding at high-latitude (Inuvik; *white boxes*) and midlatitude (Revelstoke; *gray boxes*) sites between 2009 and 2011. Values are categorized by sex-class; depleted signatures suggest mesic habitat use on the wintering grounds

initiation date. Although local weather conditions in May were not notably different among years, male arrival dates were later in 2009 than in 2010 or 2011 ("Year," Table 1). Female clutch initiation dates were delayed in 2011 in response to a period of freezing temperatures in early June ("Year," Table 1). After controlling for arrival date, males with enriched δ^{15}N signatures obtained mates who initiated clutches earlier than the mates obtained by males with depleted δ^{15}N signatures ($p = 0.01$; Table 1). Male δ^{13}C signatures showed no direct relationship with clutch initiation date.

δ^{13}C and δ^{15}N signatures were not directly related to the number of fledglings produced by either sex. Productivity of males and females varied among years and was significantly lower in 2011 when subzero temperatures in June killed eggs and led to the abandonment of clutches initiated before the freeze (Table 1). Unexpectedly, we found little evidence that the number of fledglings produced by male or female warblers declined significantly with later clutch initiation dates (Table 1). There were some suggestions that, in males, seasonal effects on fledgling number varied among years ("Year × Clutch Initiation," $p = 0.06$; Table 1). However, this interaction was not caused by seasonal declines in productivity in any of the 3 years, but rather a positive relationship between clutch initiation date and male productivity in 2011 when males whose social mates initiated their first clutch after the freeze experienced greater success.

The δ^{13}C signature of either social mate was not directly related to the average condition of their nestlings at day 7 post-hatch. For males, none of the variables we considered explained any of the variation in nestling condition (Table 1). Among females, there was an indication that δ^{15}N influenced nestling condition in some years, but not others ("Year × δ^{15}N," $p = 0.05$; Table 1). This interaction was the product of a negative relationship between δ^{15}N and nestling condition in 2010. Overall, the female model did not explain a significant amount of the variation in nestling condition.

Comparison with midlatitude sites

Our power to detect winter habitat effects on the breeding phenology of young female Yellow Warblers in Inuvik of the same magnitude as that observed in young females in Revelstoke, British Columbia, was high (δ^{13}C alone: $1 - \beta = 0.97$; δ^{15}N alone: $1 - \beta = 0.92$; joint effect: $1 - \beta = 1.0$; $n = 50$). Similarly, a winter habitat effect on arrival date among older males in Inuvik of comparable strength to that observed in older male American Redstarts in Chaffy's Lock, Ontario, would have been detectable given our sample sizes ($1 - \beta = 1.0$; $n = 106$).

The relationship between clutch initiation date and productivity differed significantly between Inuvik and our midlatitude site. Fledgling number decreased with clutch initiation date in Revelstoke but did not vary with clutch initiation date in Inuvik ("Location × Clutch Initiation": males, $p = 0.02$; females, $p = 0.03$; Table 2, Fig. 4).

Discussion

We predicted that carry-over effects of winter habitat use would be more pronounced among migrant Yellow Warblers breeding in the arctic. We anticipated this because northern breeders are likely to travel further during migration and encounter harsher environmental conditions upon arrival (Boulet et al. 2006; Sandberg 1996). Both factors should result in higher energetic costs. Migrants in the north additionally experience a shorter breeding season, which we assumed would strongly penalize delayed reproduction. Instead, we found little support for an effect of winter habitat use on the breeding phenology or productivity of Yellow Warblers in the far north. Our study instead offers convincing support for the concept that increasing migration distance dampens carry-over effects.

We found no evidence that δ^{13}C and δ^{15}N signatures in winter-grown tissue influenced male arrival, female clutch initiation dates or pair productivity in Inuvik. Any effect sizes, if present, were weaker than those reported among midlatitude warbler populations. The absence of a winter habitat effect on older males in our arctic population was not completely unexpected as there is also no support for such an effect among older male Yellow Warblers breeding further south (Drake et al. 2013). The disparity between the

Table 1 Multiple regression analyses testing the influence of winter habitat (inferred from δ^{13}C and δ^{15}N) on Inuvik Yellow Warbler breeding metrics

Model	Males						Females					
	r^2	df, *n*	*p*	Std *B*	*F* ratio	Prob > *F*	r^2	df, *n*	*p*	Std *B*	*F* ratio	Prob > *F*
Arrival	0.20	2, 133	<0.001				–	–	–			
Year				–	15.94	<0.001				–	–	–
Wintering signature contribution to fit												
δ^{13}C	0.22	3, 115	<0.001	0.04	0.24	0.62	–	–	–	–	–	–
δ^{15}N	0.23	3, 115	<0.001	0.11	1.81	0.18	–	–	–	–	–	–
Clutch Initiation	0.50	4, 108	<0.001				0.27	2, 127	<0.001			
Year				–	26.09	<0.001				–	23.38	<0.001
Arrival				0.51	40.53	<0.001				–	–	–
δ^{15}N				−0.18	6.23	0.01				–	–	–
Wintering signature contribution to fit												
δ^{13}C	0.50	5, 108	<0.001	0.03	0.13	0.72	0.36	3, 105	<0.001	0.06	0.58	0.45
δ^{15}N	–	–	–	–	–	–	0.35	3, 106	<0.001	0.05	0.37	0.54
Fledgling number	0.09	5, 124	0.06				0.06	2, 126	0.02			
Year				–	3.04	0.05				–	4.28	0.02
Clutch Initiation				−0.02	0.04	0.84				–	–	–
Year × Clutch Initiation				–	2.83	0.06				–	–	–
Wintering signature contribution to fit												
δ^{13}C	0.07	6, 107	0.28	−0.10	0.35	0.34	0.06	3, 105	0.08	0.15	2.37	0.13
δ^{15}N	0.06	6, 107	0.35	0.04	0.18	0.68	0.05	3, 105	0.18	0.07	0.48	0.49
Fledgling Condition	–	–	–				0.08	5, 82	0.24			
Year				–	–	–				–	0.02	0.98
δ^{15}N				–	–	–				0.01	0.01	0.92
Year × δ^{15}N				–	–	–				–	3.17	0.05
Wintering signature contribution to fit												
δ^{13}C	0.00	1, 92	0.43	0.08	0.79	0.43	0.09	6, 82	0.28	0.11	0.86	0.36
δ^{15}N	0.00	1, 92	0.62	−0.05	−0.51	0.62	–	–	–	–	–	–

For predicted relationships see Fig. 2. Age and Year plus second-order interaction terms were included in initial models and dropped sequentially if they did not contribute to fit. Below each model (italics), we report the effect strength and contribution of δ^{13}C and δ^{15}N to model fit if these variables were to be independently added back into the final model. Whole model r^2, sample size and significance are reported for these inflated models besides each isotope

response of males in these populations and male American Redstarts in eastern North America, where carry-over effects have been well documented (Marra et al. 1998, Norris et al. 2004; Reudink et al. 2009), may relate to differences in species ecology or migration routes rather than to migration distance. However, the disparity in the relationship between δ^{13}C and δ^{15}N and young female clutch initiation dates between our arctic site and Revelstoke would suggest that migration distance reduces the importance of wintering habitat use. This counter-prediction finding warrants further study. It is possible that increased migration distance increases the relative contribution of migratory events to individual arrival date and condition and therefore dampens wintering effects. Additionally, low levels of anthropogenic disturbance (Hannah et al. 1995) and higher invertebrate densities (Currie and Fritz 1993) at northern latitudes may create favorable migratory conditions that help to mitigate disadvantages acquired by individuals over winter. This may not be true for populations moving through highly fragmented habitats further south.

Evidence of condition-mediated carry-over effects in Inuvik was limited. δ^{13}C had no effect on the speed with which males obtained a mate and initiated reproduction. δ^{13}C and δ^{15}N also had no direct impact on male or female

Table 2 Location effects on the relationship between first-clutch initiation date and productivity in Yellow Warblers from the perspective of (a) breeding males and (b) breeding females. For both sexes, the best-fitting model predicts a negative relationship at our midlatitude (Revelstoke) site and a weak positive or no relationship at our high-latitude (Inuvik) site. See also Fig. 4

	r^2	df, *n*	*p*	Std *B*	*F* ratio	Prob > *F*
a) Males						
Fledge number	0.15	7, 199	<0.001			
Location (Revelstoke–Inuvik)				0.36	20.50	<0.001
Clutch Initiation				−0.16	4.17	0.05
Location × Clutch Initiation				0.18	5.41	0.02
Year				–	1.80	0.17
Year × Clutch Initiation				–	0.77	0.46
b) Females						
Fledge number:	0.13	7, 190	<0.001			
Location (Revelstoke–Inuvik)				0.32	13.76	<0.001
Clutch Initiation				−0.16	3.78	0.05
Location × Clutch Initiation				0.19	4.99	0.03
Year				–	2.99	0.05
Year × Clutch Initiation				–	0.53	0.59

productivity or nestling condition. Enriched δ^{15}N signatures were associated with earlier clutch initiation in males once arrival date was accounted for. Enriched feather δ^{15}N is associated with higher feather chroma in Inuvik (Jones, Drake and Green, unpublished data). This plumage trait may have enabled δ^{15}N-enriched males to pair faster, but it remains unclear why δ^{15}N and chroma itself are related. Despite advances in breeding phenology through clutch initiation date for δ^{15}N-enriched males, this shift did not represent a condition-mediated carry-over effect as males did not experience higher productivity with earlier clutch initiation. Similarly, clutch initiation date in Inuvik was not directly associated with nestling condition. Such an association might have produced a carry-over effect for males if nestlings that leave the nest in better condition are more likely to survive and recruit into the breeding population (Magrath 1991). That advanced breeding date did not impact male fitness in Inuvik has three caveats. First, without radio telemetry, we cannot eliminate the possibility that post-fledgling survival might decline with later clutch initiation date (Brown and Roth 2002). Any such relationship might also vary with latitude due to differences in late-season food availability and fall migration costs. Secondly, it is possible that δ^{15}N-enriched males experience higher rates of extra-pair paternity if advanced pairing is the product of increased attractiveness. Genetic data would be needed to assess this. Finally, it is possible that rapid pairing is the product of rapid territory acquisition. This may mean that δ^{15}N-enriched males experience less male–male conflict, which could in turn influence their survival.

It was expected that individuals who arrived on the breeding grounds and initiated clutches early would have higher productivity than individuals arriving later in the breeding season (e.g., Smith and Moore 2005; Rockwell et al. 2012). We did not observe this pattern in Inuvik Yellow Warblers. Clutch initiation date in Inuvik was not significantly correlated with productivity even after excluding data from 2011, where freezing temperatures penalized individuals who began nesting earlier in the season (males: Spearman's $\rho = -0.16$, $p = 0.15$, $n = 83$; females: Spearman's $\rho = -0.14$, $p = 0.25$, $n = 75$). In contrast, seasonal declines in productivity are observed among Yellow Warblers in Revelstoke (Fig. 4; Drake et al. 2013). That seasonal productivity declines in Inuvik were indeed weaker than those in more southerly populations was confirmed by significant slope differences in the relationship between clutch initiation and fledgling number between Revelstoke and Inuvik (Table 2). This result is similar to that reported for ptarmigan (*Lagopus* spp.) where later first clutch dates had less of an influence on clutch size for birds breeding in the arctic than for those in the alpine at lower latitudes (Martin and Wiebe 2004) but counter to consistent seasonal declines in first clutch size reported for American Pipits (*Anthus rubescens*) across latitudes (Hendricks 1997). There are several reasons why productivity declines might not be observed in our Inuvik population. First, inhospitable conditions in the early spring may mean that northern birds arrive and initiate reproduction more synchronously than more southerly populations. In the 3 years of our study, Inuvik birds initiated nests over a 22-day period while Revelstoke birds began to breed a week earlier in the season and initiated nests over a 27-day period (Fig. 4). This reduced spread in clutch initiation dates in Inuvik would reduce productivity differences among individuals if timing effects were present. Secondly, Inuvik Yellow Warblers, like other birds breeding in the

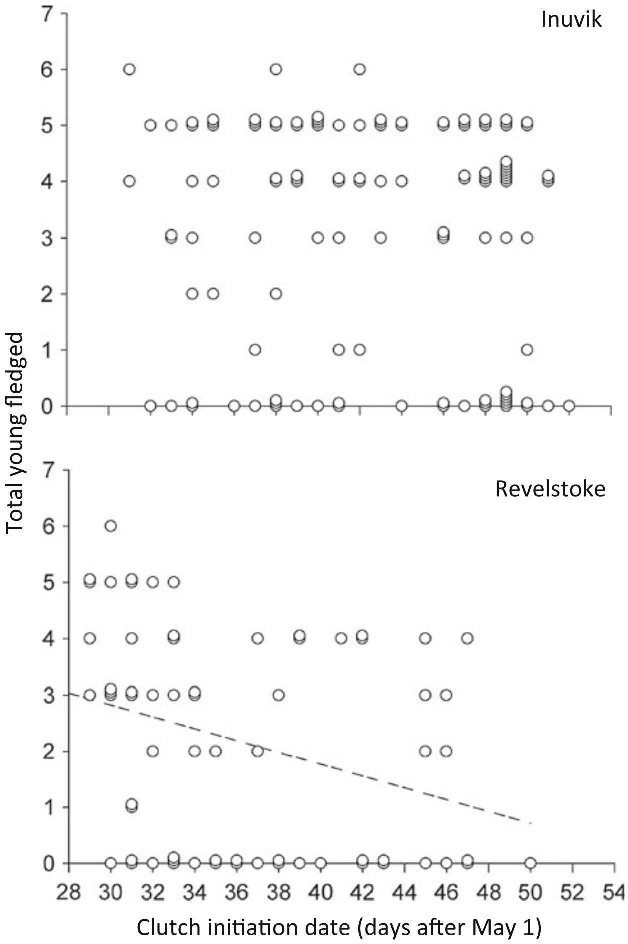

Fig. 4 The relationship between first-clutch initiation date and annual productivity (total number of young fledged) among Yellow Warbler females within our high-latitude breeding population (Inuvik; *top*) and our midlatitude breeding population (Revelstoke; *bottom*). See also Table 2

north, experience lower predation rates than more southern populations (Martin 2013; McKinnon et al. 2010; Salgado-Ortiz et al. 2008). This means that fewer first nests fail (39 % (Inuvik, $n = 128$ nests over 3 years) vs. 52 % (Revelstoke, $n = 152$ nests over 6 years)) and, consequently, additional time for renesting is not necessary for the majority of individuals. Among females in Inuvik who failed in their first nesting attempt, individuals who initiated their first clutch later in the season were less likely to successfully fledge a subsequent clutch ($\chi_1^2 = 12.9$, $p < 0.001$, $n = 45$); however, these individuals represented too small a proportion of the breeding population to influence overall trends. Yellow Warblers in Inuvik are almost always single-brooded; in 3 years only one female in our study reared a second clutch after successfully fledging a first. Fledging first nests early was therefore not associated with the production of second broods, which might have contributed to total fledgling number. Finally, clutch size in Inuvik is a quadratic function of clutch initiation date, with early clutches containing fewer eggs than midseason clutches (Martin 2013). This pattern suggests that early clutch initiation dates are costly, possibly due to the shorter window of suitable climatic conditions and food availability in the north. Small, early clutch sizes followed by a midseason peak and decline may flatten any negative linear relationship between clutch initiation date and fledge number.

In conclusion, we found no evidence of an effect of wintering habitat use on individual productivity among Yellow Warblers at northerly extreme of their range. This was due to (1) any potential effect of winter habitat use on breeding phenology being weaker than that observed among warblers at midlatitudes and (2) productivity patterns in the north that undermine the time-mediated pathway through which carry-over effects have previously been shown to act in passerines (Norris et al. 2004, Saino et al. 2004, Drake et al. 2013). We found some support for a non-breeding season effect on male condition, which advanced male breeding phenology from the point of clutch initiation. This effect did not translate into increased productivity or improved nesting condition. In total, the absence of a detectable winter habitat effect on fledgling number in Inuvik indicates that timing effects are weaker in this population than in populations where declines in fledgling number have been shown. Increased migratory distance therefore appears to dampen the impact of winter habitat use on breeding phenology, while productivity advantages associated with breeding in the far north appear to reduce the role of phenology in breeding success.

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