HABITAT SELECTION AND MIGRATORY CONNECTIVITY OF A NEOTROPICAL MIGRANT SONGBIRD

by

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ABSTRACT

Addressing population declines in Neotropical migratory birds requires information on breeding demography and connectivity throughout the annual cycle. For species breeding in North American riparian habitats, anthropogenic changes to breeding habitat and indirect carry-over effects from the previous winter can both influence demographic rates. I examined whether a human-altered floodplain was an ecological trap by assessing habitat preferences and their reproductive consequences for yellow warblers (*Dendroica petechia*). I found that male settlement patterns were positively related to habitat cues that predicted breeding productivity, suggesting that extant riparian habitat was not attracting birds to poor quality sites. I then used stable hydrogen isotopes (δD) to show that warblers moulted some feather blocks on breeding grounds and others during their tropical overwintering period. Assignment tests using δD values in winter-grown feathers showed that most individuals originated from regions throughout Central America. However, interannual variation in isotope signatures limited further assignment accuracy.

Keywords: yellow warbler, riparian habitat, breeding productivity, British Columbia, stable-hydrogen isotopes, migration

Subject Terms: birds, yellow warbler, British Columbia; stable isotopes, migration

To Mom and Dad

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CHAPTER 1: GENERAL INTRODUCTION

Long-term declines in the abundance of many Neotropical migratory songbirds since 1966 (Robbins *et al.* 1989; Sauer *et al.* 2008) has prompted a growing body of research dedicated to better understand the mechanisms explaining these declines (Greenberg & Marra 2005; Rappole 1995; Holmes 2007). Many of these studies have focused on (1) identifying at what point during the annual cycle populations are most limited (Martin & Finch 1995; Sherry & Holmes 1995) and (2) examining within-season causal factors that may negatively influence population trends (Newton 2004; DeSante *et al.* 2001; Saracco *et al.* 2008; Sherry & Holmes 1996). Many studies have hypothesized that populations are influenced by events on the tropical wintering grounds (Sherry & Holmes 1996; Rappole & Mcdonald 1994). For example, tropical deforestation (Askins *et al.* 1990) and habitat-mediated food limitation (Sherry *et al.* 2005) may act to reduce over-winter survival by hatch-year and adult birds. Some studies suggest that stopover areas and weather hazards experienced during migration have significant consequences on populations (Sillett & Holmes 2002; Moore *et al.* 1995; Newton 2004). Lastly, studies have shown that fecundity on the breeding grounds may be important in maintaining population sizes despite spending about three months in these temperate habitats during their annual cycle (Holmes 2007). However, a growing body of evidence suggests that events on the wintering grounds could be influencing individual fitness on the breeding grounds (Webster *et al.* 2002; Norris & Marra 2007; Marra *et al.* 1998; Marra *et al.* 1998). These and other findings demonstrate the importance of factors occurring during all periods of the annual cycle and present new challenges for developing conservation strategies for effectively managing species in decline.

On the temperate breeding grounds of North America, breeding success and productivity are regarded to have important influences on Neotropical migratory bird populations (Askins 2000). Anthropogenic habitat fragmentation has been shown to reduce breeding productivity through increased exposure to nest predators and cowbird nest parasitism in eastern populations (Robinson *et al.* 1995; Faaborg 2002) which can negatively influence population demography (Schmidt 2003). However, fragmentation may not affect western landscapes in a similar way because topographic variation and natural disturbance regimes maintain naturally heterogeneous and patchy habitats (George & Dobkin 2002). For example, Tewksbury *et al*. (1998) tested the effects of fragmentation on breeding demography for a suite of riparian-dependent bird species. The more common species included song sparrow (*Melospiza melodia*), common yellowthroat (*Geothlypis trichas*), warbling vireo (*Vireo gilvus*), and yellow warbler (*Dendroica petechia*) breeding on floodplain habitats of Montana. They found that patch size, edge and landscape effects had opposite patterns on breeding productivity compared to those documented in eastern landscapes. That is, fragmented agricultural habitat had lower predation and parasitism rates than more contiguous forest tracts. Thus, if population declines are not related to fragmentation effects cited for many eastern Neotropical migrant songbirds in decline, alternative hypotheses are required to determine how changes to breeding habitat influence key demographic rates such as breeding productivity.

As one of the most endangered ecosystems in the world, riparian landscapes have experienced myriad anthropogenic disturbances (Nilsson *et al.* 2005). In western North America over 95% of existing habitat has been lost or degraded (Knopf *et al.* 1988; Ohmart 1994). Habitat loss and degradation have been suggested as the most important causes of population declines among landbird species in western North America (DeSante & George 1994). Factors such as overgrazing by domestic livestock is frequently stated as a primary source of degradation in the semi-arid United States, affecting between to 70 to 90% of all natural riparian habitat (Hirsh & Segelquist 1978; Dobkin *et al.* 1998). By contrast, large rivers and bottomlands of mesic landscapes in the Northwest US and Canada have been modified by widespread dam construction for flood control, power generation, and irrigation purposes among others (Fullerton *et al.* 2006; Graf 1999; Scott *et al.* 2003). Despite the wealth of research examining the grazing impacts on migrant bird communities in these disturbed habitats, considerably less research has been done to explore the how modified hydrologic regimes influence habitat selection and breeding success in these disturbed habitats. These few studies have focused mainly on bird distribution and abundance (Fletcher & Hutto 2008; Hatten & Paradzick 2003; Scott *et al.* 2003) in riparian habitat but do not address the breeding consequences related to these use patterns. Consequently, additional information is required on breeding productivity in relation to habitat features to understand how these disturbances influence annual fecundity.

In Chapter 2, I determined whether habitat characteristics were related to selection patterns of yellow warblers in order to test the ecological trap hypothesis that reproductive performance was lower in more preferred nest-sites and territories.

Commonly found throughout North American riparian habitats, this Neotropical migrant passerine has shown broad declines among western populations (Webb 1985; Ortega & Ortega 2000; Sauer *et al.* 2008). I therefore, investigated the reproductive consequences for individuals breeding in remnant riparian habitats modified by hydroelectric reservoir operations in British Columbia, Canada. I examined the extent to which individual preference for structural vegetation and habitat cues reliably predict habitat quality in a riparian landscape that has underdone significant ecological change.

Several studies have demonstrated that breeding performance in long-distance migratory birds is strongly influenced by factors related to arrival timing (Lozano *et al.* 1996) and body condition upon arrival (Smith & Moore 2005; Smith & Moore 2003), which are presumed to be influenced by events outside the breeding season. In some species, individuals arriving late to the breeding grounds and in poor condition have been linked to poor winter habitat quality (Marra *et al.* 1998). Climatic patterns affecting weather conditions on the wintering grounds have also been linked to productivity the following summer (Nott *et al.* 2002; Sillett *et al.* 2000). Thus, in addition to habitat quality on the breeding grounds, events during the previous winter should also influence reproductive success.

Until recently, obtaining information on the wintering grounds has been limited to banding recaptures of individuals at different periods to make direct connections between populations. Stable isotope analysis studies are now taking a leading role in exploring these connections by making inferences with intrinsic markers found in body tissues formed in particular seasons (Hobson & Wassenaar 2008). In Chapter 3, I use stable isotope analysis of deuterium ratios (δD) in feathers collected on the breeding grounds but grown in previous seasons to examine patterns of geographic connectivity to the wintering grounds. Moulting chronologies among some species of the Parulidae family (i.e., New world wood-warblers) involves a second moult during the overwintering period that allowed me to use δD values to link breeding birds to their previous wintering and breeding origins. Using feathers of unknown origin (prealternate) and known origin (prebasic), I tested whether sampling these multiple feathers can link individuals to their wintering and breeding grounds, respectively.

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CHAPTER 2: YELLOW WARBLER BREEDING PERFORMANCE IN HUMAN-ALTERED RIPARIAN HABITAT: ASSESSING THE POTENTIAL FOR AN ECOLOGICAL TRAP

Abstract

The loss and degradation of riparian habitat throughout the Inter-mountain West has been suggested as the most important cause of population declines among landbird species in western North America. However, studies suggest fragmentation of western landscapes may be less important than in eastern landscapes. An alternative explanation for declines is that human-modification to water flow leads to a mismatch between habitat cues and breeding productivity in migratory birds that creates an ecological trap. I evaluated whether riparian habitat on an actively managed reservoir along the Columbia River in British Columbia attracted yellow warblers to settle in habitat with low nesting success and productivity. Breeding territories and nests sites varied in their physical characteristics and potential effects on reproductive performance. Using male settlement order to estimate habitat preference, I found that birds settled earlier in territories with greater riparian habitat cover and less canopy cover. The habitat characteristics that predicted settlement order were also the characteristics that predicted reproductive performance. Specifically, I found that nest success increased with decreasing canopy cover, and riparian habitat was positively related to the number of young fledged during the breeding season. These results are consistent with the null hypothesis that disturbed riparian habitat does not act as an

ecological trap because males appear to settle preferentially in high quality territories and nest sites with increased reproductive performance. These results highlight the importance of measuring individual preference and multiple fitness metrics when testing for ecological traps.

Introduction

When animals select breeding habitat they are faced with the complex task of assessing the relative quality of sites differing in many attributes. Models of habitat selection tend to assume that individuals have evolved to recognize and settle preferentially in the highest quality habitat available (Fretwell & Lucas 1970). Mechanistically, the decision to settle in a particular environment is thought to be influenced by environmental cues that reliably link to increased subsequent reproductive success and survival (Stamps & Krishnan 2005; Clark & Shutler 1999). For example, individuals may select habitat based on food availability (Marshall & Cooper 2004) or the absence of predators (Martin 1998) and consequently raise more young or have higher survival. However, in many cases the factors that ultimately determine fitness may not be evident at the time habitat is selected, effectively forcing individuals to use indirect cues to predict subsequent habitat quality. In recently modified environments, indirect cues can become uncoupled from their suitability for survival and reproduction, such that preferred habitats may be less productive than other habitats available (Robertson & Hutto 2006). In an experimental study Weldon and Haddad (2005) measured site fidelity and settling patterns of indigo buntings (*Passerina cyanea*) to show that older males preferred to nest in forest patches with artificially-increased forest edge where reproductive success was lower. Similarly, in chestnut-collared longspurs (*Calcarius ornatus*), individuals were equally likely to settle in high quality native grassland and exotic wheatgrass despite experiencing lower nesting success and producing lower quality nestlings in the wheatgrass habitat (Lloyd & Martin 2005). Such maladaptive habitat selection has been termed an “ecological trap” (Dwernych & Boag 1972; Gates & Gysel 1978) and has recently received considerable attention in the literature as a behaviourally-mediated mechanism contributing to population declines in species occupying disturbed landscapes (Battin 2004).

Ecological traps have been shown theoretically to influence population sizes that may lead to extinction if initial population sizes are low (Pulliam & Danielson 1991; Delibes *et al.* 2001; Kristan 2003; Donovan & Thompson 2001). However, strong empirical evidence for the existence of ecological traps remains limited. This may be because ecological traps are rare and restricted to heavily modified environments (Robertson & Hutto 2006; Kristan 2003). Alternatively, the lack of evidence for ecological traps has been attributed to difficulties in measuring habitat preferences of individuals (Robertson & Hutto 2006), the need to link apparent cues to reliable fitness estimates (Arlt & Part 2007) or because the links between habitat preferences and fitness outcomes are measured at the wrong spatial scales (Kristan 2003).

The majority of empirical studies investigating ecological traps have used use-availability data or individual density within a habitat patch as a measure of preference (Robertson & Hutto 2006). In some circumstances density measurements may accurately gauge preference for high quality habitats but this cannot always be assumed (Bock & Jones 2004). Tracking individual decision-making is a more direct and potentially more reliable method of gathering information about habitat preference. In migratory birds the order in which individuals settle on territories has been used to infer habitat preferences but has been notoriously difficult to obtain for most species (Schlaepfer *et al.* 2002; Battin 2004; Robertson & Hutto 2006).

Nesting success is an accurate measure of habitat quality in avian systems because it provides information on the relative predator pressures or availability of safe nesting sites (Martin 1993). While nesting success has obvious fitness consequences for breeding birds, individuals can also select habitats based on other resources. Food abundance, for example, can limit a parent's ability to produce sufficient offspring during a breeding season (Marshall & Cooper 2004; Hart *et al.* 2006; Thomas *et al.* 2001) and therefore represents an additional fitness component that can influencing preference. However, quantifying seasonal breeding productivity can be difficult for many bird species because pairs may re-nest after failure or double brood and linking breeding attempts to particular pairs requires tracking throughout the season.

Ecological traps are thought to be more common in modified environments where human activities introduce new competitors or predators, change agricultural practises or other types of land use (Gates & Gysel 1978; Battin 2004; Schlaepfer *et al.* 2002). Riparian ecosystems are considered to be one of the most degraded and modified habitat types in North America (Dobkin *et al.* 1998; Goodwin *et al.* 1997; Saab 1999; Tewksbury *et al.* 2002). Modifications to water flow by dams and diversions have significantly affected these ecosystems (Goodwin *et al.*1997). Because water is the single most important factor controlling the growth of riparian vegetation (Hupp & Osterkamp 1996) restricting or controlling its influence affects recruitment of willow and cottonwood (Rood *et al.* 1995), controls vegetation structure through forest succession (Stromberg *et al.* 2007) and consequently, the structural and vegetative diversity.

Riparian landscapes in the west also provide critical nesting habitat to more than 60% of western Neotropical migratory bird species (Saab 1999; Dobkin *et al.* 1998; Johnson *et al.* 1977), many of which have experienced pronounced downward trends as measured by North American Breeding Bird Surveys (Sauer *et al.* 1996). Although habitat loss and degradation are implicated in these declines (DeSante & George 1994; Sanders & Edge 1998), ecological traps may further reduce breeding success by attracting individuals to settle in areas that mimic high quality habitat but lead to negative breeding outcomes. Habitat preferences may be influenced by attributes at different spatial scales such as structural diversity of vegetation or continuous shrub associations (Stauffer & Best 1980; Sanders & Edge 1998; Saab 1999). Consequently, developing *a priori* hypotheses on which attributes may be negatively influencing selection patterns presents a major challenge.

In this chapter, I investigated habitat preferences of yellow warblers breeding in highly modified riparian habitat on the Columbia River, British Columbia, Canada and assessed whether there was a mismatch between apparent cues used in selecting breeding habitat and their fitness consequences. Because drastic changes to the flow regime have altered remaining habitat, I predicted a negative outcome to habitat selection patterns in which individuals preferentially settle in habitat with lower reproductive performance. To estimate preference, I contrasted two different models of habitat selection to reveal how different approaches predicted which habitat cues were important for settlement. I then evaluated the relationships between potential habitat cues with two fitness components (nesting success and seasonal fledgling productivity). A negative association between preference and its fitness outcome would provide evidence for an ecological trap. Alternatively, if preferences were unrelated to cues predicting breeding success, this would provide evidence for the ideal free habitat model because earlier birds had equal fitness as later arriving individuals. Lastly, a positive association between preference and fitness outcomes would be evidence of an ideal despotic model because fitness is predicted to be consistently high in the most preferred habitats (Petit & Petit 1996).

Methods

Species & study area

Yellow warblers are one of the most common passerine species breeding in wet, deciduous habitats within the Rocky Mountain west (Tewksbury *et al.* 2002) and the species is recognized as a management indicator of functional sub-canopy/shrub habitats in riparian areas by the USDA Forest Service and Partners in Flight. While most eastern populations remain stable, western populations appear to be declining based on abundance data from North American Breeding Bird Surveys (Remsen, Jr. 1978; Dunn & Garrett 1997; Robbins *et al.* 1989). Province-wide surveys of British Columbia show significant declines over the past four decades [-1.9%, $P < 0.05$, total number of survey routes = 119, 1966 – 2007 (Downes & Collins 2008)]. Loss and degradation of habitat leading to higher nest predation and parasitism are cited as the main causes of declines among western populations (Sauer *et al.* 1996; Ortega & Ortega 2000; DeSante & George 1994). However, analysis of MAPS and BBS data by Saracco *et al.* (2008) show that adult survival may also be an important driver of recent population trends (1992-2003) among different geographic strata of its breeding range.

I monitored habitat selection and breeding of yellow warblers at three sites within the drawdown zone of Arrow Lakes Reservoir, a 240-km long reservoir system in the upper Columbia River valley near Revelstoke, British Columbia, Canada (Fig. 2.1). Water levels in the reservoir, formed in 1968 after the downstream construction of the 52 m high Hugh Keenleyside Dam, range in elevation (ASL) from 422 to 441 m. Flow into the study site is regulated by the power-generating Revelstoke Dam, located less than 20 km upstream. I established three study plots, 30-39 ha in size, in riparian habitat located in the upper reaches of the floodplain (435-441 m) that are periodically disturbed by inundation due to downstream reservoir operations. The site at the highest elevation, Machete Island (437-442 m), included a patch of mature cottonwood forest (*Populus trichocarpa*) with an understorey of riparian-associated shrub species such as dogwood (*Cornus stolonifera*), snowberry (*Symphorycarpos alba*), twinberry (*Lonicera spp.*), and willow (*Salix spp.*). The forest block was edged by willow shrubs, grading out into smaller groupings of isolated willow patches. The Illecillewaet site (436-439 m) was located at the confluence of the Columbia and Illecillewaet rivers less than 2 km from the town of Revelstoke. Habitat here graded from young, regenerating willow along the river course to a narrow strip of mature mixed riparian forest. The third site centred at the mouth of Drimmie Creek (434-439 m) and contained a patchy network of willow-dominated habitat with a narrow band of mixed riparian forest adjacent to upland coniferous forest. When water levels are sufficiently low, riparian patches of all sites are imbedded within a matrix of open grassland habitat consisting of planted fall rye (*Secale cereale*) and reed canary grass (*Phalaris arundinacea*), with horsetail and sedges.

Monitoring arrival dates and breeding performance

All three sites were monitored throughout the breeding season beginning in late April, when migrant birds were observed moving north through the Columbia River valley (Campbell *et al.* 1990), until early August in 2004 to 2006. Each site was surveyed every 1-2 days to determine when males returned to establish breeding territories, band new arrivals, and to resight previously banded birds for subsequent territory mapping. Returning males are easily identifiable because they sing from prominent perches to advertise their presence and aggressively defend territories by chasing other con-specifics (Studd & Robertson 1988). Rigorous attempts were made to capture territorial males within 1-2 days of their return to the study area. Captured birds were banded with a numbered metal Canadian Wildlife Service-issued band and a unique combination of three colour bands. The vast majority of territorial males were banded at all three sites (80% in 2004 and 100% in 2005 and 2006). I recorded the arrival date of all males and tracked the order in which territories were occupied at all three sites. Occupied territories were then ranked based on this settlement order. If several territories were settled on the same day, they were assigned the same mean rank.

Intensive nest-searching and monitoring of all nesting attempts began in mid-May after females arrived to the study area. Nests were typically located by following females while nest-building. Most females and any unmarked males were subsequently captured as they moved to and from the nest. I recorded the UTM locations for all nests using a GPS and checked them daily during egg-laying to determine when clutches were initiated (defined here has the first egg laid by the female), document occurrences of brood-parasitism and record clutch size. I checked nests every 2-4 days during the incubation and nestling phase to determine whether the nests were active, their hatch dates, and brood size. Nests that could not be checked with the aid of a stepladder and pole-mounted mirror were monitored from a distance with a spotting scope. Where possible, nestlings were weighed and banded on day 7of the 9-day nestling period (Lozano & Lemon 1996), the last day to handle young safely without causing premature fledging. I assumed nests fledged all young banded or observed at nests on day 7 if there were no signs of predation and parents were subsequently observed carrying food to fledglings within their territory. Nests were considered successful if they fledged at least one young. Territory productivity was defined as the sum of fledged young from all nesting attempts within a season.

Measuring vegetation and habitat characteristics

At the end of each breeding season I assessed the vegetation cover and habitat characteristics surrounding all nests found within each territory and at random points within each site. To compare vegetation and habitat characteristics of potential nest sites, random locations were chosen by selecting a representative nest substrate within a 5 m distance from a randomly generated coordinate. Initially, overlapping of random locations was a concern because much of the available habitat was represented by smaller patches within the grassland matrix relative to floodplain area. I therefore surveyed points that fell greater than 20 m from previously established points to reduce repeated sampling of the same habitat (Boyce 2006) and maximize coverage of available habitat. However, all random points that fell near existing nest sites were surveyed to comply with use-availability approaches to evaluate habitat selection (Wiens 1984; Martin & Roper 1988). The centres of all random points were required to be within riparian habitat.

Vegetation was measured within circular sample plots at two spatial scales: the nest patch and the territory. At the patch level, I quantified seven variables describing the shrub/understorey layer within a 5 m radius of the nest or random point and six variables describing the forest/canopy structure measured within an 11.3 m radius (Table 2.1). Vegetation was measured by using a modified BBIRD vegetation sampling design for shrub/ground nesting passerines (Martin *et al.* 1997). I also measured two habitat characteristics at the territory scale defined as the two-dimensional riparian habitat coverage within a 50 m radius centred on the nest or random point. These were calculated from a digital vegetation map of the study area developed by walking boundaries of all core riparian areas and larger periphery patches using the tracking feature on a handheld GPS. I defined boundaries as the transition between woody, deciduous vegetation and herbaceous/grassy fields, upland habitat, or waterways. I mapped smaller habitat patches by assigning each to a small, medium, or large patch size class (1.5m, 2.25m, or 3.5m radius circles, which are equivalent to patch coverage of 7, 16, and $38m^2$, respectively) and recorded a UTM waypoint at the approximate centre of each isolated habitat patch. I then downloaded all GPS data into the GIS software package ArcView version 5.1 (ESRI, Redlands, California) and developed a single riparian habitat layer of core and periphery patches. A 50 m radius buffer centred at the nest or random point was used to calculate the territory scale characteristics.

Statistical analyses

I used a multivariate discriminant function analysis (DFA) to assess whether points centred on nests (n = 76) and random points (n = 65) could be distinguished using vegetation and habitat variables. I included the first or only nesting attempt initiated within a territory in each year in this analysis to avoid over-representation of selected habitat. Prior to this analysis, I first transformed all vegetation variables to better approximate normality and assessed the relationships between the 15 measured variables (Table 2.1). Specifically, proportions were arcsine transformed, continuous variables were log-transformed, and count data were square root transformed. Three variables describing forest structure were highly correlated (total cottonwood trees, average canopy height, and percentage canopy cover; $r > 0.70$; Table 2.1); I subsequently selected percentage canopy cover for further analysis because this structural attribute has been shown in other habitat selection studies to be an important predictor of riparian bird species abundance and diversity (e.g., Pearson & Manuwal 2001). The resulting thirteen vegetation and habitat variables were then entered into a stepwise DFA that sequentially removed variables that did not contribute to differences between nest-sites and random locations based on the Mahalanobis distances (Manly 2002; Martin & Roper 1988). I subsequently determined the predictive power of this analysis using the significance of the function, Wilks' Lambda, and the proportion of correctly classified cases. I evaluated the relative importance for each habitat variable by its absolute correlation with the discriminant function, where a loading of 0.3 or greater was considered important in contributing to between-group differences (e.g., Misenhelter & Rotenberry 2000).

I initially used generalized linear mixed models to examine whether the order in which territories were settled, nest success or seasonal fledgling productivity were influenced by vegetation or habitat characteristics. Female identity was entered as a random term in these models as females could be monitored in more than one year of the study and/or initiate more than one nest per year. However, in all models, there was little variance associated with the random term (estimated variance components were close to zero with considerably larger standard errors) so I dropped the random term and used generalized linear models to simplify analyses. Generalized linear models examining settlement order and seasonal fledgling productivity were fitted using a Poisson distribution and logarithmic link function. In these models I used average vegetation and habitat values if data had been collected from more than one nest in a given year. Generalized linear models examining nest success (success = 1, failure = 0) were fitted using a binomial distribution with a logit link function. In each case, I initially fitted a full model containing the 13 vegetation and habitat variables. The final minimal model was obtained by sequentially removing non-significant terms until only significant effects remained. Significance was assessed using the change in deviance that approximates a Chi-square distribution. Variables that had been dropped were back-checked against the minimal model to ensure that order effects did not influence the final model selected. In all models, I examined residuals to confirm assumptions about normality and variance. Analyses were performed in SPSS and Genstat software statistical programs. I report untransformed summary statistics for vegetation/habitat variables for ease of interpretation.

Results

Patterns of territory and nest-site selection

There was considerable variation in the vegetation and habitat characteristics centred on nesting locations within yellow warbler territories and random points within our three study sites (Table 2.2). Five variables helped discriminate between points centred on nests and random points. Overall, the high canonical correlation coefficient (0.770) and Wilks' Lambda (0.640) indicated that the DFA produced a meaningful statistical model a ($P < 0.001$). The variable with the highest loading was shrub stem density, (loading = 0.703), with points centred on nests having higher stem densities than random points. Proportion of riparian habitat cover had the second highest correlation with the DFA (loading = 0.498), with breeding territories having greater coverage of riparian vegetation within a 50 m radius of the survey point. Points centred on nests were also located further from habitat edges (loading = 0.449), placed in vegetation with greater understorey cover (loading = 0.314), and in areas with fewer small patches of riparian habitat (loading = -0.449). The other eight habitat variables had no ability to separate differences between groups (i.e., were poorly correlated with the discriminant function).

Male territory settlement patterns

Males returned to the study area over a 3-4 week period between May 5 and the first week in June. Males maintained their territories throughout the breeding season, with no documented territory switching. Three vegetation and habitat variables were related to male settlement order. Males settled earlier in territories with a higher percentage of riparian habitat cover (effect: -0.51± 0.23, $\chi^2 = 4.64$, $P = 0.035$; Figure 2.2a). Males also settled earlier in territories with less canopy cover (effect: 0.78 ± 0.21, $P < 0.001$; Figure 2.2b) and in habitat with lower proportion of willow shrub stems (effect: 0.36 ± 0.15, $\chi^2 = 5.77$, $P = 0.019$). Order of territory establishment was not related to any other habitat variable.

Influence of habitat characteristics on breeding productivity

Nesting success

I determined the fates for 104 of 107 nests monitored during the study (2004, n=23; 2005, n =35; 2006, n=46) by 78 different pairs. Overall nesting success was 55.8% and was consistent among years ($\chi^2 = 0.311$, $P = 0.696$, df = 2) and did not vary with date ($\chi^2 = 1.09$, P = 0.297). Predation accounted for 69.4% (34/46) of nest failures, nine losses were attributed to abandonment following a parasitism event, and three nests were flooded due to increasing reservoir levels. Thus, differences in predation caused the majority of observed variation in nesting success among territories.

The probability of fledging at least one young decreased when nests were placed within vegetation surrounded by a greater proportion of willow shrubs (effect: -1.31 ± 0.47, $\chi^2 = 8.68$, $P = 0.003$). Nest success also increased when nests were placed under less canopy cover (effect: -1.67 ± 0.75, $\chi^2 = 5.25$, $P = 0.022$).

Fledgling productivity

I monitored breeding performance of 19 pairs in 2004, 24 in 2005, and 35 in 2006 (n = 78). All but two males formed monogamous pairs. Yellow warbler females fledged, on average 2.45 ± 2.03 SD (n = 75, 2 unknown fates) offspring per season. The average number of young fledged per pair did not vary between years ($\chi^2 = 3.57$, df = 2, P = 0.543). I found that only one habitat variable was related to the number of fledglings produced in a season. Amount of riparian habitat cover at the territory scale had a positive effect on fledgling productivity (Fig. 2.3; effect: 0.885 ± 0.072, $\chi^2 = 9.20$, $P = 0.002$). The impact of riparian habitat cover could result simply because high quality individuals return earlier and select territories with high riparian cover. However, the impact of this habitat characteristic remains after controlling for the Julian date of clutch initiation ($\chi^2 = 6.18$, $P = 0.013$), a proxy for male arrival date ($r = 0.660$, $P < 0.001$, $n = 53$) which was a variable not measured in all years. Furthermore, the effect on fledgling productivity could be influenced principally by the reproductive performance of successfully double-brooded territories ($n = 3$). However, when removing the second-brood observations, the model remained robust ($\chi^2 = 7.23$, df = 1, $P = 0.007$). No other vegetation characteristics were important in explaining variation in fledgling productivity.

Discussion

This study showed that yellow warbler habitat use is non-random and demonstrated that habitat features on the floodplain predicted settlement order of territorial males. By settling earlier in territories with greater amounts of riparian vegetation cover, and placing nests in vegetation with less canopy cover, warblers experienced higher overall breeding productivity. These findings are not in agreement with the ecological trap hypothesis because male settlement order was positively related to potential habitat cues in territories that reliably predicted fitness. Instead, habitat selection behaviours by yellow warblers are consistent with the ideal despotic model of habitat selection (Fretwell & Lucas 1970) because individuals settling earlier had higher seasonal reproductive success.

Recent literature suggests that disturbed habitat can still produce maladaptive habitat selection behaviours but in less extreme ways. For example, unlike the classic ecological trap scenario where poor habitats are preferred over high-quality habitats, animals may ‘mismatch’ potential cues by preferring those that confer no fitness benefits while ignoring ones that do. This has been termed ‘non ideal’ habitat selection by Arlt and Part (2007), or ‘equal preference trap’ by Robertson and Hutto (2006) and has been suggested for birds breeding in exotic grassland systems (Lloyd & Martin 2005) and natural shrub steppe habitats (Chalfoun & Martin 2007). Contrary to these studies, yellow warblers were only attracted to habitat characteristics with positive reproductive outcomes. Similar results were noted by Leston and Rodewald (2006) who found no evidence for maladaptive habitat selection for northern cardinals (*Cardinalis cardinalis*) nesting in urban riparian forests.

The relationship between canopy cover and male settlement order illustrates the potential importance of continuous shrub associations rather than mature deciduous forests for yellow warblers settling early on the floodplain of the Upper Arrow Lakes Reservoir in British Columbia. Relationships between deciduous forest canopy structure are well documented (James & Wamer 1982) and generally show Neotropical migrant birds responding positively to moderate levels of canopy cover (Hennings & Edge 2003) . At one extreme, red-eyed vireos (*Vireo olivaceous*), consistently show preferences for territories associated with a high degree of canopy cover/closure associated with mature deciduous forests. Work by Marshall and Cooper (2004) further show that the three dimensional volume of canopy was the best predictor of preference and food abundance, suggesting that canopy cover offers a reliable cue for selecting high quality territories for vireos. Interestingly, results from this study indicate that yellow warblers show preference for the opposite gradient of the same structural attribute. Where vireos appear to select canopy cover based on food abundance, the link I found between nesting success and canopy cover suggests that predator avoidance (or, perhaps parasitism avoidance) influences these preferences. This pattern makes sense because numerous studies show predator densities to be higher in forested riparian patches (Heltzel & Earnst 2006; Cain *et al.* 2003) and high canopy cover can provide perching sites for brown-headed cowbirds to observe movements of host species near nest sites (Ortega & Ortega 2000).

The male settlement results also show the potential importance of the area of riparian habitat for yellow warbler selection behaviour. I argue that earlier males may be selecting for prey abundance indirectly using riparian area as a cue. For a yellow warbler breeding pair, the greatest food demand will likely be during the rearing of chicks. Thus, prey abundance is likely to have its greatest influence on habitat quality later in the season during brood rearing. Because prey abundance can vary greatly from when territories are settled to chick-rearing, cues that remain relatively constant over time are likely to provide reliable information, such as riparian area used in this study. My assertion is further supported by demonstrating how area of riparian habitat at the level of the territory predicts seasonal fledgling production (Fig. 2.3).

The use of two different fitness metrics in this study revealed how yellow warbler breeding productivity was influenced by habitat features at different scales that may represent preference for different resources. As previously mentioned, males that showed preferences for territories with greater riparian cover were able to produce more young during a breeding season. The analysis of warbler nest success, on the other hand, showed that nests placed in more open shrub habitats that included shrubs other than willows were more likely to avoid predation and fledge at least one young, suggesting that smaller scale habitat features were also important for avoiding nest depredation. Taken together, these results indicate that warblers in this study make use of cues at different scales to maximize offspring quantity and potentially reduce the risk of losing a brood to nest predators or parasitism.

By demonstrating links between settlement order, habitat characteristics, and fitness consequences of yellow warbler habitat selection, I provided important evidence to reject the ecological trap hypothesis. To demonstrate unequivocally that an ecological trap exists, however, researchers must verify that because of individual preference for low quality habitat, fitness is reduced leading to a decline in the population (Battin 2004; Kristan 2003). Although warblers appeared to prefer higher quality sites in which breeding productivity was high, I did not measure survival metrics for these individuals, which is a necessary component of an individual's lifetime fitness potential. While most studies focus on fecundity to estimate fitness consequences, such as nest success and clutch/fledgling productivity (Chalfoun & Martin 2007; Remes 2003; Robertson & Hutto 2007), others have assessed fitness consequences of preferred habitats more comprehensively by including survival estimates (Leston & Rodewald 2006; Jones & Bock 2005; Arlt & Part 2007). Given that the fitness metrics used here reflect only recruitment, it is possible that the higher productivity in preferred territories was a compensation for lower survival in these habitats.

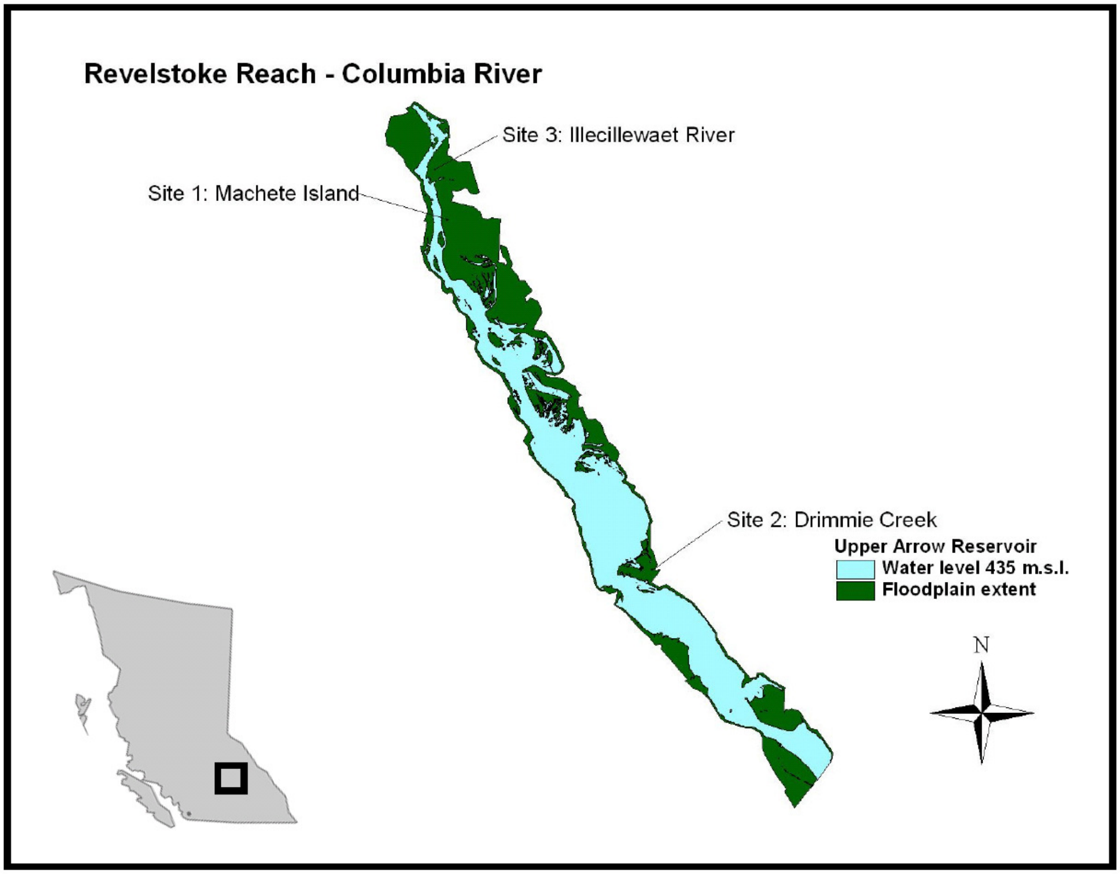


Figure 2-1: Location of floodplain habitat monitored for yellow warbler habitat selection and reproductive productivity from 2004 to 2006.

The study site was located on the northern reach of Upper Arrow Lakes Reservoir near Revelstoke, British Columbia (black box on grey inset). Water levels shown here represent the lowest elevation at which perennial woody vegetation persists following recent flooding events. Site 1 and 2 were established in 2004 and Site 3 was established in 2005. Approximately 20 kilometres separates Site 3 from Site 1.

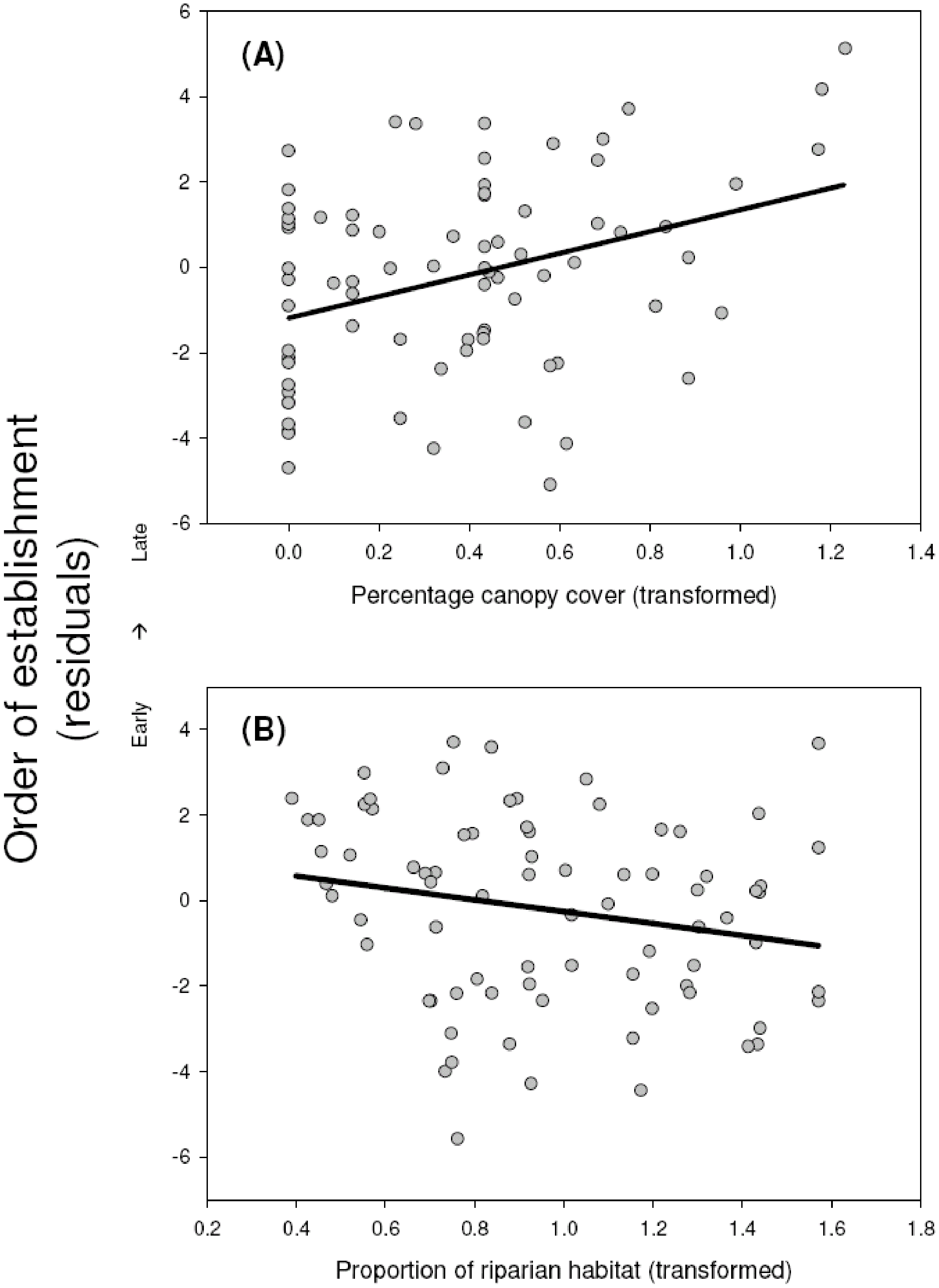
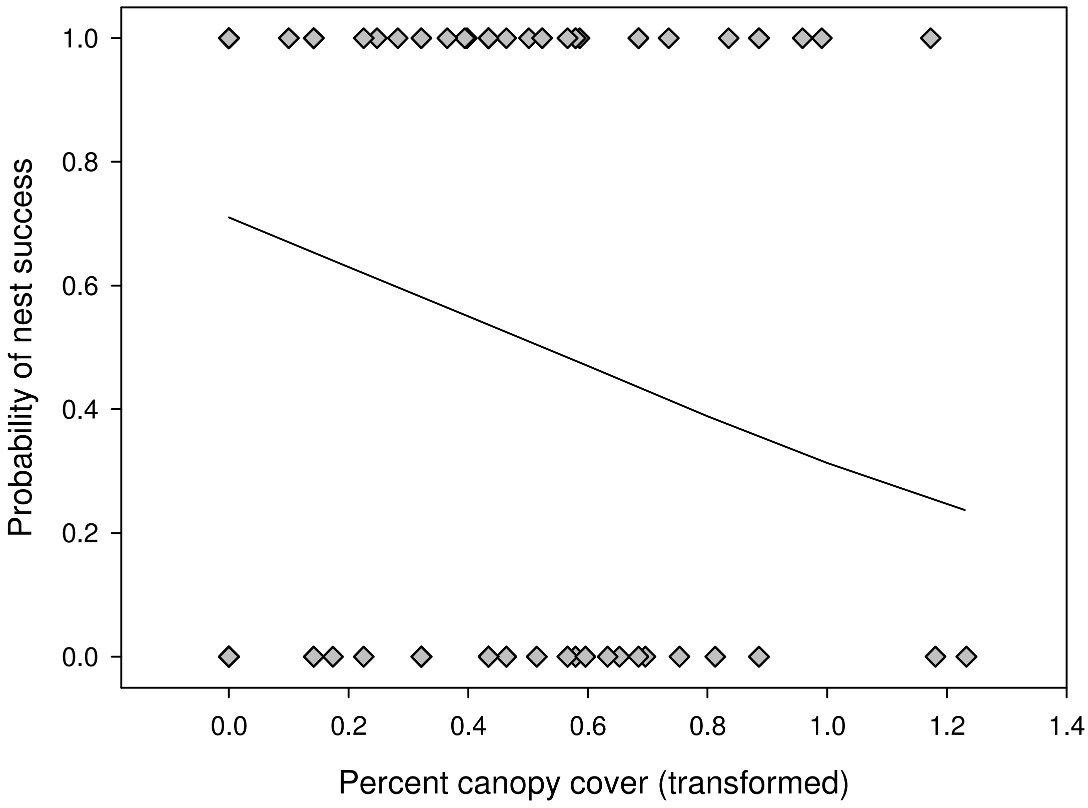

(A)
(B)
Order of estabishment (residuals)
Late
Early
6
4
2
0
-2
-4
-6
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Percentage canopy cover (transformed)
4
2
0
-2
-4
-6
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
Proportion of riparian habitat (transformed)

Figure 2-2: **Relationship between arcsine transformed habitat variables and order of territory establishment by male yellow warblers breeding on Upper Arrow Lakes Reservoir, British Columbia, Canada, 2004–2006.**

Residuals of order of establishment were plotted to control for other variables in final model. Low residual values correspond to early establishment in relation to (A) Percentage of canopy cover and (B) Proportion of riparian habitat area (percentages were arcsine-transformed prior to analysis).


Probability of nest success
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Percent canopy cover (transformed)

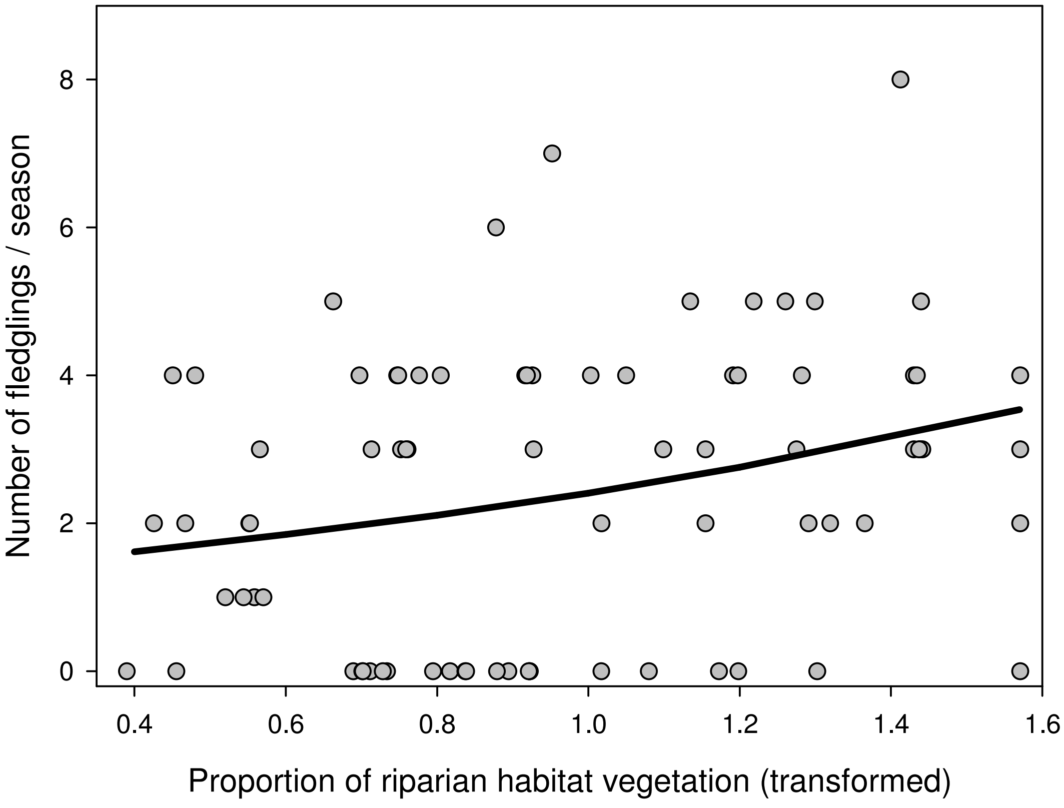

Number of fledglings / season
8
6
4
2
0
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Proportion of riparian habitat vegetation (transformed)

Figure 2-3: **Relationship between arcsine transformed habitat variables and metrics of reproductive performance by yellow warblers breeding on Upper Arrow Lakes Reservoir, British Columbia, Canada, 2004–2006.**

Probability of nest success in relation to percentage of canopy cover above the nest site and (B) seasonal fledgling productivity (no. young fledged per pair) in relation to proportion of riparian habitat coverage within a 50 m radius from the nest site (both arcsine transformed).

Scale	Habitat Characteristic	Explanation
Nest Patch	Nest height* (m)	Measured with ruled meter stick or climometer
	Substrate height^ (m)	Height of nesting substrate measured using a ruled pole.
	Distance from foliage edge (m)	Horizontal distance from the nest site to nearest clear opening of foliage.
	Distance from habitat edge* (m)	distinct transition of open grassland, open water, or upland/coniferous forest.
	Shrub stem density	Number of deciduous stems < 8 cm DBH within 5 m radius of nest or random substrate.
	Percent willow stems (%)	Proportion of willow shrub stems < 8 cm DBH comprising the total number of shrub stems within a 5 m radius of nest or random substrate.
	Shrub stem diversity	Number of shrub species within a 5 m radius. All willow species were categorized as a single species due to limitations in species identification.
	Ground cover (%)	Visual estimation of ground cover as a percentage of total ground within a 5 m radius from nest or random substrate. Area was separated into quadrats to facilitate accuracy.
	1) Forb cover	
	2) Leaf litter cover	
	Understorey cover (%)	maximum height of 5 m. Measured using a densiometer placed at arms' length.
	Canopy cover (%)	subtracting the total overall foliage cover from the understorey cover value (Martin et al. 1997).
	Number of trees	Number of trees > 8 cm DBH within an 11.3 m radius (0.04 ha) from the nest or random substrate.
	1) Cottonwood	
	2) Other deciduous spp.	
	3) Coniferous trees	
	Canopy height^ (m)	Height of substrate selected within an 11.3 m radius representative of overall canopy height.
Territory	Number of patches	Isolated riparian patches within the 50 m radius territory plot including nest patch where applicable.
	Percent riparian cover (%)	Proportion of the riparian vegetation covering total maximum area of the sample territory plot (7812 m^2).

Table 2-1: **Explanations of habitat characteristics measured at nest sites and random locations and the scales at which variables were measured, Upper Arrow Lakes Reservoir, British Columbia, Canada, 2004–2006.**

Proportional variables were arcsine transformed, counts were square root transformed, and continuous variables were transformed using their natural log. ^Measured using ruled pole or clinometer.*Measured only at nest sites.

	NEST (76)			RANDOM (65)		
		95 % CI			95 % CI	
Habitat variable	**Mean**	**Lower**	**Upper**	**Mean**	**Lower**	**Upper**
Nest height (m)	**3.2**	2.3	4.1			
Substrate height (m)	**5.7**	4.3	7.0	**4.7**	3.6	5.9
Distance to foliage edge (m)	**1.5**	-0.2	0.3			
Distance to habitat edge (m)	**21.8**	16.4	27.1	**11.1**	6.9	15.4
Stem diversity	**3.2**	2.6	3.7	**2.9**	2.3	3.4
No. stems	**249.3**	213.9	284.8	**120.1**	94.8	145.4
Willow stem composition (%)	**71.1**	62.7	79.5	**66.6**	57.1	76.1
Forb cover (%)	**3.8**	2.9	4.7	**2.6**	1.8	3.4
Leaf cover (%)	**17.9**	13.1	22.7	**19.0**	13.7	24.4
Understorey cover (%)	**46.3**	34.6	58.0	**36.8**	25.6	48.0
Canopy cover (%)*	**19.6**	14.4	24.9	**25.5**	17.8	33.1
No. cottonwood trees*	**5.2**	3.0	7.4	**7.8**	4.8	10.8
No. conifer trees	**0.4**	0.0	0.8	**0.32**	0.0	0.7
No. Tall shrubs	**1.7**	1.0	2.5	**1.17**	0.5	1.8
Canopy height (m)*	**7.1**	5.8	8.4	**8.1**	6.4	9.8
No. habitat patches	**2.2**	1.3	3.1	**5.2**	3.8	6.6
Riparian cover (%)	**64.6**	58.4	70.8	**44.5**	36.5	52.6

Table 2-2: Means (bold) and 95% confidence intervals (CI) for habitat variables within vegetation plots of nest sites and random locations, Upper Arrow Lakes Reservoir, British Columbia, Canada, 2004–2006.

Sample sizes are shown in brackets. Raw data is presented in table but was transformed prior to analysis. Asterisk indicates intercorrelated variables; only canopy cover was retained for statistical analyses.

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CHAPTER 3: USING MOULT PHENOLOGY AND STABLE ISOTOPE ANALYSIS TO TRACK A NEOTROPICAL MIGRANT THROUGHOUT ITS ANNUAL CYCLE

Abstract

Stable-hydrogen isotopes have become an important tool for tracking individuals and populations of migratory birds throughout their annual cycle. Knowledge of moult phenologies combined with continental gradients of stable-hydrogen (δD) isotopes have the potential to expand the utility of this approach. Using multiple feather tracts from individual yellow warblers, I investigated whether δD in feathers can be used to identify different moulting areas of a Neotropical migratory songbird captured on its breeding grounds. I found that two feathers types presumed to be moulted on the wintering grounds had distinctly different δD values from locally moulted breeding ground feathers. Using likelihood-based assignment tests, I examined whether feather δD values assigned to their predicted regions of growth using expected δD values based on interpolated maps of continent-wide growing season δD values in precipitation and adjusted using a standard discrimination factor. Eighty-eight percent of breeding ground feather samples were positively assigned to their predicted region of moult and only nineteen percent of winter-grown feather samples. However, assignment tests based on winter precipitation δD data estimated that over half of yellow warblers overwintered in Mexico with fewer assigned to southern Central America. Interannual variation in winter-grown feather signatures may reflect ENSO-related changes in climate

potentially introducing bias to assignment tests. Researchers should consider the role of temporal variation in future stable isotope studies when attempting to link Neotropical migrants to their wintering origins.

Introduction

Migratory animals that travel long distances between seasonal habitats are likely to face numerous factors that influence survival and reproductive success at all periods of their annual cycle. Considerable debate has centred on identifying factors influencing population regulation of migratory populations (Sherry & Holmes 1995; Newton 2004; Greenberg & Marra 2005). Long-term declines in species that migrate from temperate breeding grounds to tropical overwintering areas have emphasized the importance of documenting how and where these limiting processes occur (Newton 2004). For Neotropical species, most studies suggest that declines can be attributed to human-induced habitat changes on the breeding grounds. In contrast declines of Palaearctic species have been attributed to drought and desertification on their African wintering grounds (Newton 2004). More recently, however, it is generally agreed that habitat-related processes are likely operating throughout the annual cycle to influence key population demographic rates (Holmes 2007).

Identifying the connections between individuals or populations between seasons has become an important consideration in our understanding of population dynamics in migrant birds (Webster *et al.* 2002). Recent empirical findings demonstrate that events in one season can carry-over and influence reproductive success and/or survival in subsequent seasons (Norris *et al.* 2004a; Marra *et al.* 1998; Saino *et al.* 2004) and theoretical evidence suggests that seasonal interactions may play an important role in population dynamics (Runge & Marra

2005; Norris 2005). However, the degree to which populations are affected by seasonal interactions requires information on the level of geographic connectivity between migratory populations (Webster *et al.* 2002). For example, wintering habitat loss is expected to have greater influences on population dynamics for species with strong connectivity (Esler 2000; Dolman & Sutherland 1995) and therefore, should be important to quantify for species of conservation concern.

Over the past decade, stable isotope analysis of animal tissues has been increasingly used to infer information on past environments for many migratory species (Bearhop *et al.* 2005; Hobson *et al.* 2001; Kelly *et al.* 2002; Chamberlain *et al.* 2000; Hobson & Wassenaar 1997) and advanced our understanding of their migratory ecology (Hobson & Wassenaar 2008). In birds, the collection of feathers (and, to a lesser extent, claw tissue) has proven particularly useful for tracking individuals because these tissues are replaced at specific periods in the annual cycle, which are generally known for most species. The isotopic make-up of these newly grown tissues should therefore reflect the diet or habitat of the animals during the time of synthesis, which, for feathers are generally only a few weeks (Pearson et al. 2003). In particular, measurement of stable hydrogen isotopes (δD) in tissues can be useful for inferring the geographic origins of long-distance migratory organisms. This is due to the recognition that δD values in growing season precipitation gradually decrease (or become 'depleted') from the Gulf of Mexico across the North American continent to higher latitudes in a Northwest direction (Rozanski *et al.* 1993). At the global scale, δD values follow a pattern of enrichment toward the equator.

Using these pronounced latitudinal gradients of precipitation δD (δD_p) pioneering studies by Hobson and Wassenaar (1997) and Chamberlain *et al.* (1997) showed how small Neotropical migrant songbirds captured on their wintering grounds could be traced to their breeding or natal origins using δD values in feathers (δD_f) grown during the previous breeding season. Since these publications, there has been a proliferation of studies using stable-hydrogen isotopes to delineate temperate breeding origins of many North American songbird species (Hobson & Wassenaar 2008). However, this approach has rarely been used to track breeding populations to their previous wintering origins (but see Jones *et al.* 2008; Mazerolle *et al.* 2005).

Results of some studies suggest that δD_f markers may not be useful for tracking migratory wildlife to regions outside North America where broad-scale patterns do not follow well-defined latitudinal gradients (Rocque *et al.* 2006). For example, Pain *et al.* (2004) found high variation and no detectable patterns in δD_f data to infer unknown wintering locations in the aquatic warbler (*Acrocephalus paludicola*). In contrast, wintering populations of blackcaps (*Sylvia atricapilla*) in the British Isles and Portugal where shown to have distinct δD signatures in their claw tissue when sampled upon return to their sympatric breeding grounds in south-central Europe (Bearhop *et al.* 2005). In addition, a recent study by Jones *et al.* (2008) showed how cerulean warblers (*Dendroica cerulea*) captured on their breeding grounds could be linked to their previous overwintering areas in South America with the aid of stable isotope base maps of regional precipitation.

Maps describing ‘isoscapes’ at the level of the continent (Bowen *et al.* 2005; Meehan *et al.* 2004) have reached the scientific literature only recently but represent a potentially powerful new tool to understand how global patterns in δD_p relate to those in animals tissues. Specifically, isoscape maps are visual representations of models that express a continuous, predicted surface of δD_p values over large spatial scales using δD_p data collected from stations situated around the globe. However, in some areas, such as parts of Central and South America, there are much fewer stations collecting data adding uncertainty to spatial interpolations in these regions (Wunder *et al.* 2005). Nonetheless, spatial patterns in δD_p for these regions do exist and may be sufficient for linking individuals to broad regions in their tropical wintering range (Kelly *et al.* 2008).

In this study, I attempt to use δD in feathers to identify tropical wintering regions of individual yellow warblers captured on their breeding grounds in southern British Columbia (Fig. 2.1) and test the utility of existing base maps for these purposes. Yellow warblers are small Neotropical songbirds that breed across North America and overwinter in Mexico, Central America, and northern South America (Lowther *et al.* 1999). Based on known moulting patterns in which some or all of the feathers are moulted during the breeding and wintering periods (Froehlich *et al.* 2005; Ryder & Rimmer 2003; Rimmer 1988; Rohwer *et al.* 2008), I evaluated whether yellow warblers caught on spring migration or upon arrival to the breeding grounds could be linked to both seasons based on differences in δD_f that reflected isotope signatures in these respective environments. Specifically, I predicted that body feather δD values of crown and greater coverts (body feathers) would be enriched whereas tail and primary covert feather (flight feathers) δD values would be depleted relative to body feathers. Based on these predictions, I used likelihood-based assignment tests (Wunder & Norris 2008) to test the hypothesis that continental isotopic base maps provide an accurate reference from which to source feathers of known (summer) and unknown (winter) origin. I then assigned body feathers of unknown origin to different wintering regions using two different sources of information on δD in precipitation: (1) isotope base maps and (2) precipitation δD data obtained over the wintering period at specific sampling stations. My second objective was to explore interannual, age-, and sex-related variation in δD values as these have been shown in other studies to influence interpretation of isotope signatures in feathers.

Methods

Study species

Yellow warblers are a suitable species to evaluate the utility of δD in multiple feather blocks to link breeding and wintering seasons for three reasons: First, yellow warblers have a large wintering range (Mills 2006) in Central and South America, which should increase the probability of detecting differences in winter-grown isotope values. Second, western populations of Neotropical migrants have been suggested to moult-migrate; analysing δD from multiple feather blocks may provide researchers with important information as to whether this is a common strategy for these populations. Third, populations overwinter at relatively low elevations throughout their range (Lynch 1989; Greenberg & Ortiz 1994; Greenberg *et al.* 1996), which should minimize the confounding effect of elevation on isotope signatures during feather growth.

A marked population of breeding yellow warblers has been studied in riparian habitat along the Revelstoke Reach Wetlands (RRW) in south-eastern British

Columbia since 2004 (see Ch. 2). The Wetlands are situated on a floodplain in the upper reaches of the Upper Arrow Lakes Reservoir (49.088 N, 115.678 W; elevation 435-440 m) and surrounded by sleep slopes of coniferous forest to elevations exceeding 2000 m (Fig. 2.1).

Feather collection

I collected feather samples from territorial birds captured in May through July of 2005 and 2006. Males were lured into mistnets using call playback shortly after their arrival while females were captured passively near their nest sites. Unbanded birds were marked with a United States Geological Survey (USGS) aluminium band and a unique combination of three colour bands. The gender and age (SY: second-year or ASY: after second-year) of captured birds was assigned based on morphological and plumage characteristics. I distinguished between males and females based on the presence of an enlarged cloacal protuberance and/or a brooding patch, and SY from ASY birds based on feather wear of the primary coverts, the presence of secondary moult limits, and tail feather shape (Pyle 1997). I obtained feather samples from a maximum of four feather tracts. Specifically, I removed the third outer right tail/rectrix feather (also REC3) and the innermost (proximal or PC1) primary covert[1] that are thought to be replaced during the prebasic moult following the breeding season of the previous year. I also collected 5-6 crown feathers (CRN) and one of the innermost (proximal or GC) greater covert that are thought to be replaced on the wintering grounds between December and April (Pyle 1997) as part of an extensive prealternate moult (Froehlich *et al.* 2005). Crown

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[1] Primary feathers were not sampled because I did not want to influence the flight capabilities of individuals that were surveyed for breeding productivity (See Ch. 2).

feather sampling was limited to the bright orange cap on males and pale yellow crowns contrasting with the greenish-yellow nape in females. I ensured the greater-covert feather collected had broad, uniform yellow edging and avoided feathers having dull olive edges that may not have been replaced during the pre-alternate moult (Fig. 3.2). Feathers were placed in individually labelled paper envelopes and stored in a freezer prior to being transported to a laboratory for cleaning and analysis. The numbers of feather tracts sampled per individual varied because I did not begin to collect greater coverts until midway through the 2005 season and some birds were released if they showed any signs of stress. I monitored all individuals sampled throughout the breeding season to confirm their local breeding status (see Ch. 2).

Laboratory methods and stable isotope analysis

Feather samples were soaked in 2:1 chloroform:methanol solution for 24h, drained and air-dried in a fume hood for an additional 24h to remove excess solvent (Kelly *et al.* 2002). Prior to isotope analysis, I cut and weighted 350 ± 10 μg of feather material into 3.5 x 5-mm elemental analyzer silver capsules. Because feather types differed by size and proportion of vane vs. rachis, I attempted to cut mostly vane to minimize bias related to intra-feather variation in δD composition (Wassenaar & Hobson 2006). Samples collected from the 2005 and 2006 field seasons were analysed at the National Water Research Institute in Saskatoon, Canada in May and December of 2006, respectively. The deuterium composition of the nonexchangeable component of a feather sample was measured using the online pyrolysis and continuous-flow isotope-ratio mass spectrometry (CFIRMS) techniques described by Wassenaar and Hobson (2003). During analysis samples of similar feather types were run together to eliminate potential bias from drift in feather δD values. Repeated analysis of in-house hydrogen isotope intercomparison material was routinely included as a check to eliminate variation owing to isotope exchange with ambient water vapour. Stable-hydrogen isotopes are reported in per mil notation (‰) relative to Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW–SLAP) according to the following notation:

$$\delta X_{\text{std}} = (R_{\text{sample}}/R_{\text{std}} - 1) \times 1000$$

where δX_{std} is the isotope ratio in delta units relative to standard R_{sample} and R_{std} are the absolute isotope ratios of the sample and the standard, respectively. The standard deviation for repeated measurement of an in-house standard was 1.8‰ (n = 30). In addition to these standards, duplicates of the same yellow warbler feather sample (n = 18; CRN and REC3) were analysed and produced a mean difference of 3.2‰ (±0.6 SE).

Data analysis

I first used general linear mixed models (GLMM) to evaluate whether δD_f values varied with feather type. Individual identity was included as a random term in models because individuals contributed up to four feather samples per year and some breeders were sampled in both years. GLMMs were also used to examine whether variation in the δD values of feathers grown on breeding grounds (PC1) and wintering grounds (GC) varied between years or with the sex and age (GC only) of the individual. Significance of the explanatory variable was assessed using the Wald statistic, which approximates a Chi-square distribution. I expected that isotope ratios would differ between sexes because previous research has found latitudinal sex segregation in yellow warblers and other migratory songbird species on the wintering grounds (Catry *et al.* 2004; Cristol *et al.* 1999; Komar *et al.* 2005) but had no *a priori* expectation for how age differences affected δD_f values. I restricted these analyses to PC1 and GC as these feather groups exhibited less variation that could be attributed to moult migration or sampling error (see Results, Ch. 3).

To explore whether different feather tracts of the same moult had similar δD_f values (and hence, were likely replaced at the same time), I investigated correlations using Pearson r-values between δD_f values of REC3 and PC1 samples, and CRN and GC, obtained from the same individual.

Assignment tests to region of moult

I tested whether feathers purported to be grown in either the breeding or wintering grounds have isotope signatures consistent with those expected based on interpolated isotopic base maps available at (www.waterisotopes.org) for North and South America. Specifically, I used a likelihood-based assignment test to estimate the probability that a feather with a given δD_f value originated from its expected range. I first derived expected mean and SD values of δD_p from an equal-area grid of long-term average growing season δD_p (Bowen *et al.* 2005) for the breeding and wintering region using ARCGIS software (ESRI, Redlands, California). Because I expected PC1 samples to reflect a local breeding site signature I conservatively defined a 500 km buffer centred on Revelstoke, British Columbia constrained by the western slope of the Rocky Mountains where the highest number of breeders in summer occur (Campbell *et al.* 1990). I defined the potential wintering range to include mainland areas defined by Ridgely *et al.* (2003) from Mexico, Central America and northern South America. I further constrained these regions by the elevational ranges yellow warblers are known to occupy in each season (Breeding grounds: < 1450 m in British Columbia, Campbell *et al.* 1990: wintering grounds: < 600 m; Greenberg *et al.* 1996; Lynch 1989; Greenberg & Ortiz 1994). I adjusted means using a discrimination factor of -19‰ to account for isotopic fractionation of deuterium when it is transferred and propagated from precipitation into animal tissues (Wassenaar & Hobson 2001; Langin *et al.* 2007; Mazerolle & Hobson 2005; Hobson & Wassenaar 1997). Using the adjusted mean (δD_X) and SD values for the breeding and wintering regions, I then calculated the likelihood that each δD_f observation (two for each individual: breeding- and wintering-grown feather) originated from a region's expected probability distribution of δD_X values as:

$$f(y^* \mid \mu_b, \sigma_b) = \frac{1}{\sqrt{2\pi}\sigma_b} \exp\left[-\frac{1}{2\sigma_b^2}(y^* - \mu_b)^2\right]$$

where μ and σ are the mean and SD of δD_X for each region and y^* is the δD value for a given feather sample (Royle & Rubenstein 2004). I normalized the likelihood values using Bayes' Rule to interpret these results in terms of probabilities of assignment (Wunder & Norris 2008). Each δD_f observation was considered to have originated from the predicted region of moult if its probability of assignment was > 50%.

Assigning birds to winter regions

I also calculated likelihood-based assignments for two sub-regions of the yellow warbler wintering range: Mexico and Central America (Figure 3.3) using the same methods described above. I limited assignment tests to these regions because previous work on yellow warblers suggested that South American regions (Venezuela) were dominated by individuals with the eastern haplotype and none with a western form (Boulet *et al.* 2006). However, after deriving the mean ± SD for these sub-regions, there was little difference between expected δD_X values (Table 3.2). Significant overlap between the probability distributions for the wintering regions may be related to uncertainty associated with the spatial interpolation of the isotope base maps (Wunder & Norris 2008), which were developed more recently than the North American maps. Thus, in order to maximize the predictive resolution of the assignment-based likelihood tests, I chose to develop complimentary probability distributions for the same regions using non-interpolated δD_p data sampled only during the wintering period from the GNIP/ISOHIS database (IAEA 2007). To do this, I extracted monthly mean δD_p values collected between October and March at the following three locations: Veracruz, Mexico; 10 sites in North-west Costa Rica; and Panama Canal, Panama (all sites were < 600 m elevation). I then calculated mean δD_X values ± SD for each location over the 6-month period to reflect a winter-season specific signature[2]. I made certain that all sites had rainfall measured for δD_p over multiple years (in some cases, over decades) to reduce influences of climatic variations in δD_p values (Farmer *et al.* 2008). The resulting δD_X mean ± SD values showed greater variability among regions than from the

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[2] Although I initially considered limiting this ‘isotope window’ to overlap more realistically with the winter-moult period (Jan-Mar) as done by Greenberg et al. (2007), Hobson (2005) suggested researchers resist breaking down the IAEA data set into monthly averages because we expect food webs to reflect seasonal patterns in δDp rather than short-term variations.

interpolated GIS-based data, thereby increasing the confidence of assignments (Table 3.2). Lastly, I completed assignment tests based on the probability distributions derived from (1) the interpolated map and (2) precipitation data from the GNIP database using the same methods described above. I assigned each feather to the region for which it had the highest probability of assignment [i.e., $> f(y^* | b)$] and calculated the proportion of birds estimated to be wintering in each sub-region. To asses which approach yielded the most accurate results, I examined the magnitude of assignment probabilities, with the highest probabilities having the highest confidence of assignment.

Results

Feather moults

I collected 216 feathers from 70 individuals breeding in the Revelstoke Reach Wetlands in 2005 and 2006. Twenty-eight birds sampled were known breeders the previous year and were thus of known breeding origin and fourteen of those were sampled in 2005 and 2006. The isotope data was stratified by sex (male = 36, female = 34), and age (SY = 20, ASY = 49; unknown = 1). I found large differences in the δD_f values of yellow warbler feathers collected from different feather blocks (Fig. 3.5; Wald = 1877, df = 3, $P < 0.001$). As predicted based on expected moult phenologies, δD_f values were most depleted in REC3 and PC1 samples and most enriched in CRN and GC samples with little overlap between samples (Fig. 3.5). This indicated that summer- and winter-grown feather blocks were grown in temperate and tropical regions, respectively. There were two highly enriched REC3 samples, representing 5% of the sampled population, suggesting that, in rare cases, some tail feathers are moulted on migration. Similarly, two CRN samples had relatively depleted values (Fig. 3.5; -113.4 and 101.7‰) suggesting either these were moulted on migration or because of sampling error (e.g., one or more of the crown feathers in sample were adventitiously replaced during spring migration).

Individual isotope signatures in prebasic feather and prealternate feathers were correlated (prebasic: r = 0.348, n = 42, *P* = 0.012; prealternate: r = .478, n = 56, *P* = 0.001). The correlation for prealternate feathers was strengthened when the outliers were removed (r = 0.611, n = 55, *P* < 0.001).

The δD_f values of PC1 samples did not vary significantly between years (Wald = 1.19, n = 42, *P* = 0.282; Fig. 3.6). There was also no evidence that δD_f values varied with gender (male: -132.0 ± 7.2, female: -131.0 ± 7.5, Wald = 0.17, n = 42, *P* = 0.68). Unlike REC3 or PC1 samples, however, δD_f values of GC varied significantly between years with 2006 samples more enriched than 2005 (GC: Wald = 5.62, df = 55, *P* = 0.021; Fig. 3.6). Repeated sampling of individuals across years also demonstrated the same pattern: birds returning to breed in 2006 had significantly more depleted mean δD_f values (2005: -18.7 ± 16.8‰; 2006: -42.3 ± 12.5‰, t-test = -13.2, df = 13, *P* <0.001). After controlling for differences between years, winter-grown δD_f values were not influenced by the sex or age of the individual (Age effects: Wald = -0.17, df = 1, *P* = 0.44; Sex effects: Wald = 0.21, df = 1, *P* = 0.32).

Geographic assignment of feathers to season of moult

Feathers grown in the Revelstoke region or southeast British Columbia would be expected to have δD_x values of -133.4 ± 9.4‰ based on expected interpolated data from North America isotope maps (Table 3.2). δD_f of PC1 samples known to have grown on or near the breeding grounds had δD_f values of -132.0 ± 7.1 (n = 42). Eighty-eight percent (37/42) had assignment probabilities predicting breeding ground signatures (with a probability of assignment of >0.5). When using an assignment probability of 0.8, assignment confidence of these feathers was lower (48% or 20/42). Only 19% (11/57) of the GC samples were predicted to have originated from the wintering grounds based on assignments using Central and South American isotope maps. When an 80% probability of origin was applied, only 5% were assigned to the predicted wintering origin (3/57). δD_f values of GC were more enriched than expected (δD_f: -26.6 ± 13.3‰; δD_X: -48.1 ± 6.3‰) suggesting that these feathers were not grown north or south of their wintering grounds.

Geographic assignment of feathers to wintering regions

Based on the 10 reliably assigned greater covert feathers, 100% of yellow warblers wintered in Mexico and none in Central America. Forty-four percent of these assignments were from 2005 samples (4/9) and only 14% were from the 2006 dataset (7/49). Assignment tests based on probability distributions from precipitation δD_p data estimated 55% of birds originated from Mexico (Veracruz), 28% from Costa Rica, and 17% from Panama (Table 3.3).

Discussion

This study provides evidence that feathers sampled from yellow warblers on their breeding grounds can be differentiated based on δD incorporated from local food webs during moult on the breeding and wintering grounds. These results support prior research describing seasonal moulting phenology in this species and others in the Parulidae family (Froehlich *et al.* 2005; Voelker & McFarland 2002) in which different feather tracts are replaced in different seasons as part of a biannual moulting strategy. For yellow warblers, multiple feather tracts for both the prebasic and prealternate moults show similar δD signatures, which provide future studies with a feather sampling approach to assign this species to previous breeding and wintering origins, respectively.

δD breeding-ground signatures

Stable isotope analysis of δD values in feathers has become a widely applied tool to link birds captured on the wintering grounds (or en route during migration) to their previous breeding origins (Hobson & Wassenaar 2008). The success of this approach has been supported by isotope base maps created to represent the known latitudinal gradient of spatially distinct δD patterns expressed in precipitation (Bowen *et al.* 2005) and confirmed for feathers grown in these regions (Hobson & Wassenaar 1997). By using summer-grown PC1 feathers of known origin, I found that the North American base map provided an accurate reference from which to assign yellow warbler breeding origins. Although these results were expected, they complement those of a similar study by Langin *et al.* (2007) that tested assumptions about the accuracy of North American maps for assigning birds to previous breeding origins. Furthermore, because this study was carried out in a western landscape in which topographic relief and dynamic water sources would be predicted to contribute confounding variation to δD_f samples, I show that such concerns may not be warranted (Hobson 2005).

The present study found that 12% of all breeding samples could not be accurately assigned their known origin of growth. This result was not surprising because I applied a restricted geographic range from which to estimate the likelihood-based assignments. Other studies, typically used larger regions that attempt to encapsulate continent-wide patterns in δD or centres of breeding abundance (Norris *et al.* 2006; Girvan *et al.* 2007) or even conservation regions (Girvan *et al.* 2007). Increasing the predicted origin of growth for the breeding grounds would have increased the proportion of assigned feathers because of larger standard deviations applied to the assignment tests. I also found that these misclassified samples all had enriched δD_f values, suggesting few occurrences of moult migration. However, this is not likely the case as Powell and Hobson (2006) provided a number of other competing explanations as to why one would observe enriched δD values for summer-grown feathers. They argued that enriched wood thrush (*Hylocichna mustelina*) feathers were likely caused by heat stress experienced during moult on the breeding grounds. By contrast, I might have expected that δD in yellow warbler summer-grown feather would be more depleted because of the aforementioned local effects of topography and/or influences from the large seasonally active hydroelectric reservoir adjacent to the study site. The negative effect of altitude on δD concentration in rainfall is well established (Bowen *et al.* 2005) but the fact that yellow warblers sampled in this study originated from a low elevation riparian habitat may explain why no depletion was observed in the δD values.

Moult migration has been cited as a strategy more common to populations of Neotropical migrants in western North America than eastern populations (Rohwer *et* *al.* 2008; Carlisle *et al.* 2005). The relatively consistent stable isotope ratios in yellow warbler breeding feathers provided evidence that moult-migration appears to be rare in this yellow warbler population. One could argue that the few southerly-biased enriched feathers not assigned to the breeding region reflect moult-migration. Two reasons make this interpretation unlikely. First, some of these individuals were observed to be actively moulting within their territories during the post-fledging period (SPQ, *personal observations*). Secondly, moult-migration as described by Rohwer *et al.* (2005) involves populations postponing moult until arriving to the monsoon region of southwest United States and Mexico. Because thousands of kilometres separate Revelstoke from these areas, it would be expected that moulted feathers would show more enriched δD values relative to those observed in this study. I propose that the two highly enriched outliers observed in the tail feather δD data are likely the result of adventitious regrowth of feathers on the wintering grounds. Similar results were found by Reudink et al. (2008) who re-examined results reported by Norris *et al.* (2004b) and found that infrequent δD enrichment in American redstart (*Setophaga ruticilla*) tail feathers were mistakenly interpreted as reflecting moult migration.

δD wintering-ground signatures

To date, there have been few attempts to link Neotropical birds to unknown wintering grounds using stable hydrogen isotopes. However, recent work on cerulean warblers (*Dendroica cerulea*) by Jones *et al.* (2008) provided preliminary evidence that winter-grown feathers can provide important information for describing migratory connectivity in a species of conservation concern. By confirming that greater covert and crown feathers contained similar isotopic information in yellow warblers, I demonstrated that the prealternate moult is extensive and likely occurs while birds are sedentary on the wintering grounds. Whereas crown feathers have provided wintering signatures for previous studies in migrant songbirds (Jones *et al.* 2008; Mazerolle *et al.* 2005; Greenberg *et al.* 2007) this study demonstrated that greater coverts can also provide similar isotopic information. Thus, in migratory birds that replace both feather types during the winter, greater coverts may be preferable to crown feathers because their larger size mean only one feather is required for analysis (Smith *et al.* 2008).

Geographic assignment of greater covert feathers showed that most warblers previously wintered in the northern reaches of its range but more depleted δD values also suggested considerable mixing of this breeding population to more southerly regions of Costa Rica and Panama. The large range in observed δD values relative to summer-grown feathers also indicated diffuse patterns of geographic connectivity throughout Mexico and Central American wintering areas. This result would be consistent with results by Boulet *et al.* (2006) who found that birds wintering in Panama had equal proportions of eastern- and western-breeding individuals by examining east-west haplotypes of overwintering individuals. These results indicate that although there may be considerable mixing of individuals across the wintering range, western populations may be found at higher concentrations in the northern portions of its wintering range.

Interannual variation in δD signatures

Interannual variation in δD is a fundamental source of uncertainty for stable isotope applications for studies assigning migratory animals to previous geographic areas (Farmer *et al.* 2008). In this study, I detected no interannual variation in summer-grown feathers but did for winter-grown feathers. Atkinson *et al.* (2005) reported interannual differences in δD values of red knot feathers grown on their Caribbean and South American wintering sites. These authors argued that temporal differences in δD_f were a reflection of broad-scale changes in climatic patterns across the knot wintering range. Yellow warbler δD data in my study may also be influenced by similar climate patterns. First, extreme phases of the ENSO (El Nino/Southern Oscillation) cycle are known to have important influences on precipitation patterns in Mexico (Ropelewski & Halpert 1987) and also δD concentration in rainfall (Bowen *et al.* 2005). Secondly, available data on the Pacific sea surface temperatures (SST) that define these extreme weather episodes show that the SST values reflected an El Nino event in the winter of 2005 and a La Nina event in the winter of 2006 (defined as SST consistently above or below the 0.5°C threshold for a minimum of 5 overlapping season (NOAA 2009)]. Thus strong differences experienced in Mexico during these ENSO phase extremes provide a reasonable explanation describing interannual differences in winter-grown feather δD. Although, further investigation into the relationship between δD_p and δD_f in tropical wintering regions is warranted, I suggest that sufficient climatic evidence is available to reasonably state that winter-grown feathers are likely to be influenced more strongly than feathers grown in temperate regions of western North America.

Isotopic base maps of δD_p have been used successfully as spatial references for studying movement patterns in migratory species but recent studies suggest temporal and spatial variation in these gradients need to be explicitly considered when designing isotope studies that rely on these maps (Farmer *et al.* 2008). I demonstrated that yellow warbler feathers could be assigned to their breeding grounds with higher accuracy using isotope base maps than to their wintering grounds. While the mechanisms behind the discordance are not completely clear, I propose that strong weather patterns induced by ENSO-related events are likely to confound future studies using these techniques to link birds to previous wintering origins. Of particular importance will be to collect data over multiple years because unpredictable changes in climate patterns in tropical regions may lead to misleading results for assignment tests based on long-term isotope base maps.

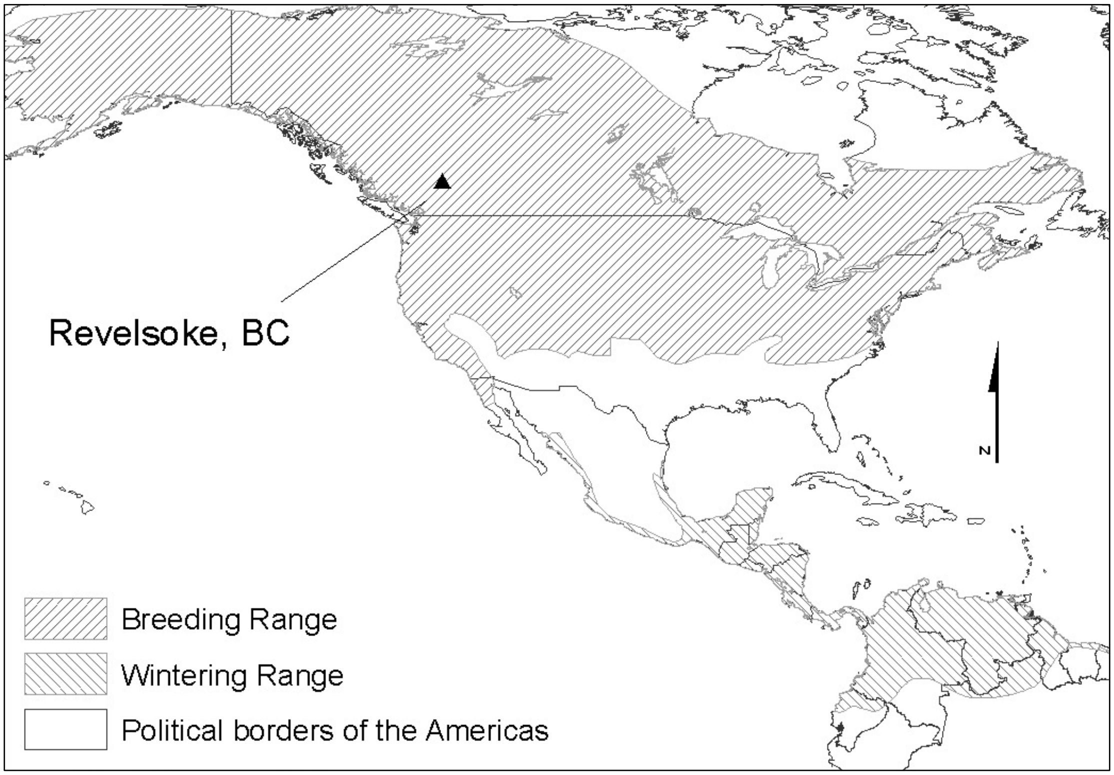

Figure 3-1 **Breeding (northeast hatch) and wintering (northwest hatch) ranges of the northern yellow warbler (*Dendroica petechia; aestiva* group).**

Yellow warbler feather samples for the study were collected near Revelstoke, British Columbia, Canada. Prebasic feathers were predicted to have been moulted on the breeding grounds near Revelstoke and prealternate feathers predicted to have been moulted on the wintering grounds.

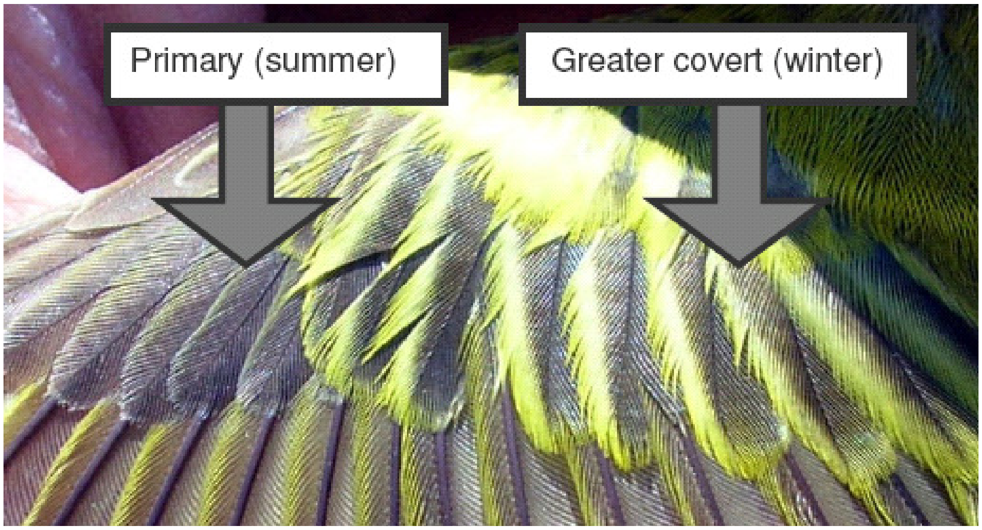

Figure 3-2 Adult (ASY) yellow warbler (*Dendroica* petechia) wing with primary covert feather (PC1) on distal and greater coverts (GC) on proximal end.

Primary coverts are replaced sequentially with primary feathers following breeding in late summer prior to fall migration. The presence of fresh broad yellow edging on primary coverts is used to identify an ASY individual. All greater coverts are usually replaced on ASY individuals and only partially replaced in many SY birds.

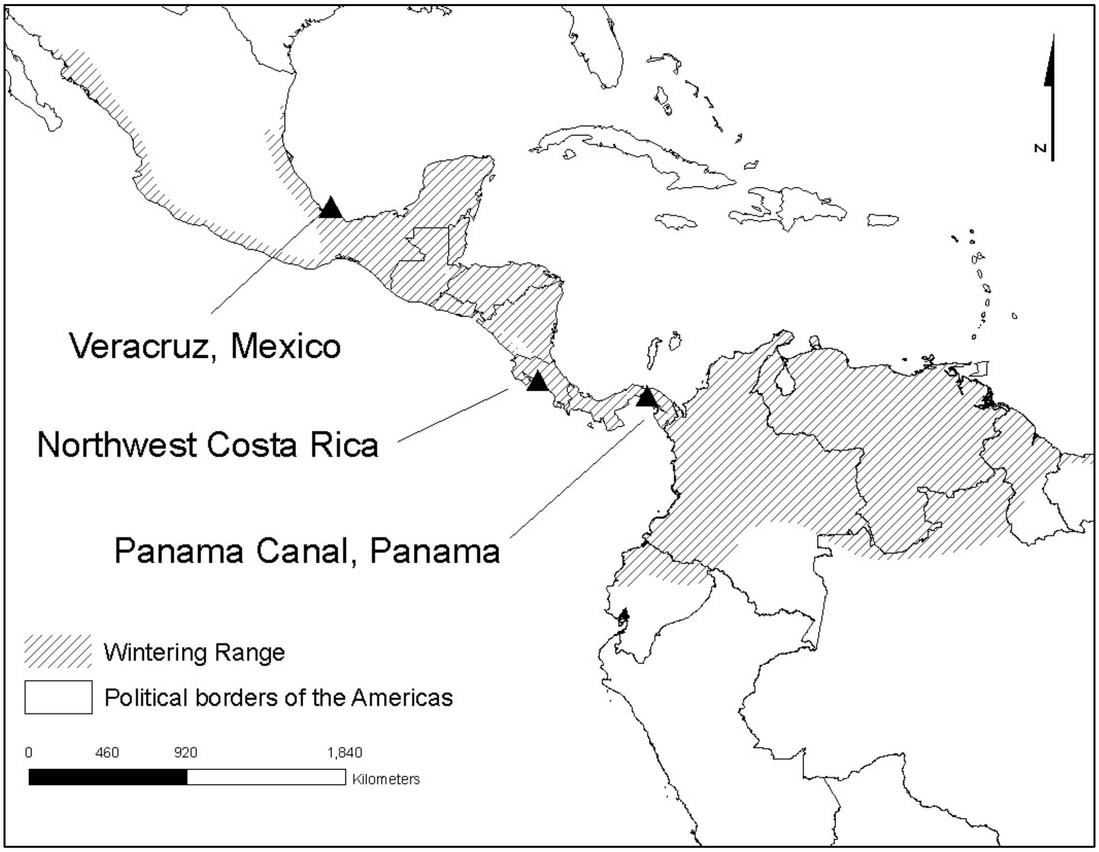

Figure 3-3: **Sampling stations reported in the Global Network Isotopes in Precipitation database from which average monthly δD_p data were obtained for winter months (October to March).**

Precipitation δD data for Veracruz was collected for 18 years (1962–1988), Costa Rica for 3 years (1990–1992), and Panama for 23 years ((1968–1997). All stations were at elevations under 600 m.

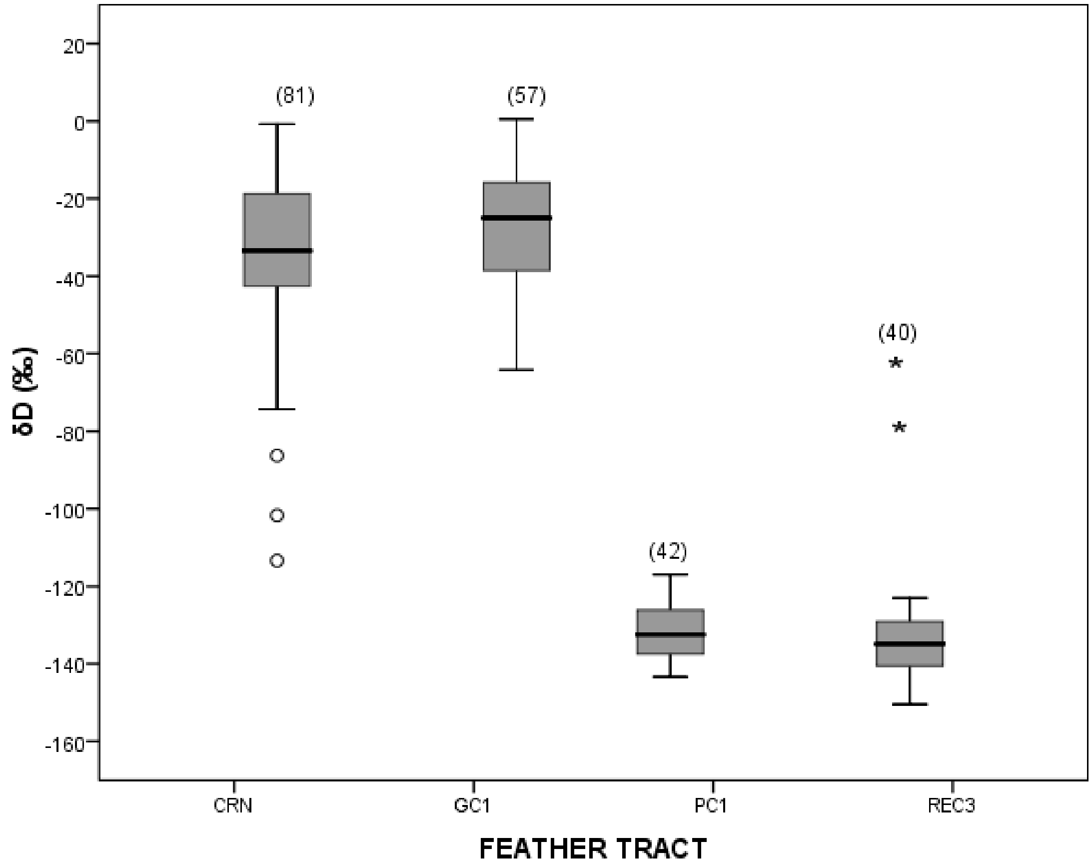

Figure 3-4 Box plot (median, interquartile ranges, and outliers) comparison of feather tracts sampled from birds captured near Revelstoke, British Columbia, Canada during the spring of 2005 and 2006.

Crown feathers (CRN) and greater coverts (GC) represent prealternate feathers moulted on the wintering grounds and primary covert (PC1) and tail feathers (REC3) represent prebasic moult on the breeding grounds.

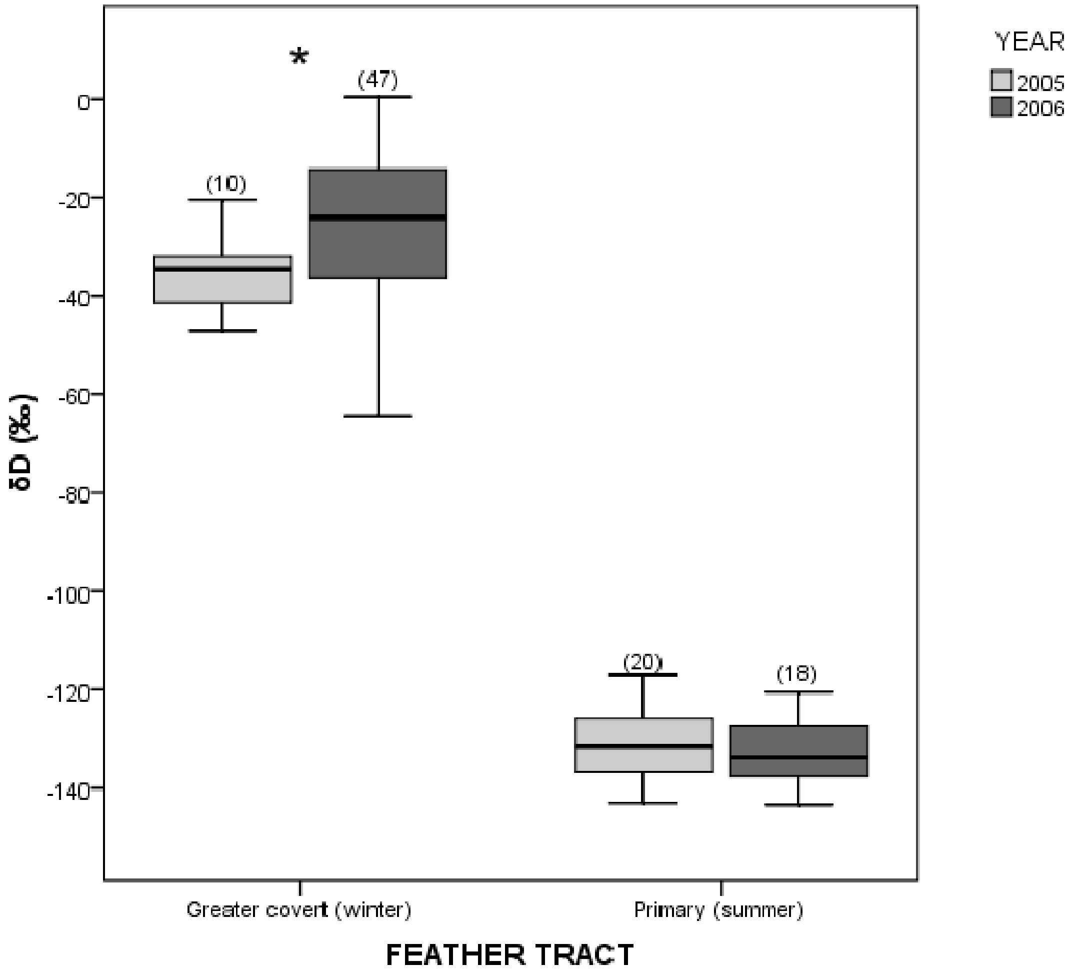

Figure 3-5: Box plot (median, interquartile ranges, and outliers) comparison of representative winter-(greater covert or GC) and summer-grown (primary covert or PC1) feather tracts sampled from birds captured near Revelstoke, British Columbia, Canada during the spring of 2005 and 2006.

The asterisk indicates a significant difference between years (Wald = 5.62, df = 55, *P* = 0.021). Sample sizes are in parentheses above box plots.

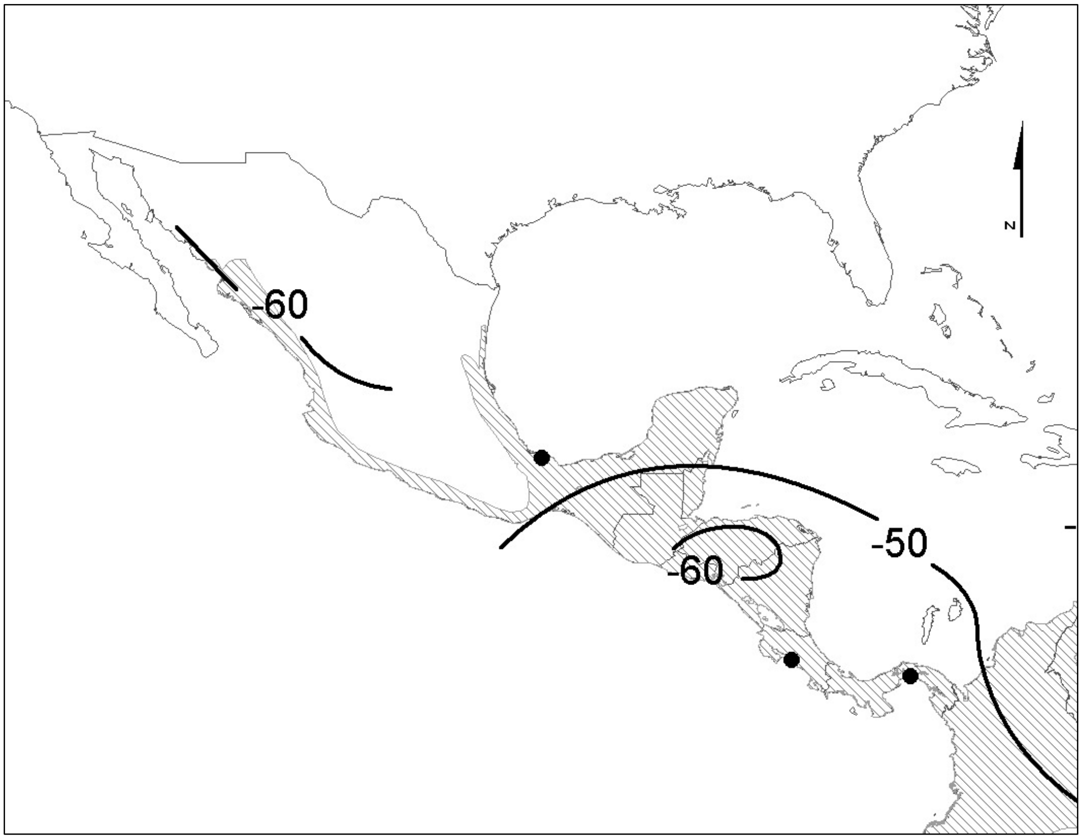

Figure 3-6: Spatial distribution of expected hydrogen isotopes (δD_X) in winter-grown yellow warbler feathers in Central and South America.

In general, isoclines of δD values show broad spatial patterns of reduced values in southern Central America and higher values in northeastern South America and Mexico (Data available at www.waterisotopes.org). Dots represent rainfall sampling stations from which interpolated GIS-based maps of predicted δD values were developed.

Table 3-1: Summary statistics for results of stable-hydrogen isotope analysis of four feather types collected from 33 and 51 individuals near Revelstoke, British Columbia, Canada, in2005 and 2006, respectively.

Means ±SD and samples sizes of δD values (‰). All samples were analyzed at the National Water Research Institute in Saskatoon, Saskatchewan, Canada.

	2005			**2006**			**TOTAL**		
Feather Type	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**
Winter-grown									
Crown	-47.1	16.4	29	-25.3	19.8	52	-33.1	21.3	81
Greater covert	-35.5	8.7	7	-25.3	13.4	50	-26.6	13.3	57
Summer-grown									
Primary	-131.3	7.7	22	-132.8	6.6	20	-132.0	7.1	42
Tail	-132.2	21.1	21	-131.0	5.4	19	-131.6	15.5	40

Table 3-2: Stable hydrogen isotope values (δD ‰) with means ± SD for summer and winter moulting regions of the yellow warbler calculated from interpolated isotope base maps and from precipitation after correcting for a discrimination factor of -19‰ .

Source	Region	Predicted mean isotope *signature* (‰)	SD
Interpolate base map	Southwest BC	-133.4	9.4
	Wintering range	-48.1	6.3
	Mexico	-48.6	5.3
	Central America	-54.2	3.7
GNIP rainfall stations	Veracruz, Mexico	-18.1	20.0
	Northwest, Costa Rica	-51.1	16.5
	Panama Canal, Panama	-36.9	15.2

Table 3-3: **Yellow warbler greater covert δD values (‰, n = 57), the year of feather sample collection, assigned winter region of moult and individual assignment probabilities.**

Feather δD values were compared to precipitation δD values extracted from three regions: Veracruz, Mexico; northwestern Costa Rica; and Panama Canal, Panama. Feather δD values were assigned to all three regions and most likely origin of moult was determined to be the assignment with the highest probability.

Greater covert deltaD value	Year	Assignment region (stations)	Assignment probability
-49.0	2006	COSTA RICA	54.4%
-47.0	2005	COSTA RICA	51.6%
-44.6	2006	COSTA RICA	48.1%
-43.3	2006	COSTA RICA	46.0%
-42.9	2006	COSTA RICA	45.4%
-42.4	2006	COSTA RICA	44.5%
-41.7	2005	COSTA RICA	43.4%
-41.5	2006	COSTA RICA	42.9%
-41.3	2006	COSTA RICA	42.6%
-41.2	2005	COSTA RICA	42.6%
-40.3	2006	COSTA RICA	41.0%
-39.1	2006	COSTA RICA	39.0%
-38.6	2006	COSTA RICA	38.1%
-38.6	2006	COSTA RICA	38.0%
-36.2	2006	COSTA RICA	34.0%
-42.2	2005	COSTA RICA	44.2%
-35.1	2006	PANAMA	37.9%
-34.3	2005	PANAMA	38.2%
-32.4	2005	PANAMA	38.7%
-31.6	2005	PANAMA	38.9%
-31.0	2006	PANAMA	39.0%
-31.0	2006	PANAMA	39.0%
-30.7	2006	PANAMA	39.1%
-29.8	2006	PANAMA	39.2%
-28.7	2006	PANAMA	39.4%
-28.6	2006	PANAMA	39.4%
-28.5	2005	MEXICO	39.5%
-26.7	2006	MEXICO	42.0%
-26.4	2006	MEXICO	42.4%
-25.0	2006	MEXICO	44.3%
-24.9	2006	MEXICO	44.4%
-24.2	2006	MEXICO	45.5%
-23.9	2006	MEXICO	45.8%
-22.4	2006	MEXICO	47.8%
-21.8	2006	MEXICO	48.6%
-20.8	2006	MEXICO	49.9%
-20.6	2006	MEXICO	50.1%
-20.4	2005	MEXICO	50.3%
-18.3	2006	MEXICO	52.8%
-18.0	2006	MEXICO	53.2%
-17.5	2006	MEXICO	53.7%
-17.3	2006	MEXICO	53.9%
-16.8	2006	MEXICO	54.5%
-15.8	2006	MEXICO	55.5%
-14.8	2006	MEXICO	56.6%
-14.2	2006	MEXICO	57.2%
-14.0	2006	MEXICO	57.4%
-13.8	2006	MEXICO	57.5%
-13.7	2006	MEXICO	57.7%
-13.4	2006	MEXICO	58.0%
-13.1	2006	MEXICO	58.2%
-12.3	2006	MEXICO	59.0%
-11.9	2006	MEXICO	59.4%
-8.5	2006	MEXICO	62.2%
-7.8	2006	MEXICO	62.7%
-6.0	2006	MEXICO	64.0%
-4.6	2006	MEXICO	64.9%
0.5	2006	MEXICO	67.9%

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CHAPTER 4: GENERAL DISCUSSION

This study addressed direct and indirect factors considered to influence breeding productivity for a Neotropical migratory songbird breeding in western North America. Using the yellow warbler as a model species, I showed in Chapter 2 that even in highly modified habitats, earlier arriving males settled disproportionately in habitats that increased their breeding productivity. These results provide evidence that the study site was not acting as an ecological trap for yellow warblers but additional research is warranted to test this hypothesis using alternate predictions (e.g., high breeding productivity is a compensatory mechanism for lower survival in juveniles). In Chapter 2, I demonstrated how warblers carried isotopic information in different feather tracts relating to both their breeding and wintering periods. Assignment tests and higher variation among winter-grown δD values showed that within a single population of breeding birds, there might be significant dispersal among geographic regions on the wintering grounds and likely weak migratory connectivity in this population. I was also able to confirm some important assumptions in isotope research, namely that feathers grown in temperate North American landscapes with high isotopic variability are useful for linking birds to these regions and interannual variation is likely to explain additional variation in winter-grown signatures.

Are dammed riparian habitats in the west ecological traps for breeding Neotropical migrants?

I found no evidence for an ecological trap but I did detect variation in productivity based on specific habitat features that are, or can be, directly impacted by reservoir operations on the Revelstoke Reach Wetlands. For example, birds appeared to prefer territories with sparse or open canopies while avoiding more forested habitats. These observations were interpreted as adaptive selection behaviour because they also increased breeding productivity. However, during flood events which have occurred in seven of the last twelve years (1994-2006), open habitats flood earlier and for longer durations. Forested habitat, which is situated at higher elevations, is consequently disturbed less frequently. It is possible that the Revelstoke Reach acts as an ecological trap only during periods of high water levels.

δD isotope signatures in winter-grown feathers

Using stable-hydrogen isotopes measured from feathers collected on the breeding grounds, this study provided baseline information for future Neotropical migrant research. First, I demonstrated that individual birds carry markers reflecting both seasons of their annual cycle. Because yellow warblers have similar moulting patterns to other Parulidae species, sampling techniques used in this study may be useful in studies of other related species, especially those of particular conservation concern. I also demonstrated that isotopic base maps of Central and South America do not provide a useful reference for assigning yellow warblers to their wintering grounds. Instead, sampling newly grown winter feathers *in situ* will allow for further investigation into the causes of this apparent variation for the tropics but not in temperate North America.

Future directions

The ability to assess how remnant habitat from dam operations impact yellow warblers would be improved by long-term data on adult and juvenile survival in relation to annual and spatial variation in water levels within individual territories. Combined with similar long-term data on productivity this approach would allow the estimation of population growth in relation to variation in water level and assess whether populations in riparian habitat function as a source or sink, or ecological trap.

In Chapter 3, I concluded that for multiple reasons, stable isotopes alone are not sufficient to track warblers to their previous wintering origins. However, by combining additional intrinsic markers, assignment methods used in this study may allow researchers to refine assignments. For example, considerable work has already used (Dawson *et al.* 1997; Gibbs *et al.* 2000) genetic markers on yellow warblers and Boulet *et al* (2006) demonstrated how they can be integrated with stable-isotope markers to explore geographic connectivity between seasonal populations. In addition, researchers may wish to move beyond the use of available isotopic base maps based on regional precipitation as a reference for assigning birds to unknown origins. Instead, by developing species-specific isotope maps, researchers will be able to bypass the speculative step of adjusting tissue δD values with discrimination factors to facilitate comparisons with δD in precipitation.

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