

**The transition from migration to breeding and
demography of yellow warbler (*Setophaga petechia*)**

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Abstract

Migration and reproduction are often considered discrete stages of birds' life cycle with unique physiological adaptations. The speed of the transition from a migratory to a reproductive physiology is likely to have significant fitness consequences. I examined the transition from migration to breeding in yellow warbler (*Setophaga petechia*), a long-distance neotropical migrant, and explored the factors and mechanisms through which migration influences annual survival, breeding phenology and productivity. I showed that females arrived on the breeding grounds with elevated plasma triglyceride levels compared to males. Some females had plasma triglyceride levels consistent with an advanced stage of yolk precursor production suggesting that they can initiate these changes while on migration. Next, I confirmed that the timing of breeding in yellow warblers is linked to weather conditions on migration and investigated potential pathways in which this carryover effect may arise. Crosswind speed experienced during the 14-day period before arriving on the breeding grounds influenced the delay between female arrival and egg laying, but not arrival timing, residual mass or their reproductive state (triglyceride levels) on arrival. However, females that arrived with higher plasma triglyceride levels took less time to initiate their first clutch. Wind speed on migration and reproductive state on arrival independently influenced the delay between arrival and egg laying, which in turn influenced productivity because initiating reproduction early increased both their chance to raise at least 1 nestling and the number of nestlings fledged. Finally, I used spatial Cormack-Jolly-Seber (CJS) models to show that sex-differences in dispersal can lead to erroneous conclusions about survival, and that incorporating dispersal can both reduce the bias and increase the accuracy of survival estimates. The spatial CJS model describing dispersal using a t-distribution that varied with sex estimated annual survival of yellow warblers to be 0.08-0.16 higher (18-42% higher than apparent survival). The longer dispersal distances of females largely explained the sex differences in apparent survival estimates obtained using conventional CJS models. Together, these findings highlight the importance of considering events that occur in previous stages of the annual cycle when analyzing demographic data.

Keywords: yellow warbler; *Setophaga petechia*; plasma triglyceride; carryover effects; breeding phenology; spatial CJS model

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Chapter 1.

Introduction

Migratory organisms often travel long distances between different regions of the globe in which they spend only a portion of their annual cycle. Seasonal movements of up to several thousand kilometres allow organisms to take advantage of temporal and geographical variation in resources (Berthold 2001, Alerstam et al. 2003), predation risk (Lank et al. 2003), parasite loads (Clark et al. 2016) and disease (Altizer et al. 2011). However, long-distance migration is energetically challenging (Wikelski et al. 2003, Butler 2016) and migration has been traditionally identified as a period of high mortality (Sillett and Holmes 2002, Klaassen et al. 2014). Long distance migrants are currently impacted by a range of anthropogenic stressors acting over a large geographic area and challenged by the need to adjust their migratory and reproductive schedules in response to a rapidly changing climate. Populations of long-distance migrants, perhaps as a consequence, have declined at a faster rate than short-distance migrants and resident birds (Ballard et al. 2003, Lemoine and Böhning-Gaese 2003, Both et al. 2009, NABCIC 2019). To better understand the drivers and mechanisms of the population declines of many long-distance migrants, factors which influence survival, fecundity, dispersal and recruitment must be identified (Newton 1998, 2004). Further, the underlying processes through which these demographic changes occur and whether there are periods throughout the annual cycle that demonstrate relatively greater impact on these vital rates must be investigated (Marra et al. 1998, Newton 2004).

Neotropical migrant songbirds have long been used to investigate avian demography and population dynamics throughout the whole annual cycle. Survival of long-distance migrants can be impacted by events on the breeding grounds (Gullett et al. 2014), wintering grounds (Sillett et al. 2000, Marra and Holmes 2001, Studds and Marra 2007, Wilson et al. 2011, Rockwell et al. 2017) and on migration (Newton 2006, Drake et al. 2014b, Halupka et al. 2017, Huang et al. 2017). Fecundity of neotropical migrants can also be affected by events on the breeding grounds as well as carryover effects from previous stages of the life cycle (Harrison et al. 2011). The loss of reproductive habitat (Vance et al. 2003, Gruebler et al. 2015), degradation and

fragmentation of habitat (Donovan et al. 1995, Robinson et al. 1995, Weinberg and Roth 1998) and edge effects (Paton 1994, Donovan et al. 1997, Hartley and Hunter 1998, Batáry and Báldi 2004) are often linked to a decline in productivity (but see Hahn and Hatfield 1995, Tewksbury et al. 1998, Friesen et al. 1999, Fahrig 2017). Many studies have also shown that carry-over effects from environmental conditions at earlier stages of the annual cycle (over-wintering and migratory periods) can affect the timing of arrival on the breeding grounds and various aspects of reproduction (Marra et al. 1998, Reudink et al. 2009, Harrison et al. 2011). For example, birds that over-winter in lower quality habitats may delay their departure for breeding grounds (Marra et al. 1998, Studds and Marra 2005), arrive on the breeding grounds later (Marra et al. 1998, Reudink et al. 2009) and in worse/inferior condition and produce fewer offspring (Norris et al. 2004, Reudink et al. 2009). Favourable climate conditions at over-wintering sites have also been linked to individuals being in better condition at the end of winter and departing for migration earlier (Saino et al. 2007, Studds and Marra 2007, 2011, Cooper et al. 2015) or arriving on the breeding sites earlier (Saino et al. 2004, González-Prieto and Hobson 2013). However, some studies argue that temperatures on the breeding grounds explain inter-annual variation in laying date better than any carryover effect due to environmental conditions on wintering grounds (e.g., winter Southern Oscillation Index values - Mazerolle et al. 2011, wintering ground precipitation - Ockendon et al. 2013). Climate conditions on stopover sites during spring migration were also identified as important predictors of arrival phenology (Marra et al. 2005, Saino et al. 2007, Robson and Barriocanal 2011, Tøttrup et al. 2012) as well as breeding phenology (Finch et al. 2014). Finch et al. (2014) suggested that carry-over effects from passage regions (warmer spring temperatures at stopover sites) may influence breeding phenology more than climate conditions (temperature) on the breeding grounds. Moreover, crosswinds experienced during migration through western North America was also documented to influence the timing of breeding (Drake et al. 2014b). While many studies have investigated carry-over effects of various environmental conditions on the timing of breeding or survival (Harrison et al. 2011) there remains little cohesion among their conclusions and the importance of these carryover effects vary not only among species (which could be due to variation in life history strategies among different species) but also among different populations of the same species (e.g., survival of American redstart [*Setophaga ruticilla*] populations in the eastern, but not western, North America were linked to the variation in the Normalized Difference Vegetation Index; Wilson et al. 2011).

Moreover, the mechanisms and pathways through which these carry-over effects impact fecundity remains largely obscure because carryover effects may be mediated by impacts on the condition of birds when they arrive on the breeding grounds that then influence the timing of breeding (e.g., female American redstart - Norris et al 2004) or through direct effects on the timing of arrival which influences the timing of breeding. As such, the mechanisms through which carryover effects influence fitness are contentious.

In neotropical migrants, the timing of breeding is often critical because any mismatch between reproduction and optimum food availability may result in a reduction in fitness (Perrins 1970, Verhulst et al. 1995, Both et al. 2006, Visser et al. 2006). Early arrival on breeding grounds is often beneficial because birds that arrive early can occupy higher quality territory (Aebischer et al. 1996, Smith and Moore 2005), are more likely to mate (Lozano et al. 1996), benefit from polygyny (Reudink et al. 2009, Canal et al. 2021), extra-pair matings (Møller et al. 2003, Reudink et al. 2009) and have in general higher reproductive success (Cooper et al. 2011, Bielański et al. 2022). Breeding early can have significant fitness benefits because earlier nesting birds tend to have greater reproductive success (Perrins 1970, Wiggins et al. 1994, Verhulst et al. 1995, Newton 1998, Öberg et al. 2014). Individuals that start nesting early often lay larger clutches (e.g., Daan et al. 1990, Crick et al. 1993), can have higher nest success (e.g., Wiggins et al. 1994, Öberg et al. 2014), and may be more likely to re-nest after a nest failure or successful first attempt (e.g., Gillis et al. 2008, Hepp et al. 2021). However, timing of breeding is thought to be dependent on arrival time because migration and reproduction are assumed to be temporally discrete life-history stages constrained by energetic costs and physiological trade-offs (Wingfield 2005, Ramenofsky and Wingfield 2006; but see Williams 2012). Moreover, the timing of breeding initiation also depends on an individual's ability to adapt their breeding schedule based on their individual condition on arrival and resource availability (Drent and Daan 1980, Stearns 1992, Rowe et al. 1994, Drent 2006). However, the extent to which individuals are able to influence the duration of the transition from arrival on the breeding grounds to egg laying and the mechanism that may allow some individuals to control this transition remains largely unknown.

In this thesis I explore the transition from migration to breeding, and the mechanisms through which migration influences annual survival, breeding phenology and productivity. The yellow warbler (*Setophaga petechia*) provides a model system for evaluating how events at different stages of the annual cycle influence survival and

reproduction. The yellow warbler has a widespread distribution throughout North America (Lowther et al. 1999) but its migratory connectivity has been reasonably described using a combination of genetic, stable isotope, and banding data (Boulet et al. 2006, Quinlan and Green 2011). In general, yellow warblers breeding in western North America overwinter in Mexico and Central America, while birds from the eastern portion of North America overwinter in Central and South America (Boulet et al. 2006). The yellow warbler is often considered an indicator species for healthy multi-layer riparian habitat in North America (e.g., KBO 2013, Roberts and Burnett 2020, FRESC 2022) and in British Columbia its preferred habitat is dense, willow-dominated riparian vegetation (Campbell et al. 2001) which is frequently influenced by high ground water levels. On the breeding ground in riparian habitat altered by reservoir operations near Revelstoke, British Columbia, reproductive success varies with the quality of the riparian habitat (Quinlan and Green 2012). Flooding of the nesting territories by water had minimal effect on fledging success (Hepp et al. 2021) but could reduce post-fledging survival and recruitment by up to 50% (Hepp et al. 2018). In addition to flooding, predation (Quinlan and Green 2012, Rock et al. 2013), and to a lesser extent, cowbird brood parasitism (Rock et al. 2013), were identified as other causes of nest failures. The yellow warbler over-winters in a wide range of natural and modified habitat (Lowther et al. 1999). Its wintering habitat in Mexico has been heavily modified (Bonilla-Moheno et al. 2012) but birds overwintering in western Mexico (which were identified as breeders from the northwestern regions of North America - Boulet et al. 2006, Valdez-Juárez et al. 2018), have a relatively high survival rate (Valdez-Juarez et al. 2019). Winter habitat use appears to have little impact on yellow warbler monthly apparent survival, which was high in both agricultural and natural habitats (Valdez-Juarez et al. 2019). During spring migration, yellow warblers breeding in the northwestern part of North America migrate through areas west of the continental divide (Boulet et al. 2006). Wind speed during the time of spring migration, specifically crosswind speed, was identified as an important factor influencing yellow warbler apparent annual survival (Drake et al. 2014b).

Carryover effects of winter habitat use have been documented in some age-classes and populations of yellow warbler and not others. In Revelstoke, BC, young females with feather isotopic signatures consistent with the use of dry winter habitat experienced later clutch initiation and lower productivity (about 0.8 fewer fledglings per year) than young females with signatures suggesting more mesic winter habitat use

(Drake et al. 2013). However, this effect was not observed in older females. In Inuvik, NWT, the carry-over effect of winter habitat quality on breeding phenology was not demonstrated for either young or older females (Drake et al. 2014a). In addition, analyzing male plumage coloration of feathers grown at different stages of the annual cycle, the carry-over effect of winter habitat quality (quantified by alternate plumage coloration – which was grown on wintering grounds) did not explain any variation in breeding phenology, mate acquisition or reproductive success (Jones et al. 2014). However, carryover effects of wind conditions experienced during spring migration (westerly crosswind) were a better predictor of breeding phenology (and apparent annual survival) than climate conditions (rainfall) on the wintering grounds or springtime breeding ground temperature (Drake et al. 2014b). Carryover effects on the timing of breeding in yellow warblers resulted in carryover effects on productivity because yellow warbler productivity is primarily influenced by the timing of clutch initiations (Drake et al. 2014b), which in turn is affected by the age of females, with older females starting to nest earlier (Drake et al. 2013). However, the pathway and physiological mechanism by which this carry-over effect takes place is not fully understood.

Given the importance of the migration period and the carry-over effects of wind speed on breeding phenology and subsequently productivity, my thesis focuses on advancing our understanding of factors and processes which influence yellow warbler transition from migration to breeding. Specifically:

Chapter 2 – Investigates the timing of transition from migratory to reproductive physiology in female yellow warbler and evaluates whether female yellow warblers are able to initiate this transition before reaching the breeding grounds. This chapter was published in *Physiological and Biochemical Zoology* 94 (2021).

Chapter 3 – Investigates whether any carryover effect of wind speed during migration arises via effects on the reproductive physiology of females and evaluates how environmental conditions on migration and on the breeding ground, as well as temporal and intrinsic factors influence the reproductive condition of females on arrival. In addition, this chapter examines how environmental conditions, temporal and intrinsic factors influence the time interval between arriving on the breeding grounds and initiating reproduction and assesses the fitness consequences of the timing of breeding in yellow warblers.

Chapter 4 - Describes breeding dispersal and assesses whether sex-differences in dispersal result in biased estimates of apparent survival and examines how incorporating dispersal improves our ability to estimate true survival. Finally, this chapter investigates whether crosswind experienced on migration influences true survival estimates, after controlling for dispersal.

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Chapter 2.

Female songbirds can initiate the transition from a migratory to a reproductive physiology during spring migration

2.1. Abstract

The high energetic costs of both migration and reproduction and the physiological changes to support these costs suggest that these life-history stages should be compartmentalized with little overlap between stages. In contrast, previous studies have shown that male birds can initiate reproductive development during migration before arrival on the breeding grounds with increases in plasma testosterone levels and testis size. However, sex-differences in seasonal gonadal function are now recognized as profound, and few studies to date have shown that females can initiate the costly, but critical, estrogen-dependent final stages of gonadal maturation and changes in liver function (yolk precursor synthesis, vitellogenesis) while on migration. Here, we show that female yellow warblers (*Setophaga petechia*) arrive on the breeding grounds with elevated plasma triglyceride levels compared with males. Some females had plasma triglyceride levels of 5-7 mmol L⁻¹, suggesting that they arrived in a relatively advanced stage of yolk precursor production. Furthermore, we show that females that arrived with higher plasma triglyceride levels took less time to initiate their first clutch. Adaptive plasticity in the timing of the transition from a migratory to a reproductive physiology might help migrant birds buffer against a mismatch between timing of arrival and conditions on the breeding grounds and allow them to advance timing of breeding to maximize breeding productivity.

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2.2. Introduction

Long-distance migration allows birds to take advantage of spatio-temporal variation in food availability (Berthold 2001; Alerstam et al. 2003). However, migration is energetically demanding (Wikelski et al. 2003; Butler 2016) and can involve increased mortality risk (e.g., Sillett and Holmes 2002; Klaassen et al. 2014). Studies on birds in wind tunnels and on migration suggest that the metabolic rate of birds during long-distance migratory flight averages 8-9 x basal metabolic rate (BMR; Piersma 2011) compared with a maximum sustained metabolic rate of 4-5 x BMR during reproduction (Drent and Daan 1980; Piersma 2002). Consequently, migratory birds possess a suite of physiological adaptations that facilitate migration. For example, migrating birds can (1) put on muscle and fat to power and fuel the flight (Klaassen and Lindström 1996; Jenni and Jenni-Eiermann 1998; Jenni-Eiermann et al. 2002), (2) reduce the size of their body organs through protein catabolism to maintain osmotic homeostasis during long-distance flight (Battley et al. 2000; Gerson and Guglielmo 2011), or (3) reduce blood viscosity by decreasing haematocrit after the onset of flight (Jenni et al. 2006).

By the time of arrival on the breeding grounds, birds must rapidly transition from a migration physiology to a reproductive physiology and start to allocate considerable energy to reproduction. Females need to develop and then mature their reproductive organs (ovary and oviduct), initiate rapid yolk development, and be able to produce eggs that can each constitute up to 15% of their body mass (e.g., Caro et al. 2009). Commitment of energetic resources to egg production is high, and in songbirds, the resting metabolic rate (RMR) during this time is increased, on average, by 18%-27% (Nilsson and Råberg 2001; Vézina and Williams 2002; Vézina et al. 2006). The high energetic demands of both migration and reproduction were traditionally thought to constrain migration and reproduction to be temporally discrete life-history stages (Wingfield 2005; Bradshaw and Holzapfel 2007; Dawson 2007; but see Williams, 2012b).

Nevertheless, several studies have shown that male birds can initiate reproductive development during migration before arrival on the breeding grounds with increases in plasma testosterone levels and testis size (e.g., Quay 1985; Raess and Gwinner 2005; Bauchinger et al. 2007, 2009). Timing and control of gonadal maturation is very different in male and female birds: both sexes respond to increasing day length in

spring with a switch on of upstream components of the reproductive axis at the level of the hypothalamus and pituitary (Williams 2012b; Perfito et al. 2015; Verhagen et al. 2019). Males then show a slow, gradual increase in testis size and function over weeks or months prior to breeding, largely dependent on the same photic cues. In contrast, in females fine-tuning of seasonal timing of gonadal maturation is regulated mostly downstream in the neuro-endocrine axis at the level of the ovary and liver (Williams 2012b; Perfito et al. 2015; Verhagen et al. 2019) and involves integration of a range of nonphotic cues (food, temperature, social factors; Farner and Wingfield 1980). Thus, onset of ovarian function, just before onset of egg laying, involves estrogen synthesis and secretion by the ovary, estrogen-dependent onset of vitellogenesis, and a shift in lipid metabolism to yolk-targeted very low-density lipoproteins (VLDLs) in the liver and, subsequently, rapid yolk development (Williams 2012b). To our knowledge, few studies – and none in small migratory passerines - have demonstrated that females initiate these critical estrogen-dependent final stages of gonadal maturation and changes in liver function while on migration (but for seabirds, see Crossin et al. 2010; Williams, 2012a; see also “Discussion”).

Here, we investigate the timing of the transition from a migratory to a reproductive physiology in female yellow warblers (*Setophaga petechia*), a small Neotropical migrant, using differences in plasma triglyceride levels as an index of egg-yolk precursor production and vitellogenesis (Williams 2012b; Crossin & Williams 2021). We describe the dynamics of female plasma triglyceride levels after arrival on the breeding grounds and in relation to timing of egg laying. We contrast female plasma triglyceride levels at arrival with those of males (which reflect only migration physiology or fattening independent of egg production) and evaluate whether female yellow warblers are able to initiate the transition from a migratory to a reproductive physiology before reaching the breeding grounds. Finally, we assess whether females that arrive with elevated plasma triglyceride levels breed earlier (i.e., take less time to initiate their first clutch).

2.3. Methods

Study System

The yellow warbler is a small (ca. 9 g) Neotropical migrant songbird with broad distribution throughout North America (Lowther et al. 1999). We have monitored the breeding biology of a population of yellow warblers at three sites near Revelstoke, British Columbia, since 2005. The three study sites, approximately 24, 27 and 30 ha in size, are situated in the drawdown zone of the Upper Arrow Lakes Reservoir on the Columbia River (435 – 441 m asl). Riparian habitat at the three sites is composed of a mosaic of mature black cottonwood (*Populus trichocarpa*) forest patches, willow (*Salix* spp.) shrub, and grassland. Details of the study sites and breeding biology of this population are provided in previous works (Quinlan and Green 2012; Drake et al. 2014).

In 2015-2017, we monitored the arrival and reproduction of yellow warblers at each of the three sites every 1 or 2 d (typically two sites were visited each day for 2-5 h per site) from the beginning of May to late July. Males started to arrive in the first week of May; the first male was observed on our study sites on May 5 in 2015 and 2016 and May 8 in 2017. Females started to arrive 1-2 wk later; the first female was observed on May 15 in 2015, May 14 in 2016, and May 20 in 2017. We attempted to capture all birds on the day they were first observed or as soon as possible thereafter. All birds were sampled only one time per season, and of the 70 females with a known laying date, 61 were captured during the prelaying period, 6 were captured during the laying period, and 3 were captured during incubation. All birds were captured using mist nets with call and/or song playback. Birds new to the study sites were banded with aluminum US Fish and Wildlife Service bands and a unique combination of three color bands. We sexed and aged birds according to plumage criteria (second year [SY]: a bird in its second calendar year; after second year [ASY]: an adult in at least its third calendar year; Pyle 1997), measured mass to 0.1g using a digital scale (Insten digital pocket scale, 0.01-100g), and collected blood samples from all birds captured. We also assigned a fat score on the basis of visible fat in the furcular depression using a nine-point scale (interpreted from Kaiser 1993): 0 = no fat visible, 1 = trace fat up to one-third furcular depression covered, 2 = one-third to two-thirds of furcular depression covered, 3 = two-thirds to full furcular depression covered but concave, 4 = furcular depression completely

covered and level/flat. We did not record any birds with fat scores above 4, so they are not described here.

We assigned each bird an arrival date assuming it arrived (1) on the day it was first observed if we had visited the site the previous day or (2) the day before it was first observed if there was a 2-day interval between site visits. We used the assigned arrival dates to calculate the number of days between arrival and capture (days after arrival [DAA]). All birds were subsequently monitored every 1-3 d, so that we could find nests and determine the date that the first egg was laid. For nests found during laying or after clutch completion, we determined the first-egg date assuming females lay one egg per day and incubate for 11 d (Martin et al. 2019). We used the assigned first-egg dates to calculate the number of days between blood sampling and when the first egg was laid (days relative to first egg [DRE]), with birds captured before laying having negative values, and the time interval between arrival and when the first egg was laid (egg after arrival [EAA]). For yellow warbler in our study site, expected clutch size is four to six eggs. Therefore, birds sampled up to the third or fourth egg would be predicted to have high or peak triglyceride levels (Challenger et al. 2001).

Blood sampling and plasma assay

We collected blood samples (<75 μ L) into heparinized 50- μ L microcapillary tubes after puncturing the brachial vein with a 26-gauge sterile needle. All birds were blood sampled within 20 min of capture. We stored the blood samples in a cooler with ice for no more than 4 h before separating the plasma from the red blood cells by centrifuging the microcapillary tubes for 10 min at 12,000 rpm. Plasma samples were then stored in a freezer at -20°C until they were processed.

We evaluated the timing of the transition from a migratory to a reproductive physiology by measuring plasma triglyceride levels. Migration requires moderate levels of plasma triglycerides (generic VLDLs) to fuel flight. In females, the onset of breeding is associated with a shift in protein and lipid metabolism and a dramatic increase in circulating triglyceride levels as estrogens trigger the production of vitellogenin (VTG) and yolk-targeted VLDL (VLDLy) by the liver (Walzem et al. 1999; Vanderkist et al. 2000; Challenger et al. 2001; Williams 2012b). Plasma VTG and VLDLy are then taken up by ovaries during vitellogenesis and egg formation.

We determined plasma triglyceride concentration following an established protocol (Williams et al. 2007). Briefly, we determined the concentration of free glycerol and total triglyceride using commercially available kits (Sigma-Aldrich free glycerol reagent kit F6428 and triglyceride reagent kit T2449, respectively). We pipetted 5 μL of plasma into wells of a 96-well microplate (400 μL , flat-bottom), and 240 μL of the free glycerol reagent was added. Plates were then shaken for 30 s and incubated for 10 min at 37°C. Each plate was then read in the plate reader (Bio-Tek PowerWave 340) to determine the free glycerol concentration. To determine the total triglyceride concentration, 60 μL of the triglyceride reagent was added, followed by an additional 30-s shake and 10-min incubation at 37°C, and read in the plate reader. Triglyceride concentration (mmol L^{-1}) was calculated by subtracting the free glycerol value from the total triglyceride concentration.

The standard curve for each plate was estimated from values obtained from a serial dilution of a 2.54-mmol glycerol standard (Sigma-Aldrich G7793). A hen plasma pool was included in each assay to assess intra- and interyear assay variation. For free glycerol assays, the intra-assay coefficient of variation was 5.6%, and the interassay coefficient of variation was 8.4%. For total triglyceride assays, the intra-assay coefficient of variation was 2.8%, and the interannual coefficient of variation was 3.8%. All samples were run in duplicate, and the mean plasma triglyceride concentration was used in analyses.

Statistical analysis

We log transformed plasma triglyceride concentrations before analyses, so that our analyses conformed to the assumptions of normality and heterogeneity. Our sample size was not sufficient to include all explanatory variables in one analysis. As such, we first examined whether male plasma triglyceride levels varied with two intrinsic factors (body mass and age) and three temporal factors (time since sunrise, Julian date, year). We then evaluated whether male plasma triglyceride levels varied depending on the number of days between arrival and capture, after controlling for any significant intrinsic or temporal covariates.

We next examined how female plasma triglyceride levels varied with the same two intrinsic factors and three temporal factors. The date of blood sampling did not vary

across years. We then examined whether female plasma triglyceride levels varied depending on the number of days between arrival and sampling and the number of days before the first egg was laid. Next, we compared the plasma triglyceride levels of females captured within a day of arrival with those of males to determine whether female levels were elevated (i.e., consistent with these birds having initiated vitellogenesis) and asked whether the plasma triglyceride levels of these females were related to the time taken to lay their first egg. We did not include female body mass as a linear covariate in these analyses because female body mass, the temporal variables DRE and DAA, and predicted changes in plasma triglyceride are confounded by development of reproductive tissues (the ovaries and oviduct; Vezina and Williams 2003). However, Challenger et al. (2001) showed that plasma VLDL (and plasma VTG) concentrations were independent of nonreproductive body mass (total body mass - mass of ovary and oviduct) in female European starlings (*Sturnus vulgaris*). We confirmed that plasma triglyceride levels in egg-laying female yellow warblers were independent of body mass (DRE from -4 to 3; $r_p = -0.30$, $P = 0.28$).

We used standard linear regression models and Loess smoothing function in our analyses, since the majority of males (73%) and females (85%) were sampled in only 1 yr of the study. We included data obtained from the 17 males and 11 females captured in more than 1 yr because there was considerable variation in when they were sampled relative to sunrise, when they arrived on the breeding grounds, and (for females) when they laid their first egg. We reran these analyses using mixed models (with bird ID as random factor) and found that they did not change the results. There was very little variation associated with the random term, so we used the simpler models in our analyses. To assess the differences in fat scores between sexes, we used the Wilcoxon ranked sum test.

Statistical models were run using the R statistical software (R Development Core Team 2018). The results were visualized using the package visreg within the R statistical framework (Breheny & Burchett 2017).

2.4. Results

Plasma triglyceride levels in males

We determined the plasma triglyceride levels in blood samples from 85 male yellow warblers over the 3 yr of the study (2015, $n = 39$; 2016, $n = 28$; 2017, $n = 18$). Male plasma triglyceride levels ranged from 0.45 to 2.36 mmol L^{-1} (median = 1.01, interquartile range = 0.77 - 1.23). Plasma triglyceride levels (log transformed) did not vary with male mass ($F_{1,78} = 0.98$, $P = 0.33$) or age (ASY vs. SY; $F_{1,83} = 0.84$, $P = 0.36$). Plasma triglyceride levels increased over the course of the day (time since sunrise: estimate = 1.75 ± 0.37 ; $F_{1,83} = 22.98$, $P < 0.001$) but did not vary seasonally (Julian date: $F_{1,83} = 0.97$, $P = 0.33$) or across years ($F_{2,82} = 2.57$, $P = 0.08$). After controlling for the time since sunrise, for males captured within 10 d of arrival ($n = 70$), plasma triglyceride levels were independent of the number of days between arrival and capture (Figure 2-1).

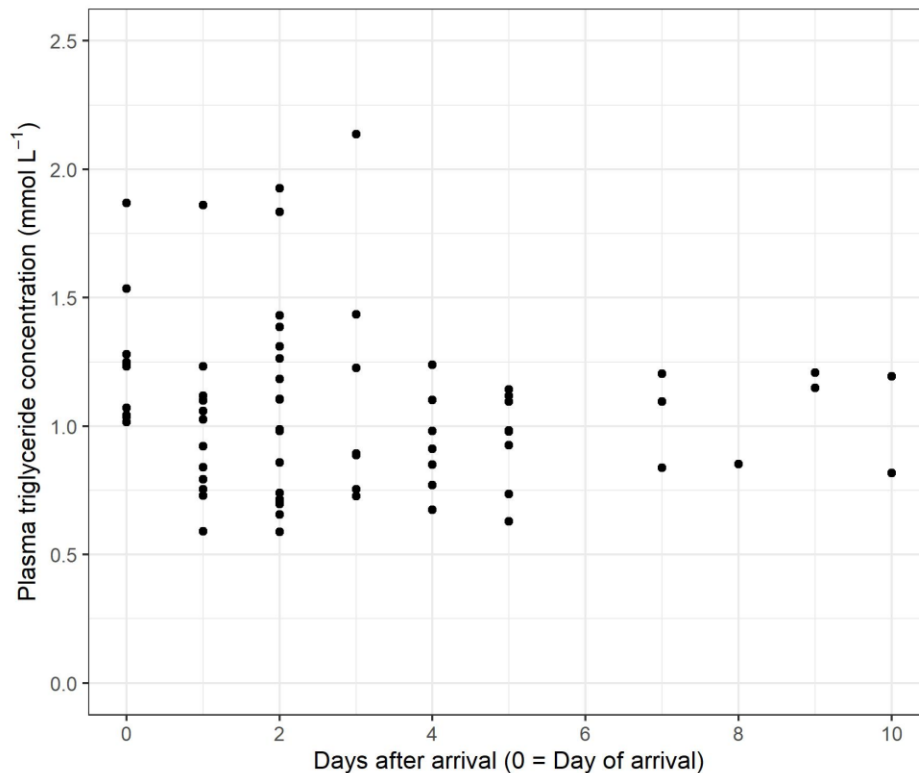


Figure 2-1: Variation in the plasma triglyceride concentration of male yellow warblers ($n = 70$) sampled within 10 d of arrival on the breeding grounds. The points show the partial residuals after controlling for time since sunrise.

Plasma triglyceride levels in females

We determined the plasma triglyceride levels in blood samples from 83 female yellow warblers over the 3 yr of the study (2015, $n = 33$; 2016, $n = 30$; 2017, $n = 20$). Female plasma triglyceride levels ranged from 0.60 to 14.22 mmol L⁻¹ (median = 2.77, interquartile range = 1.60 – 6.47). Plasma triglyceride levels (log transformed) did not vary with the time of day (time since sunrise: $F_{1,81} = 0.12$, $P = 0.73$), seasonally (Julian date: $F_{1,81} = 2.16$, $P = 0.15$), or across years ($F_{2,80} = 0.36$, $P = 0.70$). Plasma triglyceride levels increased with increasing female mass (estimate = 0.53 ± 0.08 ; $F_{1,74} = 42.14$, $P < 0.001$) but were independent of age ($F_{1,81} = 0.10$, $P = 0.75$). Female triglyceride levels were correlated with body mass in prelaying females (DRE -14 to -5; $r_p = 0.55$, $P < 0.001$) but not egg-laying females (DRE -4 to +3; $r_p = -0.30$, $P = 0.28$). For females captured within 10 d of arrival ($n = 75$), plasma triglyceride levels (log transformed) increased as the number of days between arrival and capture increased (Figure 2-2; estimate = 0.16 ± 0.043 ; $F_{1,73} = 14.19$, $P < 0.001$).

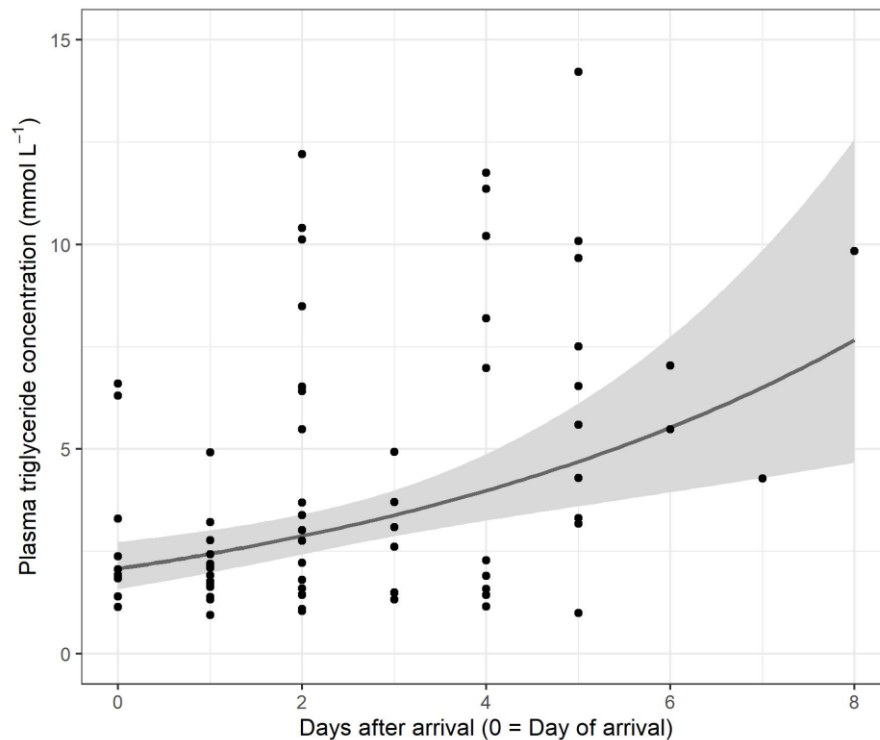


Figure 2-2: Variation in the plasma triglyceride concentration of female yellow warblers ($n = 75$) sampled within 10 d of arrival on the breeding grounds. The line shows the prediction from the model, and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

For birds captured within a day of arrival, female plasma triglyceride levels ($n = 24$) were significantly higher than those of males ($n = 22$, Figure 2-3; estimate (males) = -0.61 ± 0.12 , $F_{1,44} = 24.28$, $P < 0.001$). Fat scores of these females were also higher than those of males ($W = 436.5$, $P < 0.001$). However, plasma triglyceride levels of females were unrelated to their fat scores ($F_{1,22} = 0.99$, $P = 0.33$; fat score 1 and 2 pooled: mean \pm SD = 2.40 ± 1.70 mmol L⁻¹, $n = 18$; fat score 3: 2.61 ± 0.56 mmol L⁻¹, $n = 6$). Eight of 24 females caught within a day of arrival (33.3%) had plasma triglyceride levels that were outside the range of values detected in males caught within a day of arrival. Eleven of 24 females caught within a day of arrival (45.8%) had log-transformed plasma triglyceride levels that were more than 2 SDs higher than the mean of all sampled males.

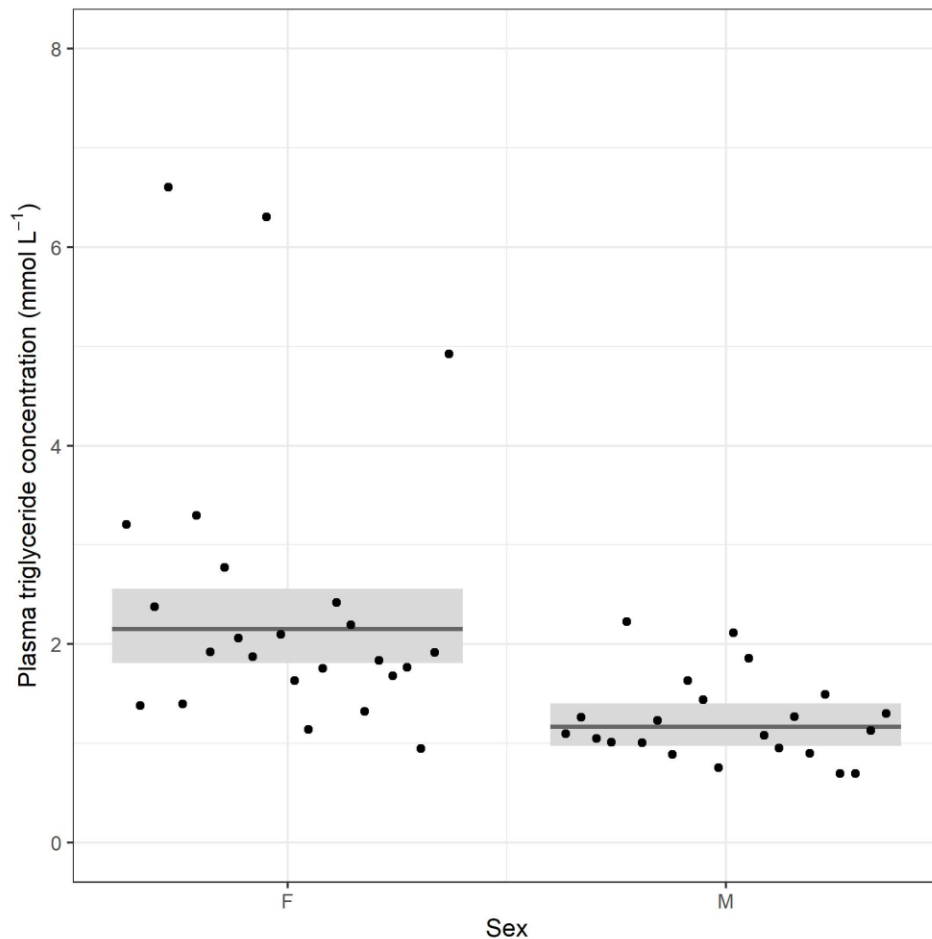


Figure 2-3: Plasma triglyceride concentrations of male ($n = 22$) and female ($n = 24$) yellow warblers sampled within 1 d of arrival on the breeding grounds. The line shows the prediction from the model, and the shaded area shows the 95% confidence interval around the prediction. The points show the partial residuals.

Female plasma triglyceride levels were also dependent on when females were sampled relative to when the first egg was laid ($n = 70$). For females sampled more than 10 d before the first egg, the mean plasma triglyceride concentration was low and relatively constant (mean \pm SD = 1.59 ± 0.52 mmol L⁻¹, $n = 9$). In general, plasma triglyceride levels began to increase 10 d before females laid their first egg, increased most rapidly 6–3 d before egg laying, peaked around 2 d before egg laying, and then declined (Figure 2-4). Mean plasma triglyceride concentration during the peak period of triglyceride concentration (from 3 d before the first egg to the day of the first egg) was 9.53 ± 2.58 mmol L⁻¹ ($n = 11$). The maximum recorded triglyceride concentration was 14.22 mmol L⁻¹.

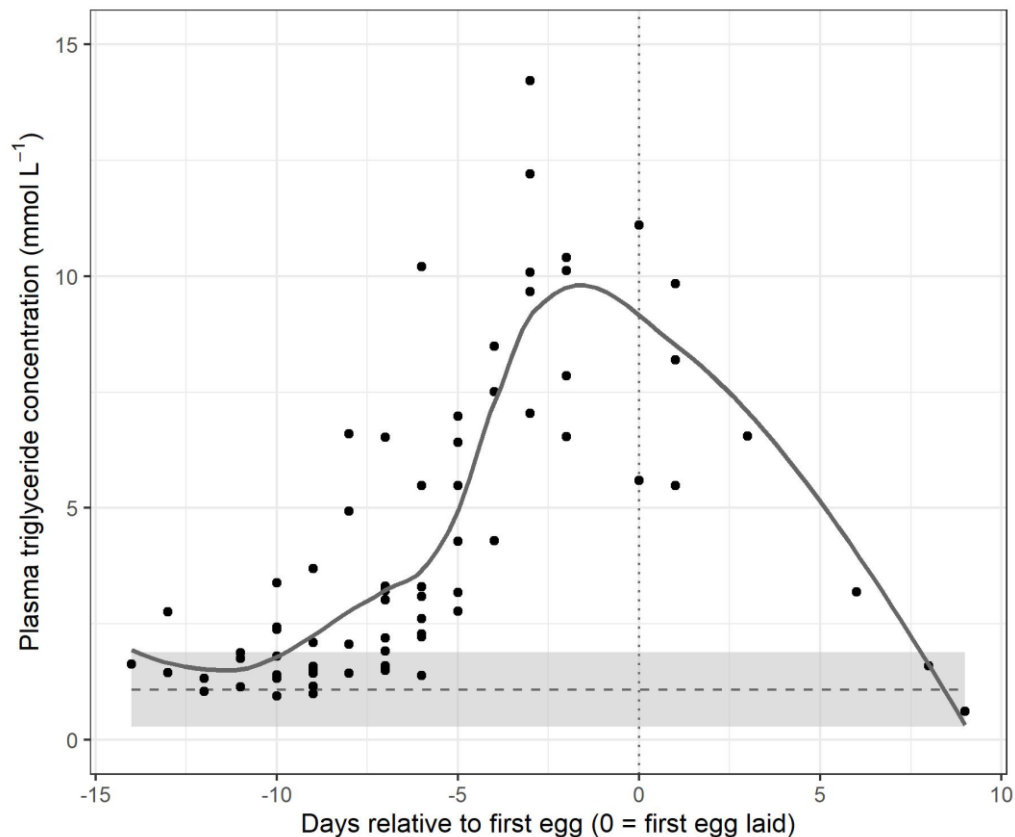


Figure 2-4: Plasma triglyceride concentrations of female yellow warblers ($n = 70$) in relation to the day they laid their first egg. The solid line is the Loess smoother (span = 0.5). The dashed line and shaded area show the mean plasma triglyceride concentration \pm 2 SDs of males (1.08 ± 0.80 mmol L⁻¹; $n = 85$).

For females that were blood sampled within a day of arrival and where first-egg dates were known ($n = 18$), the time interval between arrival and the day they laid their first egg (EAA) tended to decline as plasma triglyceride levels increased (Figure 2-5, estimate = -0.82 ± 0.431 , $F_{1,16} = 3.66$, $P = 0.07$). This relationship was not driven by the one female with a plasma triglyceride concentration that was more than double the concentration of the other 17 females in this sample. Excluding this observation, the effect became stronger (estimate = -2.06 ± 0.773 , $F_{1,15} = 7.10$, $P = 0.02$).

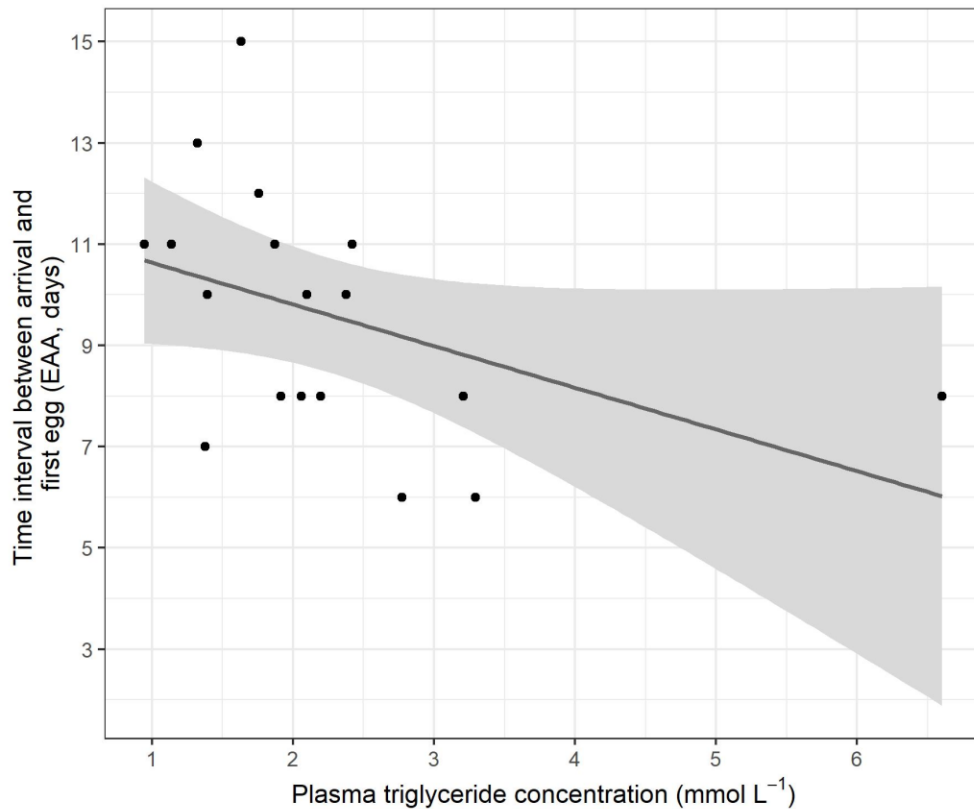


Figure 2-5: Relationship between the plasma triglyceride concentration of female yellow warblers sampled within 1 d of arrival on the breeding grounds ($n = 18$) and the time interval between arrival and the day they laid their first egg (EAA). The line shows the prediction from the model, and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

2.5. Discussion

In this study, we describe the postmigration and prebreeding dynamics of blood plasma triglyceride levels as a measure of reproductive readiness in a free-living population of a small migratory songbird. Quantifying the concentration of triglycerides in plasma allowed us to examine the timing of the transition from a migratory to reproductive physiology in female yellow warblers. This is possible because the onset of vitellogenesis is associated with a shift in lipid metabolism as females switch from producing low ($<3 \text{ mmol L}^{-1}$) levels of generic VLDL that fuel migration to high ($>10 \text{ mmol L}^{-1}$) levels of VLDL necessary for vitellogenesis and egg formation (Williams, 2012b; Crossin and Williams 2021). We show that females arrive on the breeding grounds with plasma VLDL levels that are already elevated in comparison to those of males and that females that arrive with elevated plasma VLDL levels take less time to initiate their first clutch. Our study therefore suggests that, despite the high energetic demands of both migration and reproduction, some female yellow warblers are able to initiate the transition from a migration to a reproductive physiology before they arrive on the breeding grounds. These females likely obtain a fitness benefit because productivity declines with the date that females initiate reproduction in yellow warblers (Drake et al. 2014).

Early field endocrinology studies evaluated whether female songbirds can initiate vitellogenesis while on migration by measuring plasma luteinizing hormone levels, estrogens, and ovarian follicle size. Wingfield and Farner (1978b) found that newly arrived but already paired females of short-distance migrant white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) in Washington had plasma luteinizing hormone similar to wintering females sampled in February. Although plasma estrone and estradiol levels in these females were high enough to be detected, ovarian follicles were previtellogenic ($<1 \text{ mm}$ in diameter), and it was concluded that vitellogenesis (yolk synthesis) and yolk deposition occurred on the breeding grounds (see also Ramenofsky and Wingfield 2006). In long-distance migrant *Zonotrichia leucophrys gambelii*, Wingfield and Farner (1978a) found that newly arrived females in Alaska had elevated blood plasma luteinizing hormone, estrone, and estradiol levels and slightly enlarged but still previtellogenic ovarian follicles ($<2 \text{ mm}$ in diameter) compared with those of wintering females, and they also concluded that vitellogenesis and yolky follicle development

occurred on the breeding grounds. More recently, Covino et al. (2017, 2018) used GnRH challenges and measurements of circulating testosterone to explore seasonal variation in pituitary and gonadal sensitivity to hypothalamic signalling during spring migration. Testosterone is central to male reproduction, but also acts as a prohormone for estradiol and influences female reproductive behavior (Rosvall et al. 2020). While there was evidence that male migrants prepare for breeding during their vernal migration, there was no relationship between plasma testosterone levels, or the capacity to elevate testosterone levels in response to exogenous GnRH, and breeding ground proximity in female black-and-white warblers (*Mniotilta varia*) and female Swainson's thrushes (*Catharus ustulatus*; Covino et al. 2017, 2018). Kimmitt et al. (2019) compared migrant and resident dark-eyed juncos (*Junco hyemalis*) in their sympatric nonbreeding range (which is also the breeding grounds for the residents) before migration and found no difference in plasma triglyceride (VLDL) levels. VLDL levels in all birds were typical of nonbreeding or premigratory, hyperphagic birds (2-4 mmol L⁻¹) and very low compared with values in laying females (~15 mmol L⁻¹). Only two birds in this study had yellow (yolky) follicles, and these were resident females (A. Kimmitt personal communication). In summary, no studies to date have measured yolk precursors directly at the migration-reproduction transition as an indicator of onset of vitellogenesis to show that female birds initiate yolk precursor production before their arrival on their breeding grounds.

In birds, the onset of reproduction in females can be monitored by quantifying the concentration of triglycerides in plasma (Vanderkist et al. 2000) and relating it to the dynamics of VLDL concentrations before, during, and after egg laying. Here, we describe the dynamics of plasma VLDL from before to just after egg laying in a wild population of a migratory songbird. In female yellow warblers, plasma VLDL levels are low 2 wk before egg laying. Plasma VLDL levels begin to rise 10 d before egg laying but accelerate dramatically 6 d before egg laying. Plasma VLDL levels then peak about 2 d before the first egg is laid at concentrations six times higher than baseline levels before declining again. The dynamics of plasma VLDL in this small Neotropical migrant expected to follow an income breeding strategy (i.e., relying on daily food intake for egg production) has both similarities to and differences from the patterns observed in yolk precursor levels in captive songbirds (zebra finch, *Taeniopygia guttata*; Salvante and Williams 2002; Salvante et al. 2007), nonmigratory songbirds (European starling; Challenger et al. 2001), and wild populations of large birds (Vanderkist et al. 2000;

Gorman et al. 2009; Hennin et al. 2015; Lamarre et al. 2017) with a capital breeding strategy (i.e., using endogenous, stored body reserves for egg production) or a mixed capital and income breeding strategy. In yellow warblers, we observed first a slow and then a rapid increase in VLDL levels. The initial slow increase occurs later than increases observed in peregrine falcons (*Falco peregrinus*; Lamarre et al. 2017) and common eider (*Somateria mollissima*; ca. 18 d before laying; Hennin et al. 2015), while the rapid increase occurs slightly earlier than increases observed in European starlings (4 d before laying; Challenger et al. 2001). Peak plasma VLDL levels in yellow warblers (9.5 mmol L⁻¹) are intermediate between those measured in greater scaup (*Aythya marila*; 7.3 mmol L⁻¹; Gorman et al 2009) and European starlings (ca. 33 mmol L⁻¹; Challenger et al. 2001). However, these peaks occur later than those in peregrine falcons (8 d before laying; Lamarre et al. 2017) and common eiders (5 d before laying; Hennin et al. 2015) and earlier than those in European starlings (during laying; Challenger et al. 2001). Although in this study the females were targeted and sampled primarily during the prelaying period, a smaller sample of postlaying data was also obtained. The declines in yellow warbler plasma VLDL levels parallel those observed in common eiders (Hennin et al. 2015) but contrast with European starlings, where VLDL levels do not start to decrease until just before ovulation of the last follicle (Challenger et al. 2001), and greater scaup that maintain high VLDL levels through the whole egg-laying period (Gorman et al. 2009). Given the varied patterns observed across taxa and our limited postlaying sample size, further work is required to describe and understand the mechanism behind the changes in VLDL levels during egg laying in free-living passerines.

Previous studies have shown that despite the high energetic costs of both migration and reproduction and the potential hormonal conflicts (Williams, 2012b), females of a few larger bird species are able to initiate vitellogenesis during migration (e.g., macaroni penguin, *Eudyptes chrysolophus* [Crossin et al. 2010]; surf scoter, *Melanitta perspicillata* [Williams, 2012a]). Here, we show that female yellow warblers are also able to initiate the transition from migration to reproduction physiology before reaching their breeding grounds: female yellow warblers arrived at the breeding grounds with significantly elevated VLDL levels compared to males. This is in contrast with data recorded in the same area during fall migration, where no sex difference in triglyceride levels was documented and mean triglyceride concentration was less than 1.00 mmol L⁻¹

(Wagner et al. 2014). Furthermore, in three cases, females arrived with plasma VLDL levels around 5-7 mmol L⁻¹, suggesting that they arrived in relatively advanced stages of yolk precursor production. In migrating birds, there is no indication that triglyceride levels in males and females differ (e.g., Williams et al. 2007; Wagner et al. 2014). While there are some differences in triglyceride levels between spring and fall migrants (e.g., Seewagen et al. 2011; Smith 2013), these differences are not at the scale we recorded in our study (with some females having VLDL of up to 7 mmol L⁻¹). Females that initiate this transition before arrival should be able to start reproduction earlier than females that arrive with baseline levels of plasma VLDL. Indeed, we documented that, independent of age, females arriving on the breeding grounds with higher VLDL levels took less time to initiate their clutches. The shortest interval we recorded between arrival and clutch initiation was 3 d. For yellow warblers, this can be important because annual productivity declines over the course of the breeding season (Drake et al. 2014). For this population, the ability to advance the clutch initiation by 1 d would be expected to increase annual productivity by, on average, 0.11 fledglings for SY females and 0.09 fledglings for ASY females (Drake et al. 2014).

Our conclusion is dependent on the assumption that we detected females as soon as they arrived on their breeding territories and that females with elevated triglyceride levels are not individuals that remained undetected for several days. We believe that this assumption is warranted and that our estimates of female arrival dates are accurate to within 1 d for five reasons. First, we visited our sites every 1 or 2 d, and two or three observers located, followed, and identified all males and females observed. Second, males are highly vocal but modify their behavior after the arrival of a prospective mate. Males with no females sing incessantly; however, males with females sing less and closely follow their prospective mates. Therefore, females are rapidly detected by tracking changes in male behavior and by the loud and easily identifiable chip contact calls made by both males and females. Third, females rapidly select and settle on a territory in part because females that move between territories risk high levels of harassment by all males in the area. Fourth, if females were spending time near but not at our monitored breeding site before being detected, we would then expect to catch females at our sites which move on and do not attempt to breed. We rarely catch females that later disappear, and the few that do so are then often resighted or recaptured on our sites the following year, suggesting they bred just outside our study

area. Returning color-banded females (that can be identified on first detection) are almost always observed in the territory where they subsequently breed, with minimal within-season movement around the breeding area. Finally, we observe no age effects on triglyceride level on arrival (in actual territory), which we would expect to see if younger females spend more time nearby looking for a suitable place to breed, whereas older returning birds go directly to their previous breeding location. Therefore, females could possibly remain undetected for a day or arrive between visits to a particular site but are unlikely to remain undetected for long enough to bias the interpretation of our results.

This study adds to the growing evidence that migration and breeding are not entirely discrete life-history stages constrained by energetic costs and physiological trade-offs, even in small songbirds. Both the elevated VLDL concentrations at arrival and the fact that females with higher VLDL levels are able to nest earlier after arrival suggest that at least some female yellow warblers are able to switch into a reproductive physiology and initiate vitellogenesis (yolk formation) before arriving on their breeding grounds. While for larger birds the initiation of rapid yolk development (surf scoter; Williams 2012a) and egg production (macaroni penguin; Crossin et al. 2010) before arrival on the breeding grounds have been documented previously, this study is the first to confirm that even small income-breeding migrants are capable of initiating the critical estrogen-dependent final stages of gonadal maturation and changes in liver function (yolk precursor synthesis and yolky follicle development) while still on migration. This raises questions about the magnitude of the energetic costs and the mechanisms that prevent any potential hormonal conflicts (Jubinville et al. 2020). Our study also shows that there is considerable variation in timing when females switch to reproductive physiology, with some females arriving on breeding grounds in more advanced stages than others. The adaptive plasticity in the timing of a transition from a migratory to a reproductive physiology in long-distance migrants may help birds buffer against a mismatch between arrival timing and the conditions on breeding grounds by adjusting the timing of egg laying to maximize breeding productivity. However, further work is required to understand the factors that explain the variation and fitness benefits associated with the timing of this transition.

2.6. Literature

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Chapter 3.

Crosswinds during spring migration influence the timing of reproduction of a neotropical migrant due to carryover effects that increase the time interval between arrival and egg laying

3.1. Abstract

Events on the wintering grounds and on migration can influence the timing of reproduction and the productivity of migratory songbirds. We show, using data from a 12-year study in Revelstoke, BC, Canada, that the onset of breeding in yellow warblers (*Setophaga petechia*) is linked to weather conditions on migration, specifically the speed of crosswinds experienced over the western flyway during a 2-week period at the end of May. During 2015-2017, we investigated whether this carryover effect was due to crosswind effects on the timing of arrival, the reproductive state and condition of females on arrival, or a combination of other effects that delayed egg laying. In these years, female arrival dates varied with age, but were independent of year, growing degree days or crosswinds on migration. Though crosswind experienced by females during the 14-day period before their arrival on the breeding ground had no significant influence on female plasma triglyceride levels (which reflected their reproductive state) or female residual mass on arrival, it did have an effect on the time interval between arrival and egg laying. This time interval was also shorter if females arrived with elevated plasma triglyceride levels and longer if females arrived early in the season. Both wind speed experienced on migration (14-days before arrival) and reproductive state on arrival (plasma triglyceride concentration) independently influenced the delay between arrival and egg laying. Crosswind effects that delay breeding have a significant effect on reproductive success; female yellow warblers that initiate reproduction late decrease both their chance to raise at least 1 nestling and the number of nestlings fledged.

3.2. Introduction

In a seasonal environment, the timing of breeding often has consequences for reproductive success and juvenile survival (Perrins 1970, Verhulst et al. 1995). For birds, individuals that breed early often lay larger clutches (e.g., Daan et al. 1990, Crick et al. 1993), have higher nest success (e.g., Wiggins et al. 1994, Oberg et al. 2014), and are more likely to re-nest after a nest fails or young fledge (e.g., Gillis et al. 2008, Hepp et al. 2021). Juveniles from early nesting attempts can also have higher survival and are more likely to recruit to the breeding population (e.g., Norris 1993, Oberg et al. 2014). However, individual decisions on when to breed are the outcome of complex trade-offs between the costs and benefits of reproducing early for both parents and their offspring (Drent 2006) and consequently likely to vary with parental quality (e.g., age - Ratcliffe et al. 1998, condition - Descamps et al. 2011), environmental conditions on the breeding grounds (e.g., Le Vaillant et al. 2021) and carryover effects from environmental conditions at earlier stages of the annual cycle (Harrison et al. 2010).

Carryover effects on breeding phenology could arise due to environmental conditions before, during, and immediately after migration or the condition of individuals which could delay the transition from a migratory to a reproductive physiology. In migratory birds, food availability on the wintering grounds can influence the timing of departure (e.g., Studds and Marra 2007, 2011, Cooper et al. 2015). Headwinds on the wintering grounds and en-route can delay departure and slow migration (e.g., Gronroos et al. 2012, Rotics et al. 2018). Conditions experienced during migration can also influence arrival dates and the timing of breeding. For example, more favorable stopover conditions in North Africa advanced the arrival dates of barn swallows (*Hirundo rustica*) in Spain (Balbontin et al. 2009), while warm temperatures in the Mediterranean promoted earlier breeding by common redstarts (*Phoenicurus phoenicurus*), spotted flycatchers (*Muscicapa striata*) and wood warblers (*Phylloscopus sibilatrix*) in Europe (Finch et al. 2014). Similarly, strong winds on migration through the western United States delayed breeding of yellow warblers (*Setophaga petechia*) and yellow-breasted chats (*Icteria virens*) in Canada (Drake et al. 2014, Huang et al. 2017; respectively). Less is known about how events on the wintering grounds combine with the conditions experienced on migration to influence the condition of individuals when they arrive on the breeding grounds. However, winter habitat use, inferred from stable carbon isotope

values, can influence the arrival body condition of some songbirds (e.g., American redstart [*Setophaga ruticilla*, Marra et al. 1998], black-throated blue warbler [*Setophaga caerulescens*, Bearhop et al. 2004], palm warbler [*Setophaga palmarum*, González-Prieto and Hobson 2013]) and waterfowl (e.g., northern pintail [*Anas acuta*, Yerkes et al. 2008]).

Despite the high energetic costs of migration and reproduction and the potential for hormonal conflicts (Williams 2012b, Jubinville 2020), females of some species can initiate the transition from a migratory to a reproductive physiology while on migration (Williams 2012a, Pavlik et al. 2021). During the non-breeding season bird reproductive organs are inactive and it takes several weeks to fully re-activate them (Williams 2012b). Because of this, females begin to develop and mature their reproductive organs (ovary and oviduct) prior to or on migration (e.g., Bluhm et al. 2000, Raess and Gwinner 2005). Females of some species can also initiate vitellogenesis (a much later stage of gonadal development dependent on estrogen synthesis and secretion by the ovary) and the subsequent production of yolk-targeted very low-density lipoproteins (VLDL_y) by the liver (Williams 2012b), during migration. For example, Crossin et al. (2010) argued that female macaroni penguins (*Eudyptes chrysolophus*) must initiate vitellogenesis while at sea because females lay their first egg only 7-14 days after their return to the breeding colony whereas yolk formation is estimated to take approximately 16 days. Williams (2012a) provided more direct evidence that female surf scoters (*Melanitta perspicillata*) initiate vitellogenesis on migration, since females had elevated blood vitellogenin levels when captured 1200 km from their breeding grounds.

Previous studies on yellow warbler suggest that climatic conditions can influence the annual survival, timing of breeding and productivity (Mazerolle et al. 2011, Drake et al. 2014). In British Columbia, stronger crosswinds during the migration period were associated with lower apparent annual survival rates and later female clutch initiation dates (Drake et al. 2014). Moreover, we have recently demonstrated that some female yellow warblers (ca. 17 %) can initiate vitellogenesis prior to arrival on the breeding grounds (Pavlik et al. 2021). Wind-speed effects on the timing of breeding could therefore arise because: (a) crosswinds during migration delay arrival on the breeding grounds, (b) energetic costs associated with crosswinds on migration limit the number of females that initiate vitellogenesis before arriving on the breeding grounds, or (c) cross

winds influence the condition of birds on arrival and increase the amount of time females need to build up the resources needed to produce eggs.

Here, we confirm that wind speed during migration influences the onset of reproduction and evaluate the temporal and spatial scale of wind effects on the timing of breeding. We investigate whether this carryover effect arises via effects on the reproductive physiology of females. We evaluate how environmental conditions on migration (wind speed) and on the breeding ground (growing degree days - GDD), temporal factors (day of arrival - DOA), and intrinsic factors (age) influence reproductive state on arrival, estimated using plasma triglyceride concentration of females. Next, we examine how environmental, temporal and intrinsic (age and reproductive state on arrival) factors influence the time interval between arriving on the breeding grounds and initiating reproduction. Finally, we assess the fitness consequences of the timing of breeding in yellow warblers.

3.3. Methods

Study system, study sites and field methodology

The yellow warbler is a small neotropical migrant passerine with a broad breeding distribution throughout North America (Lowther et al. 1999). Our study sites were located near Revelstoke, British Columbia, Canada, and situated in the drawdown zone of the Upper Arrow Lakes Reservoir on the Columbia River (435 – 441 m AMSL). The three sites, approximately 24, 27 and 30 ha in size, were composed of periodically flooded riparian habitat with patches of mature black cottonwood (*Populus trichocarpa*) forest, willow-dominated shrub (*Salix* spp.) and grassland.

We monitored the breeding biology of a colour-banded population of yellow warblers between 2005 and 2017. In each year, birds new to the study sites were captured in mist-nets and banded with aluminum USFW bands and a unique combination of three colour bands. We aged and sexed birds according to plumage criteria (Pyle 1997). We assigned each bird to one of three age categories:

- (1) SY second year birds - birds in their first breeding season,
- (2) ASYL local after second year birds - returning birds at least 2 years old that previously bred at the study sites, and
- (3) ASYU unknown after second year birds - new birds at least 2 years old that were new to the study population.

For all captured individuals, we measured body mass to 0.1 g using a digital scale (Insten digital pocket scale, 0.01–100 g), wing chord, tail length and tarsus length. In all years with the exception of 2007, we documented male arrival dates, the identity of individuals in all pairs that formed, and attempted to find and monitor the fate of all nests made by each female. Pairs and their nests were monitored every 1-3 days. For nests found during egg laying or after clutch completion, we estimated the date that the clutch was initiated assuming females lay one egg per day and incubate for 11 days (Martin et al. 2020). We used this information to determine the onset of reproduction (the date the first egg was laid, DFE) and the annual productivity (total number of young fledged from all nesting attempts) for 16-35 females per year ($n = 305$ female years in total). More details of the three study sites and the breeding biology of this population are provided by Quinlan and Green (2012) and Hepp et al. (2021).

In 2015-2017, we increased our monitoring effort and also documented female arrival dates (date of arrival, DOA). In these three years, study sites were visited every 1-2 days (typically 2 sites were visited each day for 2-5 hours per site) from the beginning of May to late July. We attempted to capture all females on the day they were first observed or as soon as possible thereafter. Females ($n = 83$) were captured using mist-nets combined with call and/or song playback. We assigned each female an arrival date assuming it arrived on the day it was first observed if we had visited the site the previous day or the day before it was first observed if there was a 2-day interval between site visits. We then used these arrival dates to calculate the number of days between arrival and capture (days after arrival, DAA) and the time interval between arrival and when females laid their first egg of the season (egg after arrival, EAA).

Physiological state of females on arrival

Physiological state of females when they arrived on the breeding ground was assessed by measuring their plasma triglyceride levels. While migration requires low (<3 mmol L⁻¹) levels of triglycerides (generic VLDLs), the transition to a reproductive physiology is associated with a dramatic increase in circulating triglyceride levels as estrogens trigger the production of vitellogenin (VTG) and yolk-targeted VLDL (VLDL_y) by the liver (Vanderkist et al. 2000; Challenger et al. 2001, Williams 2012b). This shift in lipid metabolism allowed us use differences in plasma triglyceride levels as an index of egg-yolk precursor production and vitellogenesis (Williams 2012b; Crossin and Williams 2021).

Blood samples (<75 μ l) were collected in heparinized 50- μ l microcapillary tubes after puncturing the brachial vein with a 26-gauge sterile needle. All birds were sampled within 20 min of capture and the blood samples were stored in a cooler with ice for no more than 4 h before separating the plasma from the red blood cells by centrifuging the microcapillary tubes for 10 min at 12,000 rpm. Plasma samples were then stored in a freezer at -20°C until they were analyzed.

Plasma triglyceride concentration was determined following an established protocol described in detail by Williams et al. (2007). This protocol corrects for the presence of free glycerol by subtracting the free glycerol concentration from the total triglyceride concentration. We determined the concentration of free glycerol and total triglyceride using a Sigma-Aldrich free glycerol reagent kit - F6428 and triglyceride reagent kit - T2449, respectively. To determine free glycerol concentration, 5 μ L of plasma was pipetted into wells of a 96-well microplate (400 μ L flat-bottom) and 240 μ L of the free glycerol reagent was added to each well. Microplates were then shaken for 30 seconds and incubated for 10 minutes at 37°C . Each plate was then read in the absorbance plate reader (Bio-Tek PowerWave 340) to determine optical density measurements of samples from which free glycerol concentration was determined using a standard curve. The standard curve for each plate was estimated from values obtained from a serial dilution of a 2.54-mmol glycerol standard (Sigma-Aldrich G7793). To establish the total triglyceride concentration, 60 μ L of the triglyceride reagent was added to each well, followed by an additional 30-second shake, 10-minute incubation at 37°C , and the plates were re-read in the plate reader.

A hen plasma pool was included in each assay to assess intra- and inter-year assay variation. For free glycerol assays, the intra-assay coefficient of variation was 5.6% and the inter-assay coefficient of variation was 8.4%. For total triglyceride assays, the intra-assay coefficient of variation was 2.8% and the inter-annual coefficient of variation was 3.8%. All assays were run in duplicate and the mean plasma triglyceride concentration was used in analyses.

Wind speed on the migration flyway

The wind conditions experienced during spring migration were quantified using modeled wind speed data extracted from the National Center of Environmental Prediction (NCEP) Reanalysis 1 data archives at the NOAA-CIRES Climate Diagnostics Center at Boulder, Colorado, USA (Kalnay et al. 1996) using the RNCEP package for R statistical software (Kemp et al. 2012). These data have a spatial resolution of 2.5° latitude and longitude and temporal resolution of six hours. Because songbirds migrate at night and mostly at elevations from close to the surface up to 2100 m (Alerstam et al. 2011, Bruderer et al. 2018) depending on terrain and environmental conditions, we used average nighttime (1800, 0000 and 0600) westerly (U-wind) and southerly (V-wind) components at the 850 mb (~1500 m AMSL) and 925 mb (~700 m AMSL) levels. For the crosswind (U-wind) absolute values of the wind vector were used, however for the headwind (V-wind) original wind values were used reflecting a difference between headwind (positive values) or tailwind (negative negative).

We defined the western flyway for our population as the overland region west of the easternmost portion of the continental divide (107°W), beginning at the northern extent of the yellow warbler wintering range (25°N) and ending at the latitude of our study site (50°N). We calculated average annual U-wind and V-wind components for 3 geographical areas:

- (1) ALL – the entire flyway area (25°N - 50°N),
- (2) N2/3 - the northern 2/3 of the flyway (35°N - 50°N), and
- (3) N1/3 - the northern 1/3 of the flyway (45°N - 50°N; Figure 3-1).

Each of these areas had 4 temporal windows: (1) 2 months (April-May), (2) 1 month (May), (3) 14 days (May 18-31), and (4) 7 days (May 25-31). We chose the

geographical area and temporal window based on the best model in the candidate set examining spatio-temporal effects of wind conditions on lay dates in this population (see below and Results). We also calculated the likely crosswinds experienced by each individual on their northern migration by averaging the U-wind components over the entire flyway over the 14 days prior to their arrival on the breeding grounds.

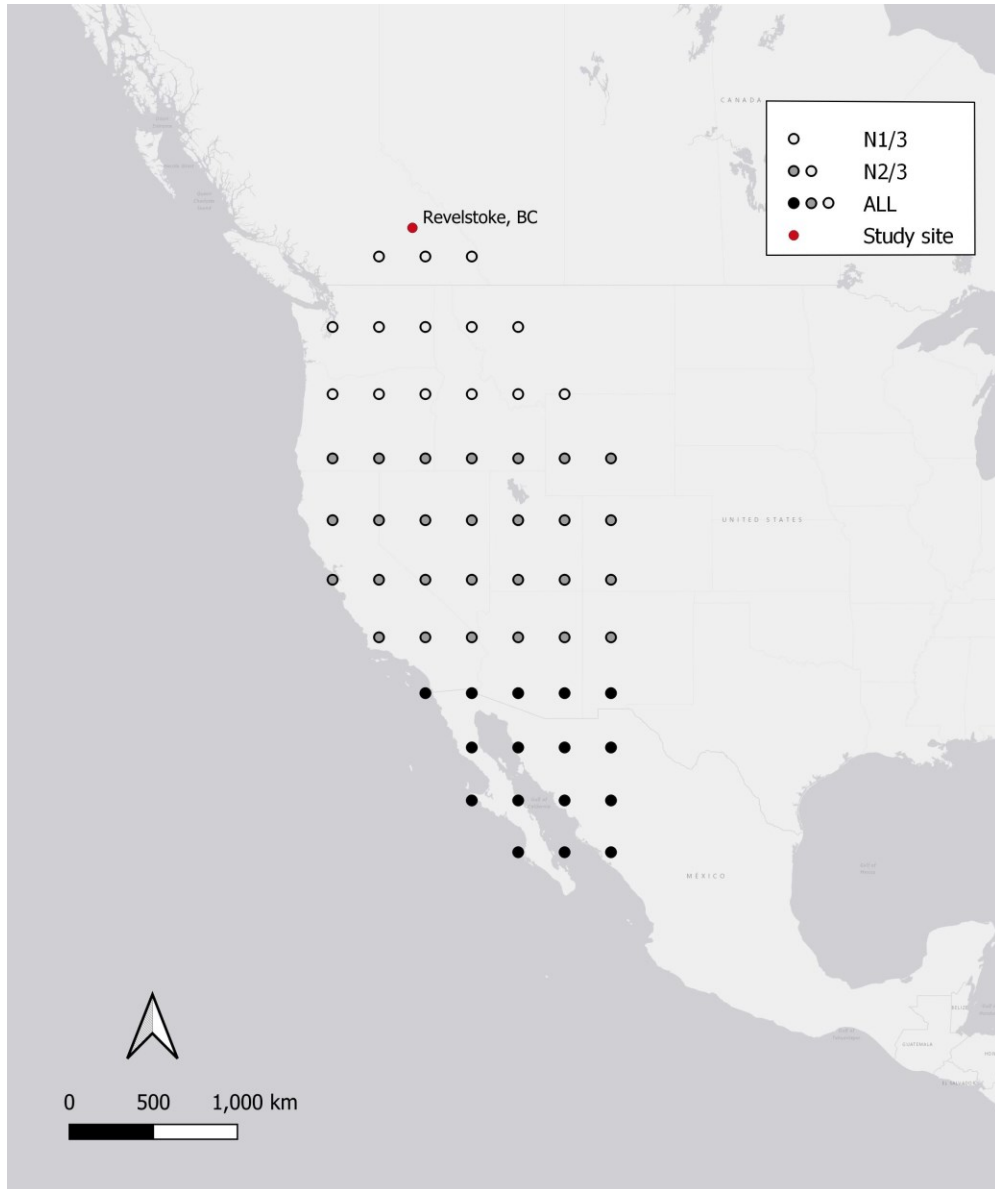


Figure 3-1: The location of the study area in Revelstoke, BC and the points used to calculate the wind speed values during migration for the three geographical areas (N1/3 = the northern 1/3 of the flyway, N2/3 = the northern 2/3 of the flyway, and ALL = the entire flyway).

Environmental conditions on the breeding ground

For each year, we used growing degree days (GDD) as a measure of thermal accumulation over time that reliably predicts plant phenology on the breeding ground (e.g., bud break in trees; Hakkinen et al. 1998, Linkosalo 1999) which in turn supports the arthropod prey abundance of yellow warblers (e.g., Hodgson et al. 2011, Clayton et al. 2015). GDD was calculated as a cumulative sum of mean daily temperatures exceeding 5°C (i.e., threshold as in Hodgson et al 2011) at the start of the breeding season (set as June 1) and for the day when individual females arrived on the breeding grounds in 2015 to 2017.

$$\text{GDD} = \text{Sum} ((T_{\text{max}} - T_{\text{min}}) - 5)$$

for each day from Jan 1 – May 31 or Jan 1 – DOA

Daily maximum and minimum temperatures for Revelstoke (Revelstoke A station, 50°58' N, 118°11' W; WMO id = 71685) were downloaded from the Environment and Climate Change Canada website (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html?Month=12&Day=4&Year=2022&timeframe=2&StartYear=1840&EndYear=2022).

Statistical analyses

We created a series of candidate model sets. The first candidate model set examined spatio-temporal effects of wind-speed on the laying date (DFE) of female yellow warblers ($n = 226$) over 12 breeding seasons ($n = 305$ female years). The linear mixed effect models in this set used the same model structure as previous work (i.e., included the two wind components [U-wind and V-wind] and age class [SY, ASYU, ASYL] as fixed main effects and female identity as a random term; see Drake et al. 2014). Candidate models differed in the geographic area and temporal window used to calculate average U- and V-wind-speeds (see above).

The second candidate model set examined annual variation in the date of arrival of females ($n = 65$) in the three years with more extensive monitoring (2015 - 2017; $n = 81$ female years). The linear mixed effect models in this candidate set included combinations of age category, year, U-wind (best spatio-temporal window from previous

analysis), GDD at the start of each breeding season and a null model. Female identity was included as a random term in all models.

The third candidate model set examined factors influencing variation in the plasma triglyceride levels of female yellow warblers captured on or very soon after arrival on the breeding ground (within 2 days of arrival; $n = 40$ female years). The general linear models in this candidate set all controlled for the time interval between arrival and capture (DAA). Triglyceride values were log-transformed to conform to the assumptions of normality and heterogeneity. The candidate model set included models with all univariate and multivariate combinations of age category, year, date of arrival (DOA), and crosswinds experienced over the entire flyway in the two weeks prior to each female's arrival (U-wind). We used average wind speeds over the entire flyway in the two weeks prior to arrival since this spatio-temporal scale best described variation in laying dates in the first candidate set (see Results). This candidate model set also included models with term GDD (calculated for the time interval when individual females arrived on the breeding ground), however we did not include any combination of term GDD with term DOA (since individual GDD is highly correlated with the date of arrival). In addition, we used the same candidate set to assess the effect of different factors on residual mass of yellow warblers. Residual mass was calculated from regression of body mass and tarsus length assuming: (1) mass increased linearly with tarsus length, and (2) proportion of body mass made up of energy stores is independent of tarsus length.

The fourth candidate set examined factors influencing variation in the time interval between arrival and egg laying ($n = 35$ female years). This candidate model set included general linear models with all univariate and multivariate combinations of age category, year, U-wind experienced over the entire flyway in the two weeks prior to arrival, date of arrival (or GDD on arrival) and adjusted triglyceride levels (or residual mass). Triglyceride levels and residual mass were adjusted to control for differences in triglyceride (residual mass) levels of females captured on the day of arrival (DAA= 0 and 1) and those captured after arrival (DAA = 2) by the differences in mean triglyceride concentration (residual mass) between the two groups.

Finally, we created a candidate model set to examine the fitness consequences associated with advancing the day of the first egg. We examined variation in annual productivity (the total number of fledged nestlings) using 'hurdle' models (Zeileist et al.

2008) where a binomial distribution was used to model failure/success and a Poisson distribution was used to model the number fledged. We used annual productivity data from 226 females over 12 breeding seasons (n = 305 female years). Candidate models included all combinations of age category, year and lay date (DFE) as main effects and a null model.

All analyses were conducted using the R statistical software (R Core Team 2022). Mixed effects models were fitted using 'lme' function from 'nlme' package (Pinheiro et al. 2022) and general linear models were fitted using standard linear regression function. All parameters of the models were estimated using maximum likelihood (ML) method. Models in the candidate set were ranked using Akaike's Information Criterion corrected for small sample sizes (Burnham & Anderson (2002)). Only results from the best performing models based on AICc are interpreted, although standardized effect sizes for all models within 2.5 Δ AICc are presented in Supplemental Table 3-A. Relationships in the top models were visualized using package 'visreg' within the R statistical framework (Breheny and Burchett, 2017).

3.4. Results

The top model in the candidate set examining spatio-temporal effects on egg laying date suggested that the variation in female first egg date between 2005 and 2017 was best described by the model with wind speeds over the entire flyway during the 14-day period (May 18-31). This model received substantially more support than models with a larger time window or the null model with no migration wind effects (Table 3-1). The first egg dates tended to be later as crosswinds increased; an increase in average U-wind speed of 1 m/s delayed the date of the first egg by 3.76 days (95% CI = 2.24 - 5.29) (Figure 3-2). The date of the first egg was not impacted by headwinds (effect = -0.42 days [95% CI = -1.91 - 1.08]; Supplemental Figure 3-A). The date of the first egg also varied with age category (Supplemental Figure 3-B). Older returning local females laid their first egg before older females that had not been banded and were likely new to the study population and young females breeding for the first time (ASYU effect = 3.29 days [95% CI = 1.58 - 5.00], SY effect = 7.16 days [95% CI = 5.48 - 8.84]).

Table 3-1: Comparison of support for models in the candidate set examining spatio-temporal effects of crosswinds (U-wind) and headwinds (V-wind) on the date of the first egg of female yellow warblers (2005-2017). Models vary in the geographic area and temporal time window used to calculate average wind components and all models include the age category term. Models are ranked according to the difference from the best model based on Akaike's Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight.

Model	K	AICc	Δ AICc	w_i
ALL – 14 days	7	1969.47	0	0.70
ALL – 1 month	7	1971.99	2.52	0.20
N2/3 – 14 days	7	1974.31	4.84	0.06
ALL – 2 months	7	1975.68	6.21	0.03
N2/3 – 7 days	7	1979.56	10.09	0
N2/3 – 2 months	7	1980.06	10.59	0
N1/3 – 2 months	7	1980.48	11.01	0
N2/3 – 1 month	7	1981.90	12.43	0
ALL – 7 days	7	1982.38	12.91	0
N1/3 – 7 days	7	1986.63	17.16	0
N1/3 – 14 days	7	1989.02	19.55	0
Null (age only)	5	1989.79	20.32	0
N1/3 – 1 month	7	1989.91	20.44	0

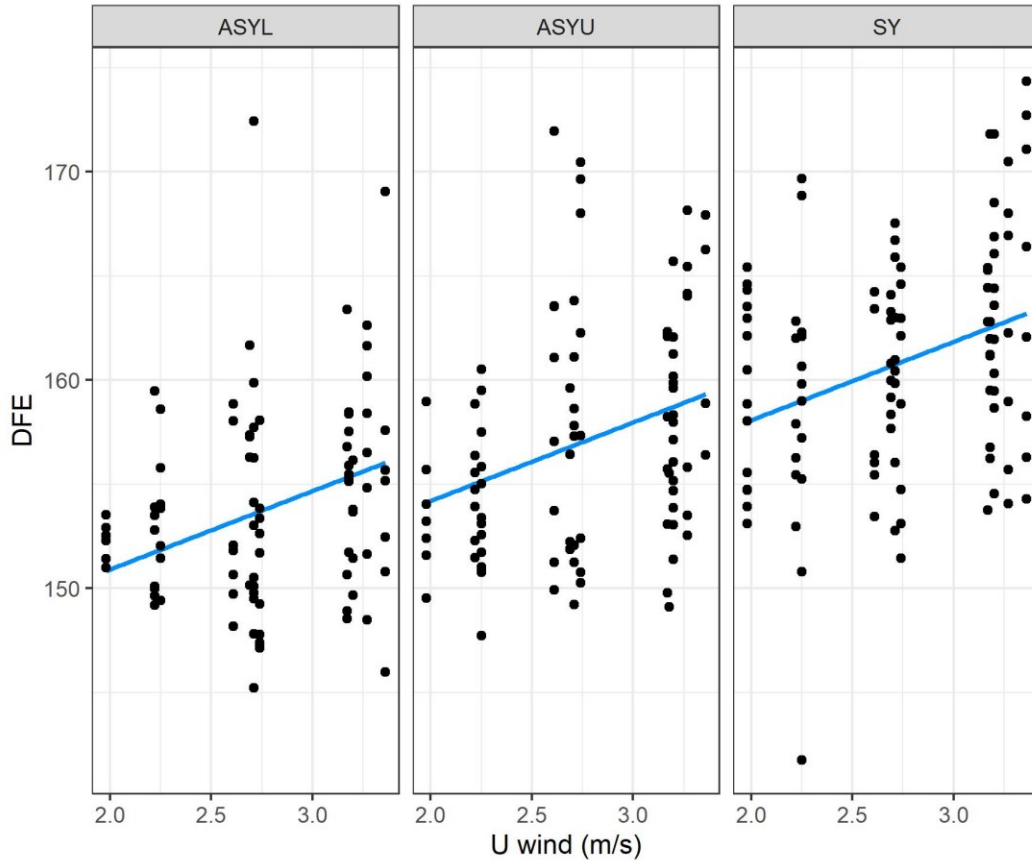


Figure 3-2: Relationship between westerly wind speed during migration (U-wind) and date of the first egg (DFE) in yellow warblers (2005-2017). The line shows the prediction from the model (controlling for age category and V-wind) and the points show the partial residuals.

The top model in the candidate set examining variation in female arrival dates in the three years from 2015 to 2017 included only the age category term. The top model received more than 2.5 times the support of models with year, growing degree days at the start of the breeding season or average U-wind speed over the entire flyway in the last 14 days of May (Table 3-2). Older females, whether they had been banded previously or not, arrived before young females (ASYU effect = 0.82 days [95% CI = -1.83 – 3.46], SY effect = 6.72 days [95% CI = 3.93 – 9.52]; Figure 3-3). For these three years (2015, 2016 and 2017), there was some variation in growing degree days at the start of the breeding season but little variation in average U-wind.

Table 3-2: Comparison of support for models in the candidate set examining variation in the arrival dates of female yellow warblers (2015-2017). Models are ranked according to the difference from the best model based on Akaike's Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight.

Model	K	AICc	Δ AICc	w_i
Age	5	497.69	0	0.51
Age + GDD	6	499.66	1.97	0.19
Age + U-wind	6	499.86	2.17	0.17
Age + Year	7	501.82	4.13	0.06
Age*GDD	8	503.24	5.55	0.03
Age*U-wind	8	503.73	6.04	0.02
Age*Year	11	510.55	12.86	0
null	3	518.91	21.22	0

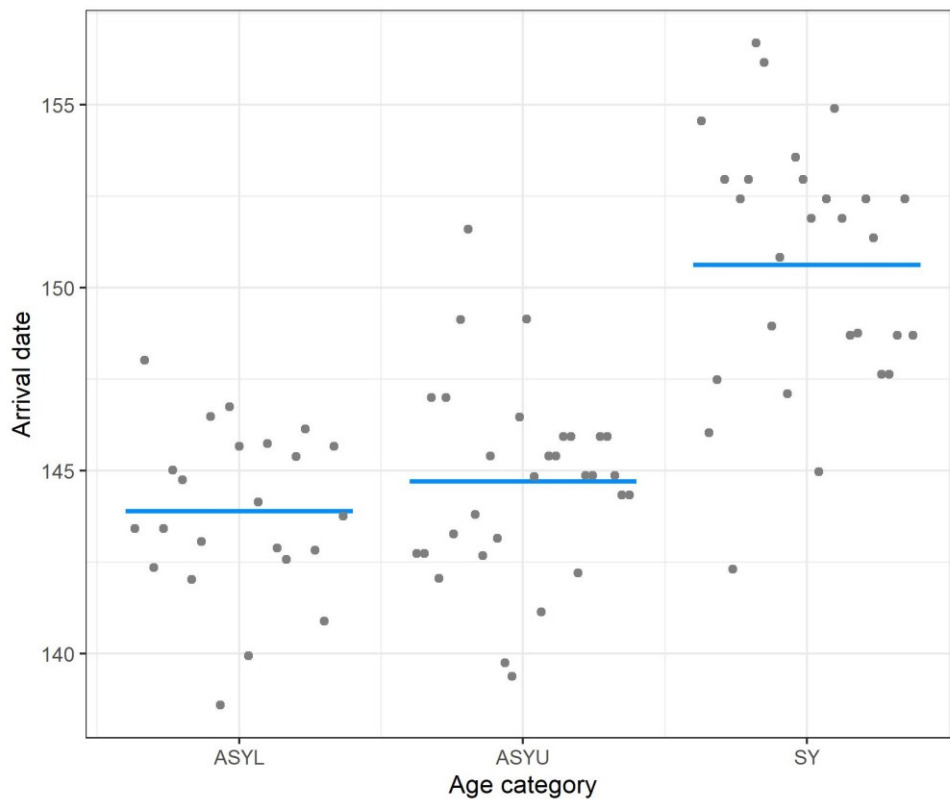


Figure 3-3: Variation in the arrival date among age categories (ASYL = after second year local, ASYU = after second year unknown, SY = second year) in female yellow warblers (2005-2017). The line shows the prediction from the model and the points show the partial residuals.

The top model in the candidate set examining plasma triglyceride concentrations of female yellow warblers captured within 2 days of arrival included the date of arrival (DOA) and days after arrival (DAA) terms. This model received almost 2 times the support of the model that also included the U-wind term (Table 3-3). Females that arrived later had higher plasma triglyceride levels (log transformed) than those arriving earlier in the season (DOA effect = 0.05 [95% CI = 0.01 – 0.08]; Figure 3-4). Females captured a day after arrival also tended to have higher plasma triglyceride levels (log transformed) than those captured on the day they arrived (DAA effect = 0.32 [95% CI = 0.08 – 0.73]). The model that included the U-wind term in addition to the date of arrival and day of capture terms received some support, however, the estimated effect of crosswinds was slight (effect = -0.20 [95% CI = -0.57 – 0.17], Figure 3-5). Models that included other terms received little support (Table 3-3).

Table 3-3: Comparison of support for models in the candidate set examining variation in the plasma triglyceride concentration of female yellow warblers captured within 2 days of arrival on the breeding grounds. All models control for the time of capture (days after arrival, DAA). Models are ranked according to the difference from the best model based on Akaike’s Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight.

Model	K	AICc	Δ AICc	w_i
DOA (+DAA)	4	83.56	0	0.49
DOA + U-wind (+DAA)	5	84.80	1.24	0.26
DOA + Year (+DAA)	6	87.34	3.78	0.07
null (DAA)	3	88.04	4.49	0.05
DOA + Age (+DAA)	6	88.86	5.31	0.03
GDD (+DAA)	4	89.71	6.15	0.02
U-wind (+DAA)	4	90.30	6.74	0.02
DOA + Age + U-wind (+DAA)	7	90.41	6.85	0.02
Year (+DAA)	5	91.27	7.71	0.01
Age (+DAA)	5	91.71	8.15	0.01
Year + U-wind (+DAA)	6	91.78	8.22	0.01
GDD + U-wind (+DAA)	5	92.29	8.73	0.01
Age + GDD (+DAA)	6	94.14	10.59	0
Age + U-wind (+DAA)	6	94.44	10.88	0
Age + Year (+DAA)	7	95.27	11.71	0

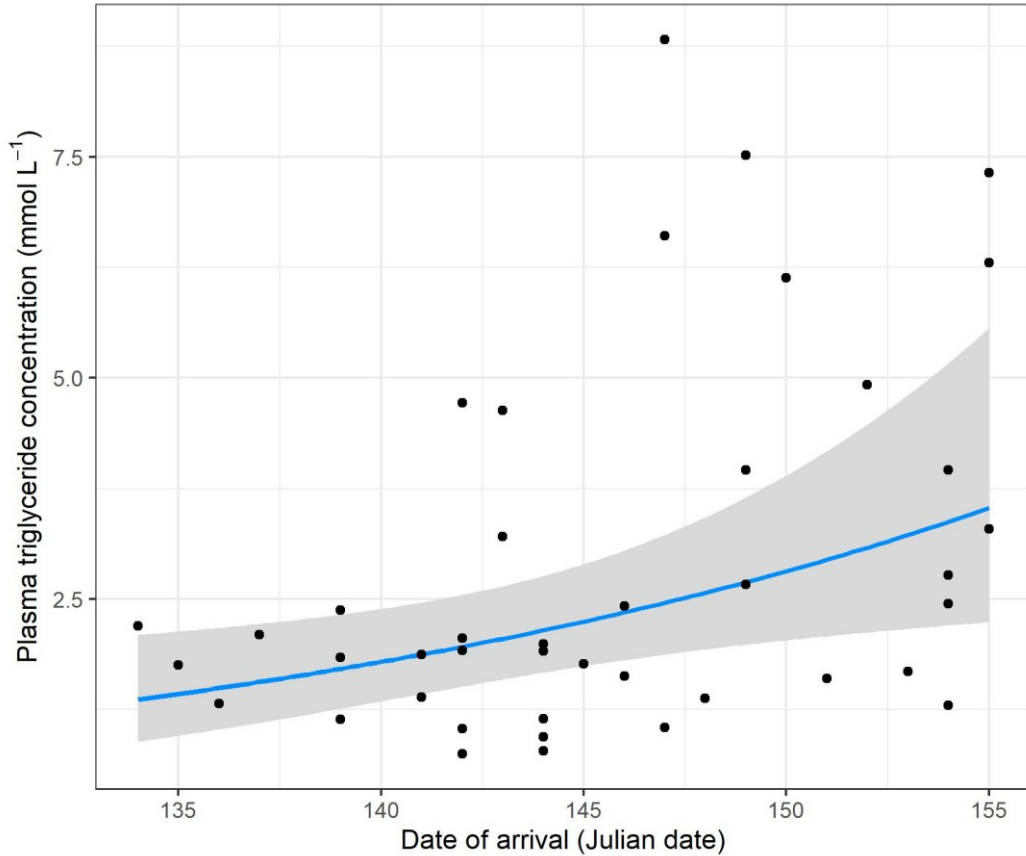


Figure 3-4: Relationship between the plasma triglyceride concentration of female yellow warblers sampled within 2 days of arrival on the breeding grounds ($n = 42$) and the date of arrival on the breeding grounds. The line shows the prediction from the model (controlling for DAA) and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

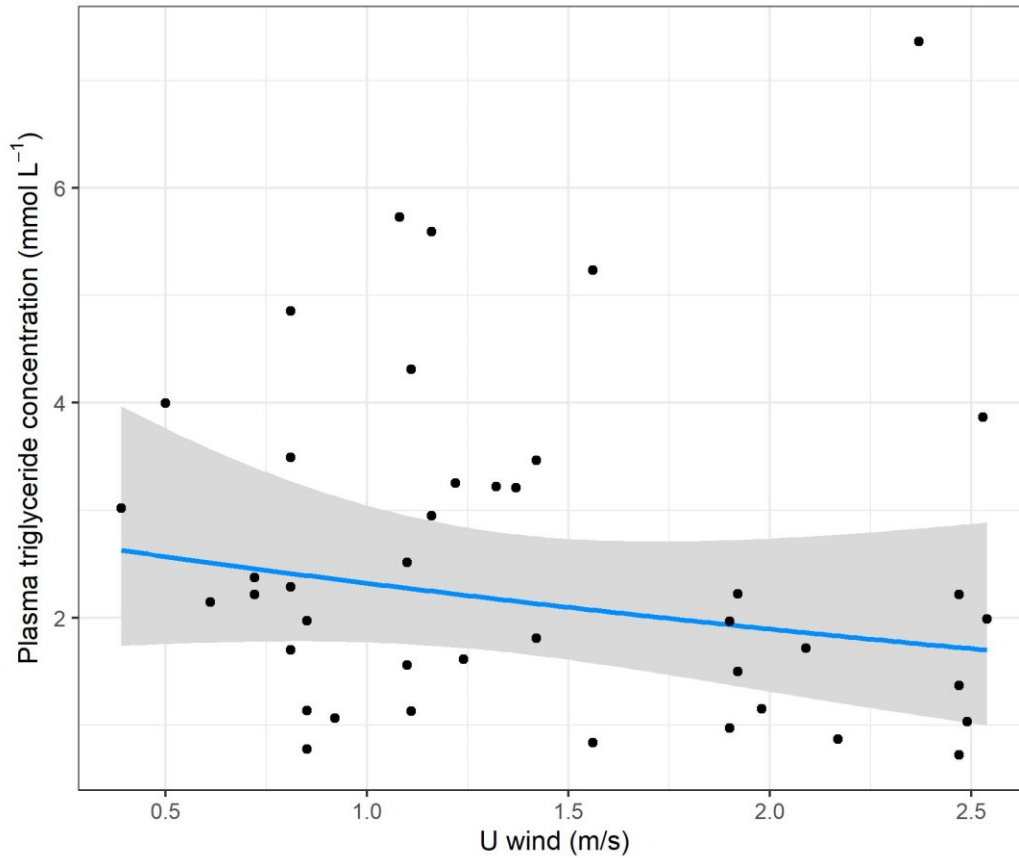


Figure 3-5: Relationship between the plasma triglyceride concentration of female yellow warblers sampled within 2 days of arrival on the breeding grounds ($n = 42$) and U-wind experienced during migration (14 days period prior to arrival for the entire area). The line shows the prediction from the model (controlling for DAA and DOA) and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

Using the same set of candidate models to describe variation in residual mass, the top model included growing degree days at the time of arrival (GDD) and days after arrival (Supplemental Table 3-B). The top model suggested a positive relationship between growing degree days on arrival and residual body mass (GDD effect = 0.0019 [95% CI = 0.0002 – 0.0036]; Supplemental Figure 3-C). In the model that included the effect of crosswind during the 14 days before arrival, wind did not influence residual mass.

The top model in the candidate set describing variation in the time interval between arrival and egg laying in female yellow warblers included the U-wind, adjusted

triglyceride, and date of arrival terms. This model received almost three times the support of the next best model, which did not include the U-wind term. (Table 3-4). The top model suggested that crosswinds experienced on migration during the 14-day period before arrival on the breeding grounds increased the time interval between arrival and egg laying; a 1 m/s increase in U-wind was estimated to delay laying by 1.79 days (95% CI = 0.58 – 3.00; Figure 3-6). This model also suggested that females arriving with higher plasma triglyceride or arriving later were able to reduce the time interval between arrival and egg laying, with a 1 mmol/L increase in plasma triglyceride concentration advancing laying by 0.80 days (95% CI = 0.53 – 1.06; Figure 3-7), and a 1-day delay in arrival advancing laying by 0.17 day (95% CI = 0.05 – 0.29).

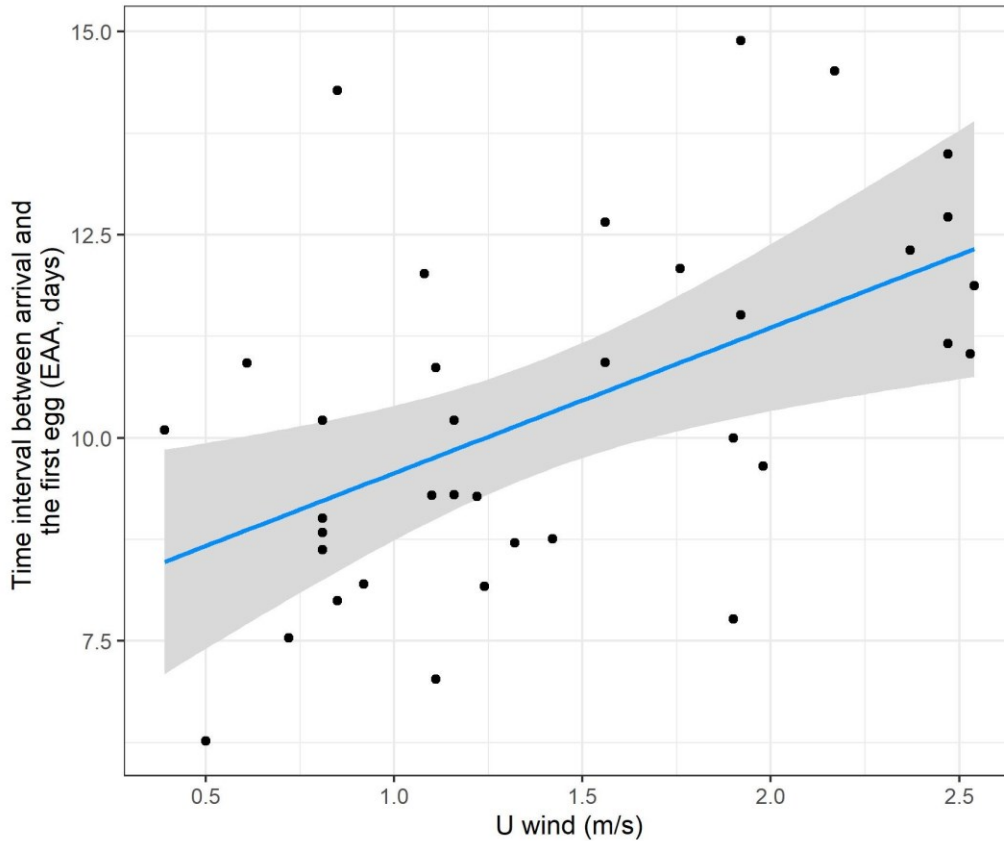


Figure 3-6: Relationship between U-wind experienced by female yellow warblers sampled within 2 days of arrival on the breeding grounds ($n = 36$) and the time interval between arrival and the day they laid their first egg (EAA). The line shows the prediction from the model (controlling for adjusted triglyceride and DOA) and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

Table 3-4: Comparison of support for models of delay between arrival and egg laying in female yellow warblers captured within 2 days of arrival on breeding grounds (controlling for DAA). Models are ranked according to the difference from the best model based on Akaike's Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight (Trig* = adjusted triglyceride, MassR = residual mass).

Model	K	AICc	Δ AICc	w_i
U-wind + Trig* + DOA	5	153.14	0	0.60
Year + Trig*	5	155.08	1.94	0.23
Trig*	3	158.62	5.47	0.04
U-wind + Trig*	4	158.72	5.57	0.04
DOA + Trig*	4	159.17	6.03	0.03
Year + MassR	5	159.71	6.56	0.02
Year + Trig* + Age	7	160.62	7.47	0.01
GDD + Trig*	4	160.85	7.71	0.01
U-wind + GDD + Trig*	5	161.41	8.27	0.01
Trig* + Age	5	163.90	10.76	0
U-wind + MassR + DOA	5	168.93	15.79	0
U-wind + MassR	4	170.16	17.02	0
U-wind + MassR + GDD	5	171.00	17.86	0
MassR	3	172.19	19.05	0
Year + DOA	5	173.66	20.51	0
DOA + MassR	4	174.26	21.12	0
Age + MassR	5	176.16	23.02	0
Year	4	177.30	24.15	0
U-wind + DOA	4	177.33	24.19	0
DOA	3	178.35	25.21	0
U-wind + Year	5	178.72	25.58	0
null	2	179.61	26.46	0
U-wind	3	181.81	28.67	0
GDD	3	181.94	28.80	0
Age + Year	6	182.53	29.38	0
Age + DOA	5	183.23	30.09	0
Age	4	183.98	30.84	0
U-wind + GDD	4	184.37	31.23	0
U-wind + Age	5	186.42	33.28	0
GDD + Age	5	186.61	33.46	0

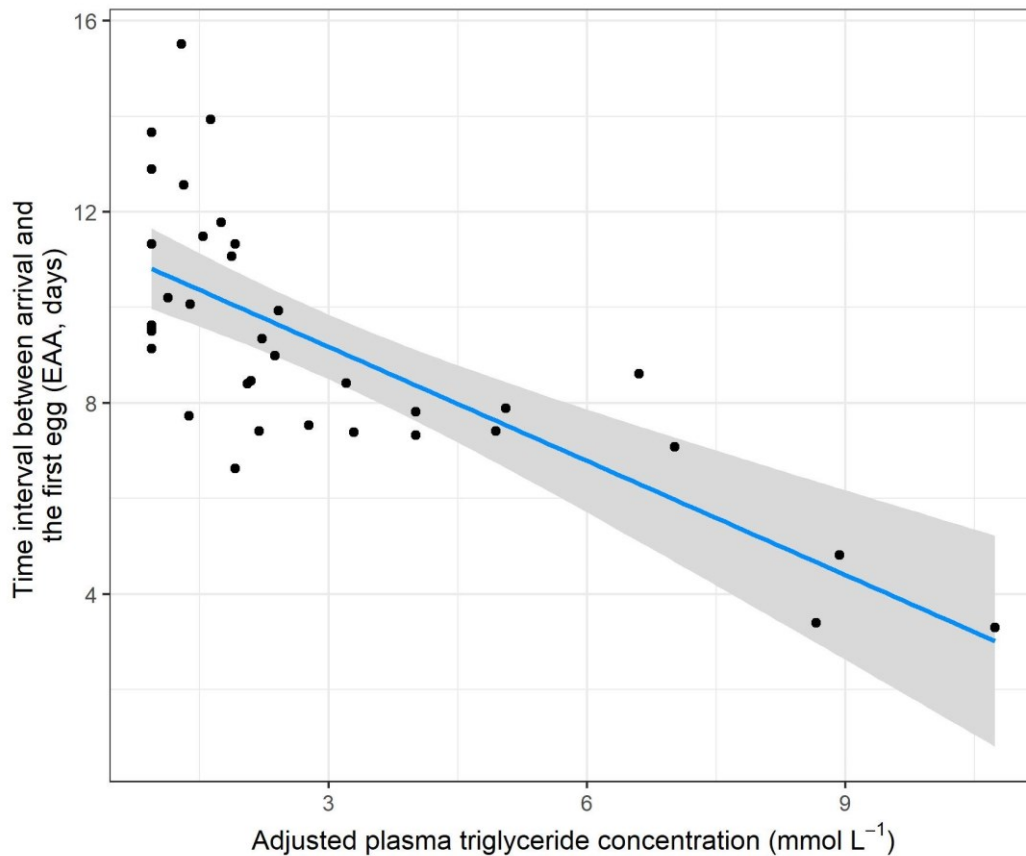


Figure 3-7: Relationship between the plasma triglyceride concentration of female yellow warblers sampled within 2 days of arrival on the breeding grounds ($n = 36$) and the time interval between arrival and the day they laid their first egg (EAA). The line shows the prediction from the model (controlling for U-wind and DOA) and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

The top hurdle model in the candidate set examining variation in annual productivity of female yellow warblers contained only the day of the first egg term. This model received more than 3 times the support of the next best model which also included the age category term (Table 3-5). Laying early increased both the probability of fledging at least one nestling and the number of young fledged if females were successful (Figure 3-8 and Figure 3-9).

Table 3-5: Comparison of support for hurdle models in the candidate set examining variation in the annual productivity of yellow warblers (2005-2018). Models are ranked according to the difference from the best model based on Akaike's Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight.

Model	K	AICc	Δ AICc	w_i
DFE	4	1023.00	0	0.79
DFE + Age	8	1025.71	2.71	0.21
Age	6	1036.44	13.44	0
null	2	1046.01	23.01	0
DFE + Year	26	1058.19	35.19	0
DFE + AGE + Year	30	1063.75	40.75	0
AGE + Year	28	1074.93	51.93	0
Year	24	1081.95	58.95	0

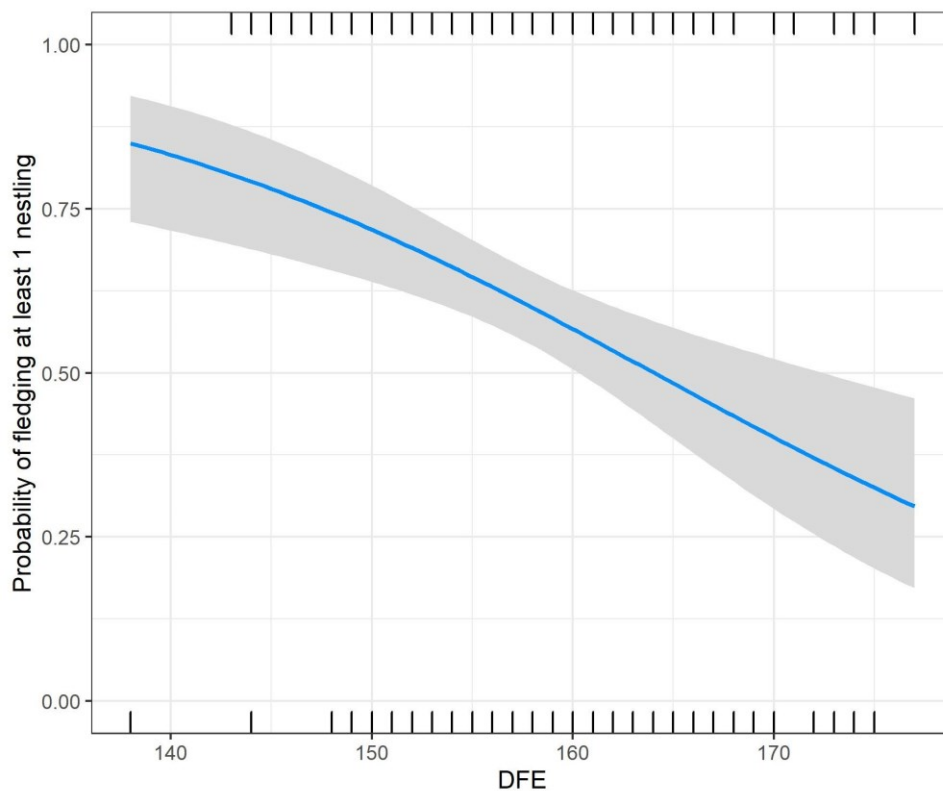


Figure 3-8: The effect of timing of breeding (date of the first egg, DFE) on the probability that yellow warblers fledge at least one nestling (2005-2017). The line shows the prediction from the model and the shaded area shows the 95% confidence interval around the predicted relationship.

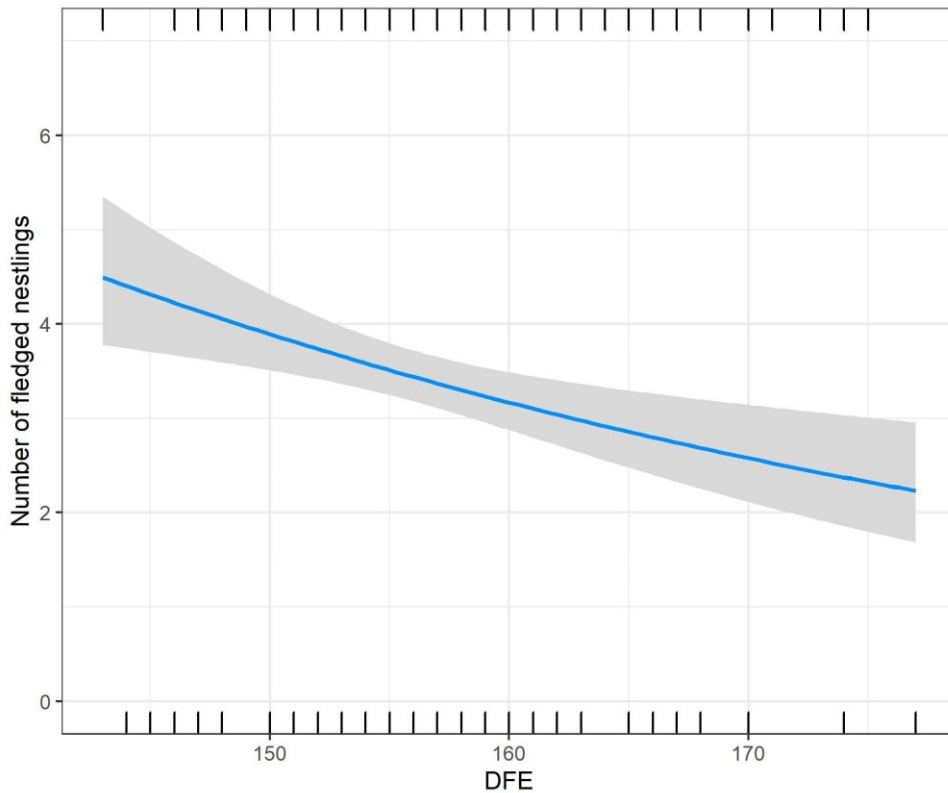


Figure 3-9: Variation in the number of fledged nestlings (if successful) over the season in yellow warblers in relation to the date of the first egg (DFE). The line shows the prediction from the model and the shaded area shows the 95% confidence interval around the predicted relationship.

3.5. Discussion

In many migratory species, females gain a fitness benefit from initiating reproduction early in the breeding season (Perrins 1970, Wiggins et al. 1994, Newton 1998, Öberg et al. 2014). Female yellow warblers are no exception; females that initiate reproduction early increase both their chance to raise at least 1 nestling and the number of nestlings fledged. In this study we confirm that timing of breeding in yellow warblers is linked to weather conditions during migration, specifically the crosswind speed experienced during northward migration. We show that carryover effects of crosswind speed on the onset of reproduction could be explained, in part, by their influence on the

time interval between arrival on the breeding grounds and when females lay their first egg.

Potential carryover effects of wind during the migration period depend both on the timing and location of wind events and the amount of time migrating birds are exposed to them. Previous studies have investigated these carryover effects at the population level using interannual variation in the date of the first egg and average windspeed values during the months migration is thought to occur across the entire flyway (Drake et al. 2014, Huang et al. 2017). In this study, we show that at the population level, a shorter time period (2 weeks) performed better than longer periods (1 month or 2 months). At the individual level, crosswinds faced in the 14 days before an individual's arrival on the breeding grounds was correlated with the delay between arrival and egg laying but not with the triglyceride concentration of newly arrived females. These results are not entirely unexpected, as multiple tracking studies show that neotropical migrant songbirds can travel at rate of 250 – 350 km/day during their spring migration (Stutchbury et al. 2009, Heckscher et al. 2011, Gallo et al. 2013) and can complete their spring migration within 14 days. For example, during spring migration wood thrushes (*Hylocichla mustelina*) were documented to complete their ~3700 km migration within 13-15 days (Stutchbury et al. 2009) and the maximum duration of migration of Kirtland's warblers (*Setophaga kirtlandii*; distance of about 2200 km) was 13-23 days (Ewert et al. 2012). Comparable data is not available for yellow warblers but observation of yellow warblers on their wintering grounds in Mexico well into the second week of May (Valdez-Juarez et al. 2019) suggests that their spring migration takes a similar amount of time.

In birds, the timing of arrival on the breeding grounds can be influenced by various factors. In this study we found limited evidence that the timing of arrival on the breeding grounds varies with growing degree days (GDD), which is closely linked to the temperature on the breeding grounds and the stage of vegetation phenology at the time of arrival (Hakkinen et al. 1998, Linkosalo 1999). Female arrival dates did not vary across the three years of this study despite marked differences in GDD among years. While our findings are consistent with some studies that concluded that climate conditions on breeding grounds are not a good predictor of arrival phenology (e.g., Both et al. 2006, Weidinger and Král 2007, Møller et al. 2008), other studies demonstrated that breeding ground temperature can be an important factor in predicting arrival of

migratory songbirds on the breeding grounds (e.g., Ahola et al. 2004, Marra et al. 2005, Mazerolle et al. 2011, Mihoub et al. 2012, Connare and Islam 2022). Previous work with yellow warblers demonstrated that wind conditions experienced during migration affect the arrival timing of males (Drake 2014). While arrival dates for yellow warbler males are easily recorded due to their more vocal and territorial nature, arrival data for females are much more difficult to obtain. In this study we attempted to carefully document female arrival. While conditions on migration seem likely to influence the timing of arrival of both males and females, we found limited evidence that wind experienced during migration significantly influenced arrival of females. However, in the three years of this study there was little variation in the speed of crosswinds on the Pacific flyway during the time of yellow warbler spring migration.

Upon arrival on the breeding grounds female songbirds rapidly transition from a migration to a reproductive physiology in order to lay eggs (Williams 2012b). Recently, we have demonstrated that some females can arrive on the breeding grounds in a relatively advanced stage of yolk precursor production (Pavlik et al. 2021). Here, we confirm that reproductive state (plasma triglyceride concentration) on arrival influences the delay between arrival and egg laying. Delays were associated with both plasma triglyceride levels and crosswinds faced by females during the 14-day period before arriving on the breeding grounds. However, crosswind effects on delay were not caused by changes in reproductive state attributable to crosswinds experienced during migration. Plasma triglyceride levels in female yellow warblers were not correlated with crosswinds experienced during the 14-day period before arrival on the breeding grounds. Moreover, we did not find a correlation between GDD on arrival and reproductive state (plasma triglyceride) on arrival or the delay between arrival and egg laying.

Carryover effects from crosswinds experienced during migration on the timing of breeding and reproductive success of yellow warblers, are likely to arise due to their effect on arrival date and how rapidly birds can transition from a migratory to a reproductive physiological state. The delay between arrival on the breeding territory and laying of the first egg can fluctuate based on multiple factors. Later arriving females could compensate for their late arrival by shortening the delay between arrival and first egg date perhaps by taking advantage of phenologically advanced vegetation, higher temperature and more abundant food (e.g., Meijer et al. 1999, Salvante et al. 2007,

Visser et al. 2009, Deschamps et al. 2011, Dunn et al. 2011, Nightingale et al. 2023). Similarly, females arriving in better breeding condition (body condition and/or reproductive state) could take advantage of this asset by being able to shorten this delay (e.g., Drent and Daan 1980, Rowe et al. 1994, Descamps et al. 2011, Hennin et al. 2016, Lamarre et al. 2017).

In this study, we demonstrate that crosswinds experienced during the last 14 days before arrival on the breeding grounds influence the delay between arrival and the start of egg laying. How wind conditions may affect the ability of females to shorten the delay between arrival and egg laying remains unclear because crosswind effects were independent of when females arrived and their residual mass or reproductive state on arrival. Similarly, it remains to be uncovered what the mechanisms are which allow some females to arrive with high plasma triglyceride levels. This study highlights the importance of carryover effects from migration on the timing of reproduction in determining the productivity of a migratory songbird. We also provide further evidence that the benefits associated with initiating reproduction early can lead to selective pressures that favor individuals capable of a fast transition from migratory to reproductive physiology and of minimizing the delay between arrival and egg laying. However, this study also acknowledges limited understanding of the mechanisms that allow some females to transition into a reproductive physiology before reaching the breeding grounds or mechanisms through which conditions from the migration period influence delay between arrival and egg laying.

3.6. Literature

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3.7. Supplemental Tables and Figures

Supplemental Table 3-A: Standardized effect sizes for the models from the candidate sets in which multiple models had ΔAICc less than 2.5.

a) Standardized effects sizes (95 % CI) for models examining variation in the arrival dates of female yellow warblers ($\Delta\text{AICc} < 2.5$).

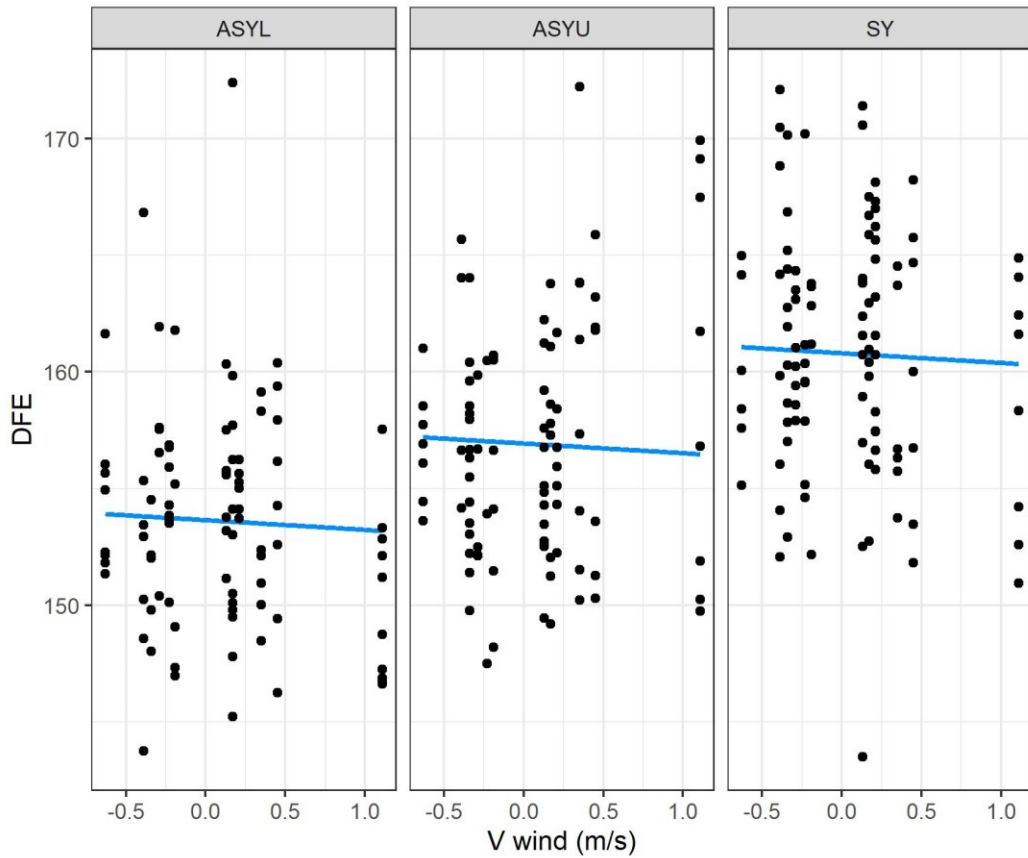
Model	Age		GDD	U-wind
	ASYU	SY		
Age	0.14 (-0.32 – 0.60)	1.16 (0.68 – 1.64)	.	.
Age + GDD	0.14 (-0.32 – 0.59)	1.14 (0.66 – 1.63)	0.05 (-0.13 – 0.23)	.
Age + U-wind	0.15 (-0.31 – 0.60)	1.16 (0.67 – 1.64)	.	0.03 (-0.15 – 0.21)

b) Standardized effects sizes (95 % CI) for models examining variation in the plasma triglyceride concentration of female yellow warblers captured within 2 days of arrival on the breeding grounds ($\Delta\text{AICc} < 2.5$).

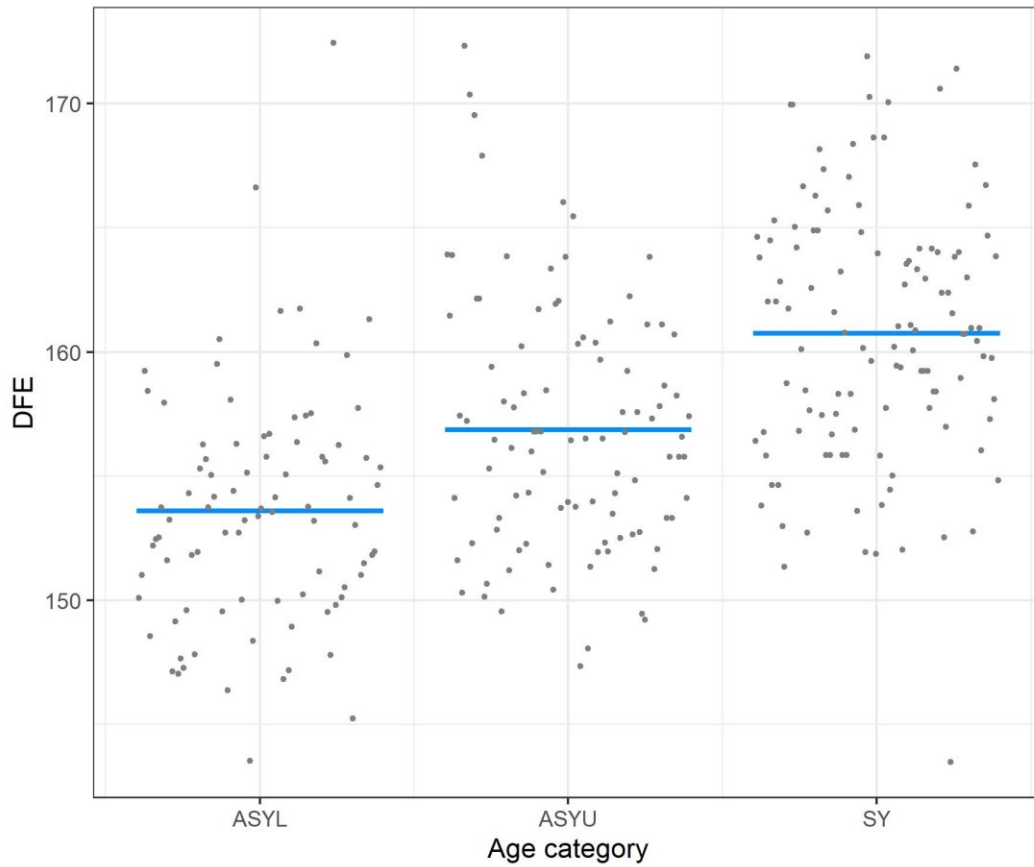
Model	DAA	DOA	U-wind
DAA + DOA	0.47 (-0.12 – 1.06)	0.38 (0.09 – 0.68)	.
DAA + DOA + U-wind	0.53 (0.07 – 1.12)	0.48 (0.14 – 0.83)	-0.19 (-0.53 – 0.16)

c) Standardized effects sizes (95 % CI) for models examining variation in the delay between arrival and egg laying in female yellow warblers captured within 2 days of arrival on breeding grounds ($\Delta\text{AICc} < 2.5$).

Model	Trig	U-wind	DOA	Year	
				Year 2	Year 3
Trig + U-wind + DOA	-0.68 (-0.90 – -0.45)	0.39 (0.13 – 0.66)	-0.38 (-0.65 – -0.12)	.	.
Trig + Year	-0.65 (-0.88 – -0.42)	.	.	0.70 (0.22 – 1.19)	0.27 (-0.47 – 1.02)



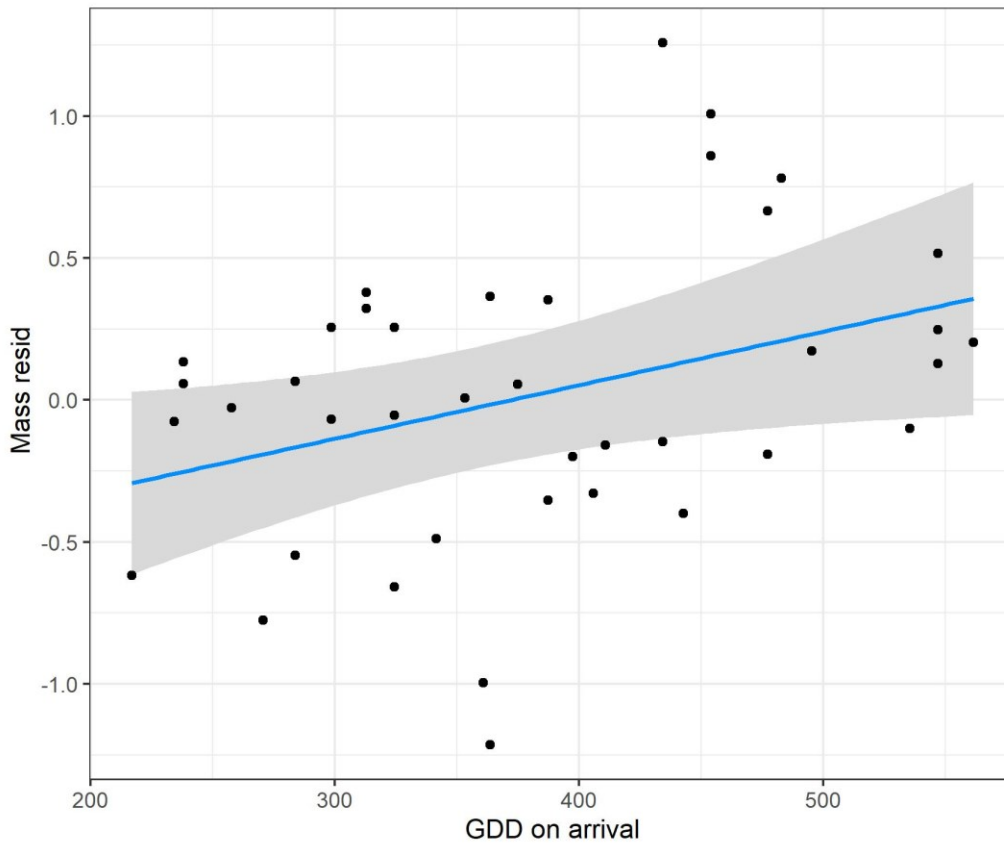
Supplemental Figure 3-A: Relationship between northerly wind speed during migration (V-wind) and date of the first egg (DFE) in yellow warblers (2005-2017). The line shows the prediction from the model (controlling for age category and U-wind) and the points show the partial residuals.



Supplemental Figure 3-B: Variation in date of the first egg (DFE) among age categories (ASYL = after second year local, ASYU = after second year unknown, SY = second year) in female yellow warblers (2005-2017). The line shows the prediction from the model (controlling for U-wind and V-wind) and the points show the partial residuals.

Supplemental Table 3-B: Comparison of support for models in the candidate set examining variation in residual mass of female yellow warblers captured within 2 days of arrival on the breeding grounds (2015-2017). All models control for the time of capture (days after arrival, DAA). Models are ranked according to the difference from the best model based on Akaike's Information Criterion corrected for small sample size (AICc). K is the number of model parameters, and w_i is the Akaike weight.

Model	K	AICc	Δ AICc	w_i
GDD (+DAA)	4	63.34	0	0.39
GDD + U-wind (+DAA)	5	65.92	2.58	0.11
null (DAA)	3	65.93	2.59	0.11
DOA (+DAA)	4	66.51	3.16	0.08
U-wind (+DAA)	4	66.84	3.49	0.07
Year + U-wind (+DAA)	6	66.99	3.65	0.06
Year (+DAA) (+DAA)	5	67.44	4.10	0.05
Age + GDD (+DAA)	6	67.86	4.52	0.04
Year + DOA (+DAA)	6	67.93	4.59	0.04
DOA + U-wind (+DAA)	5	68.75	5.40	0.03
Age (+DAA)	5	70.87	7.53	0.01
Age + DOA (+DAA)	6	70.89	7.55	0.01
Age + U-wind (+DAA)	6	72.03	8.69	0.01
Age + Year (+DAA)	7	73.04	9.69	0
Age + DOA + U-wind (+DAA)	7	73.53	10.19	0



Supplemental Figure 3-C: Relationship between the residual mass of female yellow warblers sampled within 2 days of arrival on the breeding grounds ($n = 40$) and the growing degree days (GDD) on the day of arrival on the breeding grounds. The line shows the prediction from the model (controlling for DAA) and the shaded area shows the 95% confidence interval around the predicted relationship. The points show the partial residuals.

Chapter 4.

Evaluating the use of spatial CJS models to improve the accuracy of survival estimates: a case study on yellow warblers (*Setophaga petechia*)

4.1. Abstract

Survival is often estimated from traditional Cormack–Jolly–Seber (CJS) models which do not distinguish between mortality and dispersal to sites outside the study area. Spatial Cormack-Jolly-Seber (sCJS) models have the potential to improve demographic models by providing an estimate of true survival rather than an estimate of apparent survival. To evaluate the use of spatial CJS models we used encounter history and individual spatial location data from a 14-year, multi-site study on yellow warblers (*Setophaga petechia*) near Revelstoke, BC. We show that sex-differences in dispersal can lead to erroneous conclusions about survival, and that incorporating dispersal can both reduce the bias and increase the accuracy of survival estimates. Breeding dispersal of yellow warblers was best modelled using a t-distribution which captured the rare longer distance dispersal events. Median estimated breeding dispersal distance was 39.0 m for males and 95.0 m for females. Our model predicted that 4.7% males and 11.3% females disperse further than 500 m, and 0.3% males and 0.7% females further than 5 km. The spatial CJS model that described dispersal using a t-distribution estimated annual survival probabilities of ASY males at 0.65 (95% CI: 0.59 – 0.71), ASY females at 0.62 (0.54 – 0.72), SY males at 0.48 (0.39 – 0.57) and SY females at 0.44 (0.35 – 0.55). True survival estimates of yellow warblers were 0.08-0.16 higher (18-42% higher) than apparent survival estimates and varied with age but not sex. The longer dispersal distances of females, which make them more likely to permanently leave the study areas than males, thus largely explained the sex differences in apparent survival estimates obtained using conventional CJS models. We confirmed that true survival of yellow warblers is reduced in years with stronger crosswinds during spring migration. We also show that while spatial CJS models are data hungry they provide an opportunity to examine correlates of annual variation in survival.

4.2. Introduction

Fecundity, survival, and dispersal of individuals combine to determine the trajectory of populations. Identification of factors responsible for variation in these demographic rates is important because it can inform conservation and management. For example, knowledge of local and landscape effects on breeding success can be used to help designate protected areas (Ferrer-Sánchez et al. 2019), inform or test the efficacy of restoration activities (Forrester et al. 2017, Severson et al. 2017), and assess the environmental impact of anthropogenic activities (Bonnot et al. 2018, Kleist et al. 2018). Similarly, estimates of survival can be used to assess the quality of natural and modified habitat (Valdez-Juarez et al. 2019, González et al. 2020) and the impact of climatic conditions throughout the year (Santisteban et al. 2012, Hill et al. 2019). Finally, understanding and mitigating landscape level effects on dispersal may be critical in maintaining patch occupancy in fragmented landscapes (Lees and Peres 2009, Pavlacky et al. 2012).

Survival is frequently estimated from mark-recapture data using traditional Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992, Grosbois et al. 2008) that allow the probability of survival and recapture to be estimated separately. However, annual survival estimated using CJS models combines two demographic rates, true survival and permanent dispersal from the study area. The estimated parameter, apparent annual survival, is therefore likely to be lower than true survival, and conclusions regarding sex, age and environmental effects on survival will be biased if dispersal is non-random. The inability of CJS models to incorporate sex (Clarke et al. 1997), age (e.g., Calabuig et al. 2008, Cline et al. 2013) or environmental effects on dispersal (e.g., Møller et al. 2006, Dugger et al. 2010) is therefore a major limitation of this approach (Schaub and Royle 2014).

Studies on multiple taxa highlight the importance of including information on dispersal when estimating annual survival. For example, Weldy et al. (2022) found that age and sex specific survival estimates for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) can be biased if emigration differs among these classes. Cilimburg et al. (2002) showed that permanent dispersal of yellow warblers (*Setophaga petechia*) from their original study site was common (7% of males and 12% of females dispersed further than 1.5 km between

years), and that using multiple study sites and an extended search area increased annual apparent survival estimates by 7-23%. More recently, using a spatial CJS (sCJS) model that allows estimation of both dispersal and true survival, Reidy et al. (2018) estimated that 10% of male golden-cheeked warblers (*Setophaga chrysoparia*) dispersed further than 1 km between years and the true annual survival estimate was 21% higher than the apparent annual survival estimated using a traditional CJS model. Even when the dispersal distances are short compared to the size of the study area, spatially explicit survival model estimates are more precise than non-spatial survival estimates (e.g., field vole - *Microtus agrestis*; Ergon and Gardner 2014).

Here, we use and extend the spatial CJS model (sCJS) developed by Schaub and Royle (2014) to assess the degree to which sex differences in breeding dispersal bias estimates of true survival. We address this question using data from a 14-year, multi-site study on yellow warblers, a small neotropical migrant (Quinlan and Green 2012, Hepp et al. 2021). Previous studies on yellow warblers suggest that annual apparent adult survival varies with sex (Cilimburg et al. 2002, Salgado-Ortiz et al. 2008, Martin et al. 2020), age (Drake et al. 2014) and ENSO associated variation in wind-speed during spring migration (Drake et al. 2014). Observational data (Cilimburg et al. 2002) as well as analysis of genetic markers (Gibbs et al. 2000) also provide evidence for sex-differences in breeding dispersal of yellow warblers. We combined the encounter histories and spatial location data (x and y-coordinates) from banded yellow warblers to estimate true survival probabilities and dispersal parameters using the sCJS modelling approach developed by Schaub and Royle (2014). This model extends traditional CJS models by explicitly modelling the dispersal process and estimating true survival after accounting for the fraction of dispersal events that result in permanent dispersal from the study area. Specifically, we (1) describe breeding dispersal and assess whether dispersal is best modelled by normal, exponential, t-distribution or double normal distribution; (2) assess whether sex-differences in dispersal result in biased estimates of apparent survival and examine how incorporating dispersal improves our ability to estimate true survival; and (3) examine whether crosswind experienced on migration influences true survival estimates, after controlling for dispersal.

4.3. Methods

Study species, site and field methodology

The yellow warbler is a small, insectivorous neotropical migrant with a broad breeding distribution in North America (Lowther et al. 1999). We studied yellow warblers breeding at three sites near Revelstoke, British Columbia, Canada (118°W 50°N) from 2004 to 2017. The three sites, each of approximately 30 ha, are located in riparian habitat (435 – 442 m AMSL) composed of a mosaic of mature black cottonwood (*Populus trichocarpa*) forest patches, willow (*Salix* spp.) dominated shrub and seasonally flooded grassland along the edge of the Arrow Lakes Reservoir in the Columbia River valley. These sites, separated by 1.7, 13.8 and 15 km, support a total of approximately 35 (range = 24 – 42) breeding pairs each year. Yellow warblers begin to return to our study sites in early May (with males arriving, on average, a few days before females). Females initiate their first clutches from mid-May to mid-June, can re-nest after the failure or success of their first nest, and continue to initiate replacement and occasionally second clutches until early-July (Hepp et al. 2021).

We captured and re-sighted birds in all years, although our monitoring effort was less extensive in 2007. We visited sites every 1-3 days from early-May to late-July in 2004-6 and 2008-2017, and every 1-3 days between 1-21 May and 7-21 June in 2007. We caught birds using mist nets with call and/or song playback, and banded birds with a unique combination of color bands and a Canadian Wildlife Service-issued aluminum band. We aged and sexed birds using plumage criteria (Pyle 1997). We subsequently noted when and where birds were re-sighted on territory maps and recorded the location of each nest found using a GPS unit. Where possible we used the location of the first nest initiated by a pair as the spatial reference for each member of the pair in that year. In the rare cases where a bird was re-sighted but disappeared before initiating a nest, we used the location where the bird was first re-sighted as the spatial reference.

Spatial survival modelling

We estimated the true survival probabilities and dispersal parameters using the sCJS modelling approach developed by Schaub and Royle (2014). This model combines spatial locations with encounter histories of all individuals to model true survival

independent of dispersal. The model assumes that survival does not vary spatially, locations are recorded without measurement error, that re-sighting events can occur anywhere within the study area, and that the study area is defined as the area in which animals are marked and re-sighted (Schaub and Royle 2014).

The survival component of the sCJS model describes the state (z ; alive = 1 or dead = 0) of each individual i in each year t as the outcome of a Bernoulli process, defined by survival probability s . The model conditions on first capture and the previous state of each individual such that only marked individuals alive at time $t-1$ may be alive at time t .

The dispersal component of the sCJS model treats dispersal as a random walk where the location (x and y coordinates of the nest or resighting location) of an individual in time t is described in relation to their location in previous year ($t-1$) by symmetric probability distributions that model movement in both the x and y direction. We tried to fit four separate sCJS models that differed in the probability distributions describing dispersal: 1) a symmetric normal distribution defined by mean and precision parameters (sCJS-N), 2) a symmetric t -distribution defined by mean, precision and degrees of freedom parameters (sCJS-T), 3) an exponential distribution and 4) a double-normal mixture distribution describing both long and short distance dispersal using two normal distributions (sCJS-M). For each model the mean of the dispersal distribution was taken to be the location of the individual in time $t-1$, while the additional parameter(s) defining the shape of the distribution are estimated. Dispersal movements are assumed to be random with respect to location within the study area so the probability that an individual leaves the study area depends on the individual previous location relative to the study area boundaries.

The observation component of the sCJS model, defined by the recapture probability (p), is estimated for individuals that are alive and present in one of the three study sites. Individual spatial locations (x and y coordinates) are known or assigned missing values in years in which an individual is not encountered. Individuals that are alive at time t ($z_{i,t} = 1$) may be inside ($r_{i,t} = 1$) or outside the study area ($r_{i,t} = 0$) depending on whether dispersal takes them outside the study area (in our case represented by an irregular, disjunct, set of 609 50x50m grid cells; Figure 4-1).

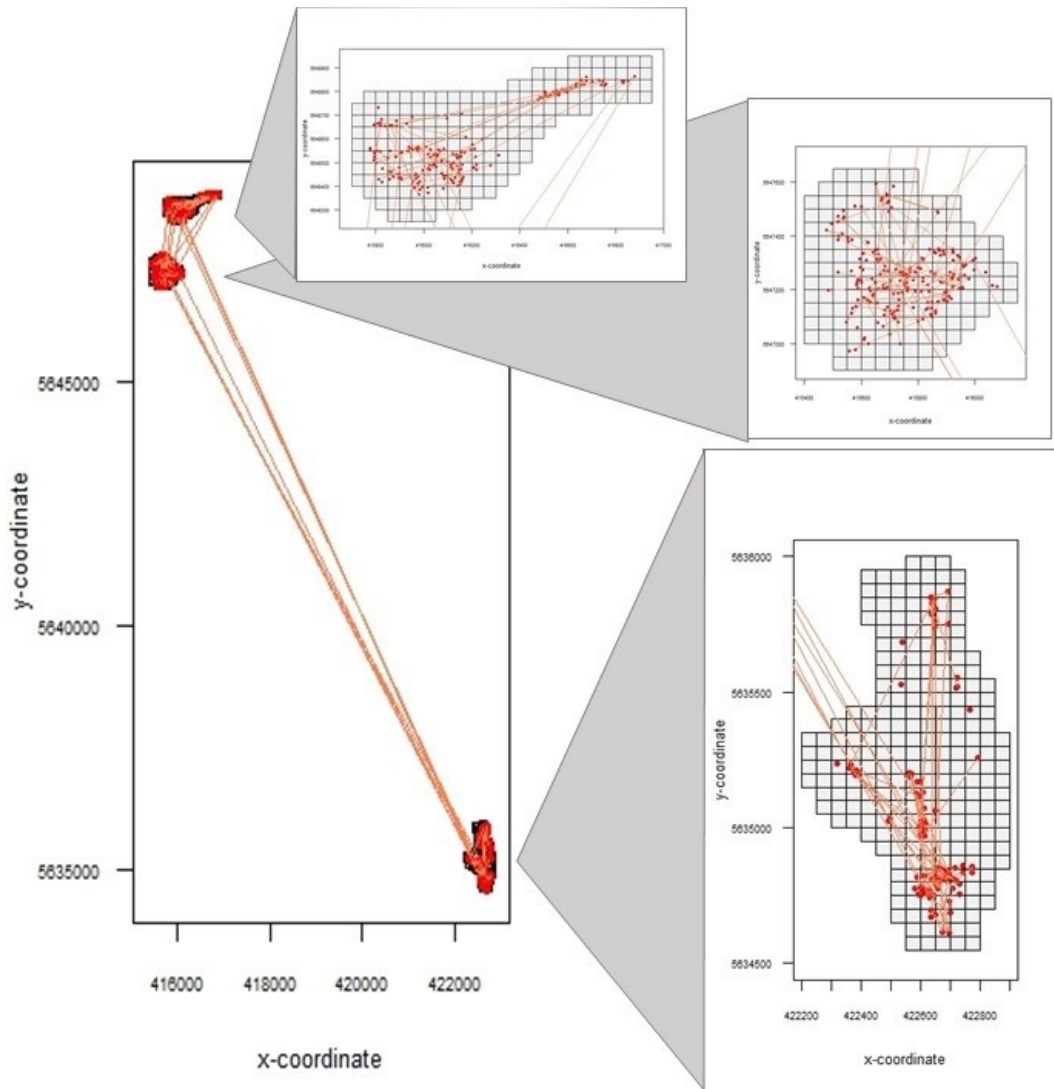


Figure 4-1 Study area near Revelstoke, BC showing 50x50m grid with individuals' locations (points) and recorded dispersal movements of yellow warblers (lines). Lines show breeding dispersal movements from year t to year $t+1$ within and between the three study sites.

Analyses

Prior to examining breeding dispersal and dispersal effects on true survival we used the encounter histories from banded yellow warblers to estimate annual apparent survival using a non-spatial CJS model. The model structure followed Drake et al. (2014); the resighting probability was allowed to vary with sex and the survival

probability was allowed to vary with age and sex. We next described the breeding dispersal of marked warblers within and among the three study sites. We compared the breeding dispersal distances of males and females and second-year (SY) and after-second-year (ASY) birds using a non-parametric Wilcoxon signed-rank test.

Next, we used the encounter histories and breeding dispersal data to fit spatial CJS models. Because sCJS models are sensitive to how the dispersal distribution is specified (Schaub and Royle 2014), initial models assessed four potential dispersal structures (sCJS-N, sCJS-T, sCJS-E or sCJS-M). For these models, we allowed annual survival to vary with sex and age, and resighting probability to vary with sex, and assumed that survival and dispersal parameters were constant over time. We then extended the best fitting sCJS model by allowing male and female dispersal distributions to be described by different functions (while allowing annual survival to vary with sex and age, resighting probability to vary with sex, and assuming that survival and dispersal parameters were constant over time). We compared the true survival estimates obtained for the four age-sex classes using this sCJS model with the estimated apparent annual survival from the non-spatial CJS model.

Finally, we used this spatial CJS model to assess whether sCJS models are able to incorporate environmental covariates and test whether annual variation in wind-conditions on migration was still an important factor influencing the true annual survival. We used the mean U-wind speed for the entire western flyway for April and May as an indicator of conditions faced on spring migration (Drake 2014). We used April-May, rather than the March-May used by Drake et al. (2014) as recent work suggests yellow warblers using the western flyway do not leave their wintering grounds in Mexico until April (Valdez-Juarez et al. 2019). Wind-speed values were obtained from the National Center of Environmental Prediction (NCEP) Reanalysis 1 data archives at the NOAA-CIRES Climate Diagnostics Center at Boulder, Colorado, USA (Kalnay et al. 1996) using the RNCEP package for R statistical software (Kemp et al. 2012). We defined the western flyway for our population as the overland region west of the easternmost portion of the continental divide (107°W), beginning at the northern extent of the yellow warbler wintering range (25°N) and ending at the latitude of our study site (50°N). Wind data have a spatial resolution of 2.5° latitude and longitude and temporal resolution of six hours. Because songbirds migrate at night and mostly at elevations from close to the surface up to 2100 m (Alerstam et al. 2011, Bruderer et al. 2018) depending on terrain

and environmental conditions, we used average nighttime (1800, 0000 and 0600) westerly (U-wind) components at the 850 mb (~1500 m AMSL) and 925 mb (~700 m AMSL) levels. Absolute values of the U-wind vector were used, and we calculated the overall crosswind values by averaging the U-wind components over the entire flyway over the April-May period.

All models were fitted in a Bayesian framework using the program JAGS (Plummer 2003) and run within R programming environment (R Core Team 2022) using package “runjags” (Denwood 2016). Uninformative priors were used throughout for all parameters. Posterior distribution for all models were simulated from 3 parallel Markov chains. We discarded the first 50,000 iterations as burn-in, ran each chain for a total of 50,000 adaptive phase iterations and then thinned the samples at a rate of 1 in 5,000. To confirm convergence of models we used the Gelman-Rubin diagnostic statistic indicating adequate convergence if R_{hat} for all model parameters was less than 1.1 (Gelman and Rubin 1992) as well as visually inspecting plotted chains for signs of problems with convergence.

4.4. Results

Over the 14 years of this study, we marked a total of 494 breeding adults (male: $n = 244$; female: $n = 250$). Approximately half of these birds were first captured as second-year birds (male: $n = 131$; female: $n = 143$). Of all the birds marked, 36% ($n = 176$) were re-sighted in at least one year after capture (ASY males 48% [$n = 54$], ASY females 35% [$n = 37$], SY males 37% [$n = 48$], SY females 26% [$n = 37$]). At the maximum, two males were resighted seven times, and one male and one female were resighted 6 times.

The conventional CJS model estimated that the resighting probability for males was 0.97 (95% credible intervals [CI]: 0.93 – 0.99) and for females it was 0.78 (95% CI: 0.67 – 0.87). This model estimated the annual apparent survival of males to be higher than that of females and ASY birds to be higher than that of SY birds (Figure 4-2). The apparent annual survival of SY males was 0.40 (95% CI: 0.32 – 0.48), for SY females it

was 0.31 (0.25 – 0.39). For ASY males the apparent annual survival was 0.55 (0.50 – 0.61) and for ASY females it was 0.46 (0.39 – 0.52).

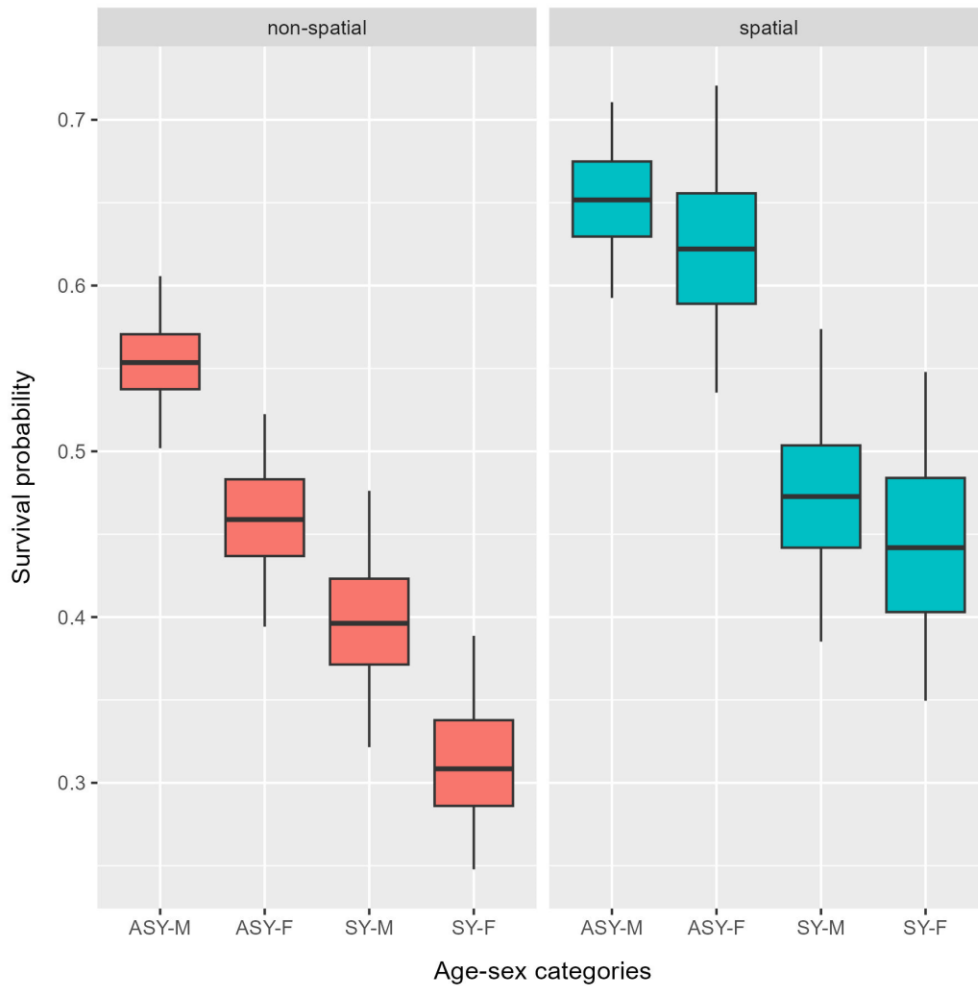


Figure 4-2: Posterior distributions of annual survival probabilities of yellow warblers estimated from non-spatial Cormack–Jolly–Seber (CJS) and spatial CJS-T survival models. ASY-M = after-second-year male, ASY-F = after-second-year female, SY-M = second-year male, SY-F = second-year female. Boxplots show the median (line in the centre of the box), the 25% and 75% quantiles (boxes) and 95% credible interval (whiskers).

We observed a total of 329 dispersal events (male = 215, female = 114) of which 13 were dispersal events between study sites (6 males and 7 females). Males were recorded to disperse a shorter distance than females (median [Q1-Q3]; male = 58.2 m [29 – 134], female = 112.3 m [49 – 228]; $W = 15,232$, $p < 0.0001$). Also, second-year

birds were recorded to disperse further than after-second-year birds (median [Q1-Q3]; second-year birds = 121.1 m [49 – 284], after-second-year birds = 61.1 m [29 – 139]; $W = 7,792.5$, $p < 0.0001$).

We used a spatial CJS model to draw conclusions about yellow warbler survival and dispersal. The initial sCJS models incorporating dispersal and modelled using a normal, exponential and double-normal distribution all failed to converge. However, the initial sCJS model incorporating dispersal using a t-distribution (sCJS-T) converged successfully. We therefore used the model with a t-distribution function for dispersal to evaluate whether dispersal could be allowed to vary with sex and/or age. The sCJS-T model incorporating dispersal that varied with both sex and age failed to converge. However, the simpler model where dispersal varied with sex converged successfully. This sCJS-T model which described dispersal that varied with sex, resighting that varied with sex, and survival that varied with sex and age was therefore used to draw any conclusions about dispersal and survival probabilities.

The sCJS-T model incorporating sex differences in dispersal estimated resighting probabilities of males and females to be high. Resighting probability for males was estimated to be 1.00 (95% CI: 0.96 – 1.00) and for females it was 1.00 (95% CI: 0.86 – 1.00). True annual survival estimated from the sCJS-T model was higher than annual apparent survival in all four age-sex categories (Figure 4-2). True survival varied with age but not sex (Figure 4-2). The estimated survival probabilities of ASY birds (ASY males: 0.65 [95% CI: 0.59 – 0.71], ASY females 0.62 [0.54 – 0.72]) were higher than those of SY birds (SY males: 0.48 [0.39 – 0.57], SY females: 0.44 [0.35 – 0.55]).

Estimated dispersal kernels from the sCJS-T model captured observed sex differences in dispersal (Figure 4-3). Median estimated dispersal distance for males was 39.0 m (Q1-Q3: 16.0 – 93.5 m) and for females it was 95.0 m (39.5 – 224.5 m). Our model predicted that 4.7% of males disperse further than 500 m, 2.2% of males disperse further than 1 km and 0.3% of males further than 5 km. For females, 11.3% were predicted to disperse further than 500 m, 5.4% further than 1 km and 0.7% further than 5 km.

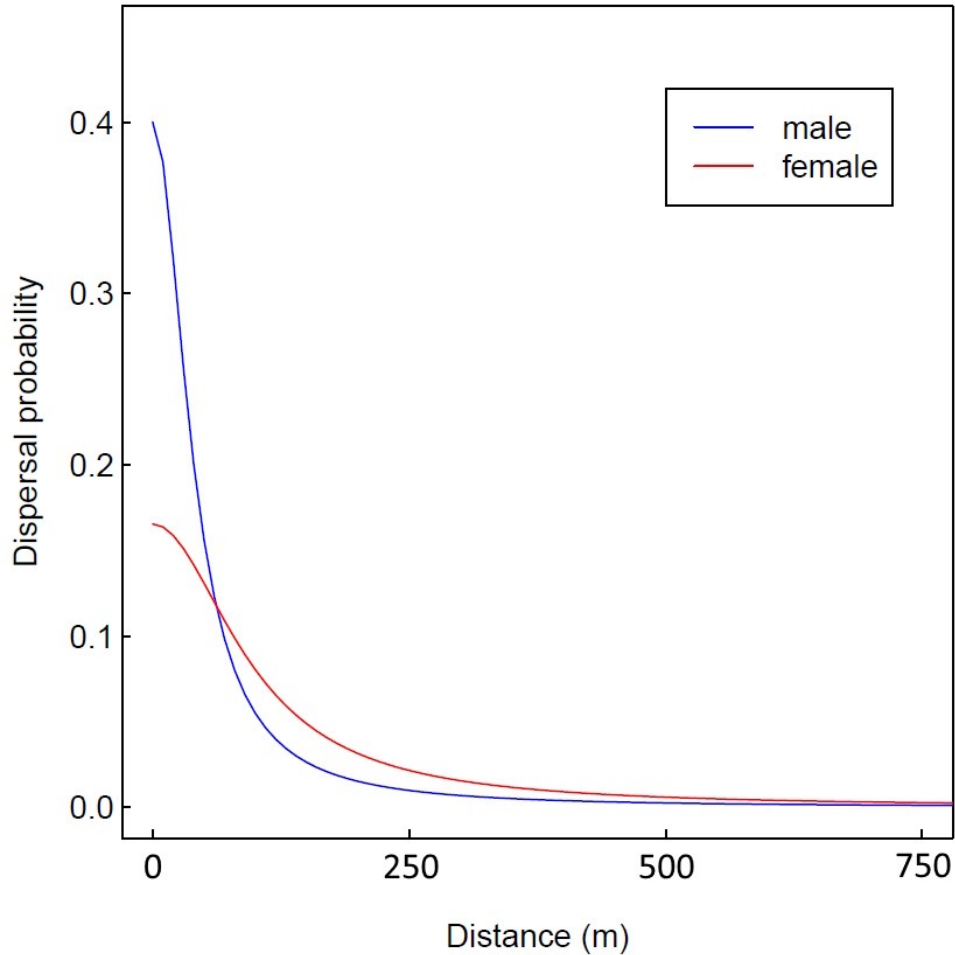


Figure 4-3: Distribution of dispersal distances (dispersal kernels) of yellow warbler males (blue line) and females (red line) predicted by the sCJS-T model.

The sCJS-T model that described dispersal that varied with sex, and survival that varied with sex and age could be extended to evaluate whether windspeed during spring migration influences yellow warbler survival. Our model estimated that an increase in the average speed of crosswinds during spring migration had a negative effective on true annual survival of yellow warbler (Figure 4-4).

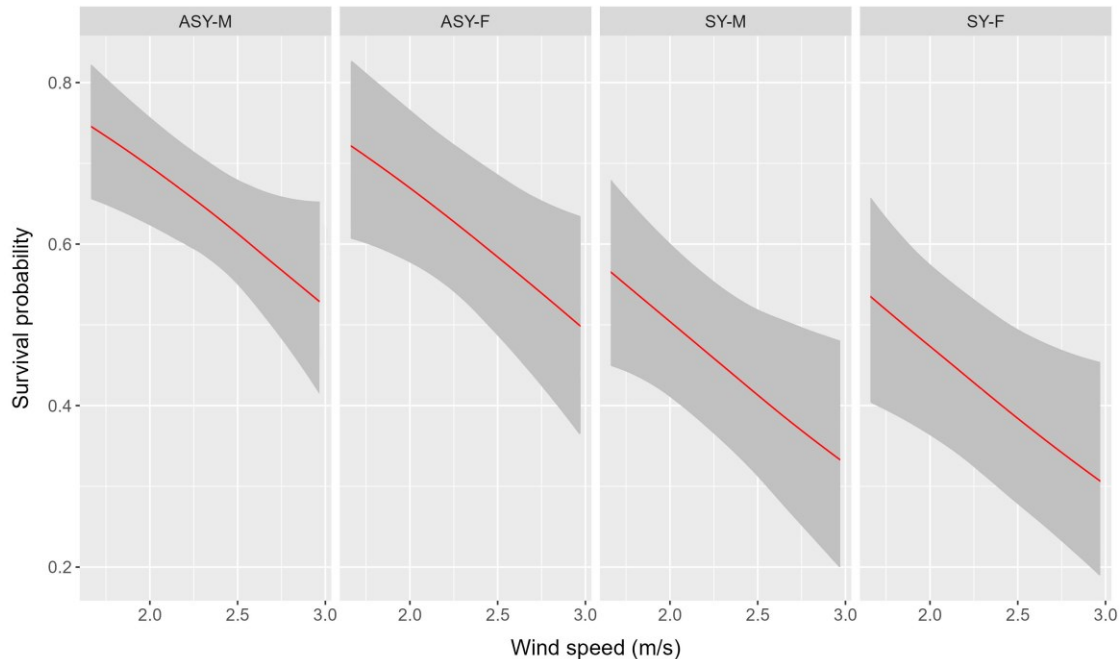


Figure 4-4: Annual survival probability of yellow warblers estimated from the spatial CJS model in relation to the average wind speed during spring migration. Red line shows Loess smoother for the predicted mean survival with 95% credible intervals.

4.5. Discussion

Spatial CJS models have the potential to improve demographic models by providing an estimate of true survival rather than an estimate of apparent survival which does not distinguish between mortality and dispersal to sites outside the study area. In this paper we show that sex-differences in dispersal can lead to erroneous conclusions about survival, and that incorporating dispersal can both reduce the bias and increase the accuracy of survival estimates. True survival estimates of yellow warblers were 0.08-0.16 higher (which is about 18-42% higher) than apparent survival estimates and varied with age but not sex. We also show that while spatial CJS models are data hungry they provide an opportunity to examine factors that influence variation in annual survival. Specifically, we confirmed that true survival of yellow warblers decreased with increasing wind speed during spring migration.

Breeding dispersal movements, defined as a shift in territory location between two breeding seasons, frequently vary with sex and age (Greenwood 1980, Greenwood and Harvey 1982, Cline et al. 2013) but are notoriously difficult to measure (Holmes et al. 1996, Walters 2000, Nathan 2001, Fajardo et al. 2009). In birds, natal and breeding dispersal is frequently female-biased (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997, Cilimburg et al. 2002, Schaub and von Hirschheydt 2009, Cline et al. 2013). In our population, although breeding males dispersed shorter distances than females, the dispersal events by both sexes that we observed primarily involved short within-site movements with medium distance between-site movements being less common. This pattern is consistent with breeding dispersal of other populations of yellow warbler (Montana, Cilimburg et al. 2002) as well as other species of migratory songbirds (e.g., hooded warbler [*Setophaga citrina*, Howlett and Stutchbury 2003]; barn swallow [*Hirundo rustica*, Schaub and von Hirschheydt 2009]; black-throated blue warbler [*Setophaga caerulescens*, Cline et al. 2013], red-backed shrike [*Lanius collurio*, Schaub and Royle 2014]). Perhaps unsurprisingly, dispersal of yellow warblers was therefore best modelled using a t-distribution which captured the skewed distribution and rare longer distance dispersal events. Previous studies that have modelled dispersal with different distribution functions (e.g., normal, double exponential and t-distribution) have also concluded that the t-distribution is best suited to describing the dispersal of migratory songbirds (red-backed shrike - Schaub and Royle 2014, golden-cheeked warbler - Reidy et al. 2018). However, modelling dispersal using two normal distributions would allow estimation of both the frequency and dispersal distances of short and long-distance dispersal events, perhaps further improving true survival estimates. Unfortunately, we found that a model with two normal distributions (one for short distance dispersal and one for long distance dispersal) failed to converge, likely because we had insufficient data to properly model both dispersal components. Studies with larger datasets should explore the use of double normal distributions which may better capture the common short distance and rare long distance dispersal events of over 100 km documented using stable isotope analysis of feather tissue (Hobson et al. 2004, Girvan et al. 2007, Rushing et al. 2015, Bairlein et al. 2016, Jones and Islam 2023).

Conventional CJS models that do not account for sex-differences in breeding dispersal may both underestimate true survival and exaggerate differences in the survival of males and females. Sex differences in apparent survival have been

documented in many taxa where dispersal is sex-biased (e.g., birds - Sillett and Holmes 2002, Cilimburg et al. 2002, Drake et al. 2014, Wilson et al. 2018; mammals - Kraus et al. 2008, Le Cœur et al. 2016). To date, relatively few studies have compared estimates of true survival, which account for dispersal, and estimates of apparent survival. In this study true survival estimates of yellow warblers were 18-42% higher than apparent survival estimates. This is consistent with other studies where true survival estimates are also far higher than apparent survival estimates. For example, Reidy et al. (2018) estimated true survival of male golden-cheeked warblers to be about 21% higher compared to apparent survival estimates from the same area and Schaub and Royle (2014) estimated true survival of red-backed shrikes to be about 20-50% higher than the apparent survival estimates. In addition, Cilimburg et al. (2002) estimated survival probability of yellow warblers increase by 7-23% when resighting data from areas outside of the study site were included in CJS models. We also found that the longer dispersal distances of females, which make them more likely to permanently leave the study areas than males, largely explained the sex differences in apparent survival estimates obtained using conventional CJS models. This is in line with findings from previous studies (e.g., Schaub and Royle 2014) which also suggested that the sex differences in apparent survival are a consequence of sex-biased dispersal.

Studies on neotropical migrants, and wood warblers (Parulidae) in particular, have been at the forefront of attempts to use a whole-life cycle approach to the study of avian demography. Migration has been identified as a key period with high mortality that varies depending on environmental conditions (Sillett and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017, Rushing et al. 2017). Studies partitioning mortality across periods of the annual cycle frequently combine estimates of annual apparent survival and estimates of survival during the two stationary periods to determine mortality on the two migrations. Sillett and Holmes (2002) argued that the mortality of black-throated blue warbler is highest during the migration period and indicated that 85% of the apparent annual mortality can occur during the migration periods. Since then, multiple other studies also suggested that migration is the period of the annual cycle with the highest mortality rates. For example, Paxton et al. (2017) estimated that willow flycatcher (*Empidonax traillii*) mortality during migration is about 62% of the annual mortality and Rockwell et al. (2017) assessed the migration mortality of Kirtland's warbler (*Setophaga kirtlandii*) to be about 44% of annual mortality. Similarly, Rushing et al. (2017) suggested

that the mortality level for wood thrush (*Hylocichla mustelina*) during migration periods is about 50% of their annual mortality for adults and 60% for juveniles. These studies however are reliant on estimates of apparent survival that are likely underestimates of true survival and examine environmental correlates of variation in apparent rather than true survival.

If true estimates of annual survival are 1.2 to 1.4 times apparent estimates of annual survival, mortality on migration would be substantially less. For example, in our population of yellow warblers and assuming birds spend 7 months on the wintering grounds with monthly apparent survival between 0.93 and 0.97 (e.g., Valdez-Juarez et al. 2019) and 3 months on the breeding grounds with monthly apparent survival of 0.92-0.98 (D.J. Green, unpublished data), a 20% increase in annual survival can lead to estimates of mortality during migration periods that are about 2/3 lower and in line with mortality during other parts of the annual cycle. Studies examining correlates of annual variation in survival can also be improved by using spatial CJS models. For warblers that migrate along the Pacific flyway, wind speed during migration (Drake et al. 2014, Huang et al. 2017) and precipitation at stopover sites (LaManna et al. 2012) have been identified as important factors affecting apparent annual survival. Here we show that true survival is reduced in years with stronger crosswinds during spring migration, as has been documented using conventional CJS models (Drake et al. 2014). Unfortunately, we had insufficient data to assess whether stronger crosswinds during migration also affect permanent dispersal.

Spatial CJS models, despite producing more accurate estimates of annual survival, have some limitations. First, these models are sensitive to how dispersal is modelled (Schaub and Royle 2014, Ergon and Gardner 2014, Efford and Schofield 2022). T-distributions appear to do an adequate job of describing breeding dispersal, but further work is required to determine whether models combining two distributions (long and short distance dispersal) would better describe the range of dispersal movements. Second, true survival estimates can be underestimated if the dispersal data is limited or insufficient to document the span of dispersal distances (Schaub and Royle 2014, Efford and Schofield 2022). Here we show that the use of multiple study sites allows some longer dispersal events to be captured, as has been demonstrated previously by Cilimburg (2002). Stratification of our three study sites allowed us to document short distance (within-site) dispersal movements as well as medium distance (between-site)

dispersal events, up to a distance of about 15 km. However, dispersal modelled using these data may underestimate the frequency of long distance dispersal events. Our analyses predicted 0.3% of male dispersal events and 0.7% of female dispersal events are longer than 5km whereas some studies using stable isotope analysis to classify individuals as residents or immigrants suggest that long distance dispersal events may be more common (Hobson et al. 2004, Girvan et al. 2007, Rushing et al. 2015, Bairlein et al. 2016, Jones and Islam 2023). Data on the frequency of short and long distance dispersal events, perhaps through a sample of satellite tagged individuals, could help determine the extent to which true survival is underestimated. Third, true survival may be overestimated if dispersal leading to permanent emigration is less likely than expected based on the modelled dispersal distribution. Our models assume that the dispersing individuals find and occupy suitable habitat and may settle anywhere outside the study area. However, natural suitable habitat is often patchy and even larger tracks of suitable habitat are geographically restricted. At least basic habitat suitability mapping may be required to create a matrix of suitable and unsuitable habitat outside the study sites and use this information to further improve dispersal and survival modelling. Finally, spatial CJS models require extensive data to allow more complicated modelling. This study spanning 14 years and monitoring 494 individuals had insufficient data to model dispersal as a process that varies with both sex and age.

Spatial CJS models have considerable potential (Ergon and Gardner 2014, Schaub and Royle 2014). Many long-term studies of birds collect resighting data and the spatial data necessary to quantify dispersal. Large long-term studies may be able to model dispersal in more detail and examine sex and age-biased dispersal or sex and interannual variation in dispersal associated with environmental conditions. Alternatively, large datasets may be able to model dispersal using two distributions (short and long-distance dispersal as two processes) as suggested by Schaub and Royle (2014). Estimates of true survival may also improve efforts to identify habitat source-sink dynamics (Paquet et al. 2020) which can be useful in conservation efforts and wildlife management and estimate more accurate seasonal mortality rates of migrants. Spatial CJS models have been applied to a diversity of taxa (Efford et al. 2022) and further work assessing both the limitations and potential of this modelling approach appear likely to shed light on biases in dispersal that can alter conclusions about survival estimates as

well as help distinguish mortality from permanent emigration which is critical to accurately parameterize population models.

4.6. Literature

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Chapter 5.

Summary and future directions

Migration is often considered an energetically demanding part of the annual cycle (Wikelski et al. 2003, Bishop et al. 2015, Butler 2016; but see Brown et al. 2023) and the metabolic rate of birds during active flapping migration flight can be 7-9 times (Norberg 1996, Piersma 2011, Brown et al. 2022, Elowe et al. 2023) or even 16 times (Meir et al. 2019) higher than the basal metabolic rate. Reproduction is also energetically expensive and the maximum sustained metabolic rate during reproduction is expected to be about 4-5 times higher than the basal metabolic rate (Drent and Daan 1980, Piersma 2002), but can be as much as 7 times higher (Ellis and Bowman 2021). During migration, birds can adjust their physiology to facilitate long-distance flight. For example, birds may increase muscle mass and fat content to power and fuel flight (Klaassen and Lindström 1996; Jenni and Jenni-Eiermann 1998; Jenni-Eiermann et al. 2002), birds may decrease hematocrit to reduce blood viscosity (Jenni et al. 2006), and may atrophy some non-essential organs to reduce maintenance costs (Piersma and Lindström 1997, Piersma et al. 1999). However, upon reaching breeding grounds, birds must transition from migration physiology to a reproductive physiology. Females must mature their reproductive organs and initiate rapid yolk development to be able to produce and lay eggs (Williams 2012b). My thesis is composed of three chapters, all of which advance current understanding of the transition from migration to breeding, and the mechanisms through which migration influences annual survival, breeding phenology and productivity.

In the **second chapter**, I describe the transition from a migration to reproductive physiology by quantifying plasma triglyceride levels as an index of egg-yolk precursor production and vitellogenesis (Williams 2012b; Crossin and Williams 2021). This is the first study to quantify yolk precursor levels directly at the migration-reproduction transition for any free-living small migrant songbird. I found that some females arrived on the breeding grounds with elevated triglyceride values compared to males and that females that arrived with elevated levels took less time to initiate their first clutch. These findings show that despite the high energetic demands of both migration and reproduction and potential hormonal conflict (e.g., between red blood cells production and vitellogenesis; Williams 2012b, Jubinville et al. 2020), some female yellow warblers

are able to initiate the transition from a migration to a reproductive physiology before they arrive on the breeding grounds. Previous studies have shown that females of a few larger species of seabirds are able to initiate vitellogenesis during migration (Crossin et al. 2010, Williams 2012a). However, this is the first time that anyone has documented the capability of small neotropical migrants to initiate these changes in liver function (yolk precursor synthesis and yolky follicle development) while still on migration.

This chapter raises several questions that warrant further investigation. First, the magnitude of energetic expenditure and fitness costs associated with the transition to breeding physiology during migration and the mechanisms which may prevent any potential hormonal conflicts needs further investigation. Unfortunately, for birds from a local study population any direct measurements of individual energetic expenditures/dynamics during their spring migration are currently not obtainable. However, if individuals could be equipped with precise satellite trackers to document their wintering area, departure date, migration route as well as detailed spatial and temporal data on flight and stopover events during migration, informed assumptions could be made about their energetic dynamic during their migration. Second, the reasons behind why some females transition during migration while others don't and the mechanisms behind the ability of some females to switch remain to be studied. One possibility is that females which arrive with elevated triglyceride concentrations are able to do so during the final stages of migration, perhaps by observing environmental cues and adjusting the speed of migration to allow for diverting more energy toward changes in reproductive physiology. With recent advances in technology, satellite trackers may soon be sufficiently small to document the speed of the last leg of migration, and even compare the migration speeds between females that arrive with elevated triglyceride levels and those who don't. Future studies should focus on uncovering mechanisms which allow some females to control this transition.

Chapter 3 further expands on the investigation of the transition from migration to breeding physiology. I confirmed that wind speed during migration influences timing of breeding in yellow warbler and investigated potential pathways in which this carryover effect may arise. I found that crosswind speed experienced during migration did not significantly influence females' arrival timing (although wind speed varied only slightly in the years when arrival timing was examined), residual mass or reproductive state (triglyceride levels) on arrival. However, wind speed on migration influenced the delay

between arrival and egg laying. This delay was also affected by females' reproductive state on arrival (triglyceride levels). Both wind speed on migration and reproductive state on arrival independently influenced the delay between arrival and egg laying. These findings highlight the importance of carry-over effects from the migration period because the timing of breeding affects productivity in yellow warbler. Indeed, in this chapter I demonstrated that females which start nesting earlier are more likely to fledge at least one offspring and are more likely to produce a higher number of offspring.

Further investigation may be able to reveal how wind speed on migration affects female condition or their ability to shorten the delay between arrival and nest initiation. Neither residual mass nor plasma triglyceride concentration appear to be directly influenced by the wind conditions on migration. While mass may be a poor measure of an individual's condition (Green 2001, Labocha and Hayes 2012, Beauchamp et al. 2021), obtaining information for a wider range of plasma metabolites could help better explain any potential differences in physiological state that may be associated with variation in wind condition on migration. In addition, including information about each female's mate, perhaps time interval between male's arrival and female's arrival and male's testosterone level on arrival could be explored and linked to the variation in delay. While current findings suggest that some females may be able minimize the delay between arrival and egg laying based on environmental conditions more studies are needed to uncover the underlying mechanism.

Chapter 4 shows, using a spatially explicit CJS model, that crosswinds experienced on migration influence true survival. Carryover effects of conditions on migration can therefore influence both the productivity and survival of neotropical migrant songbirds. The use of spatial CJS models has been limited to a handful of small long-distance migrant species (e.g., Schaub and Royle 2014, Reidy et al. 2018) but this modelling approach is able to distinguish between mortality and dispersal to sites outside the study area and has the potential to reduce bias in survival estimates when emigration varies among age or sex groups. In this chapter, I was able to show that sex differences in dispersal can bias conclusions about survival and that including dispersal data increases the accuracy of survival estimates and lowers bias in estimates between sexes. I showed that the longer dispersal distances of females mostly explained the sex differences in apparent survival estimates obtained from standard CJS models and that true survival estimates were higher than traditional apparent survival estimates.

Moreover, I was able to confirm the crosswind experienced during migration influences variation in true annual survival.

Spatial CJS models have some limitations. To obtain precise survival estimates, dispersal data of individuals need to be modelled accurately. First, dispersal data needs to span the whole range of dispersal movements. If only limited or skewed dispersal data is available (e.g., only short dispersal movements are recorded by a study) the survival may be underestimated (Schaub and Royle 2014, Efford and Schofield 2022). As such, obtaining accurate data on the frequency of short- and long-distance dispersal events (perhaps through the use of satellite trackers) is important. Conversely, survival can also be overestimated if dispersal that leads to permanent emigration is less likely than modelled. These models assume that birds are able to find and occupy territories in habitat anywhere outside the study area. However, if suitable habitat outside the study area is not available or is patchy, birds may not be able to settle there. Therefore, to improve accuracy of survival estimates at least a basic habitat suitability mapping may be required to create a matrix of suitable habitat outside the study sites which could be used to further improve dispersal and survival modelling. Second, spatial CJS models are sensitive to which distribution function is used once accurate dispersal data is obtained (Schaub and Royle 2014, Ergon and Gardner 2014, Efford and Schofield 2022). While t-distributions appears to do an adequate job of describing breeding dispersal, further work is needed to determine whether models combining two distributions (modelling long and short distance dispersal) would better describe the range of dispersal movements and allow dispersal to vary with both sex and age. Finally, this study could also be improved by equipping birds with satellite-based tracking devices that do not require recapture which would allow an evaluation of whether conditions experienced on migration impact breeding dispersal and return rates rather than annual survival.

Overall, this thesis provides a significant contribution to our understanding of the transition from migration to breeding in a long-distance migratory songbird. The importance of considering potential carry-over effects from events that occur in previous stages of the annual cycle when analyzing breeding season events and processes is highlighted. In particular, this thesis shows how effects from the migration stage (crosswind) affect timing of arrival, timing of clutch initiation, productivity and survival. Moreover, this thesis tries to unravel if the carryover effect of wind on productivity is due

to the condition of individuals on arrival or because of the variation of the timing of arrival, and tries to uncover the mechanism in which this carryover effect influences productivity. In addition, this thesis describes, for the first time, the patterns of triglyceride levels of females of a free-living small neotropical migrant songbird on their arrival on breeding grounds. This thesis also highlights the need for future work to not only identify carryover effects that may influence fecundity but also to understand the mechanism and pathways with which these carryover effects work. This can be especially important in the changing world climate where individuals' adaptive plasticity in timing of egg laying could help long-distance migrants to buffer against discrepancies between arrival timing and conditions on breeding grounds by adjusting the timing of egg laying to maximize breeding productivity.

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