

SEASONAL EVENTS AND ASSOCIATED CARRY-OVER EFFECTS IN A
NEOTROPICAL MIGRATORY SONGBIRD,
THE YELLOW WARBLER (*DENDROICA PETECHIA*)

A Thesis

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ABSTRACT

The ability to determine how events during a bird's life cycle are linked and to identify ecological factors that limit populations has received much recent attention due to declining populations of many species of migratory songbirds. Ecological events occurring during any stage of a migratory bird's life cycle have the potential to carry-over and affect an individual during a subsequent season. As a result, evidence of relationships between breeding and non-breeding (i.e., winter and migration) events has become increasingly important in advancing conservation efforts for migratory songbirds.

The quality of habitat used by songbirds during the winter has been shown to have important consequences for migratory birds. For example, the quality of winter territories (as measured by moisture and resource availability) held by American Redstarts (*Setophaga ruticilla*) determines physical condition in wintering areas and timing of migratory departure (Marra and Holmes 2001), as well as arrival date and physical condition upon reaching the breeding grounds (Webster et al. 2002; Hobson 2005b).

Male plumage coloration and ornamentation functions in territoriality, dominance, and aggression in male-male interactions, and signals attractiveness, individual quality, and reproductive strategy, status, and potential to females. Birds wintering in higher quality habitat should be more able to allocate resources to the formation of intensely

colored alternate feathers grown in wintering areas (Saks et al. 2003), which in turn should allow males to more effectively attract females and increase their breeding success (Hill et al. 1998).

Stable-carbon isotope analysis measures the ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) in plant and animal tissues, and can reflect local vegetation types, diet, and habitat quality and usage where these tissues are grown (Hobson et al. 2004). Values of $\delta^{13}\text{C}$ are transferred up the food web and incorporated into growing tissues, so that analysis of inert tissues (e.g., feathers) can provide information about habitat conditions during previous seasons. Stable-carbon isotope ratios in feathers grown in Neotropical wintering areas during prealternate molt will reflect habitat conditions of birds across a mesic to xeric habitat gradient (Marra et al. 1998). Using stable-carbon isotope analysis of alternate feathers, it is possible to examine relationships between winter habitat conditions and events occurring in previous seasons. My research focused on seasonal events and associated carry-over effects in a Neotropical migratory songbird, the Yellow Warbler (*Dendroica petechia*). My research objectives were to 1) assess winter habitat conditions of breeding Yellow Warblers using stable-carbon isotope analysis of feathers grown in tropical wintering areas, 2) examine direct and indirect relationships among winter conditions, plumage characteristics, molt status, and reproductive parameters in Yellow Warblers, and 3) determine how age, plumage coloration and ornamentation, and nest initiation date are associated with reproductive success.

This study was conducted along the southwestern shore of Lake Erie at the Ottawa National Wildlife Refuge, Ottawa County, Ohio from late April through June of 2007 and 2008. To determine reproductive success of Yellow Warblers, nests ($n = 252$) were located and monitored in willow and dogwood shrubland within 5 km of the Lake Erie shoreline. I estimated daily survival rates of nests using logistic exposure models, and recorded number of young fledged per adult. Adults males ($n = 154$) and females ($n = 148$) from each nest were captured and banded, morphological measurements were taken, and greater coverts replaced during prealternate molt were counted. A series of digital photographs of each adult bird was taken to quantify streaking and yellow coloration on the breast using the computer programs ImageJ and AdobePhotoshop, respectively. The two innermost greater coverts replaced in prealternate molt were collected for stable-carbon isotope analysis.

Stable-carbon isotope values ranged from -25.25‰ to -18.10‰ , which broadly overlaps with $\delta^{13}\text{C}$ values reported in other studies of seasonal interactions in migratory birds (e.g., Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004a), except that approximately 25% of values fell in a more xeric range. I used path analysis to examine direct and indirect effects of winter habitat conditions on reproductive measures. Path analysis indicated that for males, winter habitat conditions had direct positive effects on streaking and molt but no effects on number of young fledged per male. Streaking and fledging date had direct negative effects on number of young fledged. The pathways

explained 23% of the variation in number of young fledged from each nest. For females, path analysis indicated that streaking had a direct negative effect and molt had a direct positive effect on first egg date, but winter habitat conditions had no effects on plumage variables or reproductive measures. The pathways for the female model explained only 8% of the variation in number of young fledged from each nest. The path models for both males and females provided a good fit (males: $\chi^2 = 2.52$, d.f. = 8, $p = 0.962$; females: $\chi^2 = 4.90$, d.f. = 4, $p = 0.297$) when observed values were compared to predicted values.

I used an information theoretic approach and multi-model averaging to determine which models were important in explaining variation in daily nest survival rates and number of young fledged per adult for both males and females. I found that age ($\beta = 1.127$, SE = 0.562, Relative Importance Value (RVI) = 0.562) was important in explaining variation in daily nest survival for males, but that none of the measured variables was important in explaining variation in daily nest survival for females. Breast streaking ($\beta = -0.0000360$, SE = 0.0000151, RVI = 0.790) and hue ($\beta = -0.213$, SE = 0.104, RVI = 0.790) were most effective in explaining variation in number of young fledged for males, but none of the measured variables was important in explaining variation in number of young fledged per female, despite high relative variable importance values for hue (RVI = 0.594) and molt (RVI = 0.594).

Previous research has shown that male Yellow Warblers with more breast streaking are more territorial and achieve more extra-pair copulations, whereas males

with less breast streaking spend more time caring for young at the nest and are cuckolded more often (Studd and Robertson 1988; Yezerinac and Weatherhead 1997b). I suggest that since males in this study with less breast streaking fledged more young, females may assess streakiness of males and choose a mate based on his perceived potential to fledge young, regardless of who sires the young. Because breast streaking, yellow coloration, and age of males helped explain variation in reproductive measures, males may employ multiple messages in signaling quality to females and to other males (i.e., yellow breast coloration signals age and reproductive experience while breast streaking signals reproductive strategy).

My study indicates that plumage coloration and age may be important factors in predicting reproductive success in male Yellow Warblers, but that these attributes had little apparent impact on reproduction in females. I found neither a direct effect nor strong indirect effects of winter habitat conditions on reproduction in Yellow Warblers. However, I did observe direct effects of winter habitat conditions on plumage characteristics and of plumage characteristics on reproductive measures in males. Seasonal interactions, although moderate, were detected in this population of Yellow Warblers, and this underscores the importance of conserving habitats used throughout the annual life cycle of migratory birds.

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CHAPTER 1

INTRODUCTION

Declining populations of many migratory songbirds have created a need to understand the factors that affect reproduction and survival within and between seasons so that conservation efforts can focus on areas where populations are most limited (Marra et al. 1998; Hobson et al. 2001). Events occurring during any stage of a migratory bird's life cycle can potentially affect events during subsequent seasons (Fretwell 1972; Webster et al. 2002; Clegg et al. 2003). However, until recently it has been nearly impossible to follow migratory birds throughout their annual cycles to understand the relationships between events occurring in breeding, wintering, and migratory periods (Chamberlain et al. 2000; Kelly et al. 2002).

Extensive research on songbirds has demonstrated that birds arriving later to breeding sites have diminished breeding success (e.g. Rowe et al. 1994; Sandberg and Moore 1996). In contrast, little work has examined direct connections between wintering and breeding seasons. Studies of Neotropical migrant birds indicate that physical condition in wintering areas prior to initiation of migration is negatively associated with departure date (Marra and Holmes 2001; Hobson 2005b), and that physical condition is

dependent on the quality of wintering habitat (as measured by moisture and resource availability) that birds are able to secure (Hobson 2005b). Birds that winter in more xeric habitats often migrate later and are less likely to secure optimal breeding territories than birds that winter in more mesic habitats (Marra et al. 1998; Norris et al. 2004a; Hobson 2005b). Thus, winter habitats may limit a songbird's ability to survive and reproduce (Marra et al. 1998; Rubenstein et al. 2002; Bearhop et al. 2004). Birds that winter in more xeric habitats may have reduced energetic condition, postponed spring migration departure dates, later dates at which breeding is initiated, and therefore reduced breeding success, indicating that winter habitat may be limiting and that this limiting factor has implications across seasonal events (Marra et al. 1998).

My research has examined relationships between winter habitat conditions (as assessed by stable-carbon isotope analysis), prealternate molt, plumage coloration, and reproduction in a Nearctic-Neotropical migratory songbird, the Yellow Warbler (*Dendroica petechia*). The Yellow Warbler is an abundant breeding bird throughout much of North America, winters in both mesic and xeric habitats, exhibits strong variation in plumage characteristics (including breast streaking and intensity of yellow coloration; Figure 1.1), and has predictable prealternate and prebasic molt sequences making it well-suited for this study. Using stable-isotope analysis, it may be possible to link winter habitat occupancy, physical condition, timing of migration, and ultimately, breeding success (Sillett et al. 2000). Conservation of migratory songbird populations requires knowledge of seasonal interactions across annual cycles, linking breeding, wintering, and migration events (Hobson and Wassenaar 1997; Smith et al. 2003b).

LITERATURE REVIEW

Population Limitation, Seasonal Interactions, and Carry-over Effects

The ability to identify ecological factors that limit populations of Nearctic-Neotropical migratory songbirds has received much recent attention in avian conservation due to population declines of many species (Rubenstein et al. 2002; Mazerolle et al. 2005). It is evident that seasonal events are interrelated, each potentially affecting survival and reproductive success (Mazerolle and Hobson 2005), and that effective conservation of migrant populations occurs only through an understanding of connections between seasonal events and a knowledge of limiting factors (Rappole and McDonald 1994; Rubenstein et al. 2002; Smith et al. 2003b; Sillett and Holmes 2005). These limiting factors affect population size (Sillett and Holmes 2005) because differential survival rates between seasons affects overall population survival (Sillett and Holmes 2002) and the ability to successfully reproduce to sustain population size (Kelly et al. 2005).

There are several hypotheses about the seasonal periods that are most limiting to bird populations (Rappole and McDonald 1994). For example, habitat fragmentation and loss on breeding grounds may lead to diminished breeding success and lower population numbers. Similarly, availability of habitat on wintering grounds may be limiting because not all individuals will be able to find resources necessary for survival (Marra et al. 1993; Sherry and Holmes 1995). Sherry et al. (2005) demonstrate that habitat quality and food availability year-round can be limiting, and that events during migration may certainly

have a role in survival (Sillett and Holmes 2002). However, there is evidence that events occurring on wintering grounds may also limit migratory bird populations (Marra and Holmes 2001; Rubenstein et al. 2002; Bearhop et al. 2004). In a study of migratory connectivity, Rubenstein et al. (2002) found that breeding populations of Black-throated Blue Warblers (*Dendroica caerulescens*) segregate on the wintering grounds, indicating that northerly and southerly breeding populations winter in different areas. The populations are limited differently by habitat loss on the wintering grounds, with more southerly breeding populations, which winter in areas with the most deforestation, showing more severe population declines. Bearhop et al. (2004) found that dominance and territoriality on wintering grounds, along with habitat availability, can limit populations of Black-throated Blue Warblers. Dominant individuals exclude less dominant birds from mesic habitats, so that segregation between high- and low-quality habitats occurs. Using stable-carbon isotope analysis, Bearhop et al. (2004) found that the individuals that wintered in mesic habitats tended to be in better condition during migration, and suggested that these birds would arrive earlier to breeding grounds and obtain better breeding territories than those that wintered in more xeric habitats, indicating that loss of mesic-type habitat on the wintering ground may limit populations. Similarly, Marra and Holmes (2001) discovered that American Redstarts (*Setophaga ruticilla*) are limited by winter habitat availability, with dominant older males occupying high quality, mesic habitat, and females and young males using scrubby xeric habitats with lower resource availability, where they have poorer physical condition and lower survival. This pattern could create populations with a higher proportion of males, lower female survival, and consequently, lower reproductive success. From these studies of

American Redstarts and Black-throated Blue Warblers, it has been suggested that wintering habitats may be limiting for all *Dendroica* species (Rubeinstein et al. 2002; Bearhop et al. 2004).

Carry-over effects are events or conditions during one period (or during migration) that directly affect survival or reproductive success during subsequent seasons (Smith and Moore 2005; Kelly 2006). These seasonal interactions link events on wintering and breeding grounds, and during migration (Kelly 2006), and have the potential to explain how events during one season affect events during successive seasons. For example, winter survival tends to affect reproductive success (Webster and Marra 2005), and reproductive success and other events during the breeding season can affect survival in the subsequent winter (Fretwell 1972; Webster et al. 2002).

There has been extensive work relating the arrival timing of migratory birds to aspects of breeding success, but efforts to link wintering, migratory, and breeding events have been restricted somewhat due to the difficulty of tracking migrants year-round (Marra et al. 1998; Rubenstein et al. 2002; Webster et al. 2002). This has resulted in a large gap in our understanding of seasonal interactions and the ecology of migratory birds (Kelly et al. 2002; Norris et al. 2004a; Kelly 2006). Addressing this gap is difficult because migrant songbirds are too small for conventional radio (Chamberlain et al. 1997; Kelly et al. 2002; Webster et al. 2002) and satellite transmitters (Hobson 1999; Graves et al. 2002; Kelly et al. 2005), and the recovery and resighting of banded birds is extremely infrequent (Holmes and Sherry 1992). Tracking is further complicated by the small body size of migrant songbirds but large population numbers and expansive geographic distributions (Webster et al. 2002; Clegg et al. 2003), and, in many species, lack of

morphological population identification traits (Graves et al. 2002; Webster et al. 2002). These constraints have made it difficult to examine relationships between breeding, wintering, and migration events (Hobson and Wassenaar 1997), however, all seasonal events are interrelated and may impact each other (Marra et al. 1998; Hobson 2005b) at the individual and population levels (Webster et al. 2002). Analysis of stable-isotopes in the tissues of migratory birds undoubtedly will give insight into possible links in winter habitat quality, physical condition, timing of migration, and ultimately, breeding success (Sillett et al. 2000).

Stable-carbon isotopes incorporated into feathers grown on the wintering grounds prior to the initiation of spring migration have been used as an indicator of winter habitat occupancy (Bearhop et al. 2004). For example, Marra et al. (1998) reported that feathers with enriched $\delta^{13}\text{C}$ values corresponded to those birds that wintered in xeric habitats, and feathers with depleted $\delta^{13}\text{C}$ values corresponded to those birds that wintered in mesic habitats. Birds that had wintered in poorer-quality habitats, i.e. had enriched values of $\delta^{13}\text{C}$ in their tissues, generally arrived later to breeding grounds (Marra et al. 1998; Bearhop et al. 2004), indicating that birds wintering in mesic habitats may be in better physical condition prior to and during migration, and may initiate migration earlier than those wintering in xeric habitats (Marra et al. 1998). American Redstarts that wintered in more mesic habitats initiated migration and arrived earlier in better condition than those wintering in xeric habitats (Marra et al. 1998; Norris et al. 2004a). Individuals that are in better condition prior to and during spring migration probably are able to migrate more quickly and spend less time in stopover habitats, and therefore arrive to breeding grounds earlier than those that are in poor physical condition (Bearhop et al. 2004), obtaining

breeding territories in higher quality habitat. Populations that winter in harsh locations may be adapted to cope with the adverse weather and temperature conditions on breeding grounds that may occur early in the season and are thus able to initiate migration and arrive earlier to obtain higher quality territories than populations that winter in less harsh locations (Bearhop et al. 2005). Poor weather encountered during earlier migration may be energetically costly, but late arrival may cause reduced breeding success due to lack of availability of high quality territories (Gunnarsson et al. 2006) so that migrants must assess tradeoffs between reproductive costs and energetic costs related to suboptimal climatic conditions prior to initiation of migration (Norris et al. 2004a, 2004b).

Fitness increases with energetic condition and early arrival to breeding grounds (Marra et al. 1998; Bearhop et al. 2004), suggesting that timing of migration is an important link in connecting breeding and wintering ground quality (Gunnarsson et al. 2006). Early arrival to breeding grounds positively influences the quality of habitat obtained and the timing of breeding, and increases breeding success (Webster et al. 2002; Hobson 2005b). Early arrival to breeding grounds increases the likelihood of obtaining a mate (Lozano et al. 1996) of high quality (Rowe et al. 1994). Smith and Moore (2005) found that female American Redstarts arriving early to breeding grounds had more males on territories to choose from and thus obtained high quality males and territories, since males tend, on average, to arrive to breeding grounds before females (Gauthreaux 1982; Francis and Cooke 1986). Early-arriving females generally initiate breeding earlier (Bensch and Hasselquist 1992) and have higher reproductive success than their later-arriving counterparts (Rowe et al. 1994). Early arrival is likely a carry-over effect of higher quality wintering and breeding habitats (Gunnarsson et al. 2006), and arrival times

are dependent upon timing of departure as well as events encountered *en route* (Marra and Holmes 2001; Hobson 2005b). Genetic factors likely cue initiation of migration, however, variation in timing of initiation of migration is caused by events on wintering grounds (Gunnarsson et al. 2006), and departure times may be correlated with winter habitat quality (Marra and Holmes 2001; Hobson 2005b).

Stable Isotopes in the Environment

Research on movements of migratory animals throughout annual cycles is possible because heavy stable-isotopes, those with higher numbers of neutrons, have measurable abundances relative to the lighter forms of these isotopes. These relative abundances vary predictably with latitude, altitude, or habitat, and are present at the base of food webs so that with uptake by primary producers, isotope signatures (isotope value, or ratio of heavy to light isotopes) are passed up the food web and incorporated into growing tissues of higher organisms (Wassenaar and Hobson 2000; Hobson et al. 2001; Webster et al. 2002; Norris et al. 2005).

Stable-carbon isotopes measure the ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) in primary producers. $\delta^{13}\text{C}$ varies among plant types due to the rate at which plants assimilate ^{13}C into their tissues, becoming more ^{13}C enriched in the absence of water (Webster et al. 2002) resulting in less negative $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values incorporated into tissues vary according to the proportions of C_3 , C_4 , and CAM (Crassulacean acid metabolism) plants in local habitats, the presence of each plant type determined by local climate and amount of moisture in the habitat (Hobson 1999; Bearhop et al. 2004). These plant types

have different photosynthetic pathways so that fractionation, or a difference in the amount of atmospheric $^{13}\text{C}\text{O}_2$ each plant assimilates into its tissues, occurs (Lajtha and Michener 1994). C_3 plants are characteristic of mesic habitats, those that are cooler and water-dominated, and are generally considered to be of higher quality because of a higher availability of food resources (Marra et al. 1998). C_3 plants differ predictably in their stable-carbon isotope signatures from C_4 and CAM plants, which are associated with more xeric (arid and dry) habitats, and of generally poorer quality (Marra et al. 1998; Chamberlain et al. 2000). In addition, $\delta^{13}\text{C}$ values can vary latitudinally (Chamberlain et al. 1997). However, stable-carbon isotopes are complex and exceedingly difficult to use to track birds geographically (Wassenaar and Hobson 2001; Hobson 2005b), and there is no map for $\delta^{13}\text{C}$ values. Often, the interpretation of the geographical distribution of stable-carbon isotopes can be contradictory, owing in part to local variation in plant types. Wassenaar and Hobson (1998) reported a slight trend of ^{13}C enrichment to the north, whereas Still et al. (2003) indicate that in Central and northern South America, the distribution of the fraction of C_4 plants to other vegetation increases to the south and east. $\delta^{13}\text{C}$ values can be used sparingly in specific instances because C_3 and C_4 plant occurrence shows limited geographic variation within certain habitat types (Webster et al. 2002; Still et al. 2003) but it is almost impossible to determine these latitudes using $\delta^{13}\text{C}$ signatures alone, as the signatures from C_3 - and C_4 -dominated habitats can be confounded by seasonal wet and dry periods. For example, a xeric habitat during a rainy season can reflect more mesic signatures (Hobson 2005a).

Transfer of ^{13}C up the food web occurs from plants to herbivores (including insects) to higher organisms, such as birds, with $\delta^{13}\text{C}$ values being incorporated into

growing tissue. Thus $\delta^{13}\text{C}$ in tissue reflects the $\delta^{13}\text{C}$ values in plants (Hobson 1999; Rocque et al. 2006), and therefore the habitat in which birds foraged. Analysis of tissue samples shows biome characteristics, including dominant vegetation, growing conditions, and land use of the areas birds used during specific periods of growth (Hobson et al. 2004). Variations in diet during molt reflect prey choice and may result in variations in ^{13}C values in feathers (Hobson et al. 2004; Rocque et al. 2006). Increasing $\delta^{13}\text{C}$ values signify a relatively higher proportion of C_4 than C_3 plants indicating that foraging occurred in a dryer, xeric habitat (Hobson 2005c), and more negative values indicate that foraging occurred in a more moist, or mesic, habitat. Alternate feathers, those that are grown on the wintering grounds prior to spring migration, incorporate local $\delta^{13}\text{C}$ ratios during prealternate molt, and therefore provide a record of winter habitat. Alternate feathers enriched with $\delta^{13}\text{C}$ suggest a xeric, or poorer quality, wintering habitat, and those with depleted $\delta^{13}\text{C}$ suggest more mesic, or better quality, wintering habitats (Bearhop et al. 2004).

Isotope Markers in Feathers and Other Tissues

Analysis of stable-isotopes in tissue samples is providing new information on seasonal interactions by pinpointing the location or habitat in which stable-isotopes were assimilated into tissue. Stable-isotope analysis can provide information about feeding origins and movements of migratory animals throughout annual life cycles. For example, stable-carbon isotopes in animal tissues can reflect local vegetation types, diet, and habitat quality and usage (Hobson et al. 2004) so that movements between habitat types,

or information about habitats during previous seasons, can be inferred. Likewise, stable-hydrogen isotopes reflect deuterium ratios in local precipitation, which varies geographically, so that origins and dispersal of individuals can be inferred (Wassenaar and Hobson 2001; Kelly et al. 2002). This method compares the ratio of deuterium to hydrogen in the tissue, and this value plotted on a map of deuterium ratios in average annual growing season precipitation reveals the approximate location at which the tissue was grown (Hobson 2002; Clegg et al. 2003). Stable-hydrogen isotope analysis is accurate with respect to latitude, but often provides much less longitudinal resolution, and some researchers have suggested using additional isotopes (e.g. oxygen, carbon, strontium), genetic information (Clegg et al. 2003; Kelly et al. 2005; Yohannes et al. 2005; Boulet et al. 2006), or band encounter (Smith et al. 2003a) to pinpoint tissue origin. By combining analyses of different isotopes, broader information at the individual or population level becomes available so that tracing habitat, diet, and geographic area usage can be accomplished across seasons (Rubenstein et al. 2002; Clegg et al. 2003). Other stable-isotopes used to deduce movements of animals include nitrogen, which is used to determine diet composition and trophic relationships (Kelly 2000), and strontium, which can be used to determine whether resources are derived from terrestrial or marine food webs (Hobson 1999). Stable-isotope values are reported in delta per mil notation, or $\delta(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where R is the ratio of heavy to light isotopes (Kelly 2000).

Stable-hydrogen and –carbon isotope values are reflected through the food chain from primary producers to consumers (Hobson and Bairlein 2003), so that tissues in birds represent the location and habitat conditions, along a xeric to mesic gradient, where the

tissue was grown (Wassenaar and Hobson 2000; Hobson et al. 2001; Webster et al. 2002; Norris et al. 2005). Isotopic signatures in the diet of birds are reflected in a variety of metabolically active and inactive tissues. These isotopes are fixed in the keratin of inert tissues, such as feathers and claws, and are also present in metabolically active tissues such as blood, muscle, and bone (Marra et al. 1998), where isotopic signatures may change over short time periods due to continual turnover as cells are replaced. These tissues can reflect shifts in habitats or diets (Bearhop et al. 2003), however, varying metabolic rates within and among species complicate the determination of habitat and dietary change. Turnover rates of metabolically active tissues are unknown for wild birds (Hobson 2005a), but there is evidence that turnover rates in captive birds reared in windtunnels and those reared without exercise are similar (Hobson and Yohannes 2007). In addition, sampling metabolically active tissues typically is more invasive, sometimes involving sacrifice of individuals (Marra et al. 1998; Bearhop et al. 2003; Mazerolle and Hobson 2005), and does not provide isotopic signatures from further back in time, rendering sampling of these tissues less useful for linking seasonal interactions (Mazerolle and Hobson 2005).

Metabolically inert tissues assimilate isotopic signatures similarly while growing, but after growth, the signatures are fixed and reflect a discrete time period in the animal's life (Bearhop et al. 2003). Avian claw material has been used in isotopic analysis (Bearhop et al. 2003), although unknown rates of growth, especially for ground-foraging species, complicate the signal of origin and therefore identification of the latitude or habitat in which they were grown (Norris et al. 2005). Newly grown feathers are also inert and reflect the isotopic signatures of the latitude or habitat in which they were

grown until they are replaced (Hobson 1999; Hobson 2005a). As a result, the geographic location or habitat use of the bird at or just before initiation of northbound or southbound migration can be sampled throughout the year (Hobson 2002).

Molt within the Annual Cycle

For most migratory birds, complete feather molt occurs at least once each year (Pyle 1997), usually at or near breeding grounds (Hobson 1999) prior to fall migration (prebasic molt) and, in many species, an incomplete molt occurs on the wintering grounds prior to spring migration (prealternate molt) (Pyle 1997; Rubenstein et al. 2002). For wood-warblers, and many other families, the adult prebasic molt is complete (i.e., all feathers are replaced). However, the first prebasic molt in hatching year birds is incomplete: body feathers and most wing coverts are replaced, but all flight feathers are retained, creating a molt limit, or clear demarcation between feathers that were replaced and older feathers that were retained during molt (Pyle 1997), most often between the alula covert and the second alula feather. Prealternate molt in many wood-warblers is similar in adults and second-year birds and includes body feathers and most wing coverts, although generally fewer wing coverts are replaced than in first prebasic molt, creating a molt limit most often within the greater coverts (R.C. Leberman and R.S. Mulvihill pers. comm.).

Plumage Coloration

Secondary sexual traits, such as male plumage color and ornamentation, are most evident in high quality birds (Hill et al. 1998). These traits can function in mate acquisition and territoriality, signaling differently in inter- and intra-sexual interactions (Pryke et al. 2001), and within and between seasons (Marchetti 1998). In yellow birds, carotenoid pigments obtained through diet are incorporated into feathers and expressed as yellow plumage coloration (Hill and Montgomerie 1994). Yellow coloration can indicate male quality because individuals expressing the brightest plumage have acquired sufficient resources to satisfy nutritional demands before allocating carotenoids to ornamentation (Hill 2000; Saks et al. 2003; Alonso-Alvarez et al. 2004). For such species, bright coloration is beneficial, as it is associated with acquisition of higher-quality territories, both of which females may prefer when choosing mates (Greene et al. 2000). Thus, brighter males, or those expressing secondary sexual traits more intensely, tend to more effectively attract females (Andersson 1994), and have higher breeding success (Hill et al. 1998). Since carotenoid coloration is a direct result of diet (McGraw 2006) and nutritional status (Hill 1999), birds that have access to higher quality food sources generally express more intense carotenoid coloration (Saks et al. 2003). In Yellow Warblers, two plumage characteristics that may be related to resources acquired on the wintering grounds may serve as advertisements of quality on the breeding grounds: intensity of yellow coloration and quantity of breast-streaking.

Carotenoid-based plumage coloration is a result of resource availability, which may be related to winter habitat quality and the mesic-xeric habitat gradient. Prealternate molt in Yellow Warblers occurring during the winter includes many body feathers (including yellow breast feathers) (Pyle et al. 1997), and the intensity of yellow coloration in alternate body feathers may be a carry-over effect from the wintering grounds. The quantity of male breast-streaking may also indicate potential reproductive success, as females may relate this coloration to perceived ability to successfully fledge young when choosing a mate. An analysis of the relationship between alternate plumage coloration and stable-carbon isotope signatures could yield a valuable relationship, linking coloration of breeding plumage with winter habitat conditions.

Male ornamentation and coloration may be related to the reproductive tactics males employ and thus may provide a basis for female mate choice (Lozano and Lemon 1996). In Yellow Warblers, females may use the extent of brown streaking on the breast as a cue to the amount of parental care or territoriality a male provides. Studd and Robertson (1985a) found that, in a Yellow Warbler population in Ontario, males with lightly-streaked breasts allocated more time to parental care, and heavily-streaked males allocated more time to territorial defense (Studd and Robertson 1985b, 1988), so that there is a tradeoff between territorial defense and caring for young (Lozano and Lemon 1996). Studd and Robertson (1989) suggest that this tradeoff is intrinsic, that males with differing intensity of breast-streaking simply use different reproductive strategies. However, Lozano and Lemon (1996) did not find the same tradeoff in a Quebec population and concluded that females depend on both territorial behavior and parental care from their mates in successfully fledging young.

Yellow Warbler Natural History

The Yellow Warbler (*Dendroica petechia*) is a small (8-11 gram) insectivorous songbird and one of the most abundant breeding wood-warblers (Parulidae) in North America (Kaufman 1996). The species breeds from Alaska and northern Canada to the east coast of North America, south to northern Georgia and Alabama, and west to northern California (Curson et al. 1994; Dunn and Garrett 1997), and breeds in high densities in the counties of the northwestern Ohio lakeshore (Peterjohn 2001). Yellow Warblers breed in both mesic and xeric habitats (Peterjohn and Rice 1991) including brushy deciduous thickets, shrubby wetlands, riparian woodlands along ponds and streams, old fields and orchards, woodland edges, residential shrubs, and early-successional forests, frequently in association with willows (*Salix* spp.; Peterjohn and Rice 1991; Howell and Webb 1995; Kaufman 1996; Dunn and Garrett 1997; Peterjohn 2001).

Yellow Warblers winter in Mexico and southern Baja California, south through Central America to northern South America to Peru and Brazil east of the Andes (Curson et al. 1994; Howell and Webb 1995; Dunn and Garrett 1997). Using stable-hydrogen isotope analysis combined with geographic information obtained through mitochondrial DNA analysis of wintering Yellow Warblers, Boulet et al. (2006) suggest that northern Ohio populations of Yellow Warblers winter in Venezuela, the Yucatan, and Panama. In winter, Yellow Warblers utilize mesic and xeric habitats including brushy and scrubby habitats, riparian woodlands, wooded marshes, mangroves, transitional habitats and habitat edges, farmland second-growth, and other semi-open habitat (Curson et al. 1994;

Howell and Webb 1995; Dunn and Garrett 1997). Yellow Warblers defend territories in both breeding and wintering areas (Greenberg and Salgado Ortiz 1994) and show site fidelity during both seasons (Lowther et al. 1999).

Yellow Warblers initiate migration relatively early (Leberman 1976) and arrival to the Midwest and Mid-Atlantic occurs in mid-April with the bulk of migrants reaching the Great Lakes region by early May (Dunn and Garrett 1997; Peterjohn 2001). In fall, Yellow Warblers depart the Great Lakes region in mid- to late June or early July, peaking in late July and early August (Harrison 1984; Dunn and Garrett 1997).

As in other passerines, male Yellow Warblers tend to arrive to the breeding grounds earlier than females (Harrison 1984; Chandler and Mulvihill 1990), and, within sex classes, older individuals arrive earlier than younger individuals (Kelley 1991). Males establish and aggressively defend breeding territories almost immediately upon arrival to the breeding grounds. Females initiate nest building soon after arrival to territories. Nests are cup-shaped and constructed from grasses, bark, and plant down, and are lined with mammal hair, feathers, and seed fibers (Curson et al. 1994; Baicich and Harrison 1997; Lowther et al. 1999), and are occasionally constructed from materials obtained from failed or old nests (pers. obs.; Harrison 1984; Kaufman 1996). Nests are generally built 0.5-2.5 meters above the ground (Lowther et al. 1999) and are typically placed in the forks of sapling trees or shrubs (Baicich and Harrison 1997; Kaufman 2000), often in dogwoods (*Cornus* spp.) (pers. obs.) or multiflora rose (*Rosa* spp.) (Harrison 1984). Male courtship behavior consists of chasing and displaying to females, with receptive females responding by crouching and quivering their wings, resulting in copulation late in the nest building stage (Ficken and Ficken 1965). Extra-pair

copulations occur to varying degrees in different regions, with the territorial male usually chasing the intruder from his territory (Lowther et al. 1999). However, Yezerinac and Weatherhead (1997) found that in Ontario, about half of Yellow Warbler clutches contained extra-pair young, but that only about one-third of offspring resulted from extra-pair copulations.

Whitish, oval eggs with a ring of brown flecks are laid from late April into July (Baicich and Harrison 1997). Females lay one egg per day at approximately sunrise (Lowther et al. 1999) until a clutch of 4-5 eggs (Goosen and Sealy 1982) is laid, at which point the female begins incubation (Shrantz 1943). Males defend nests, mates, and territories from intruding males, and males, and to a lesser extent females, defend nests from predators by chasing intruders (Hobson and Sealy 1989). Rarely, some males are able to successfully maintain and defend two territories, each with females (Ford 1996). Males and females both defend the nest by performing distraction displays in the presence of potential predators (Lowther et al. 1999). Eggs hatch within 24 hours of each other after approximately 11 days of incubation (Baicich and Harrison 1997), and nestlings are fed mostly Lepidopteran larvae by both parents (Lowther et al. 1999). The nestling period continues for 8-10 days until fledging (Baicich and Harrison 1997; Lowther et al. 1999), after which fledglings remain with the parents for 17-21 days (Smith 1943). Pair bonds persist through the fledgling stage, after which they separate (Rimmer 1988). Yellow Warblers may re-nest and raise a second brood after successfully fledging young (Peterjohn and Rice 1991), but this occurs very rarely (Goossen and Sealy 1982). Breeding efforts are complicated by frequent brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Yellow Warblers are adapted

to cope with parasitism; they bury cowbird eggs under new layers of nest material (Harrison 1984; Lowther et al. 1999).

Yellow Warbler molt strategy is similar to that of other wood-warblers (Rimmer 1988). Juvenal feathers are grown in the nest, and upon fledging, a first prebasic molt occurs, replacing some body feathers and most secondary coverts, including lesser and median coverts, all greater coverts, the carpal covert, and usually the alula covert, but no flight feathers or primary coverts. Body feathers are continuously replaced on wintering grounds (October-April), but most prealternate molt occurs prior to spring migration in December-April (Pyle et al. 1997), and includes most body feathers, most lesser and median coverts, some inner greater coverts, and sometimes 1-3 tertials (R.C. Leberman and R.S. Mulvihill pers. comm.; Pyle 1997). Howell and Webb (1995) report that Yellow Warblers are in alternate plumage from March through the summer, and from March to May, second-year birds have duller and more worn primaries, greater coverts, and retrices than those of after-second-year birds (Sheppard and Klimkiewicz 1976). A complete prebasic molt occurs on the breeding grounds prior to fall migration (Curson et al. 1994; Howell and Webb 1995; Pyle et al. 1997), although flight feather replacement is suspended during migration in some species and completed on the wintering grounds (Pyle et al. 1997). Flight feather molt begins with the innermost primary and proceeds outward; midway through primary replacement, the outermost secondary is dropped and molt proceeds inward (Rimmer 1988; Ryder and Rimmer 2003).

STUDY AREA

My research was conducted on the Ottawa National Wildlife Refuge, located in northwestern Ohio on the southwest shore of Lake Erie in the Western Lake Erie Basin. Together with other national wildlife refuges, state parks, and wildlife areas, the Ottawa National Wildlife Refuge contains some of the last remnants of the Great Black Swamp. The refuge is a series of managed marshes and wetlands connected by canals and dikes, and is interspersed with small mature woodlots, shrubland, and grassy fields. Dominant woody vegetation includes dogwood (*Cornus* spp.), willow (*Salix* spp.), multiflora rose (*Rosa* spp.), and cottonwood (*Populus deltoides*) along the edges of wetlands, dogwood and rose in shrubby fields, and oak (*Quercus* spp.), maple (*Acer* spp.), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), and cottonwood in the mature woodlots. Ottawa National Wildlife Refuge is located in a highly fragmented landscape and is surrounded by agriculture and lakeshore development, which makes it a valuable refuge for many wildlife species. During spring and fall migration, Ottawa provides an important stopover area for migrating waterfowl, shorebirds, and passerines, and hosts high densities of breeding songbirds in the summer.

SIGNIFICANCE

Effective conservation of migratory songbirds can be accomplished only with a better understanding of links between breeding, wintering, and migration events (Sillert et al. 2000; Smith et al. 2003b). Although conservation efforts are needed in all areas, focus

should be on those areas in the annual cycle where populations are most limited (Hobson and Wassenaar 1997). Evidence of population declines in migrant species that winter in areas with high deforestation may indicate that loss of high quality wintering habitat is an important limiting factor to populations of migratory birds (Rubenstein et al. 2002), although events during all seasons are certainly related to survival (Sherry and Holmes 1993).

My research examined events across all seasons in a migrant's life cycle to determine whether wintering events can carry-over and affect reproduction in Yellow Warblers. Through analysis of stable-carbon isotope signatures of feathers grown on the wintering grounds, and measures of reproduction on breeding grounds, I have demonstrated moderate carry-over effects of winter habitat conditions on breeding success through coloration/ornamentation and age effects. Such interactions between seasonal events can affect other stages in a migrants' life, and major disturbances on wintering grounds have the potential to affect reproduction. Similarly, habitat loss on breeding grounds can decrease reproductive success, increase mortality rates in juveniles, and therefore decrease recruitment of new individuals into populations. My research findings underscore the importance of conserving appropriate habitats throughout the annual life cycle of migratory songbirds.

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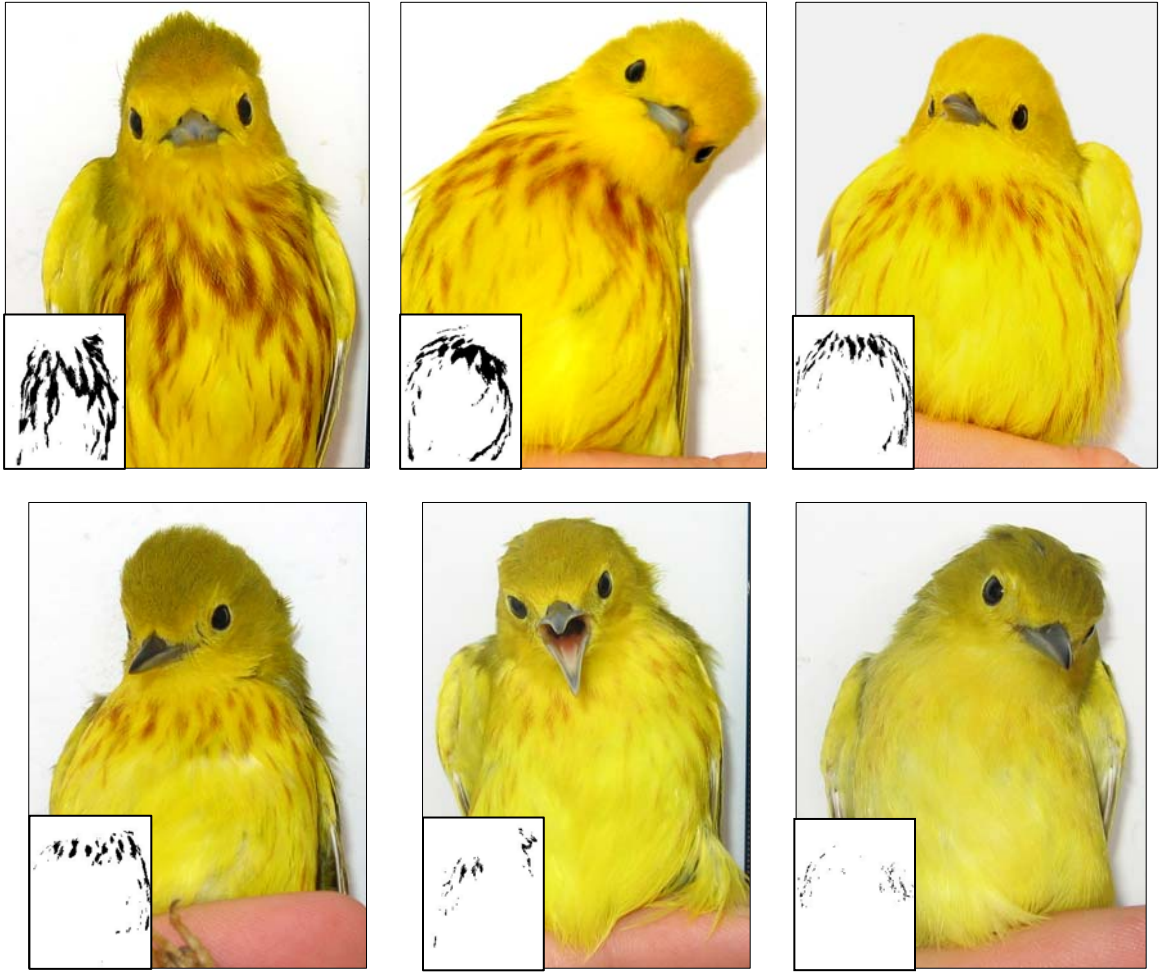
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Photographs by A. Lindsay and L. Koerner.

Figure 1.1. Variation in yellow plumage coloration and extent of breast streaking in male (top row) and female (bottom row) Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio. Black-and-white images were created in ImageJ by converting each picture to an 8-bit grayscale image and adjusting the threshold value so that yellow feathers appeared white and brownish streaking appeared black.

CHAPTER 2

EFFECTS OF WINTER HABITAT CONDITIONS ON PLUMAGE CHARACTERISTICS AND REPRODUCTIVE MEASURES IN YELLOW WARBLERS (*DENDROICA PETECHIA*)

INTRODUCTION

Until recently, it has been nearly impossible to follow migratory songbirds throughout their annual cycles and to understand factors that affect events across breeding, wintering, and migratory periods (Chamberlain et al. 2000; Kelly et al. 2002). Determining how events during a bird's life cycle are linked and identifying ecological factors that limit populations has received much recent attention due to declining populations of many species of migratory songbirds (Rubenstein et al. 2002; Mazerolle et al. 2005). Populations may be limited during any season due to habitat quality (Sherry et al. 2005), resource availability (Marra et al. 1993; Sherry et al. 2005), territoriality and competition (Greenberg and Salgado Ortiz 1994), and weather (reviewed in Sherry and Holmes 1995). Habitat loss and fragmentation on the breeding grounds can lead to increased nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Bayne and Hobson 1997, 2001), and decreased apparent annual survival (Bayne

and Hobson 2002), pairing success (Bayne and Hobson 2001), and food and nest site availability (reviewed in Sherry and Holmes 1995), all of which can diminish productivity of songbird populations. Similarly, on wintering grounds, populations may be limited by habitat loss and dominance-mediated sexual habitat segregation (Marra et al. 1998; Bearhop et al. 2004) because females and some younger individuals are less able to procure territories and obtain resources necessary for survival (Sherry and Holmes 1995). Events occurring during migration can strongly influence annual survival and therefore may limit populations (reviewed in Moore et al. 1995; Sillett et al. 2000). Determining how the ecological events during one season carry-over and affect individuals during subsequent seasons is needed to advance conservation efforts for migratory songbirds (Norris et al. 2004b).

The quality of habitat used by migratory birds during winter can influence physical condition, migratory timing, and reproduction (Webster et al. 2002; Hobson 2005). For example, birds that winter in mesic habitats tend to be in better physical condition than birds that winter in xeric habitats (Bearhop et al. 2004) due to increased resource availability. Songbirds that winter in mesic habitats initiate spring migration earlier, arrive on breeding grounds earlier, and obtain higher-quality breeding territories (Marra et al. 1998; Norris et al. 2004a; Hobson 2005), and thus initiate breeding earlier and have higher reproductive success (Rowe et al. 1994; Sandberg and Moore 1996), often fledging more young (Reudink et al. 2008), relative to birds that wintered in xeric habitats.

Using stable-carbon isotope analysis, it is now possible to remotely study events that occurred during previous seasons and link habitat conditions and resource

availability on wintering grounds to events on breeding grounds (Sillett et al. 2000). Stable-carbon isotope analysis can measure the ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) in animal and plant tissues, and can reflect local vegetation types, diet, and habitat quality and usage (Hobson et al. 2004). Stable-carbon isotopes are transferred up the food web and incorporated into growing tissue, so that analysis of inert tissues (e.g., feathers) gives information about habitat conditions during the period of growth (Hobson 1999; Wassenaar and Hobson 2000; Rocque et al. 2006). Signatures of $\delta^{13}\text{C}$ vary between plant types depending on specific photosynthetic pathways, with plant types tending to occupy a predictable habitat type. C_3 plants, which have more negative (depleted) carbon-isotope values are found in cooler and more moist (i.e., mesic) habitats, which are generally considered to be of higher quality (Marra et al. 1998). In contrast, C_4 and CAM (Crassulacean acid metabolism) plants, which have less negative (enriched) $\delta^{13}\text{C}$ values, are found in warmer and more arid (i.e., xeric) habitats, which are considered to be of lower quality (Marra et al. 1998). Stable-carbon isotope ratios in feathers grown during prealternate molt in wintering areas will reflect occupancy of birds across a mesic to xeric habitat gradient (Marra et al. 1998; Bearhop et al. 2004).

I used stable-carbon isotope analysis of feathers grown in wintering areas to determine winter habitat conditions of Yellow Warblers (*Dendroica petechia*) that breed in northwestern Ohio. I used path analysis to examine direct and indirect relationships between winter habitat conditions, plumage characteristics, and reproductive measures in Yellow Warblers. This species winters in mesic and xeric habitats (shrublands, riparian woodlands, wooded marshes, mangroves, habitat edges, and farmland second growth) in Mexico, Central America, and northern South America (Curson et al. 1994; Howell and

Webb 1995; Dunn and Garrett 1997), and breeds in a variety of shrubby habitats, including brushy deciduous thickets, shrubby wetlands, edges of upland and riparian forest, and shrub/sapling-stage forests throughout much of North America (Peterjohn and Rice 1991; Howell and Webb 1995; Dunn and Garrett 1997). Yellow Warblers exhibit wide variation in plumage characters, including amount of breast streaking, intensity of yellow coloration, and extent of prealternate molt, and winter in both mesic and xeric habitats, making it well-suited for examining winter habitat conditions and how effects may carry-over to the breeding season.

METHODS

Field Data Collection

My research was conducted on the southwest shore of Lake Erie at the Ottawa National Wildlife Refuge, located in Ottawa County, Ohio (41° 36' 56" N, -83° 12' 58" W). Ottawa National Wildlife Refuge contains some of the last remnants of the Great Black Swamp and consists of a series of managed marshes and wetlands connected by canals and dikes, and interspersed with small mature woodlots and shrubby fields. Study sites were located in willow (*Salix* spp.) and dogwood (*Cornus* spp.) shrubland within 5 km of the Lake Erie shoreline.

To assess reproduction of Yellow Warblers, nests (n = 117) were located and monitored throughout suitable habitat from April 23 – June 30 in 2007. Empty nests were checked daily to determine the date of first egg-laying so that the hatch date could

be estimated (11-day incubation period; Lowther et al. 1999). Nests found during incubation were checked every 2 days to determine hatching date (Mallord et al. 2007). Active nests were checked at a distance of > 5 m for an incubating female every 3-4 days, and nest contents were checked if no incubating female was present. Nests were checked at the estimated hatch date, and monitored every other day until fledging (Martin and Geupel 1993). I determined the number of young that fledged from each nest by counting the nestlings on the expected fledging date, and when possible, confirmed this number by resighting young after fledging (Norris et al. 2004a). I considered a nest “successful” if it produced at least one young, or “failed” if it produced no fledglings.

Adult Yellow Warblers from each nest were target netted using 2.6 x 12 m or 2.6 x 6 m mist nets (30 mm mesh), and banded with a U.S. Geological Survey aluminum leg band and a unique combination of plastic colored leg bands. The location, date, and time of capture were recorded for all banded birds. Specific measurements were taken for each adult bird: metatarsus (using calipers; 0.01 mm accuracy), unflattened wing chord (using wing rules; 0.5 mm accuracy), and mass (using digital scales; accuracy 0.1 g). Visual examination of furcular and abdominal fat were rated using a 6-point scale (Helms and Drury 1960). Each adult was aged, and then sexed, using an adaptation (Leberman and Mulvihill pers. comm.) of the guidelines described by Pyle et al. (1997).

A digital photograph of each adult bird’s breast was taken to quantify the intensity of yellow plumage coloration and extent of breast streaking, and a photograph of wing spread was taken to quantify the extent of prealternate wing molt within the greater coverts. Photographs were taken using a Canon Powershot A95 digital camera with 5 megapixel resolution, providing brightness values on red, green, and blue scales, which

were used to assign color values to each bird (Wiebe and Bortolotti 2001, 2002). The birds were held in a stable, upright position next to a ruler (for size standardization) against a white background so that all breast streaking was visible in the photographs. Lighting conditions in the field were standardized by using the camera's flash for all photographs and by holding the bird at a distance of 30 cm from the camera in a 4-sided (open at the bottom and front) 30 x 15 x 15 cm box constructed of white foam board.

The two innermost greater coverts on each wing were collected from each adult Yellow Warbler and stored in a plastic bag for stable-carbon isotope analysis. Inner greater coverts are molted and regrown on Neotropical wintering grounds prior to the initiation of spring migration (Pyle et al. 1997).

Laboratory Analysis

Feathers collected for stable-carbon isotope analysis were cleaned in a 2:1 chloroform:methanol solution for 24 hours, rinsed with methanol, then dried for at least 48 hours (Norris et al. 2005; Wassenaar and Hobson 2006). Feather material was cut from the inner and outer vanes, avoiding the rachis (Wassenaar and Hobson 2006), and 1.0 mg was weighed and packaged in a 5 x 9 mm pressed tin capsule, and placed in a 96-well plate (Costech Analytical Technologies, Inc., Valencia, California, USA). Samples were sent to the University of California-Davis Stable Isotope Facility and combusted using a PDZ Europa ANCA-GSL elemental analyzer linked to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Results were reported in

per mil (‰) deviation from the standard according to the equation: $\delta^{13}\text{C} =$
 $[(^{13}\text{C}/^{12}\text{C}_{\text{sample}})/(^{13}\text{C}/^{12}\text{C}_{\text{standard}}) - 1] \times 1000$

Photographic Analysis

Digital photographs were uploaded to a computer for analysis of breast streaking and yellow coloration. I quantified density of breast streaking using ImageJ software (Rasband 2007). Digital pictures were imported into ImageJ, converted into 8-bit grayscale images, and cropped using the ruler in the photograph to standardize size and so that only breast feathers were visible. The threshold value for ImageJ was set to between 140 and 150, so that reddish breast streaking appeared black and all other parts of the breast appeared white. ImageJ counted the number of black pixels in each photograph using the “analyze particles” function (Gering and Atkinson 2004; DeGroot and Rodewald 2008).

Intensity of yellow plumage coloration was quantified in terms of hue, saturation, and brightness (on a 0-255 red, green, and blue color scale) using Adobe Photoshop software (Villafuerte and Negro 1998; Dale 2000). Ten randomly selected squares of equal pixel size were selected from each breast photograph and analyzed for hue, brightness, and saturation (HBS) values. The ten values for each variable were averaged for each photograph so that each bird had a separate mean value for hue, brightness, and saturation (Tschirren et al. 2003).

Statistical Methods

Plumage variables were amount of breast streaking (Streaking), yellow breast coloration (Hue), and extent of prealternate wing molt (Molt). The yellow plumage variables hue, brightness, and saturation were found to be highly correlated (all p -values < 0.002), so brightness and saturation were dropped as redundant variables. Hue was chosen to represent yellow coloration. Hue is a measure of the predominant “color,” or wavelength, of a sample (0 = red, 60 = yellow, 240 = blue), indicating whether the sample is purely one color, or a blend of two colors (Senar et al. 2008). Further, hue is biologically meaningful and interpretable since it is an accurate measure of carotenoid content in feathers (Senar et al. 2008) and is related to nest provisioning and nestling growth rates in Blue Tits (*Parus caeruleus*, Senar et al. 2002).

Path analyses were performed using LISREL 8.8 (Scientific Software International 2006) to determine the relationships between winter habitat condition (as assessed by stable-carbon isotope values), plumage characteristics (Streaking, Hue, and Molt), and three reproductive measures (first egg date, fledging date, and number of young fledged per adult). Path analysis allows for determination not only of direct (DE) and indirect effects (IE) between dependent and independent variables, but also of these effects between dependent and between independent variables, thus identifying potential causal relationships between two variables using a pathway through a third variable. I constructed path diagrams using information from previous research on seasonal interactions in migratory songbirds (Norris et al. 2004a). Isotope value ($\delta^{13}\text{C}$) was used as the independent variable, and Streaking, Hue, Molt, Egg (first egg date), Fledge

(fledging date), and Fledglings (number of young fledged per adult) were used as dependent variables.

Birds that winter in mesic habitats often migrate earlier, secure high quality breeding territories (Marra et al. 1998; Norris et al. 2004a; Hobson 2005), initiate breeding earlier, and achieve increased breeding success (Rowe et al. 1994; Sandberg and Moore 1996) relative to birds that winter in xeric habitats. I predicted that winter habitat conditions (as assessed by $\delta^{13}\text{C}$) would positively influence first egg and fledging date, and negatively influence number of young fledged; i.e., birds that wintered in mesic habitats would nest earlier in the season and fledge more young.

The quality of habitat on wintering grounds determines the availability of resources that birds utilize for nutrition, feather growth, and ornamentation (Hill 2000; Saks et al. 2003; Alonso-Alvarez et al. 2004). I predicted that birds wintering in xeric habitats (less negative $\delta^{13}\text{C}$ values) would have less breast streaking and higher hue values than birds wintering in mesic habitats. Further, I hypothesized that birds that used mesic winter habitats would be able to allocate more energy to feather (wing coverts, body feathers) replacement during prealternate molt prior to spring migration than birds wintering in xeric habitats. Often, birds that more intensely express secondary sexual traits have increased reproductive success (Anderson 1994; Hill et al. 1998). Thus, I predicted that birds that have more breast streaking and/or lower hue values (more intense yellow coloration) should have earlier first egg dates and fledge more young than birds with less breast streaking and/or higher hue values.

I predicted that first egg date would be positively associated with fledging date because nests that are initiated earlier fledge earlier. First egg date and fledging date

were predicted to be negatively correlated with number of young fledged because adults that initiate nesting earlier tend to fledge more young (Barba et al. 1995; Nilsson 2000).

In males, plumage is important in territory acquisition and mate attraction, and therefore, energy resources may be allocated to production of brightly colored feathers that function in signaling in intra- and intersexual communication. Females, however, may allocate energy from resources into egg production and incubation (Fitzpatrick et al. 1995; reviewed in Amundsen and Pärn 2006). I hypothesized that the effects of winter habitat conditions would have a stronger influence on plumage characteristics for males and on reproductive measures for females, and that relationships between winter habitat conditions and plumage coloration, and between plumage coloration and reproductive measures, would be stronger in males than in females.

For path analysis, I did not include a direct pathway between winter habitat conditions and fledging date or number of young fledged, because variables associated with the breeding site should best explain variation in these reproductive measures. Path analysis for females did not include the variable “Fledge” because the effective sample size was small. For both path diagrams, unexplained variance for each variable is indicated by short arrows.

RESULTS

In May and June 2007, 117 nests were found and at least one adult from 81 of those nests was captured and banded. The remaining 36 nests failed almost immediately at the beginning of the season and adults were not captured. For nests with captured

adults, 72 males (52 after-second-year, 20 second-year) and 66 females (48 after-second-year, 18 second-year) were banded. A total of 37 nests were successful, which is a 31.6% success rate for all nests found.

Stable-carbon isotope values ranged from -25.25‰ to -18.10‰ , which is similar to the $\delta^{13}\text{C}$ range reported in other studies (Figure 2.1; Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004a). There was no difference ($p = 0.142$) in stable-carbon isotope signatures between males (mean = -22.16 ± 1.32 SE; $n = 72$) and females (mean = -22.59 ± 1.95 SE; $n = 59$), or between after-second-year (ASY) and second-year (SY) males ($p = 0.843$; ASY males $n = 52$, SY males $n = 20$). However, younger females had a more negative isotope signature than older females ($p = 0.022$; ASY females $n = 43$, SY females $n = 16$), indicating that younger females tended to winter in more mesic habitats (see Figure 2.2). Males and females differed significantly in number of replaced greater coverts ($p = 0.003$; males: mean = 8.1 ± 0.127 SE; females: mean = 7.6 ± 0.131 SE). Plumage variables (Streaking, Hue, Molt) did not differ significantly between age classes for either males or females ($p > 0.100$). Males had more breast streaking, replaced more greater coverts, and had lower hue values than females. There were no differences between the sexes in first egg date, fledging date, and number of young fledged per adult ($p > 0.100$). For males, winter habitat condition, as assessed by $\delta^{13}\text{C}$ was positively correlated with molt ($r^2 = 0.261$, $p = 0.030$), but was not correlated with the other plumage variables or reproductive measures ($p > 0.120$). None of the plumage or reproductive variables was correlated with winter habitat conditions ($\delta^{13}\text{C}$) for females ($p > 0.270$).

For males, the path model provided a good fit when observed values were compared with predicted values ($\chi^2 = 2.52$, d.f. = 8, $p = 0.962$). Winter habitat conditions were positively associated with breast streaking and extent of prealternate molt, indicating that birds with more negative isotope values (mesic conditions) had less breast streaking and less extensive prealternate wing molt; winter habitat conditions were not directly correlated with yellow coloration or first egg date. Breast streaking, in turn, had a direct negative effect on number of young fledged (birds with less breast streaking fledged fewer young), which resulted in a marginal indirect effect of winter habitat conditions on number of young fledged (Table 2.1). Plumage characteristics were not associated with fledging date or number of fledglings per adult. Fledge date, however, had a direct effect on number of young fledged, indicating that earlier nests fledged more young. Variables in the male path diagram explained 23% of the variation in the effects of winter habitat conditions ($\delta^{13}\text{C}$) on number of young fledged (Figure 2.3).

The path model for females also provided a good fit when observed values were compared with predicted values ($\chi^2 = 4.90$, d.f. = 4, $p = 0.297$). Winter habitat conditions did not have any direct effects on female plumage characteristics or on first egg date, and plumage characteristics did not have any direct effects on number of young fledged. Breast streaking in females was directly negatively associated with first egg date, indicating that birds with less breast streaking tended to initiate nesting activities later than birds with more breast streaking. The extent of prealternate wing molt was positively associated with first egg date, indicating that females that replaced fewer greater coverts nested earlier in the breeding season than birds with more extensive prealternate wing molt (Table 2.2). There was no direct correlation between yellow

coloration and first egg date for females. Isotope values and plumage characteristics explained 23% of the variation in the effects of winter habitat quality on first egg date, but these variables explained only 8% of the variation in effects of winter habitat conditions on number of young fledged (Figure 2.4).

DISCUSSION

Stable-carbon isotope ($\delta^{13}\text{C}$) values recorded in my study (-25.28‰ to -18.10‰) for feathers grown in wintering areas indicated that Yellow Warblers used a range of xeric to mesic habitats in the Neotropics. These values broadly overlap those reported in other studies of carry-over effects in migratory songbirds, but approximately 25% of $\delta^{13}\text{C}$ values, reflecting more xeric habitats (see Figure 2.1), in my study fell outside the range reported for other studies (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004a). The differences in $\delta^{13}\text{C}$ ranges between studies might be related to habitat types occupied by different species on the wintering grounds. The focal species in other seasonal interaction research, American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*), occupy woodlands, forest edges, and mangroves, whereas Yellow Warblers occupy more open, scrubby habitats (Curson et al. 1994; Howell and Webb 1995; Dunn and Garrett 1997). Forests tend to reflect mesic isotope values, whereas open, scrubland habitats tend to reflect less negative values (Marra et al. 1998). Although difficult to determine, the range of $\delta^{13}\text{C}$ values observed in my research suggests that xeric-type habitats may not be poor quality for Yellow Warblers, which are more adapted to occupying open habitats. Another possible explanation for the wider

range of $\delta^{13}\text{C}$ values observed in this study could be related to the geographical distribution of C_3 and C_4 vegetation within the winter range of Yellow Warblers. This species winters in a 31° latitudinal range (Bent 1953) and this corresponds with a higher proportion of C_4 to C_3 plants, or xeric-type habitats, to the south and east throughout this range (Still et al. 2003).

Interestingly, my study found few strong relationships between winter habitat conditions and reproductive measures despite the wide range of $\delta^{13}\text{C}$ values. This is in contrast to studies reporting that wood-warblers using poor-quality, xeric winter habitats were in lower physical condition (Marra et al. 1998; Bearhop et al. 2004), had delayed migratory departure and arrival dates (Bearhop et al. 2004; Norris et al. 2004a), later nesting initiation dates (Bensch and Hasselquist 1992; Webster et al. 2002; Hobson 2005), and lower reproductive success (Rowe et al. 1994; Webster et al. 2002; Hobson 2005).

We expected that males that wintered in mesic habitats would have had greater access to resources, thereby allowing them to incorporate pigments into streaking and yellow breast coloration, and allocate energy to wing molt, replacing more feathers. However, the direct effects observed in the path analysis were contrary to predictions and indicated that males that wintered in more mesic habitats had less breast streaking and less extensive prealternate wing molt than males from more xeric habitats (there was no apparent relationship with breast hue). Although difficult to explain, breast streaking may be more genetically determined than a product of resource availability during molt. Regardless of the factors that may have determined streaking, streaking did have a direct effect on number of young fledged, which suggested that males with less breast streaking

were able to fledge more young. This pattern is consistent with studies of male reproductive strategies in Yellow Warblers and their relationship to breast streaking. Studd and Robertson (1985a) reported a tradeoff between territory defense and nest attendance in a breeding population of Yellow Warblers in Quebec, in which lightly-streaked males allocated more time to parental care and heavily-streaked males allocated more time to territorial defense (Studd and Robertson 1985b, 1988). The direct negative effect of streaking on number of young fledged in my study suggests that males that employed the parental care strategy were able to fledge more young. However, paternity data for this population are not available, and it is unknown how many fledglings from each nest resulted from extra pair copulations by the female. Yezerinac and Weatherhead (1997a, 1997b) suggested that heavily streaked males achieve more extra pair copulations, whereas lightly streaked males are less territorial and fall victim to cuckoldry more often. Female Yellow Warblers in my study population may assess streakiness of males, and choose a mate based on his potential to fledge young.

Unlike males, I predicted that in females, winter habitat conditions, and not plumage characteristics, would be more closely related to reproductive measures. However, the direct effects observed in the female path diagram indicated that plumage characters were associated with first egg date, such that females laying earlier tended to have more breast streaking and less extensive prealternate wing molt than females with later first egg dates. Older females had earlier first egg dates than younger females, suggesting that extent of breast streaking may be a factor of age and breeding experience. There were no direct effects of breast hue on first egg date for females.

It should be noted that events occurring on the breeding grounds or during migration undoubtedly also play a role in whether an individual successfully fledged young; e.g., weather, predation, habitat conditions, and food availability. For example, surviving the winter, migrating during optimal conditions, arriving on breeding grounds early, and establishing a territory may increase chances of successful nesting, but are unlikely to protect nests from failure due to predation or weather.

My study provides evidence that winter habitat conditions can directly affect plumage characteristics of male Yellow Warblers, which function in mate acquisition and male-male interactions that in turn could affect reproductive success. However, the relationship between winter habitat conditions and breast streaking reported in this study was counter-intuitive; i.e., if streaking is a plumage ornamentation that is enhanced by food resources available during molt, we would expect a negative relationship between stable-carbon isotope values and breast streaking. There are several possible explanations, first, breast streaking may largely be genetically determined and less related to resource availability. Heavily-streaked males tend to gain more extra-pair copulations (Yezerinac and Weatherhead 1997a, 1997b), but my study shows that lightly-streaked males are able to fledge more young, and although I did not investigate the frequency of extra-pair copulations for this population, some of these young may result from extra-pair matings (thus genes from both heavily-streaked and lightly-streaked males remain in the population). Another possible explanation is rather than utilizing energy gained from resources on the wintering grounds for advertising for mates, lightly-streaked males may invest energy in parental care at the nest, similar to females (Amundsen and Pärn 2006), and may have a greater need for locating more mesic habitats on the wintering grounds.

From studies of wood-warblers in Neotropical wintering areas (American Redstarts, Marra and Holmes 2001; Black-throated Blue Warblers, Rubenstein et al. 2002, Bearhop et al. 2004), it might be expected that Yellow Warblers experience age- or sex-related exclusion during winter, since they are territorial on both breeding and wintering grounds (Greenberg and Salgado Ortiz 1994; Lowther et al. 1999). However, the positive relationship between winter habitat conditions and breast streaking in my study indicates that dominance-mediated habitat segregation may not occur in Yellow Warblers, and suggests that winter habitat conditions have fewer negative direct impacts than reported for other *Dendroica* species.

Although I found no strong associations (direct or indirect) between winter habitat conditions and reproduction, there was evidence of associations between winter habitat conditions and plumage characteristics for males, and between plumage characteristics and reproductive measures for both male and female Yellow Warblers in this population. Seasonal interactions, although moderate, were detected and are indeed occurring in this population of Yellow Warblers, and this underscores the importance of conserving appropriate habitats throughout the annual life cycle of migratory birds.

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		Isotopes ($\delta^{13}\text{C}$)	Streaking	Molt	Hue	First egg date	Fledge date
Streaking	DE	0.23					
	IE	-					
	TE	0.23					
Molt	DE	0.25					
	IE	-					
	TE	0.25					
Hue	DE	-0.08					
	IE	-					
	TE	-0.08					
First egg date	DE	0.17	0.02	0.07	0.11		
	IE	0.01	-	-	-		
	TE	0.18	0.02	0.07	0.11		
Fledge date	DE	-	-	-	-	0.07	
	IE	0.01	0.00	-0.01	-0.02	-	
	TE	0.01	0.17	0.00	0.01	0.07	
Number of fledglings	DE	-	-0.30	0.00	-0.03	-0.20	-0.32
	IE	-0.11	0.00	-0.01	-0.02	-0.02	-
	TE	-0.11	-0.30	-0.02	-0.05	-0.22	-0.32

Table 2.1. Direct effects (DE), indirect effects (IE), and total effects (TE) of winter habitat conditions (as determined by stable-carbon isotopes $\delta^{13}\text{C}$), on plumage characteristics and reproductive measures for male Yellow Warblers breeding at Ottawa National Wildlife Refuge, Ottawa County, Ohio, April-June 2007. Significant effects ($p < 0.05$) are displayed in bold.

		Isotopes ($\delta^{13}\text{C}$)	Streaking	Molt	Hue	First egg date
Streaking	DE	0.13				
	IE	-				
	TE	0.13				
Molt	DE	0.02				
	IE	-				
	TE	0.02				
Hue	DE	0.11				
	IE	-				
	TE	0.11				
First egg date	DE	0.19	-0.30	0.29	-0.20	
	IE	-0.06	-	-	-	
	TE	0.14	-0.30	0.30	-0.20	
Number of fledglings	DE	-	-0.15	0.04	0.19	0.12
	IE	0.02	-0.04	0.04	-0.02	-
	TE	0.02	-0.18	0.07	0.17	0.12

Table 2.2. Direct effects (DE), indirect effects (IE), and total effects (TE) of winter habitat conditions (as determined by stable-carbon isotopes $\delta^{13}\text{C}$), on plumage characteristics and reproductive measures for female Yellow Warblers breeding at Ottawa National Wildlife Refuge, Ottawa County, Ohio during April-June 2007. Significant effects ($p < 0.05$) are displayed in bold.

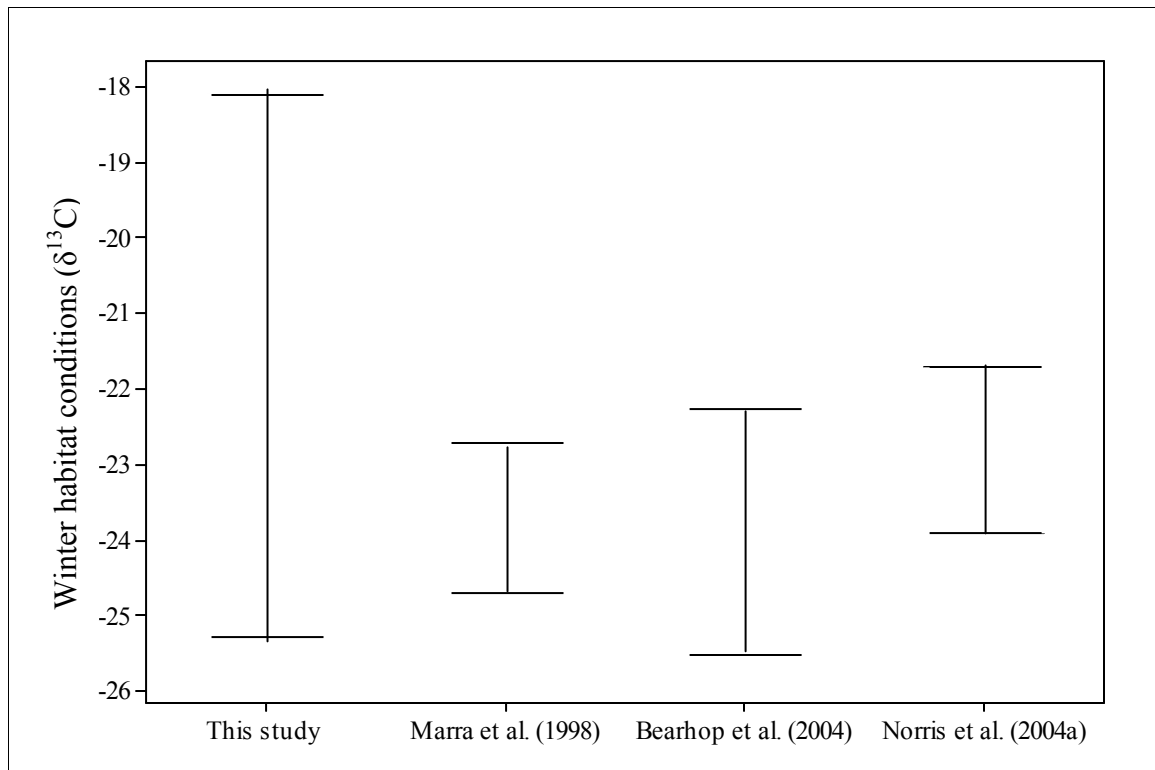


Figure 2.1. Ranges of stable-carbon isotope values ($\delta^{13}\text{C}$) reflecting habitat conditions during the previous winter for adult Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, April-June 2007, and for three similar seasonal-interactions studies of migratory songbirds: Norris et al. (2004a), American Redstarts, southern Ontario, Canada, May-June 2001 and 2002; Bearhop et al. (2004), Black-throated Blue Warblers, North Andros, Bahamas, April 2000; Marra et al. (1998), American Redstarts, central New Hampshire, spring 1997.

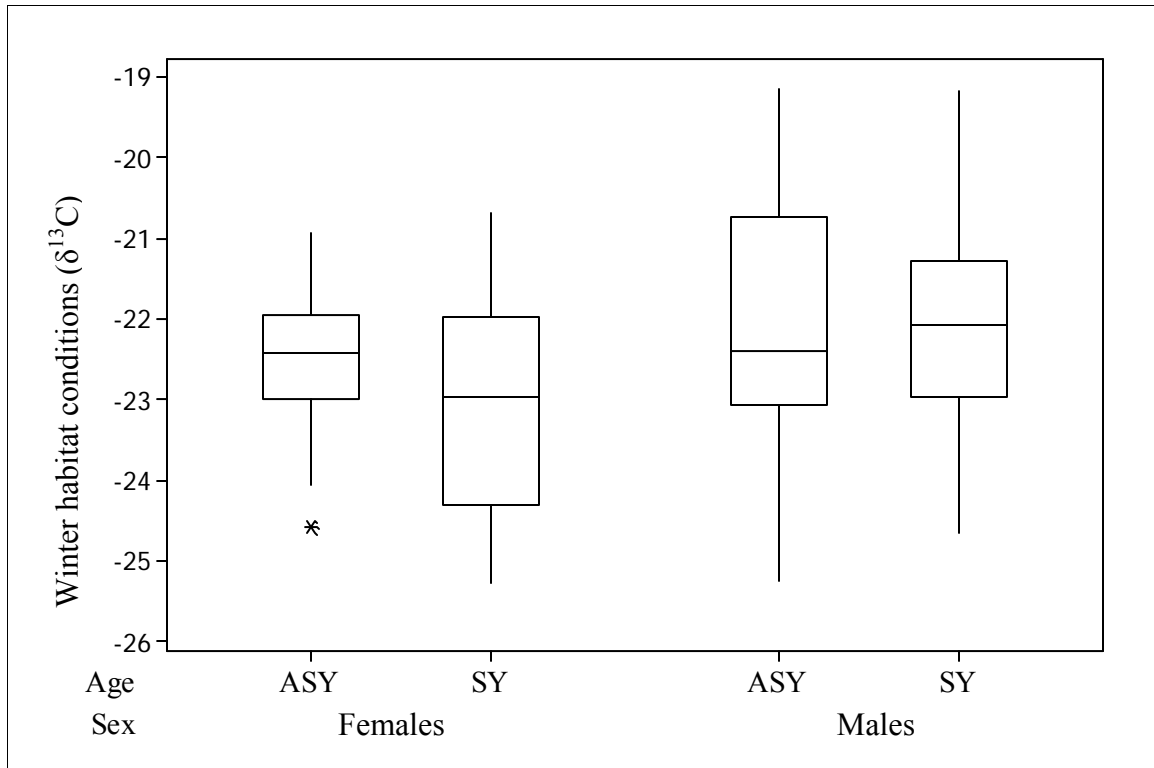
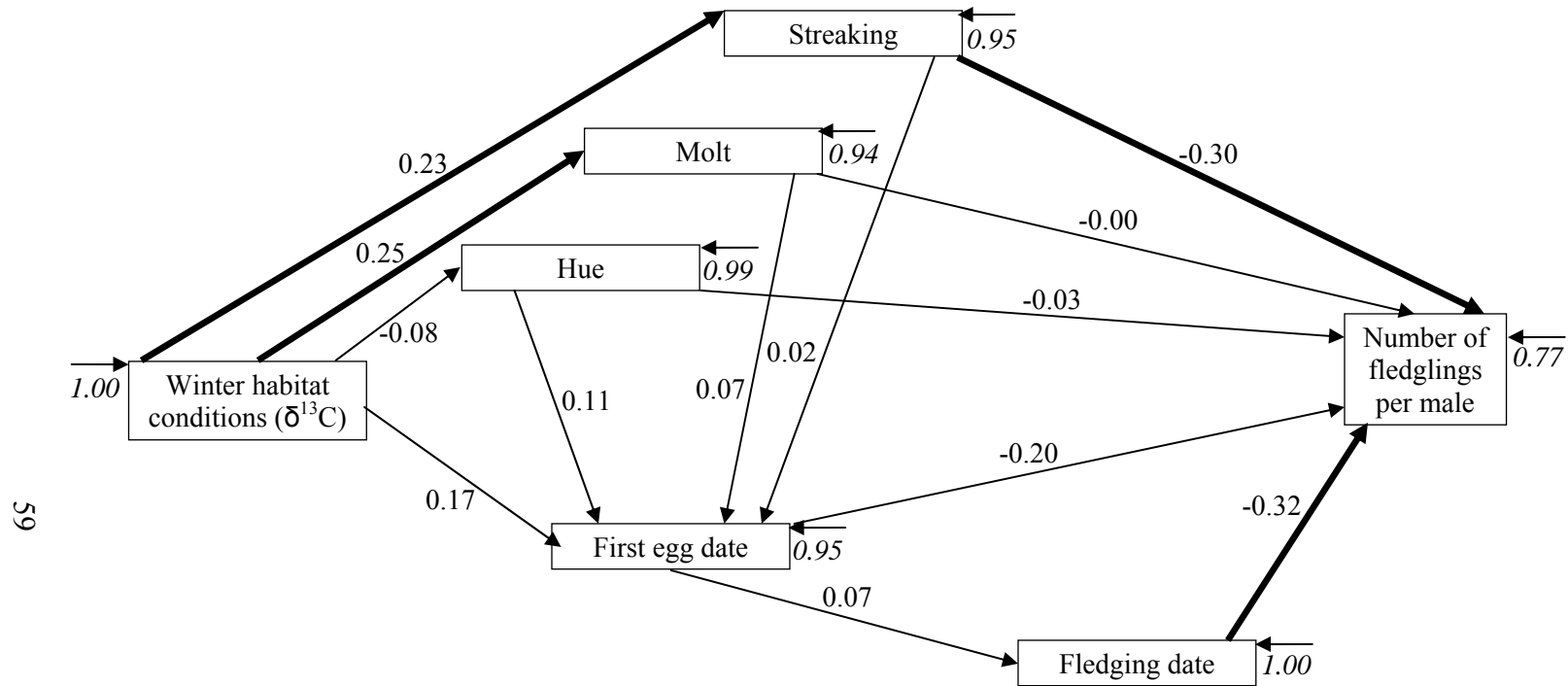


Figure 2.2. Boxplots of stable-carbon isotope values ($\delta^{13}\text{C}$) reflecting habitat conditions during the previous winter for adult Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, April-June 2007. Stable-isotope ranges are separated into age and sex categories (ASY = after-second-year; SY = second-year). The minimum and maximum, interquartile range, and median stable-carbon isotope values are represented in each boxplot, and the star represents an outlier.

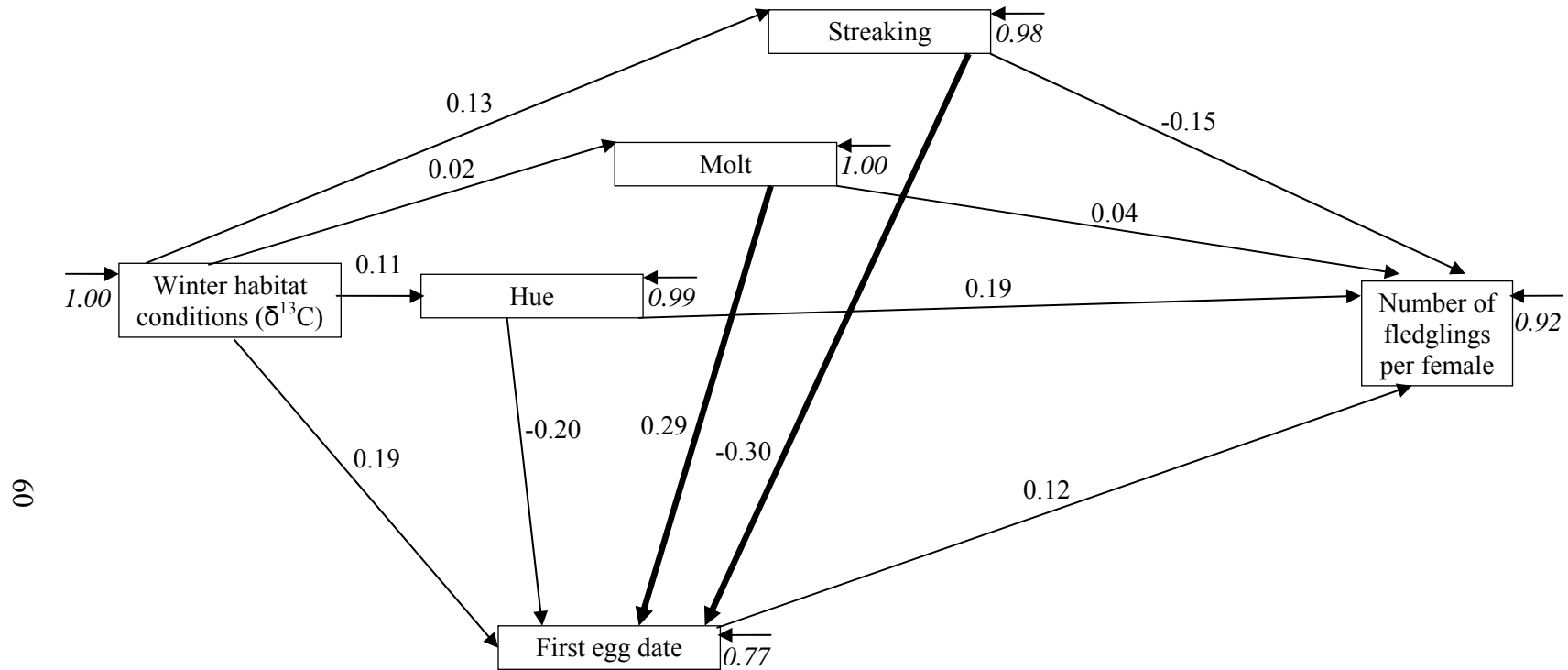
Male Path Diagram



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Figure 2.3. Path analysis diagram depicting effects of winter habitat conditions (expressed as $\delta^{13}\text{C}$) on plumage characteristics and reproductive measures of male Yellow Warblers ($n = 71$) breeding at Ottawa National Wildlife Refuge, Ottawa County, Ohio April-June 2007. The percentage of unexplained variation for each variable is represented in italics by the short arrow next to each variable. Partial regression coefficients are indicated next to each longer arrow and represent direct effects. Thick arrows represent significant direct effects ($p < 0.05$).

Female Path Diagram



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Figure 2.4. Path analysis diagram depicting effects of winter habitat conditions (expressed as $\delta^{13}\text{C}$) on plumage characteristics and reproductive measures of female Yellow Warblers ($n = 61$) breeding at Ottawa National Wildlife Refuge, Ottawa County, Ohio, April-June 2007. The percentage of unexplained variation for each variable represented in italics by the short arrow next to each variable. Partial regression coefficients are indicated next to each arrow and represent direct effects. Thick arrows indicate significant direct effects ($p < 0.05$). Note that the variable “Fledge date” was dropped from the female model due to small effective sample size.

CHAPTER 3

INFLUENCE OF PLUMAGE COLORATION AND ORNAMENTATION ON REPRODUCTIVE MEASURES IN THE YELLOW WARBLER (*DENDROICA PETECHIA*)

INTRODUCTION

Secondary sexual traits in male birds, including plumage coloration and ornamentation, function in the establishment and defense of breeding territories and in mate acquisition by signaling dominance and territoriality (Senar 2006), reproductive strategy (i.e., parental care versus territorial defense; Atkinson and Ralph 1980; Studd and Robertson 1989), reproductive status (i.e., experience and age), and reproductive potential (Hill et al. 1998), and can signal male quality or fitness (phenotypic and genetic; Hill 2000; Saks et al. 2003; Alonso-Alvarez et al. 2004). These traits signal differently in inter- (i.e., mate acquisition) and intrasexual (i.e., territoriality) interactions (Pryke et al. 2001), both within and between seasons (Marchetti 1998). Males benefit from signaling their potential reproductive quality because females base their choice of mates, in part, on appearance (Griffith and Pryke 2006). It is also beneficial to males to signal their

dominance and experience to other males in order to establish and maintain high-quality territories (reviewed in Senar 2006).

Male plumage ornamentation and coloration can indicate reproductive strategy and how a male allocates effort to territorial behavior and parental care, providing a basis for female mate choice (Atkinson and Ralph 1980; Lozano and Lemon 1996; Dale 2006). For example, in White-throated Sparrows (*Zonotrichia albicollis*), individuals with a white supercilium and throat patch are more territorial, while tan individuals invest more effort in parental care, and disassortive mating in this species increases reproductive success (Atkinson and Ralph 1980). Likewise, resident versus satellite male Ruffs (*Philomachus pugnax*) display varying color schemes depending on reproductive strategy and form cooperative leks to attract females (Lank et al. 1995). When choosing a mate, females consider visual and vocal cues, as well as territory, to assess a male's potential to successfully fledge young, and depend on both territorial behavior and parental care from their mates to achieve nesting success (Lozano and Lemon 1996). In classic mate choice experiments, Peek (1972) and Smith (1972) found that male Red-winged Blackbirds (*Agelaius phoeniceus*) with blackened epaulets were less attractive to females and less able to hold territories than non-blackened males. Similarly, both male epaulet color and resource availability on territories influenced female mate choice in Red-winged Blackbirds (Yasukawa 1981; Ewald and Rohwer 1982).

In yellow birds, carotenoid pigments present in the diet are incorporated into growing feathers during molt and expressed as yellow plumage coloration (Hill and Montgomerie 1994; McGraw 2006). The coloration of yellow plumage can indicate male quality, with highest-quality males expressing the richest pigments because more

intensely colored males have met nutritional demands and have allocated carotenoids to ornamentation (Hill 2000; Saks et al. 2003; Alonso-Alvarez et al. 2004). Richly-colored plumage is beneficial to males because it should allow them to obtain higher-quality territories and more effectively attract females (Anderson 1994; reviewed in Hill 2006), and increases reproductive success (Hill et al. 1998).

In migratory songbirds, timing of arrival to breeding grounds and initiation of nesting activities (measured by first egg date) are directly correlated (Norris et al. 2004). Birds that arrive early are more able to acquire high-quality territories, initiate breeding earlier, and thus experience increased breeding success (Bensch and Hasselquist 1992; Rowe et al. 1994; Webster et al. 2002; Hobson 2005). Energetic condition, which is likely related to resources obtained prior to initiation of northward migration as well as events during migration, and early arrival increase individual and reproductive fitness on the breeding grounds (Marra et al. 1998; Bearhop et al. 2004).

My study examined the relationships between plumage characters and both the number of young fledged per adult and daily nest survival rates to assess reproductive success of Yellow Warblers (*Dendroica petechia*) in northwestern Ohio. The Yellow Warbler is a Nearctic-Neotropical migratory bird and one of the most abundant wood-warblers (Parulidae) in North America, breeding in a variety of shrubby habitats in wetland and upland areas (Howell and Webb 1995; Dunn and Garrett 1997). This species exhibits strong variation in plumage characteristics (including amount of breast streaking and intensity of yellow coloration), and has predictable prealternate and prebasic molt sequences, making it ideal for examining relationships between plumage characteristics and reproductive success. I predicted that plumage characteristics would

be important determinants of reproductive success for males, because males use plumage coloration and ornamentation to acquire high-quality territories and mates, which are both related to breeding success (Anderson 1994; Hill et al. 1998; Senar et al. 2002). For females, I predicted that age and first egg dates would be related to reproductive success because experienced breeders (Saether 1990; Smith and Moore 2005) and birds that initiate nests earlier (Bensch and Hasselquist 1992; Rowe et al. 1994; Norris et al. 2004) tend to have higher reproductive success (Sandberg and Moore 1996).

METHODS

Field Data Collection

My research was conducted on the southwest shore of Lake Erie at the Ottawa National Wildlife Refuge, Ottawa County, northwestern Ohio (41° 36' 56" N, -83° 12' 58" W). Ottawa National Wildlife Refuge contains some of the last remnants of the Great Black Swamp, and consists of a series of managed marshes and wetlands connected by canals and dikes, and interspersed with small mature woodlots and shrubby fields. The study sites were located within the willow (*Salix* spp.) and dogwood (*Cornus* spp.) shrubland habitat ≤ 5 km from the Lake Erie shoreline.

To assess reproduction of Yellow Warblers, nests ($n = 252$) were located and monitored throughout suitable habitat from late April to late June in 2007 and 2008. Empty nests were checked daily to determine the date of first egg-laying so that the hatching date could be estimated (11-day incubation period; Lowther et al. 1999). Nests

found during the incubation stage were checked every 2 days to determine hatching date (Mallord et al. 2007). Active nests were checked at a distance of >5 m for an incubating female, and nest contents were checked if no incubating female was present. Nests were checked at the estimated hatch date, and monitored every other day until fledging (Martin and Geupel 1993). I determined the number of young that fledged from each nest by checking the nest on the fledge date and counting nestlings, and when possible, confirmed this number by resighting fledglings after leaving the nest (Norris et al. 2004). I considered a nest “successful” if it produced at least one young, or “failed” if it produced no fledglings. Each nestling was banded with a serially numbered U.S. Geological Survey aluminum leg band and a unique combination of plastic colored leg bands.

Adult Yellow Warblers from each nest were target-netted using 2.6 x 12 m or 2.6 x 6 m mist nets (30 mm mesh), and banded with a U.S.G.S. aluminum leg band and a unique combination of plastic colored leg bands. I recorded the location, date, and time of capture and measured: metatarsus (using calipers; 0.01 mm accuracy), unflattened wing chord (using wing rules; 0.5 mm accuracy), and mass (using digital scales; accuracy 0.1 g). Visual examination of furcular and abdominal fat were rated using the 6-point scale described by Helms and Drury (1960). Each bird was aged (ASY = after-second-year, SY = second-year), then sexed, using an adaptation (Leberman and Mulvihill, pers. comm.) of guidelines described by Pyle et al. (1997).

For each adult, a digital photograph the breast was taken to quantify the intensity of yellow plumage coloration and the extent of breast streaking. A photograph of the spread wing was taken to document the extent of prealternate wing molt within the

greater coverts. The birds were held in a stable, upright position next to a ruler (for size standardization) against a white background so that all breast streaking would be visible in photographs. Lighting conditions in the field were standardized by holding the bird 30 mm from the camera in a 4-sided box (30 x 15 x 15 cm; open at the bottom and front) constructed of white foam board, and using the camera's flash for all photographs. Photographs were taken using a Canon Powershot A95 digital camera with 5 megapixel resolution, providing brightness values on red, green, and blue scales, which were used to assign color values to each bird (Wiebe and Bortolotti 2001, 2002).

Photographic Analysis

Digital photographs of each adult bird were uploaded to a computer for analysis of breast streaking and yellow coloration. I quantified density of breast streaking using ImageJ software (Rasband 2007). Digital pictures were imported into ImageJ, converted into 8-bit grayscale images, and cropped using the ruler in the photograph to standardize for size, so that only breast feathers were visible. The "threshold value" was set between 140 and 150, so that reddish breast streaking appeared black and yellow areas of the breast appeared white. ImageJ counted the number of black pixels in each photograph using the "analyze particles" function (Gering and Atkinson 2004; DeGroot and Rodewald 2008).

Intensity of yellow plumage coloration was quantified in terms of hue, saturation, and brightness, on a 0-255 red, green, and blue color scale, using Adobe Photoshop software (Villafuerte and Negro 1998; Dale 2000). Ten randomly selected squares of

equal pixel size were selected from each breast photograph and analyzed for hue, brightness, and saturation (HBS) values. The ten values for each variable were averaged for each photograph so that each bird had a separate mean value for hue, brightness, and saturation (Tschirren et al. 2003).

Statistical Methods

Multiple regressions were performed using R 2.6.1 (The R Foundation for Statistical Computing 2007) and logistic exposure models (Shaffer 2004) were created using SAS 9.1 (SAS Institute Inc. 2003; reviewed in Rotella et al. 2004). Regressions for males and females were run separately because different mechanisms likely contribute to reproductive success between the sexes. Plumage variables were extent of breast streaking (Streaking), yellow breast coloration (Hue), and extent of prealternate wing molt (Molt). Hue, brightness, and saturation values were highly correlated (all p -values < 0.002), so brightness and saturation were dropped as redundant variables, and hue was chosen to represent yellow coloration. Hue measures the predominant “color” or wavelength of a sample (0 = red, 60 = yellow, 240 = blue), and indicates whether the sample is purely one color, or a blend of two colors (Senar et al. 2008). Further, hue is biologically meaningful and interpretable since it is an accurate measure of carotenoid content in feathers (Senar et al. 2008) and is related to nest provisioning and nestling growth rates in Blue Tits (*Parus caeruleus*; Senar et al. 2002). The date that the first egg was laid in each nest (Egg) was converted to a Julian date and then standardized across

the two years as the number of days after the first egg of the season was laid. Year was added as a binary variable to account for annual variation (2007 = 0, 2008 = 1).

Multiple regression was used to model the effects of plumage coloration (amount of breast streaking, yellow breast coloration) extent of prealterate wing molt, year, and age (second-year birds = 0, after-second-year birds = 1) on number of young fledged for each female or male (number of fledglings/female and number of fledglings/male). The variable first egg date (Egg) was closely correlated ($r^2 = -0.151$, $p = 0.013$) with number of young fledged and was not included in models. Logistic exposure (Shaffer 2004) was used to model the effects of plumage characteristics, age, year, and first egg date on daily nest survival rates (DNSR) of each nest. The variable number of young fledged per adult (Fledglings) was closely correlated ($r^2 = 0.888$, $p < 0.001$) with daily nest survival rate and were not included in models.

I used an information theoretic approach and Akaike's Information Criterion with an adjustment for small sample size (AIC_c) to rank candidate models; models with $\Delta AIC_c < 2$ indicated highest importance in explaining the variation in the response variables (Burnham and Anderson 2002). An *a priori* set of models was chosen (22 for daily nest survival rate; 21 for number of fledglings), including both null and full models. The full model for number of young fledged was Fledglings = Streaking + Hue + Molt + Age + Year, and the full model for daily nest survival rates of each nest was DNSR = Streaking + Hue + Molt + Age + Year + Egg.

Model averaging was performed on candidate models with $\Delta AIC_c < 2$ because these models had the highest level of empirical support. Relative variable importance

(RVI) values were calculated and 95% confidence intervals were constructed to make multimodel inferences (Burnham and Anderson 2002).

RESULTS

During 2007 and 2008, we found 117 and 135 nests, respectively. At least one adult was captured and banded at 81 of those nests in 2007, including 72 males (52 ASY, 20 SY) and 66 females (48 ASY, 18 SY). In 2008, at least one adult from 107 nests was captured and banded, including 82 males (60 ASY, 22 SY) and 82 females (62 ASY, 19 SY). A total of 37 nests (31.6%) successfully fledged at least one young in 2007, and 50 nests (37%) succeeded in 2008.

Plumage characteristics differed significantly between sex classes, males having more breast streaking than females ($p < 0.001$; males: mean = $33,948 \pm 949$ SE; females: mean = $3,564 \pm 417$ SE), more extensive prealternate wing molt than females ($p < 0.001$; males: mean = 8.27 ± 0.091 SE; females: mean = 7.40 ± 0.089 SE), and lower hue values, indicating that males have darker yellow breast feathers than females ($p < 0.001$; males: mean = 54.61 ± 0.119 SE; females: mean = 56.96 ± 0.132 SE). There were no significant differences between sexes in first egg date ($p = 0.885$) and number of young fledged per adult ($p = 0.918$), but after-second-year birds of both sexes tended to initiate nesting activities earlier than second-year birds (males: $p = 0.011$; females: $p = 0.002$). There were no significant differences in number of young fledged between age classes for both males ($p = 0.310$) and females ($p = 0.118$).

The top-ranked model explaining number of fledglings per male contained Streaking, Hue, and Molt as predictor variables (Akaike weight $\omega_i = 0.790$) (Table 3.1). Although Molt had a high relative variable importance value (RVI = 0.079), it likely was less important than Hue and Streaking because the average linear regression model indicated that the 95% confidence interval encompassed zero ($\beta = 0.213$, SE = 0.139). Variation in number of young fledged per male was best explained by the variables Streaking (RVI = 0.790, $\beta = -0.0000360$, SE = 0.0000151) and Hue (RVI = 0.790, $\beta = -0.213$, SE = 0.104) (Table 3.5a). The two candidate models receiving greatest support for explaining variation in number of young fledged per female were the models containing Hue and Molt (Akaike weight $\omega_i = 0.434$), and Streaking, Hue, and Molt (Akaike weight $\omega_i = 0.160$) (Table 3.2). However, none of the three variables in the two candidate models with ΔAIC_c were useful in explaining variation in the number of young fledged per female since 95% confidence intervals for all three variables encompassed zero (Table 3.5b).

Four models were equally probable ($\Delta AIC_c < 2$) in explaining variation in daily nest survival rates for males (Table 3.3). The predictor variable Age appeared in all four candidate models with $\Delta AIC_c < 2$, and was the only variable in the top-ranked model (Akaike weight $\omega_i = 0.193$), suggesting greater importance in explaining variation in daily nest survival rates. The average logistic exposure model revealed that the 95% confidence intervals for the variables Streaking ($\beta = 0.000$, SE = 0.000, RVI = 0.114), Hue ($\beta = 0.031$, SE = 0.074, RVI = 0.092), and Molt ($\beta = 0.016$, SE = 0.057, RVI = 0.076) encompassed zero, indicating that the variable Age ($\beta = 1.127$, s.e. = 0.562, RVI = 0.474) best explained daily nest survival rates for males (Table 3.5c). Nests associated

with after-second-year males tended to have higher daily nest survival rates than nests associated with second-year males. The null model (Akaike weight $\omega_i = 0.178$) was top-ranked among the set of logistic exposure models for daily nest survival rates for females, indicating that none of the variables measured were important in explaining the variation in daily nest survival rates for females (Table 3.4).

DISCUSSION

Secondary sexual traits, such as male plumage coloration and ornamentation, are most evident in high quality birds (Hill et al. 1998). Female birds consider a number of attributes when choosing mates, including plumage coloration and ornamentation, vocal and behavioral displays (Anderson 1994), and territory quality (Yasukawa 1981; Griffith and Pryke 2006). However, coloration and ornamentation may also serve as an indicator of female quality, as these may change or become enhanced with age, with older, more experienced or dominant individuals expressing brighter or more intense coloration (Amundsen and Pärn 2006). My study indicates that plumage coloration and age may be important factors in predicting reproductive success in male Yellow Warblers, but that these attributes in females have little apparent impact on reproductive success.

In my study, male Yellow Warblers with light breast streaking tended to fledge more young than males with heavier breast streaking. This may be a factor of how different males allocate their time during the breeding season. Studd and Robertson (1985a, 1988, 1989) found that male Yellow Warblers with lightly-streaked breasts exhibited greater parental care, spending more time foraging for young and making more

visits to the nest than heavily-streaked males which allocated more time to territorial defense. Interestingly, these differences were not related to age or to territory quality (Studd 1987; Studd and Robertson 1988, 1989). Studd and Robertson (1989) suggested that males with different amounts of breast streaking may simply use different reproductive strategies. The findings by Studd and Robertson (1985a, 1988, 1989) may imply that males in my study that allocate more time to parental care at the nest are able to fledge more young.

With respect to plumage coloration, males with darker yellow (i.e. lower hue values) breasts tended to fledge more young than paler yellow males. This may ultimately be a factor of age since after-second-year males tended have darker hue values than second-year males ($p = 0.020$), indicating that males with more breeding experience are able to fledge more young than males new to the breeding population.

Females assess a variety of factors when choosing mates, but male appearance and quality of territory are likely of high importance (Griffith and Pryke 2006). Males expressing secondary sexual traits more intensely tend to more effectively attract females (Anderson 1994), signal dominance in male-male interactions (Greene et al. 2000), and have higher breeding success (Hill et al. 1998). In Yellow Warblers, streaking and yellow coloration of the breast may signal different information regarding a male's potential for successful reproduction. The extent of streaking on a male's breast may indicate male reproductive strategy (Studd and Robertson 1985a, 1985b, 1988), and, since female songbirds depend on both male parental care and territorial behavior to successfully fledge young (Lozano and Lemon 1996), female Yellow Warblers may assess the tradeoff between these reproductive strategies by gauging breast streaking,

then choose a mate that is perceived to have the potential to fledge a greater number of young. Females may also assess yellow plumage coloration when choosing a mate, and select males with that display coloration indicating age and reproductive experience, or more richly yellow colored breast feathers.

Although first egg date is an accurate measure of timing of arrival to breeding grounds in many species (Bensch and Hasselquist 1992; Webster et al. 2002, Norris et al. 2004; Hobson 2005) and is related to reproductive success (Rowe et al. 1994; Marra et al. 1998; Webster et al. 2002; Bearhop et al. 2004), first egg date did not explain variation in daily nest survival rate for either males or females in this study. Although sample sizes were low, arrival timing was not correlated with first egg date ($r^2 = -0.012$, $p = 0.969$, $n = 18$) for Yellow Warblers in this population.

Variation in daily nest survival rates for males was age-related, with males in their second breeding season or older having higher daily nest survival rates than males in their first breeding season. This may indicate that males with more breeding experience are able to obtain better breeding territories (Smith and Moore 2005), more effectively defend nests from predators and Brown-headed Cowbirds (*Molothrus ater*), and allocate adequate time to parental care, thereby increasing nest success.

In females, plumage characteristics and age were unrelated to the number of young fledged per adult. Males and females likely employ different strategies to signal reproductive potential, and, in females, plumage characters are likely not as related to reproductive success as in males: males invest energy gained from food resources into territoriality and advertising for mates, whereas females invest energy into egg laying and incubation (Fitzpatrick et al. 1995; reviewed in Amundsen and Pärn 2006). Because the

plumage variables did not help explain the number of young fledged per female, variation was instead likely due to age-related differences in plumage and molt, as in female Cedar Waxwings (*Bombycilla cedrorum*; Mountjoy and Robertson 1988) and Red-winged Blackbirds (Johnsen et al. 1996).

Plumage characteristics, age, and timing of nest initiation were not related to daily nest survival rates for females. Plumage characteristics are likely not important in female nesting success, and the lack of effects of age and first egg date on daily nest survival rates may be due to relatively high predation that occurs at Ottawa National Wildlife Refuge and poor weather conditions (heavy rain and wind) that apparently caused nest failure. Predation and weather likely had an equalizing effect on female reproductive success and may have diminished any age, experience, or nest initiation relationships with reproduction.

My study examined how different plumage characteristics were related to reproductive performance in both males and females. Yellow Warblers may employ multiple messages (reviewed in Dale 2006) in signaling individual quality, and reflect both age and experience (through yellow coloration), and reproductive strategy and potential (through breast streaking). Although not investigated in this study, extra-pair paternity can increase or decrease a male Yellow Warbler's breeding success depending on reproductive strategy (Yezerinac and Weatherhead 1997a, 1997b), which is related to plumage ornamentation (Studd and Robertson 1985a, 1988, 1989). Males with more extensive breast streaking spend more time defending their territories (Studd and Robertson 1985a), but also elicit more extra-pair copulations (Yezerinac and Weatherhead 1997b), and ultimately sire a greater number of young (Yezerinac and

Weatherhead 1997a). In contrast, males with lighter breast streaking spend less time defending their territories (Studd and Robertson 1985a, 1988), and consequently are more susceptible to cuckoldry (Yezerinac and Weatherhead 1997b). However, because these males invest more energy into raising offspring, they may be able to fledge a greater number of young from their nests (this study), regardless of parentage. I suggest that females may choose males with lighter breast streaking because they perceive that these males will likely fledge more young. Additional studies are needed to investigate female mate choice as it relates to breast streaking and extra-pair matings, to improve our understanding of how genetics and resource acquisition interact and relate to Yellow Warbler plumage coloration and ornamentation, and to determine whether breast streaking signals divergent reproductive strategies in male Yellow Warblers as in White-throated Sparrows (Atkinson and Ralph 1980) and Ruffs (Lank et al. 1995).

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Males - Number of young fledged

Model	K	AIC	AIC _c	ΔAIC _c	ω _i
Streaking + Hue + Molt	4	550.2833	550.53	0.000	0.790
Hue + Molt	3	554.0047	554.15	3.620	0.129
Full	7	554.3928	555.11	4.576	0.080
Streaking + Hue	3	567.081	567.23	16.696	0.000
Streaking + Hue + Age	4	566.9462	567.20	16.663	0.000
Year + Streaking + Hue	4	568.7789	569.03	18.496	0.000
Hue	2	570.4202	570.49	19.960	0.000
Hue + Age	3	570.9553	571.11	20.570	0.000
Year + Hue	3	571.9184	572.07	21.534	0.000
Streaking + Molt + Age	4	579.8684	580.12	29.585	0.000
Streaking + Molt	3	580.3739	580.52	29.989	0.000
Streaking + Age	3	593.7616	593.91	43.377	0.000
Streaking	2	594.2798	594.35	43.820	0.000
Year + Streaking	3	595.0551	595.21	44.670	0.000
Molt	2	629.0757	629.15	78.615	0.000
Molt + Age	3	629.4232	629.57	79.038	0.000
Year + Molt	3	630.5453	630.70	80.160	0.000
Null	1	662.9494	662.97	112.439	0.000
Age	2	663.3072	663.38	112.847	0.000
Year	2	663.5615	663.64	113.101	0.000
Year + Age	3	664.0544	664.20	113.670	0.000

Table 3.1. Linear regression models (ranked by AIC_c) examining relationships between the number of young fledged per individual and several predictor variables for male Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, late April to late June 2007 and 2008. K is the number of parameters in the model; AIC_c is the Akaike Information Criterion adjusted for small sample sizes; ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question; ω_i is the Akaike weight indicating relative likelihood of the model (Burnham and Anderson 2002). The model with the highest level of empirical support (ΔAIC_c < 2) is displayed in bold text.

Females - Number of young fledged

Model	K	AIC	AIC _c	ΔAIC _c	ω _i
Hue + Molt	3	518.379	518.541	0.000	0.434
Streaking + Hue + Molt	4	520.262	520.534	1.994	0.160
Hue + Age	3	521.158	521.320	2.779	0.108
Hue	2	521.293	521.373	2.833	0.105
Streaking + Hue + Age	4	522.647	522.919	4.379	0.049
Year + Hue	3	523.043	523.205	4.664	0.042
Streaking + Hue	3	523.185	523.347	4.806	0.039
Full	7	523.043	523.821	5.280	0.031
Year + Streaking + Hue	4	524.947	525.219	6.679	0.015
Streaking + Molt + Age	4	545.588	545.860	27.319	0.000
Streaking + Molt	3	546.128	546.290	27.750	0.000
Streaking + Age	3	548.621	548.783	30.243	0.000
Streaking	2	549.207	549.288	30.747	0.000
Year + Streaking	3	551.075	551.237	32.697	0.000
Molt	2	583.740	583.820	65.280	0.000
Molt + Age	3	583.877	584.039	65.498	0.000
Year + Molt	3	585.733	585.896	67.355	0.000
Null	1	615.737	615.763	97.223	0.000
Age	2	615.904	615.985	97.444	0.000
Year	2	617.700	617.780	99.240	0.000
Year + Age	3	617.850	618.012	99.471	0.000

Table 3.2. Linear regression models (ranked by AIC_c) examining relationships between the number of young fledged per individual and several predictor variables for female Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, late April to late June 2007 and 2008. K is the number of parameters in the model; AIC_c is the Akaike Information Criterion adjusted for small sample sizes; ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question; ω_i is the Akaike weight indicating relative likelihood of the model (Burnham and Anderson 2002). The models with the highest level of empirical support (ΔAIC_c < 2) are displayed in bold text.

Males - Daily nest survival rate

Model	K	AIC	AIC _c	ΔAIC _c	ω _i
Age	2	108.757	108.771	0.000	0.193
Streaking + Age	3	109.789	109.817	1.046	0.114
Hue + Age	3	110.220	110.248	1.478	0.092
Molt + Age	3	110.614	110.642	1.871	0.076
Null	1	110.948	110.953	2.182	0.065
Year	1	110.948	110.953	2.182	0.065
Hue + Streaking + Age	4	110.991	111.038	2.267	0.062
Streaking	2	111.319	111.333	2.562	0.053
Egg	2	111.377	111.391	2.620	0.052
Streaking + Egg	3	112.086	112.114	3.343	0.036
Molt + Age	2	112.742	112.756	3.985	0.026
Age + Streaking + Hue + Molt	5	112.853	112.923	4.152	0.024
Hue	2	112.946	112.960	4.189	0.024
Molt + Egg	3	113.343	113.371	4.600	0.019
Hue + Egg	3	113.375	113.403	4.632	0.019
Streaking + Hue + Egg	4	114.051	114.098	5.327	0.013
Streaking + Molt + Egg	4	114.053	114.099	5.329	0.013
Full	7	114.627	114.758	5.987	0.010
Year + Streaking + Hue + Molt	4	115.139	115.186	6.415	0.008
Molt + Streaking + Hue	4	115.139	115.186	6.415	0.008
Hue + Molt + Egg	4	115.343	115.390	6.619	0.007
Egg + Streaking + Hue + Molt	5	116.030	116.100	7.329	0.005

Table 3.3. Logistic exposure models (ranked by AIC_c) examining relationships between the daily nest survival rate and several predictor variables for male Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, late April to late June 2007 and 2008. K is the number of parameters in the model; AIC_c is the Akaike Information Criterion adjusted for small sample sizes; ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question; ω_i is the Akaike weight indicating relative likelihood of the model (Burnham and Anderson 2002). The models with the highest level of empirical support (ΔAIC_c < 2) are displayed in bold text.

Females - Daily nest survival rate

Model	K	AIC	AIC _c	ΔAIC _c	ω _i
Null	1	125.044	125.051	0.000	0.178
Year	1	125.044	125.051	0.000	0.178
Egg	2	126.245	126.264	1.213	0.097
Streaking	2	126.854	126.873	1.822	0.071
Molt	2	126.956	126.975	1.924	0.068
Age	2	127.043	127.062	2.011	0.065
Hue	2	127.043	127.062	2.012	0.065
Molt + Egg	3	128.046	128.084	3.033	0.039
Streaking + Egg	3	128.204	128.242	3.191	0.036
Hue + Egg	3	128.242	128.279	3.229	0.035
Streaking + Age	3	128.854	128.892	3.841	0.026
Molt + Age	3	128.953	128.991	3.940	0.025
Hue + Age	3	129.041	129.079	4.028	0.024
Hue + Molt + Egg	4	129.999	130.061	5.011	0.014
Streaking + Molt + Egg	4	130.022	130.085	5.034	0.014
Streaking + Hue + Egg	4	130.203	130.266	5.215	0.013
Molt + Streaking + Hue	4	130.776	130.839	5.788	0.010
Year + Streaking + Hue + Molt	4	130.776	130.839	5.788	0.010
Hue + Streaking + Age	4	130.853	130.916	5.865	0.009
Egg + Streaking + Hue + Molt	5	131.984	132.078	7.028	0.005
Age + Streaking + Hue + Molt	5	132.772	132.866	7.816	0.004
Full	7	135.189	135.366	10.315	0.001

Table 3.4. Logistic exposure models (ranked by AIC_c) examining relationships between daily nest survival rate and several predictor variables for female Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, late April to late June 2007 and 2008. K is the number of parameters in the model; AIC_c is the Akaike Information Criterion adjusted for small sample sizes; ΔAIC_c is the difference in AIC_c between the top-ranked model and the model in question; ω_i is the Akaike weight indicating relative likelihood of the model (Burnham and Anderson 2002).

a) Males - Number of fledglings				
Variable	Beta hat	95% CI	RVI	SE
Intercept	12.810	1.270, 24.350		5.873
Streaking	-0.0000360	-0.0000658, -0.0000063	0.790	0.0000151
Hue	-0.213	-0.420, -0.010	0.790	0.104
Molt	0.213	-0.060, 0.490	0.790	0.139

b) Females - Number of fledglings				
Variable	Beta hat	95% CI	RVI	SE
Intercept	4.682	-7,450, 16.810		6.171
Streaking	-0.0000045	-0.0000381, 0.0000291	0.160	0.0000171
Hue	-0.048	-0.260, 0.170	0.594	0.108
Molt	-0.052	-0.350, 0.250	0.594	0.154

c) Males - Daily nest survival rate				
Variable	Beta hat	95% CI	RVI	SE
Intercept	1.635	-7.000, 10.270		4.393
Age	1.127	0.020, 2.230	0.474	0.562
Streaking	0.000	0.000, 0.000	0.114	0.000
Hue	0.031	-0.110, 0.180	0.092	0.074
Molt	0.016	-0.100, 1.130	0.076	0.057

Table 3.5. Coefficients (Beta hat), 95% confidence intervals, relative variable importance (RVI) values, and standard errors (SE) for averaging linear regression models (number of fledglings per individual) and logistic exposure models (daily nest survival rates) with $\Delta AIC_c < 2$ for male and female Yellow Warblers breeding at the Ottawa National Wildlife Refuge, Ottawa County, Ohio, late April to late June 2007 and 2008.

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