CLIMATE VARIABILITY, TIMING OF NESTING AND BREEDING SUCCESS OF TREE SWALLOWS (*TACHYCINETA BICOLOR*)

A thesis Submitted to the College of
Graduate Studies and Research in
Partial Fulfilment of the Requirements for the
Degree of Master of Science in the
Department of Biology
University of Saskatchewan
Saskatoon

By
Marie Fast

PERMISSION TO USE

In presenting this thesis in partial fulfilment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or used of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis. Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Biology
112 Science Place
University of Saskatchewan
Saskatoon, Saskatchewan S7N 5E2

ABSTRACT

Recent changes in climate have increased public attention and scientific evaluation of climate impacts on wild animals and plants. Variation in local weather and regional climate may affect breeding success in birds. Migratory species may be sensitive to these changes as breeding and wintering areas may experience different climate variations; some insectivorous species may be unable to alter timing of migration or laying dates and experience a mismatch between timing of nesting and peak insect availability for their nestlings. Therefore, I investigated the influence of local weather variables and regional climate on breeding performance of an insectivorous migrant songbird, the Tree Swallow (*Tachycineta bicolor*), and tried to examine effects of a mismatch between the timing of breeding and food availability.

I used a 14 year data set from St Denis, Saskatchewan, Canada, 1991-2004, to evaluate correlations among local weather, wetland conditions, aerial insects and regional climate indices and their relationships with variation in clutch initiation date, clutch size, and fledging success. Swallows returned to the study site in late April each year. Annual variation in median clutch initiation date was best explained by mean minimum temperatures during 1-15 May. Larger clutches were laid in years with higher pond water levels (possibly an indication of increased insect availability) and when the Southern Oscillation Index (SOI) was positive (representing La Niña conditions). Fledging success was not influenced greatly by any explanatory variable; however, fledging success tended to increase in years with higher average temperatures. Individual variation in clutch initiation date was examined using path analysis. I found high correlations between initiation date and both local environmental variables and regional climate indices; earlier nesting was associated with warmer temperatures (increased local temperatures, more positive North Atlantic Oscillation Index (NAOI) values and more negative SOI values) and decreased moisture (more positive NAOI values). Two reduced data sets, including female age or insect abundance, were also examined. Clutches were initiated earlier by older females and during springs with higher abundance of aerial insects.

I applied two heating treatments to nest boxes used by pre-laying swallows and compared reproductive measures (timing of nesting, laying sequence, clutch size, egg weight and fledging success) of birds using heated boxes to those of females attending unheated control boxes. However, I was unable to directly examine the predictions of the mismatch hypothesis because nest box heating failed to advance laying dates. Furthermore, no increases in clutch size, egg weight and fledging success were detected between treatment and control nests. Although box heating increased nest temperatures an average of 6.1 ^{o}C ($\underline{+}$ 0.8 SE) over controls, length of time females spent in heated boxes may have been too short to alleviate energetic constraints on egg production, or energy savings associated with box use were insufficient to supersede the influence of ambient environmental conditions that control food availability and energy expenditure of foraging swallows. My results demonstrated that local and regional climate variation strongly affected timing of nesting in swallows, likely via their effects on food supply.

ACKNOWLEDGEMENTS

Throughout this thesis ‘I’ is used but in all cases, it should be replaced with ‘we’ as this was, on many different levels, a group project.

Dr. R. G. Clark, my supervisor, and my mentor. You have given me the freedom to grow but your guidance, wisdom, and perspective helped me succeed. My visits to your office were thought provoking and insightful, and your comments were always constructive and positive. I was fortunate to have Drs. K. L. Wiebe and K. Machin on my advisory committee. Our discussions and your comments were constructive and invaluable – thank you.

The field research required for this project spanned 14 years and therefore I am indebted to the many people who collected swallow data at St. Denis. M. Bollinger, S. Leach, M. Leighton, R. Peterson-Wakeman, K. Waiser, and M. Yaskowich assisted me in the field - thank you for your hard work and positive attitudes. I would also like to thank the Montgomery School Grade 6 classes (2002, 2003) for making new nest boxes and for your enthusiasm and interest. I am grateful for the financial and logistical support I received from the University of Saskatchewan and the Canadian Wildlife Service. Without all of their assistance this project would never have been so enjoyable.

My fellow students in the Biology Department, your support and encouragement was appreciated and needed on many occasions. You provided discussion on biology and many other topics, comments and criticism when needed and always friendship. Katherine Mehl, and Shannon Haszard; you were my first office mates, inspiring students, wonderful friends and exceptional people. Thank you for sharing 208 with me. Chantal Gagnon – thank you. Dr. K. Dufour, thank you for your unending patience and statistical advice. Kevin, you and your family's friendship and love mean the world to us – thank you for everything.

I am also grateful to Laura McKinnon. Your editing, patience, distracting topics of conversation and laugher made completing this thesis a lot easier – thank you.

I would like to thank my family for not asking how my thesis was progressing, but for always being interested in what I was doing and asking me about my work. To my parents, your love, encouragement and devotion to our family are, as always, inspiring. Your 'ounce' of help is worth more than anything – thank you for the unending time you have made for us. To my husband, Peter, you are my co-worker, editor, sounding-board and thought-provoker. Your intelligence, humility, and perseverance are inspiring. I am forever grateful to you for your perpetual love, support, encouragement, understanding and patience. Our son, Alexander, changed our life, our perspective, and priorities. Alex, you have the ability to make me laugh, even when work was frustrating me beyond words. I couldn't imagine finishing my thesis without you both – it would have been unbearable.

DEDICATION

For my family

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

1.1 HYPOTHESES ABOUT EFFECTS OF GLOBAL WARMING ON MIGRATORY BIRDS

Climate monitoring over the past century and long-term climate reconstructions for the past millennium indicate that global warming has been accelerating (Hughes 2000). Effects of variable weather conditions and climate change on wildlife have sparked considerable interest in the past decade (e.g., McCarty 2001, Walther et al. 2002). Long-term European studies have shown that increasing air temperatures are associated with changes in body size and condition of ungulates (Post et al. 1997), and timing of both amphibian spawning (Beebee 1995) and insect emergence (Visser et al. 1998, but see Walther et al. 2002, Root et al. 2003). Climate variation also affects reproduction in bird populations. Temperature has been associated with changes in timing of laying (Crick et al. 1997, Dunn and Winkler 1999, Winkler et al. 2002), clutch size (Brown and Brown 1999, Lehikoinen et al. 2006), egg mass (Lessells et al. 2002, Saino et al. 2004) and hatching asynchrony (Ardia et al. 2006). Both local weather variables and large-scale climate indices (e.g., El Niño Southern Oscillation, North Atlantic Oscillation) indirectly affect fecundity in migratory songbirds by affecting food supply (Sillett et al. 2000, Both et al. 2006, Grosbois et al. 2006, Lehikoinen et al. 2006).

Currently, most warming in the Northern Hemisphere has occurred in Siberia and northwestern North America (Environment Canada 2003a). In Canada, the prairies are experiencing annual mean temperature variations of -0.1 to +1.0 ^{o}C from average (Hansen et al. 1998), with the greatest increases being observed in spring and summer, along with decreases in moisture due to reduced winter precipitation and higher evaporation rates (Environment Canada 2003b). Warmer temperatures are mainly attributable to rising minimum temperatures (Environment Canada 2003a). However, climate variation differs by region. Since 1900, the southern USA has experienced annual mean temperatures -0.3 to +1.0^{o}C from average (Hansen at al. 1998), with winter, spring, and summer average temperatures generally being above normal, and fall (September to November) temperatures slightly below normal (Hansen et al. 2001). Temperature increases in the Northern Hemisphere's mid-latitudes have resulted in an increase in the growing season by more than 7 days since 1970 (Environment Canada 2003a), advancing spring plant growth (Myneni et al. 1997). Spring insect emergence is also occurring earlier (Ellis et al. 1997). For insectivorous birds, a crucial determinant of reproductive success is insect abundance at the time of the maximum food requirements of their offspring (Lack 1968). For reasons explained below, differences in timing of food resource availability relative to food requirements of growing nestlings can compromise offspring quality and survival.

In several passerine and shorebird species, data suggest that changing temperatures are influencing timing of breeding (Brown et al. 1999, Dunn and Winkler 1999, Winkler et al. 2002, Pearce-Higgins et al. 2005, Both et al. 2006). Data from nest records spanning 40 years (1952 – 1992) suggest that North American Tree Swallows (*Tachycineta bicolor*; hereafter, swallows) are breeding earlier, likely due to a long-term increase in spring temperatures (Dunn and Winkler 1999). Increased spring temperatures may also affect arthropod abundance (Visser et al. 1998, Visser and Holleman 2001), the primary food of swallows (Robertson et al. 1992). Evidence suggests that increased spring temperatures may lead to a mismatch in timing of egg laying relative to food availability for nestlings, resulting in later-laying females producing fewer fledglings (Visser et al. 1998, Both et al. 2006). This may be attributable to migrant birds being unable to sufficiently shift breeding date due to the timing constraints of migration journeys: either their migration strategy is not affected by climate variation or climates at breeding and wintering areas change at different rates (Both and Visser 2001). Timing of laying has consequences not only for nestling food availability but also on clutch size which declines seasonally (DeSteven 1978, Stutchbury and Robertson 1988). Photoperiod, predation risk, precipitation, and individual characteristics (e.g., age, body condition) may also influence timing of laying (Hammer 1963, Morton 1971, Geupel and DeSante 1990, Nager and VanNoordwigk 1995, Lambrechts et al. 1997, Lloyd 1999, Dawson et al. 2001).

The purpose of my study was to evaluate effects of local spring and regional winter and spring weather conditions and insect abundance on timing of nesting and productivity of swallows. I used a 14 year data set to examine correlates of annual variation in timing of breeding and breeding success. Also, I experimentally increased nest box temperature during one breeding season to attempt to advance swallow nesting dates, and subsequently to evaluate possible effects on breeding success.

1.2 RATIONALE

Although mounting evidence suggests that climatic variation affects the fitness of animals, relatively little work has addressed this problem on the Canadian Prairies where winter and early spring warming has occurred and is expected to be more pronounced in future. I had a unique opportunity to exploit a data set spanning 1990-2004, composed of swallow nest records, including clutch initiation dates, female age, breeding success, food abundance, and weather variables. These data are unique for three reasons. First, all birds were banded each year, so age could be controlled in some analyses. Second, local and regional weather conditions could be linked to nesting date, egg production, and fledging success. Third, the data set also contained aerial insect abundance records from 1990 – 1993 and 2002 – 2003, allowing peaks in insect abundance to be compared across years with different weather conditions and wetland abundance (i.e., variation in aquatic insect emergence).

Swallows readily nest in boxes, so it is also possible to conduct experiments which attempt to advance timing of nesting, thus setting the stage to test whether a mismatch occurs between early nesting and food supply for growing nestlings. The mismatch hypothesis predicts that nestling growth and survival will be poorer in experimentally advanced nests relative to controls during near normal and warmer spring weather (Visser et al. 1998). The mechanism is low food quality and quantity during the early stages of nestling growth (i.e., in the first 1-2 weeks post-hatching). In Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*), a mismatch of egg laying date relative to nestling food availability resulted in females producing fewer surviving young (Visser et al. 1998 and Both et al. 2006, respectively).

Heating nest boxes has been conducted in few experiments. Yom-Tov and Wright (1993) heated nest boxes of laying Blue Tits (*Parus caeruleus*) and found a decrease in laying interruptions compared to females in unheated boxes. Bryan and Bryant (1999) evaluated energetic constraints on incubation behaviour; Great Tits nesting in heated boxes showed increased incubation constancy compared to those nesting in control nest boxes. Dawson et al. (2005a) used nest box heating to evaluate the effect of temperature on the population size of larval *Protocalliphora* Hough (Diptera: Calliphoridae) in swallow nests; they found a positive correlation between nestling cell-mediated immune response and number of *Protocalliphora* within nests. Dawson et al. (2005b) also experimentally heated nests during nestling-rearing and found an increase in nestling survival and growth of primaries compared to nestlings in control nests.

1.3 THE TREE SWALLOW

Swallows are cavity-nesting, migratory, aerial insectivores. Swallows breed across central and northern North America, laying a single clutch per season and migrating to wintering areas primarily in Florida and the Gulf of Mexico (Robertson et al. 1995). In natural situations, swallows typically are monogamous, forming pair bonds in breeding areas. Most nest building and all incubation duties are done by the female; however, both members of the pair feed the young (Robertson et al. 1995). Diet consists largely of insects with aquatic larval stages (Quinney and Ankney 1985). Though aerial insects are their primary food source, they eat seeds and berries during unfavourable conditions (see Robertson et al. 1995). Their use of boxes makes it easy to standardize and manipulate nests, and allows easy capture and marking of eggs, nestlings and adults.

1.4 STUDY AREA

Data were collected on the St. Denis National Wildlife Area (NWA, 52^o 13'N, 106^o 04'W; Figure 2.1) in south-central Saskatchewan, Canada, from May to July, 1991 to 2004. The 385 ha NWA contains over 100 wetland basins of varied size and permanency; vegetation includes annually cropped farmland, shrub land, groves of aspen (*Populus tremuloides*), and fields of native grasses and planted cover (mixes of brome grass, *Bromus* spp., and alfalfa, *Medicago sativa*; Clark and Shutler 1999). In 1990, 50 nest boxes ("Long Point" design) were set up; in both 1991 and 1992, an additional 25 boxes were added and, in 1993, an additional 15 nest boxes were added (total 115 nest boxes, Figure 2.1). Nest boxes were mounted on metal stakes 1–1.5 m above the ground, spaced 30 m apart along trails, most in unshaded areas, with openings facing southeast.

1.5 OBJECTIVE AND ORGANIZATION OF THE THESIS

My overall goal was to evaluate effects of annual climate variation on the timing of nesting. In Chapter 2, I examine annual variation in timing of breeding and breeding success of swallows in relation to local spring weather conditions and broad-scale climate indices, wetlands, spring food abundance, and female age. In Chapter 3, I compare

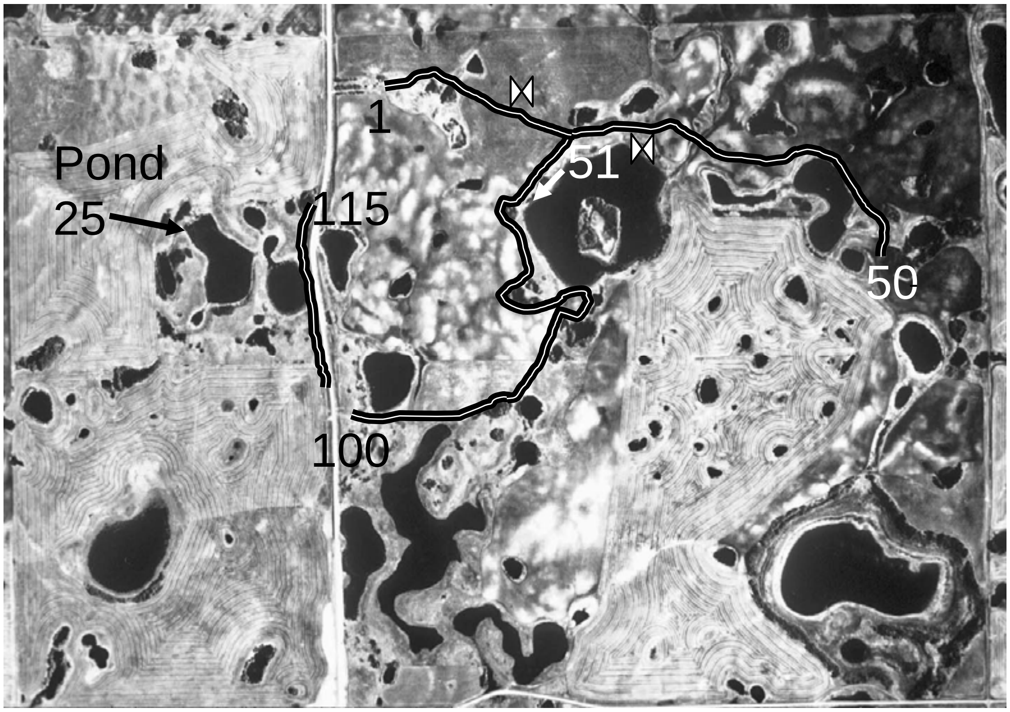

Figure 1.1 Aerial photograph of St. Denis National Wildlife Area, Canada (52°13’N, 106°04’W) showing the trails where 115 Tree Swallow(*Tachycineta bicolour*) nest boxes were located (black lines, numbers indicate nest box numbers), Pond 25, and the location of the two insect traps (⋈). The top of the photo is north; the NWA is 1.6 km from north to south, and 2.4 km from west to east.

experimentally warmed nests with unmanipulated control nests in terms of clutch initiation date, laying sequence, clutch size (quality) and fledging success. In Chapter 4, I discuss the major variables that influence swallow clutch initiation date, and suggest ways to improve future studies of climate impacts on birds.

CHAPTER 2: TIMING OF NESTING AND BREEDING PERFORMANCE OF TREE SWALLOWS: EFFECTS OF SPRING WEATHER AND AERIAL INSECT ABUNDANCE

2.1 INTRODUCTION

Many factors influence timing of breeding and breeding performance in birds. Both large and small scale climate variables may affect avian fecundity (Sillet et al. 2000, Nott et al. 2002, Hussell 2003, Both and Visser 2005, Both et al. 2006). Arrival time of breeding birds may also be affected by weather conditions experienced on their wintering grounds or during migration (Nott et al. 2002). Large scale climate indices correlate with timing of breeding (Forchhammer et al. 1998), fledgling success and mass (Sillett et al. 2000) and annual reproductive success (Nott et al. 2002, Mazerolle et al. 2005). Variation in regional and local weather conditions may affect timing of breeding (Brown et al. 1999, Crick and Sparks 1999, Dunn and Winkler 1999), egg mass (Lessells et al. 2002), clutch size (Creswell and McCleery 2003), nestling growth rates (McCarty and Winkler 1999, McCarty 2001), and nestling survival (Tyler and Green 2004, Bolger et al. 2005). However, evaluations of long-term data sets that include large scale climate indices, local conditions and breeding variables are limited.

Data from North American nest records collected over 40 years (1952 – 1992) suggest long-term increases in spring temperatures may have caused swallows to breed earlier (Dunn and Winkler 1999). Hussell (2003) found that warmer temperatures in the first 10 days of May were positively correlated with earlier nest initiation dates of swallows breeding in southern Ontario. Experimental evidence from central British Columbia has linked increases in nest box temperature to increased swallow nestling survival (Dawson et al. 2005b). Food availability has also been associated with the timing of laying by swallows; swallows in Wisconsin laid heavier eggs earlier in the season when insect abundance was relatively high (Nooker et al. 2005). In addition, female age is correlated with earlier laying dates. After-second-year (ASY, 2 years and older) swallows typically initiate nests earlier than yearlings (SY, females in their second calendar year; De Steven 1978, Stutchbury and Robertson 1988). I had a unique opportunity to examine several of these factors in concert.

I analyzed a 14 year (1991 – 2004) data set on swallows to assess putative effects of weather variables on timing of breeding and breeding success, including effects of local and regional weather, wetland depth and female age on timing of swallow nesting. I predicted earlier clutch initiation dates, at both annual and individual levels, in years with one of the following: warmer temperatures (locally or regionally (Southern Oscillation Index and North Atlantic Oscillation Index)) or increased food availability (measured directly by insect abundance or indirectly via indices of wetland conditions). I also expected that older females, presumably with more experience, would lay eggs earlier than younger females. Similarly, I expected that annual clutch size and fledging success would be positively influenced by warmer temperatures, increased food availability and female age.

2.2 METHODS

2.2.1 Tree Swallow breeding data

Laying dates and clutch size. Clean nest boxes were set up late April 1991 - 2004, prior to swallow arrival on the study area. Nest boxes were subsequently checked every 1-3 days. Swallows usually lay one egg per day early in the morning (Robertson et al. 1992), so clutch initiation dates were assigned as the day the first egg was found, or in a few cases back-dated based on number of eggs present in the nest. For example, if two eggs were found in a nest then the clutch initiation date assigned was the previous day. Nests were checked daily until clutches were complete (no new eggs appeared for 3 consecutive days). Clutches were excluded from analyses if there was evidence of predation, abandonment, or two or more females laying eggs in the same nest box (see Quinney 1983). Any nest that experienced low reproductive success due to human interference (e.g., accidental egg breakage) was also excluded. Only first nesting attempts were used.

Fledging success. To reduce disturbance, nests were not visited from early to mid-incubation. Nest visits recommenced just prior to hatch, 12 days after the last egg was laid (incubation period ranges from 11 to 19 days, 14-year mean of 14.0 days ± 1.5 SD, n = 1024) to determine hatch date and hatch success. Disturbing nestlings near the time of nest departure (ranges from 15 to 22 days after hatch) can result in premature fledging (Robertson et al. 1992), so banding and weighing of nestlings occurred when the oldest nestling in each brood was 12 days old. Nest boxes were checked at least 20 days after hatch to determine how many nestlings had successfully fledged. When no nestlings were present, I assumed they had fledged provided no evidence of predation was present (e.g., disturbed nest material, blood, feathers, or dead nestlings). When nestlings were present, nests were checked during subsequent visits until fate was determined. During the 14 year period other studies were conducted which included clutch size manipulations (Shutler et al. 2006); thus, boxes involved in egg additions or removals were excluded from fledging success results.

Female age. Adults were captured in boxes (see Stutchbury and Robertson 1986) shortly after hatching was complete. Unmarked adults were banded (using standard USFWS aluminium bands), sexed by the presence of brood patch (female) or cloacal protuberance (male), and mass (nearest 1 g, using 100 g Pesola spring scale) was recorded. Females were aged based on plumage differences as SY or ASY (Hussell 1983) or as known age from known hatch year (i.e., females that hatched on the NWA and returned to breed in subsequent years, and females banded and aged initially as SY and recaptured in subsequent years).

2.2.2 Insect biomass

Field collection. Daily aerial insect abundance was monitored during the breeding periods 1991 -1996, and 2002 - 2003; collection dates varied (start: 4 - 13 May, end: 11 July - 8 August), but each year sampling started prior to laying and continued until hatch completion. Insect collection methodology followed Quinney and Ankney (1985). Sampling occurred at two sites on the NWA (same locations each year, Figure 1.1).

Wind socks made from mosquito mesh had an opening diameter of 30 cm, were approximately 100 cm long and attached to a pole 2 m above ground (see Quinney and Ankney 1985). Insect collection jars (60 ml, filled with 70% isopropyl alcohol) were attached to the closed end of each trap. An anemometer was set up beside each wind sock. Sample jars were changed daily. In most cases, samples were collected and anemometer readings were recorded daily. If jars were not collected daily, samples were excluded from analysis. A total of 1019 insect samples was collected (locations pooled) over 8 seasons. The number of collections each year ranged from 94 to 171 (mean = 127). Although I do not know the diet composition of adults or nestlings on my study site, I have no reason to expect it would differ greatly from that collected in traps. Quinney and Ankney (1985) found the taxa and size of insects collected in traps were similar to those adults swallows delivered to nestlings.

Laboratory procedures. Insects were removed from collection jars, placed on labelled filter paper, and any plant material and insects over 13 mm long were removed at this time (following Quinney and Ankney 1985). Insect samples were dried at 90^{o} C for 3 hours (Fisher Isotemp oven). The mass of each sample was recorded to the nearest 0.001 g (Ohaus Analytical Plus scale), and insect biomass collected per hour was determined after adjusting for low wind speed following Quinney et al. (1986).

2.2.3 Local climate data and wetland conditions

A weather station on the NWA monitored temperature (^{o}C); however there was variation in data collection methods and sampling intervals. Therefore, I used Saskatoon weather station temperatures (Environment Canada 2004, minimum air temperature from the NWA and Saskatoon locations were correlated, $r^2 = 0.95$, $P < 0.0001$, n = 106 randomly selected days 1991-2004). Minimum, maximum and mean May Saskatoon daily air temperature were correlated (1991-2004, minimum and maximum; $r^2 = 0.60$, $P < 0.0001$, n = 465, minimum and mean; $r^2 = 0.92$, $P < 0.0001$, n = 465, maximum and mean; $r^2 = 0.87$, $P < 0.0001$, n = 465).

Wetland abundance was recorded on the NWA in the first 2 weeks of May 1991 - 2003. Wetlands were also counted the first 2 weeks in June except 2001 and 2004. Ponds were included in counts if they were holding water, regardless of water level. Water levels (cm) were also recorded in May, 1991 to 2004, at a semi-permanent wetland (Pond 25, Figure 1.1) using gauged stakes permanently located within the pond (Minzhen Su, Environment Canada, Saskatoon, personal communication).

2.2.4 Regional climate indices

Swallow band returns indicate that the majority of those breeding in the Canadian Prairies winter in the southern and southwestern U.S. (Brewer et al. 2000). Since swallows are migratory, it is plausible that the climatic conditions they experience on wintering grounds and during migration may affect subsequent reproductive effort. Therefore, the Southern Oscillation Index (SOI, January - May) and the North Atlantic Oscillation Index (NAOI, December - March) were used as indicators of climatic conditions in both these areas.

The SOI describes large-scale fluctuations in air pressure between the western and eastern tropical Pacific. SOI is calculated using departures from normal surface air pressure differences between Tahiti, French Polynesia and Darwin, Australia (NOAA 2005a; data from Dept. Natural Resources and Mines, State of Queensland, Australia, http://www.longpaddock.qld.gov.au/SeasonalClimateOutlook/SouthernOscillationIndex/SOIDataFiles/index.html). SOI affects both wintering and breeding areas (i.e., southern U.S. and Canadian prairies); when the SOI is more positive the southern U.S. experiences a warm dry winter/spring (December – May), while the Canadian prairies experience a cooler winter/spring (McPhaden 2002, NOAA 2005a). SOI values are also positively correlated with lake-ice break-up dates in Saskatchewan; with break-up occurring about 5 days earlier in years with low SOI values (Bonsal et al. 2006). The opposite occurs when the index is negative. During El Niño episodes (warm phase of the El Niño/Southern Oscillation (ENSO) cycle) the SOI has a large negative value and La Niña events occur when the index is positive. The extreme phases of the cycle generally last 9-12 months, and the period repeats every 3 to 4 years on average (McPhaden 2002). El Niño and La Niña are typically strongest during December-April when the equatorial Pacific sea-surface temperatures are normally warmest (NOAA 2005a).

The NAOI also affects wintering and breeding areas, and appears to be the most important teleconnection, or covariance structural pattern (i.e., shows the strongest statistical relationship between weather events) during winter and early spring (December to March, NOAA 2005b). NAOI is based on normalized sea level pressure differences between Ponta Delgada, Azores, Portugal and Stykkisholmur, Iceland. The climate impacts are presumed to be largely restricted to eastern North America through Europe and into central Russia (Hurrell 1995, Hurrell and Van Loon 1997) but Northern North America, including the Canadian prairies, are also influenced by these changes in pressure (Thompson and Wallace 2001, Sheridan 2003, Coulibaly 2006, Huang et al. 2006). Positive (negative) NAOI values correlate with warm wet (cool dry) winters in the southern U.S. (Hurrell and Van Loon 1997, Sheridan 2003, NOAA 2005b). The Canadian prairies experience warm dry winters during positive NAOI events and negative values are characterized by cold wet winters (Sheridan 2003, Coulibaly 2006, Thompson and Wallace 2006). The NAOI data are calculated monthly (data from The National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center, U.S., ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh).

2.2.5 Statistical Analyses

2.2.5.1 Annual variation in reproductive output

The 14 year data set was used to examine annual variation in timing of breeding, clutch size and fledging success. I evaluated competing models that attempted to explain variation in (1) annual median clutch initiation date (CID), (2) annual mean clutch size (CS) and (3) annual mean percent of successfully fledged nestlings (number of nestling fledged / number of eggs laid; FLEDGE) using local conditions and regional climate indices from 1991 to 2004.

Models were selected *a priori* based on my predictions regarding effects of climate indices and local weather and wetland variables. No interactions between the variables were considered due to sample size constraints, and a null model was included when building models. Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) was used to select among candidate models. The model with the lowest AIC_c value was considered to be the most parsimonious; however, models with very similar AIC_c values (< 2 AIC_c units difference) were considered well supported by data (Burnham and Anderson 2002). Models in the range 2 to 4 ΔAIC_c were weakly supported and models with > 4 ΔAICc were not considered; ΔAIC_c was calculated by subtracting the minimum observed AIC_c value from that of a given model. Normalized Akaike model weights, w_i, were calculated to provide a measure of the extent of the weight of evidence in favour of model *i* (Burnham and Anderson 2002). Weights were used to calculate evidence ratios, w_i/w_j, to provide a measure of relative likelihood of model *i* versus model *j*, suggesting which models were better representations of the data (Burnham and Anderson 2002). Within the set of candidate models, a measure of relative importance of a variable can be determined by summing the weights of all the models that include that particular variable (Burnham and Anderson 2002). General linear models (PROC GLM, SAS Institute Inc. 2001) were used to calculate residual sums of squares for use in calculating AIC_c values (Burnham and Anderson 2002).

Clutch initiation date. Variation in annual median CID was examined using female age, temperature, wetland water depth, number of wetlands present on the study area, spring SOI and winter NAOI. Since ASY generally nest earlier than SY (De Stevens 1978, Stutchbury and Robertson 1988), percent of breeding adult (ASY) females in the nesting population was included in analysis of annual variation in mean CID; unknown-age females were excluded. Given that swallows usually arrive on the study area in late April and early May, swallow activity decreases in temperatures below 15 °C (Stocek 1986), and climate change spring temperature increases are mainly due to a rising minimum temperature (Environment Canada 2003a), I included yearly mean minimum

Saskatoon temperature (°C) from 1 - 15 May (MINMAY). Swallows feed on aerial insects with an aquatic juvenile stage (Quinney and Ankney 1985). Wetland depth affects the total number of aquatic insects (Orians 1980) and NWA wetland water levels are moderately correlated with annual aerial insect biomass (1990 – 1996, 2002 – 2003, $r^2 = 0.68$, $P = 0.08$, $n = 7$). Also, insect abundance may vary with the previous winter's rainfall patterns (Blancher and Robertson 1987). Wetland water depth (cm) was recorded for Pond 25 in early May (DEPTH). May pond count is the number of wetlands holding water in early May each year (#WETMAY). Both variables were also included in the data set as an index of wetland condition and relative spring precipitation. Spring SOI (average January – May) and winter NAOI (average December – March) were used to provide information on broad-scale weather conditions on wintering and breeding areas.

Clutch size. Variation in annual mean CS was also examined using AGE, MINMAY, DEPTH, #WETMAY, SOI and NAOI. Percent of adult breeding females was included; Stutchbury and Robertson (1988) found ASY females laid larger clutches than did SYs early in the breeding season. Since egg production takes 6 to 11 days (Johnson 2000) and laying usually starts in late May (14-year mean = 30 May), MINMAY was used. Aerial insect abundance during the laying period has been shown to correlate positively with clutch size in swallows (Hussell and Quinney 1987) and was weakly correlated with NWA wetland water levels; DEPTH and #WETMAY were included in the analyses. Spring SOI and winter NAOI were also included.

Since CS decreases with advancing CID (Stutchbury and Robertson 1988) and MINMAY appeared in all of the top 4 models for CID (see results), it was possible that

MINMAY was interacting with CID. To determine if there was added variation in CS explained by MINMAY after variation due to median CID was controlled, median CID was added to all candidate models when MINMAY was included, and a model with only median CID was added to the initial set of candidate models.

Fledging success. Annual variation in mean FLEDGE was modeled using MINJUNE, MAXJUNE (mean minimum and mean maximum temperatures during 10 – 30 June, respectively), DEPTH, #WETJUNE (June pond counts were unavailable for 2001 and 2004; therefore May pond count (#WETMAY) data was used for those years), and median CID. Temperature while nestlings are still in the nest can affect their survival; nestlings in experimentally warmed (5^{o}C) nest boxes had increased survival over those in control boxes (Dawson et al. 2005b). Experimentally increased nest temperature improved nestling survival, increased 16 day old mass and length of 9th primary of nestlings in central British Columbia (Dawson et al. 2005b). Most swallows hatch on the NWA in mid June (mean = 16 June ± 4.5 days SD, range 13 – 23 June), and are present in nest boxes for at least 20 days prior to fledging (Robertson et al. 1992). McCarty and Winkler (1999) also found that daily maximum temperatures had the greatest influence on growth of nestlings younger than five days old. Therefore, the two temperatures variables (MINJUNE, MAXJUNE) include the period when most nests contained young on the study area. Two local wetland values, DEPTH and #WETJUNE, were also included. SOI was not included in this analysis because it has little effect on summer weather patterns in the northern hemisphere, especially the Canadian Prairies (McPhaden 2002). Since the NAOI most strongly influences winter weather, with low influence in the summer, it was also not included as a variable in this analysis (NOAA 2005b).

2.2.5.2 Individual variation in clutch initiation date

I evaluated CID of individual female swallows by developing structural equation models to link response and explanatory variables (i.e., temperature, wetland water depth, female age, insect biomass, spring SOI and winter NAOI; see below for details). I used path analysis (PROC CALIS, SAS Institute Inc. 2001) to illustrate causal relationships among explanatory variables and provide information about how much variation in the data is explained by *a priori* hypotheses (Figure 2.1). Path analysis uses simultaneous, multiple linear regressions to test if the hypothesis adequately describes the observations (Mitchell 1992). The standardized partial regression coefficients (or path coefficients, direct effects), correlation estimates and residual (unexplained) variance are obtained. Indirect effects are calculated by multiplying partial regression coefficients along all indirect paths. For example, using Figure 2.1, the indirect effect of spring SOI on CID, was calculated by multiplying the direct effect of spring SOI on CIDTEMP by the direct effect of CIDTEMP on CID. Total indirect effects for a variable are the sum of all indirect pathways.

The goodness of fit (GOF) of different combinations of the variables to data was directly tested. Direct, indirect and total effects of variables were also estimated. To assess the GOF of the *a priori* model and different alternative models, I used indices provided by PROC CALIS including chi-square test, Bentler and Bonnet's normed fit

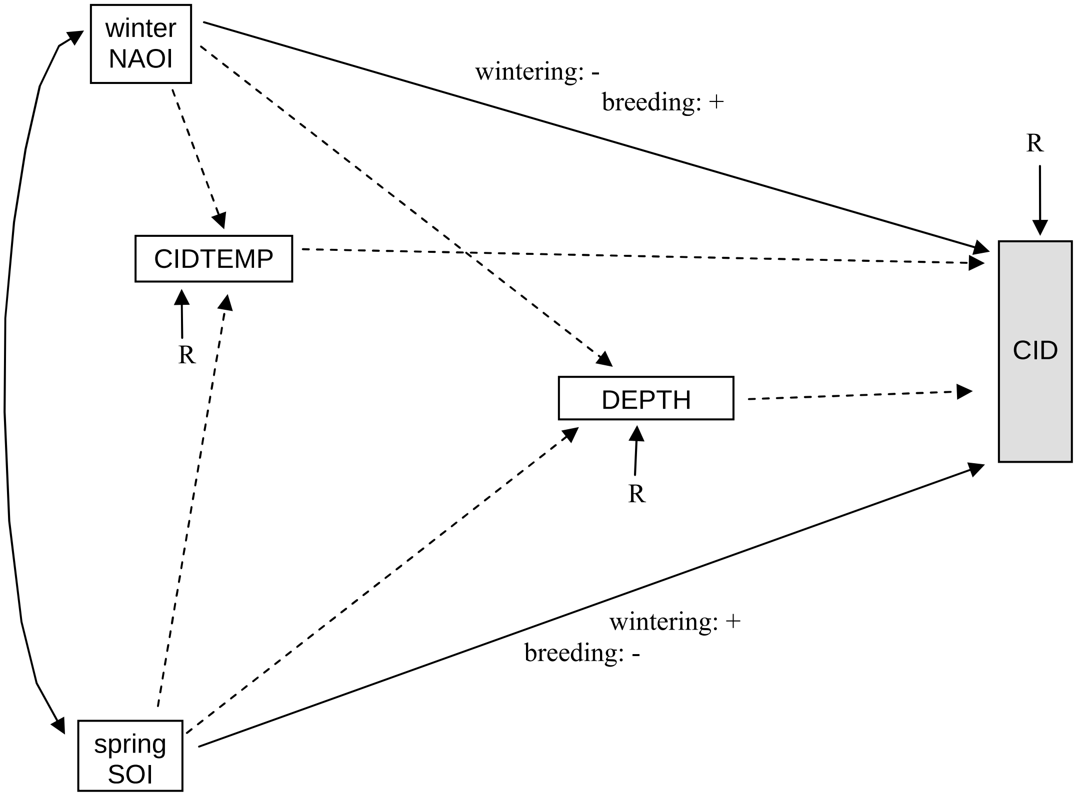

Figure 2.1 Path diagram indicating *a priori* hypotheses about relationships (direction of effect) among explanatory variables on clutch initiation date (CID) of Tree Swallows (*Tachycineta bicolor*). Dashed lines represent expected negative relationships, whereas solid lines represent positive relationships. Path coefficients (direct effects of one variable on another) are represented by single headed straight arrows, two-headed curved arrows represent correlations, and arrows not originating at a variable represent the residual variance for endogenous variables, R (unexplained). Variable definitions and deviations are described in Methods.

index (NFI) and non-normed fit index (NNFI), and Bentler's comparative fit index (CFI). The chi-square statistic tests the null hypothesis that the model fits the data. The NFI and CFI values range from 0 to 1, with values over 0.9 representing an acceptable fit of the model to the data (Hatcher 1998). Values for NNFI may range above 1 and below 0. I initially tested the *a priori* hypothesis for each data set (see below); alternative models were subsequently tested based on modifications and model fit indices.

Environmental variables. Explanatory environmental variables, spring SOI, winter NAOI, DEPTH, and CIDTEMP (see below for definition), were used in the path analyses to describe variation in the main response variable, CID. They included three previously described variables: spring SOI, winter NAOI (of the winter prior to the breeding season), and DEPTH. #WETMAY was not included in this analysis since it is highly correlated with DEPTH ($r^2 = 0.86$, $P < 0.0001$, $n = 1395$) and DEPTH was an important variable in explaining variation in CID based on AIC results (see Results section 2.2.9 and Table 2.1). An assumption of path analysis is that none of the endogenous variables be highly correlated (Hatcher 1998). Saskatoon minimum daily temperature was used to calculate a 10-day running mean deviation from the 14-year average for each initiation date (i.e., deviation of an initiation date's 10-day running mean from the 14 year 10-day running mean for that date, CIDTEMP). This analysis included 1395 nest initiations over 14 years.

Female age and environmental variables. AGE (only females with a known hatch year), along with explanatory environmental variables, spring SOI, winter NAOI, DEPTH, and CIDTEMP, were used in path analyses to describe variation in the main response variable, CID. The reduced data set including only known-age females was initially modelled using the final model from the environmental variables analysis (i.e., Figure 2.4, see Results) with the addition of AGE which directly affected CID, and was directly affected by spring SOI, winter NAOI and DEPTH.

Two key assumptions of path analysis are that the minimum number of observations is greater than 200 individuals and each endogenous variable has at least four values (Hatcher 1998). To satisfy these criteria, this analysis included 221 nests initiated by a sub-sample of females aged as 1, 2, 3 and 4 years old (most females appeared only 1-2 times in the data set).

Insect biomass and environmental variables. Insect biomass along with explanatory environmental variables spring SOI, winter NAOI, DEPTH, and CIDTEMP, were used in path analyses to describe variation in CID. Due to variation in insect collection initiation dates over the study, I was limited by number of insect collection days prior to clutch initiation. Insect monitoring started at least 5 days prior to the first CID; therefore, daily insect biomass (mg / (km/hr)) was used to calculate a 5-day running average prior to the onset of laying (BUG). The initial model including insect biomass was initially modelled using the final model from the environmental variables analysis (i.e., Figure 2.4, see Results) with the addition of BUG which directly affected CID, and was directly affected by spring SOI, winter NAOI, CIDTEMP and DEPTH. The analysis was run using 725 nest initiations from 1991 – 1996, and 2002 - 2003.

2.3 RESULTS

2.3.1. Nesting chronology and breeding success

Annual mean clutch initiation date, clutch size and number of fledglings varied over the duration of the study (Figure 2.2). A total of 1694 clutches was initiated, but due to incomplete clutches, predation, abandonment and human disturbance, only 1395 clutches were used in analyses. Over the 14 years, annual median CID varied by a maximum of 10 days, ranging from 23 May 1998 to 3 June 2002 (14-year median = 28 May). The 14-year mean CS was 6.2 (± 0.03 SE) eggs per nest, with the smallest average clutch of 5.6 (± 0.07 SE) in 2002, and the largest of 6.7 (± 0.09 SE) in 2000. The mean number of fledglings per nest (includes failed nests) ranged from 0.1 (± 0.05 SE) in 1993 to 5.5 (± 0.2 SE) in 1997, with an overall average of 4.4 (± 0.1 SE, n = 1380) fledglings per nest.

2.3.2. Environmental conditions

MINMAY averaged 1.6 °C (± 0.3 SE) and ranged from averages of -2.4 °C in 2002 and 2004 to +4.9 °C in 1993. Temperature during hatch also varied; MINJUNE ranged from minima of 6.0 °C in 2004 to 11.6 °C in 2002 (14-year mean 9.2 °C ± 0.2 SE), and MAXJUNE ranged from 19.1 °C in 2004 to 25.7 °C in 2002 (14-year mean = 22.4 °C ± 0.3 SE). DEPTH (Pond 25) also varied among years, from 0 cm in 2002 to 186 cm in 1997. #WETMAY varied from 3 to 101 and #WETJUNE ranged from 1 to 96 during the duration of the study. Spring SOI was mostly positive (mean = 3.88, range -18.78 (1998)

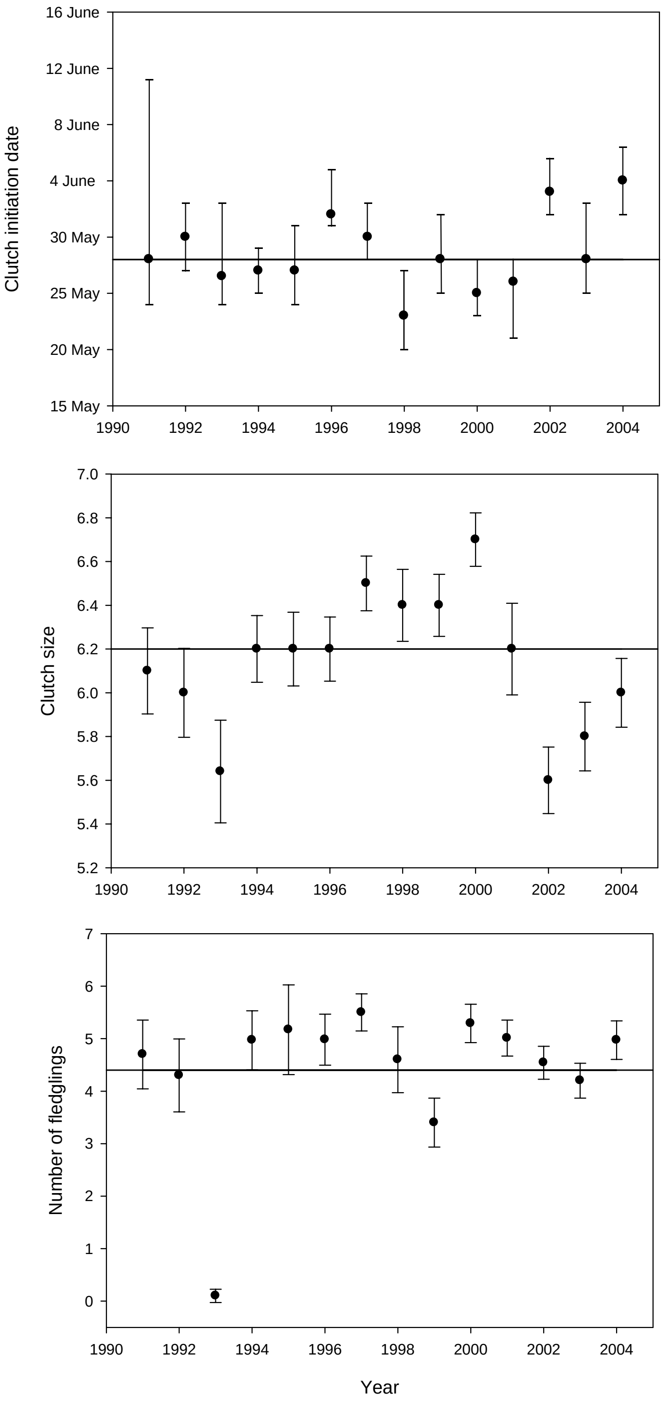

Figure 2.2 Annual median clutch initiation date (top, ± 10th & 90th percentile), mean clutch size (middle, ± 95% CL) and mean number of fledglings (bottom, ± 95% CL) for Tree Swallows (*Tachycineta bicolor*) breeding at St. Denis National Wildlife Area, Canada, 1991 – 2004 (average annual sample size = 93, range = 67 to 113). Horizontal line denotes 14-year median (top) and mean (middle, bottom).

to +9.42 (1999)), predominated by the La Niña phase with the southern U.S. experiencing a warm dry winter/spring, and the Canadian prairies experiencing a cooler winter/spring (NOAA 2005a). The winter NAOI was generally positive during the winter periods of the study (mean = 0.35, range -0.45 (1996) to +1.18 (1999)), characterized by warm wet winters in the southern U.S. (Sheridan 2003, Coulibaly 2006, Thompson and Wallace 2006).

2.3.4. Annual timing of breeding, clutch size and fledging success in relation to environmental variables

Clutch initiation date. Model selection based on AIC_c indicated that the most parsimonious model with respect to median CID included only variation in minimum May temperature (MINMAY; Table 2.1). The parameter estimates for the top model show that median annual clutch initiation date was earlier in years with warmer minimum May temperatures (Figure 2.3). This approximates a seasonal advancement in CID of one day for every one degree increase of the mean minimum temperature during 1-15 May. This model was 3 times better supported than a model that also included wetland water depth (MINMAY, DEPTH; 0.40 / 0.13 = 3.1; Table 2.1). The second two models, including MINMAY, DEPTH and MINMAY, % Adult received some support ($\Delta AIC_c \leq 2.76$; Table 2.1). A rank of importance of each variable is determined by summing the AIC_c weights, indicating that MINMAY was the most important variable followed by DEPTH ($\sum w_i = 0.98$ and 0.26, respectively).

Table 2.1 Summary of models developed to explain annual median clutch initiation date of Tree Swallows (*Tachycineta bicolor*) in relation to effects of the annual MINMAY temperatures, % Adults, pond DEPTH, #WETMAY, spring SOI and winter NAOI (see text for descriptions of variables). Only the four most parsimonious models are shown, as selected using AIC_c model selection. Data from St. Denis National Wildlife Area, Canada, 1991 – 2004.

MODEL	ΔAIC_c[a]	weight[b]	K[c]
MINMAY	0.00	0.40	3
MINMAY, DEPTH	2.19	0.13	4
MINMAY, % Adult	2.76	0.10	4
MINMAY, DEPTH, #WETMAY	3.52	0.07	5

[a] ΔAIC_c = difference in AIC_c between model and one with minimum AIC_c

[b] Normalized Akaike weight (weight of evidence in favour of model i)

[c] Number of parameters estimated in model

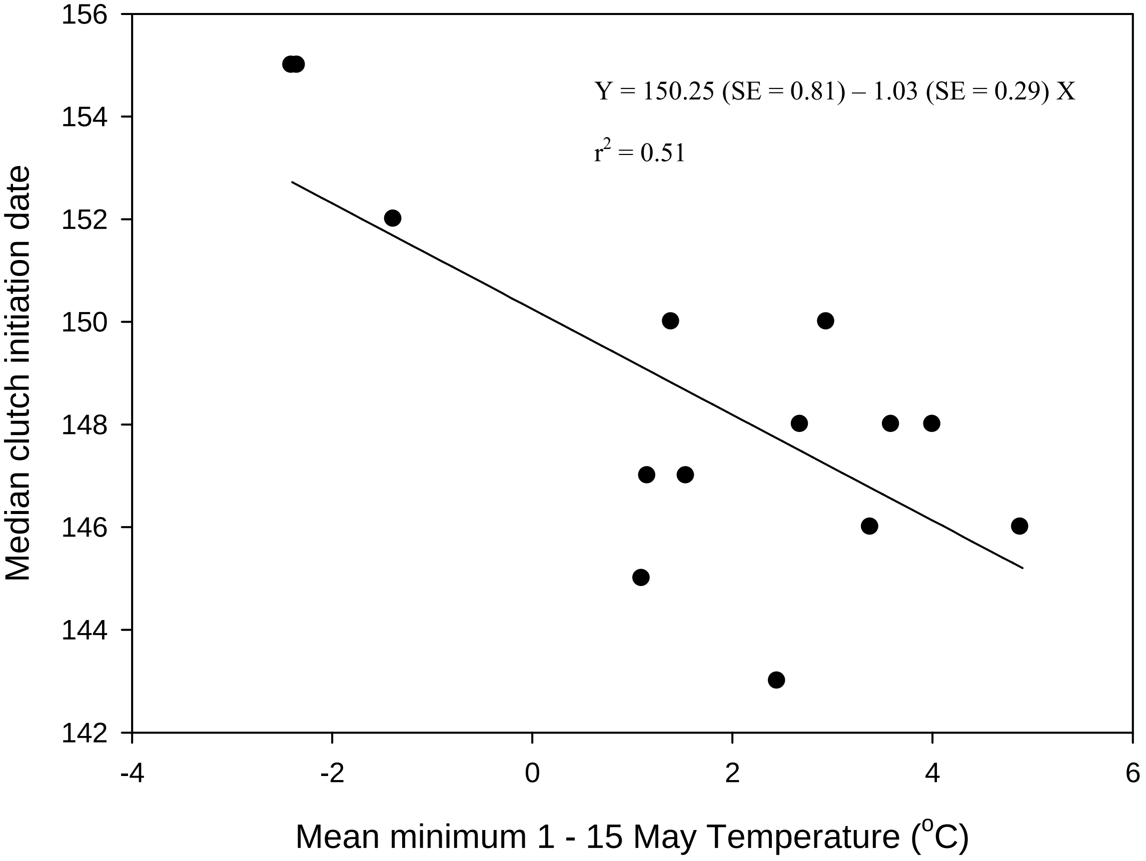

Figure 2.3 Relationship between Tree Swallow (*Tachycineta bicolor*) annual median clutch initiation date and annual MINMAY temperature (mean, °C). See text for description of variables. Data from St. Denis National Wildlife Area, Canada, 1991 – 2004.

Clutch Size. Model selection based on AIC_c indicated that the most parsimonious model with respect to mean CS included only variation in spring DEPTH (Table 2.2). The parameter estimates for the most parsimonious model show a small tendency for larger mean annual clutches to be laid in years with deeper wetland water levels (r^2 = 0.28, mean CS = 5.90 [SE = $\pm$ 0.12] + 0.006 [SE = $\pm$ 0.003] DEPTH). This model accounts for 0.16 of the model weights and was 1.5 times better supported by the data than the model that included spring SOI (0.16 / 0.11 = 1.5) and nearly 2 times better supported than the model that included only median CID (0.16 / 0.09 = 1.8). Three other models received comparable support, including the null model ($\Delta AIC_c < 2$; Table 2.2). Effects of spring SOI and median CID also received support; larger annual mean clutches were laid in years with higher spring SOI values, deeper water levels and earlier median clutch initiation date (r^2 = 0.43, mean CS = 5.95 [SE = $\pm$ 0.12] + 0.014 [SE = $\pm$ 0.009] spring SOI + 0.006 [SE = $\pm$ 0.002] DEPTH; r^2 = 0.22, mean CS = 12.6 [SE = $\pm$ 3.5] - 0.04 [SE = $\pm$ 0.02] CID).

Fledging success. The most parsimonious model for mean FLEDGE is the null model (Table 2.3), suggesting the explanatory variables I considered had little correlation with productivity. However, the model that includes MAXJUNE is well supported by the data ($\Delta AIC_c < 2.0$, Table 2.3). The parameter estimates for this model exhibit a small tendency for increased fledgling survival in years with higher maximum June temperatures (r^2 = 0.14, mean FLEDGE = -0.07 [SE = + 0.57] + 0.04 [SE = + 0.04] MAXJUNE).

Table 2.2 Summary of models developed to explain annual mean clutch size of Tree Swallows (*Tachycineta bicolor*) in relation to effects of the annual MINMAY temperatures, % Adults, pond DEPTH, #WETMAY, spring SOI, winter NAOI and median CID (see text for descriptions of variables). Only the five most parsimonious models are shown, as selected using AIC_c model selection. Data from St. Denis National Wildlife Area, Canada, 1991 – 2004**.**

MODEL	ΔAIC_c[a]	weight[b]	K[c]
DEPTH	0.00	0.16	3
DEPTH, spring SOI	0.85	0.11	4
median CID	1.14	0.09	3
Null	1.31	0.08	2
MINMAY, median CID	1.42	0.08	4
#WETMAY	2.71	0.04	3

[a] Δ AIC_c = difference in AIC_c between model and one with minimum AIC_c

[b] Normalized Akaike weight (weight of evidence in favour of model i)

[c] Number of parameters estimated in model

Table 2.3 Summary of models developed to explain annual mean percent of successfully fledged Tree Swallow (*Tachycineta bicolor*) nestlings to include effects of annual MINJUNE & MAXJUNE temperatures, % Adults, pond DEPTH, #WETJUNE and median CID (see text for descriptions of variables). Only the four most parsimonious models are shown, as selected using AIC_c model selection. Data from St. Denis National Wildlife Area, Canada, 1991 – 2004.

MODEL	ΔAIC_c[a]	weight[b]	K[c]
Intercept only	0.00	0.31	2
MAXJUNE	1.23	0.17	3
median CID	2.73	0.08	3
#WETJUNE	2.82	0.08	3

[a] ΔAIC_c = difference in AIC_c between model and one with minimum AIC_c
[b] Normalized Akaike weight (weight of evidence in favour of model i)
[c] Number of parameters estimated in model

2.3.4. *Timing of breeding in relation to environmental variables, female age and insect abundance*

Environmental variables. The final model (Figure 2.4), which included additional pathways from DEPTH to CID and the removal of a pathway from spring SOI and CIDTEMP, fit the data (CFI = 0.98, NFI = 98, NNFI = 0.93, $\chi^2 = 6.26$, P = 0.01, all standardized residuals < 2.50, n = 1395; $r^2 = 0.09$) when compared to the *a priori* model (Figure 2.1, CFI = 0.96, NFI = 96, NNFI = 0.59, $\chi^2 = 14.95$, P = 0.0001, standardized residuals < 3.86). CIDTEMP, winter NAOI and spring SOI all had strong direct effects on CID (Table 2.4). The direct path of DEPTH on CID was not significant at P = 0.05; a modified model without this pathway had similar model fit (CFI = 0.99, $\chi^2 = 6.39$, df = 2, P = 0.04, all standardized residuals < 2.50) to the final model. I performed a chi-squared difference test between the final model and modified model and found that the removal of this path resulted in no improvement in model fit ($\chi^2 = |6.26 - 6.39| = 0.13$, df = |1 - 2| = 1, P < 0.5).

Overall, winter NAOI had a negative correlation, spring SOI had a positive correlation and CIDTEMP had moderate direct, negative correlation with CID (Table 2.4). This suggest that individuals generally start laying earlier in breeding seasons associated with warmer spring temperatures (higher CIDTEMP and low SOI values) and warmer, wetter wintering area conditions (high NAOI values).

Female age and environmental variables. The final model that included female age showed similar effects to the model with only environmental effect variables

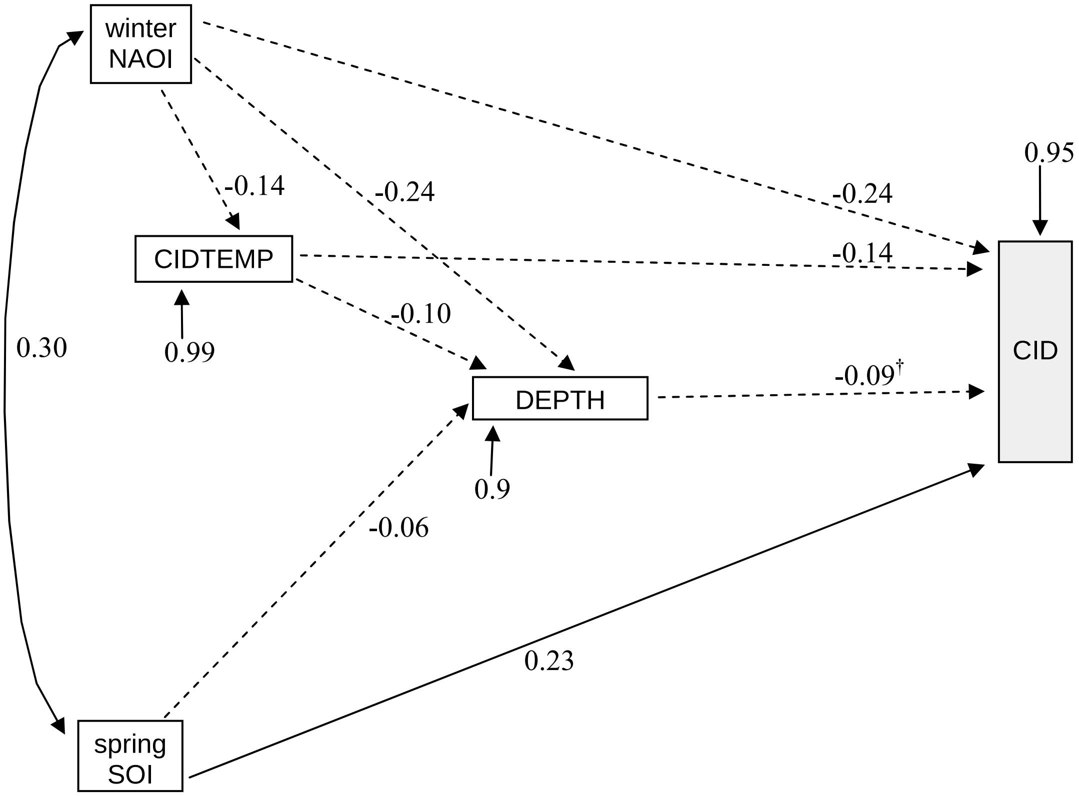

Figure 2.4 Path diagram summarizing relationships of environmental variables (see text for description) on Tree Swallow (*Tachycineta bicolor*) clutch initiation date. Path coefficients (single headed arrows; positive – solid line, negative – dashed line) and a correlation (double-headed curved arrow) are reported. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$. Data from St. Denis National Wildlife Area, Canada, 1991 – 2004.

Table 2.4 Direct, indirect and total effects from path analysis (see Figure 2.4) of environmental variables (see text for description) on clutch initiation date of Tree Swallows (*Tachycineta bicolor*, n = 1395) nesting on St. Denis National Wildlife Area, Canada, 1991 – 2004. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$.

Variable	Direct Effect	Indirect Effect	Total Effect
DEPTH	-0.09†	-	-0.09
CIDTEMP	-0.14	0.01	-0.13
winter NAOI	-0.24	0.03	-0.21
spring SOI	0.23	0.01	0.24

(Figure 2.5). The model fit to the data was significant (CFI = 1.00, NFI = 1.12, NNFI = 0.99, $\chi^2 = 1.18$, df = 3, P = 0.76, all standardized residuals < 0.94, n = 221, $r^2 = 0.14$). The direct path of DEPTH on CID was not significant at P = 0.20; a modified model without this pathway had similar model fit (CFI = 1.00, NFI = 1.12, NNFI = 0.98, $\chi^2 = 1.67$, df = 4, P = 0.80, all standardized residuals < 0.94) to the final model (Figure 2.5). A chi-squared difference test between the final model and modified model found that the removal of this path resulted in a little improvement in model fit ($\chi^2 = |1.18 - 1.67| = 0.49$, df = |3 - 4| = 1, P < 0.50).

AGE had a total negative direct affect on CID (Figure 2.5, Table 2.5), suggesting that older females initiated nests earlier. Similar to the model with only environmental effect variables, clutches were initiated later when breeding areas experienced warmer spring temperatures (high CIDTEMP and low SOI values) and warmer, wetter wintering area conditions (high NAOI values).

Insect abundance and environmental variables. The *a priori* model fit the data (Figure 2.6, CFI = 1.00, NFI = 1.00, NNFI = 0.97, $\chi^2 = 4.17$, P = 0.04, all standardized residuals < 2.03, n = 725; $r^2 = 0.24$). BUG was negatively associated with CID, indicating clutches were initiated earlier when insect abundance was higher (Figure 2.6, Table 2.6). Again females initiated clutches earlier when the breeding area had increased spring temperatures (low SOI values) and experienced warmer wetter wintering area conditions (high NAOI values). Generally, clutches were initiated earlier with increased wetland water levels (Figure 2.6, Table 2.6).

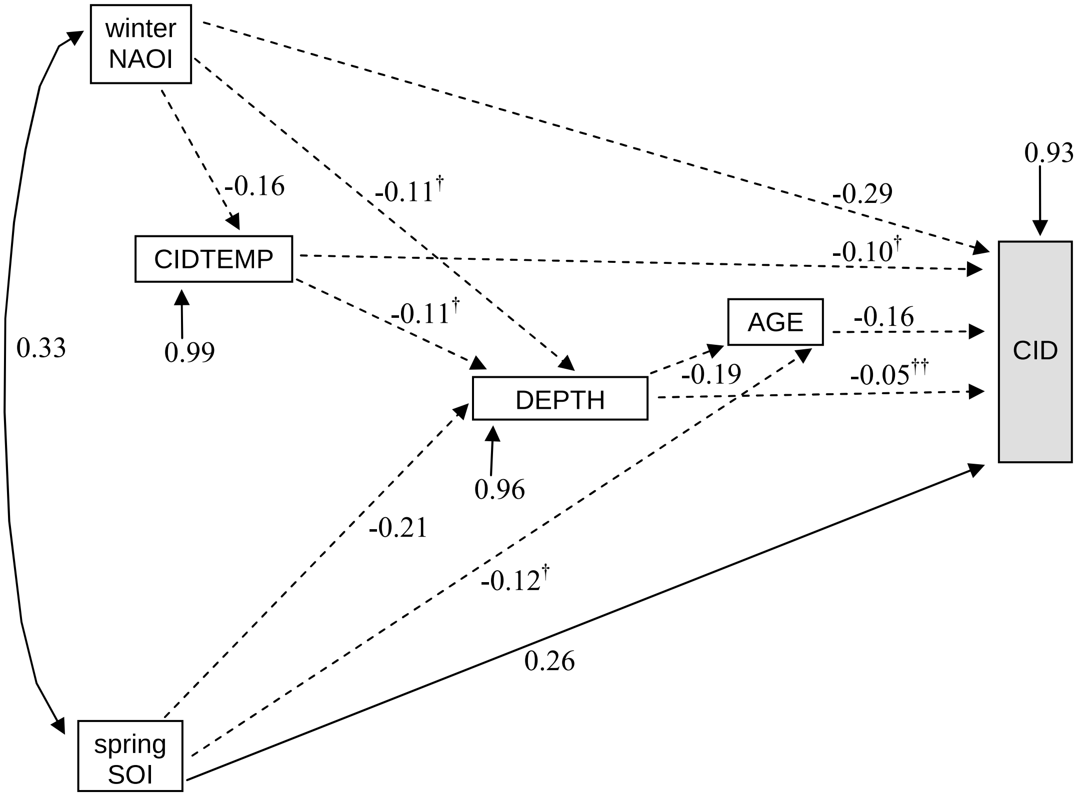

Figure 2.5 Path diagram summarizing associations of female age and environmental variables (see text for description) on Tree Swallow (*Tachycineta bicolor*) clutch initiation date. Path coefficients (single headed arrows, positive – solid line, negative – dashed line) and correlations (double-headed curved arrow) are reported. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$ and †† where $P > 0.20$. Data from St. Denis National Wildlife Area, Canada, 1992 – 2004.

Table 2.5 Direct, indirect and total effects from path analysis (see Figure 2.5) of environmental variables and female age (see text for description) on clutch initiation date of Tree Swallows (*Tachycineta bicolor*) nesting on St. Denis National Wildlife Area, Canada, 1991 – 2004. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$ and †† where $P > 0.20$.

Variable	Direct Effect	Indirect Effect	Total Effect
AGE	-0.16	-	-0.16
DEPTH	$0.05^{\dagger\dagger}$	0.03	0.08
CIDTEMP	$-0.10^{\dagger}$	-0.01	-0.11
winter NAOI	-0.29	0.01	-0.28
spring SOI	0.26	0.002	0.26

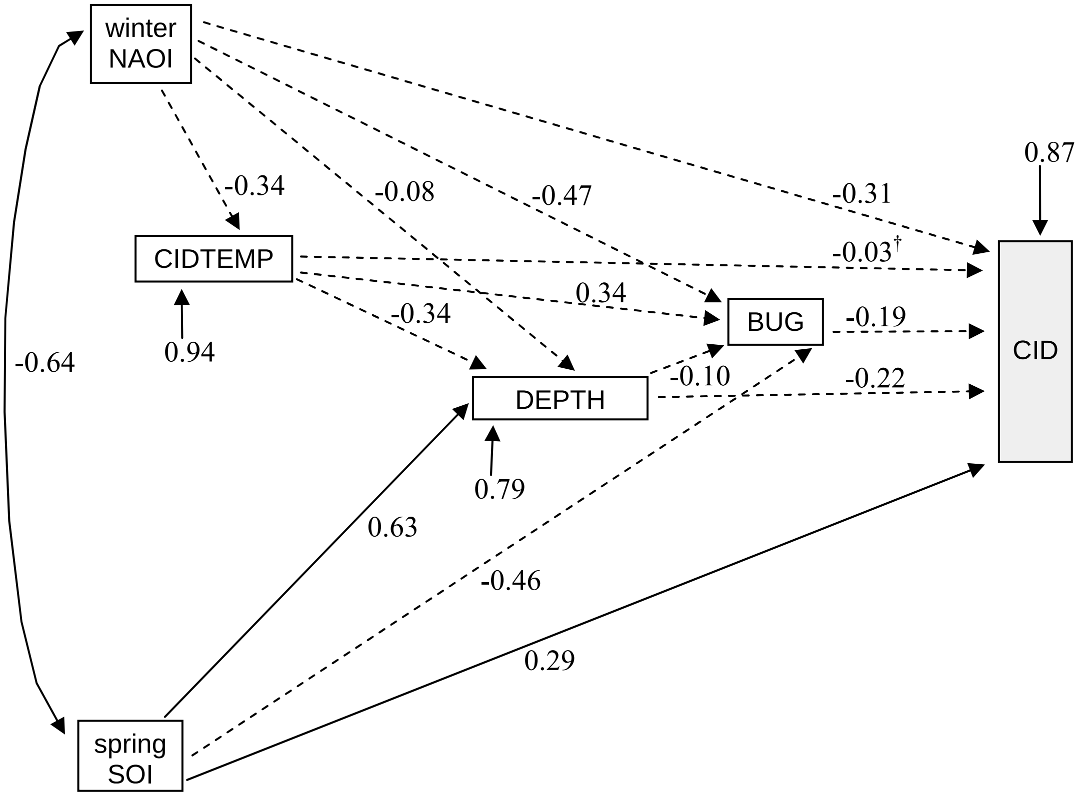

Figure 2. 6 Path diagram summarizing associations of aerial insect abundance and environmental variables (see text for description) on Tree Swallow (*Tachycineta bicolor*) clutch initiation date. Path coefficients (single-headed arrows; positive – solid line, negative – dashed line) and a correlation (double-headed curved arrow) are reported. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$. Data from St. Denis National Wildlife Area, Canada, 1991 - 1996 and 2002 - 2003.

Table 2. 6 Direct, indirect and total effects from path analysis (see Figure 2.6) of environmental variables and insect abundance (BUG; see text for description) on clutch initiation date of Tree Swallows (*Tachycineta bicolor*, n = 613) nesting on St. Denis National Wildlife Area, Canada, 1991 – 1996 and 2002 – 2003. Statistical significance of path coefficients: all $P < 0.05$, except † where $P > 0.05$.

Variable	Direct Effect	Indirect Effect	Total Effect
BUG	-0.19	-	-0.19
DEPTH	-0.22	0.02	-0.20
CIDTEMP	$-0.03^{\dagger}$	0.07	0.04
winter NAOI	-0.31	0.09	-0.22
spring SOI	0.29	-0.13	0.16

Insect abundance was also related to weather variables in the model. Insects were more abundant in years with warmer local temperatures, and shallower pond depth (Figure 2.6, Table 2.6). The effect of CIDTEMP was strengthened by its indirect effect (via DEPTH, indirect effect = 0.03, total effects = 0.37, Figure 2.6). The regional climate indices were also correlated with insect abundance when the area experienced a warm winter/spring (low SOI values) or cold wet winter (low NAOI values) insect biomass was higher (Figure 2.6).

2.4 DISCUSSION

When examining both annual and individual variation in clutch initiation dates, my results suggest that, as anticipated, temperature and moisture were the most influential factors for swallows nesting at the NWA. Increases in temperature and moisture levels, either indicated by wetland water depth or by indices values, resulted in earlier initiation dates. A larger proportion of adults and an increase in insect biomass were also correlated with earlier laying dates. Swallow clutch size and fledging success also appeared to vary with environmental conditions. There was a tendency for larger clutches to be laid in years with deeper wetland water levels and for greater fledging success to occur in years with warmer maximum June temperatures.

2.4.1. Effects of annual spring weather

Clutch initiation date. Much of the annual variation in clutch initiation dates was explained by temperatures in early May, immediately after most swallows had arrived on the study site (Table 2.1). Swallows generally nested earlier in years with warmer early May minimum temperatures, consistent with Dunn and Winkler (1999) and Hussell (2003). A mechanism driving the relationship between early May temperatures and clutch initiation dates could be an increase in insect abundance which also correlates with temperature (Roeder 1953, Visser et al. 1998, Visser and Holleman 2001). Swallows may use sufficient food resources as a cue to commence laying. If true, this lends support to Winkler and Allen's (1996) theory that swallows are income breeders (i.e., base their reproduction on resources acquired just prior to laying, Drent and Daan 1980). If swallows need to feed on the breeding area to acquire sufficient resources for clutch formation then their dependence on food prior to laying would be expected. I could not directly determine if MINMAY influenced insect biomass at NWA, since aerial insect biomass was not monitored long enough before clutch initiation dates. The relationship between temperature and clutch initiation date could also be mediated by effects of temperature on swallow and insect activity; at air temperatures <15 ^{o}C, swallows are observed less often in their nesting colony and aerial insects are less active (Stocek 1986).

Wetland water depth had a weak but positive relationship with median CID; this relationship may also be an indication of food availability. Wetland depth may affect the total number of aquatic insects (Orians 1980) and insect abundance may vary with the previous winter's precipitation (Blancher and Robertson 1987). However, the relationship between water depth and insect abundance was weak. This may be because some of the aerial insects captured in traps lacked an aquatic life stage (e.g., *Homoptera*); Quinney and Ankney (1985) reported up to 39 % of samples from traps and up to 21 % of swallow boluses contained *Homoptera*.

Timing of nesting may also be influenced by factors such as long-term cues, including photoperiod, temperature and endogenous rhythms that stimulate reproduction in birds (Immelman 1971). For example, photoperiod is thought to be partly responsible for the timing of gonad development (Immelman 1971). Predation risk, mate and nest site availability and female experience, age, and condition, may also fine-tune timing of laying (Perins 1970, Morton 1971, Meijer at al. 1990, Geupel and DeSante 1990, Nager and VanNoordwijk 1995, Winkler and Allen 1996, Lloyd 1999, Pap 2002, Hussell 2003).

Clutch Size. Swallow clutch size did not vary greatly over the 14 years, with most females laying six eggs. Swallows generally produced larger clutches in years with deeper water levels (DEPTH), presumably via wetland or precipitation effects on food availability. Again, this result lends support to the theory that swallows are income breeders; swallows laying larger clutches when breeding area food availability is increased. Females were also more likely to lay larger clutches in La Niña years, which are typified by winters and springs that are generally warmer and dryer in the southern U.S. and cooler in the Canadian prairies (NOAA 2005b). This is consistent with previous research on Yellow Warblers (*Dendroica petechia*, another migrant insectivore) which indicated that populations breeding in the Canadian prairies had higher productivity in La Niña years (Mazerolle et al. 2005). This effect may be due to a carry over effect from wintering areas (Blums et al. 1997, Smith and Moore 2003). When swallows experience dryer and warmer winters they may arrive either earlier or in better condition compared to cool, wet winters. However, swallows are thought to be income breeders (Winkler and Allen 1996), so a cross-seasonal or carryover effect from the wintering area may be less influential. Conversely, the relationship between clutch size and SOI may be due to a mismatch occurring in El Niño years. Warmer spring conditions are related to earlier spring insect emergence (Ellis et al. 1997), so when the breeding area experiences increased temperatures swallow breeding activity may be mis-timed in relationship to insect abundance, possible resulting in smaller clutches being laid.

Fledging success. Annual percent of nestlings that successfully fledged from nest boxes varied annually, but none of the variables I considered had a large influence on fledging success (Table 2.3). However, swallow nestlings were more likely to fledge successfully in years with higher maximum temperatures. This result is consistent with Dawson et al.'s (2005b) report that experimentally increased nest box temperatures (approximately 5^{o}C) for nestlings 4 to 16 days old resulted in increased nestling survival. I found weak support for an effect of clutch initiation date, suggesting that early clutches may successfully fledge more young than those laid later in the season; this is consistent with results from other studies on swallows (Winkler and Allen 1991, Stutchbury and Robertson 1998, McCarty and Winkler 1999) and higher recruitment reported among earlier-hatched nestlings (Shutler et al. 2006). Perhaps use of nestling growth rates rather than percent fledge may give more meaningful results, as growth rates may be a better indicator of subsequent survival and reproductive success (Richner 1989, Magrath 1991, Lindén et al. 1992). It is possible that some of the other variables used also affect nestling survival, but the unit of measure used was too large. For example, the minimum temperature variable used was a 20-day mean that included the period when most nests contained young. It is possible that a short cold period may not be evident over this extended period of time; this could have a large impact on fledging success when offspring are not only dependent on their parents for food but are still unable to thermoregulate (nestlings are able to thermoregulate at day 7 or 8; Robinson et al. 1992). For example, in 1993 nestling survival was extremely low due to a cold wet 3-day period (R. G. Clark pers. obs.; Shutler and Clark 2003) but this short-term, extreme event was not evident in the 20-day mean. In contrast, 2004 had the coolest mean temperatures (see results) but normal fledging rates.

2.4.2. Effects of seasonal weather, female age and insect abundance

The path model including insect abundance and environmental variables explained 24% of the variation in CID. The model including age and environmental variables explained 14%, whereas the model including only environmental effects explained only 9% of variation in CID. Clutches were initiated earlier in years with warmer temperatures, increased moisture and insect biomass. Timing of nesting of swallows has also been found to correlate positively with temperature (Dunn and Winkler 1999, Hussell 2003) and precipitation (Nooker et al. 2005).

Environmental variables. Among the environmental variables included in all three models, SOI and NAOI consistently had the strongest direct effects. Timing of breeding in swallows was positively correlated with spring SOI values, suggesting that birds nest earlier in El Niño years. This is consistent with research on reproductive output indices of temperate and neotropical wintering migrants breeding in the U.S. Pacific Northwest (Nott et al. 2002). Nott et al. (2002) suggested that El Niño may positively affect conditions on the wintering grounds and migration routes. However, Sillet et al. (2000) and Mazerolle et al. (2005) reported that La Niña years correlate positively with apparent adult survival and nestling mass in Black-Throated Blue Warblers (*Dendroica caerulescens*) and apparent adult survival and production of juveniles in Yellow Warblers, respectively.

Swallow initiation dates are negatively correlated with winter/spring NAOI values (nesting earlier in years with relatively high values). This contrasts with Weatherhead (2005), who reported that Red-Winged Blackbirds (*Agelaius phoeniceus*) in eastern Ontario started nesting later in years with higher winter NAOI values. However, Weatherhead (2005) found that higher winter NAOI values were associated with cooler spring temperatures in eastern Ontario which is consistent with the weak relationship I found (Figures 2.4, 2.5, 2.6). However, this is contrary to general patterns predicted from meteorological assessments which suggest higher winter NAOI values should correspond to warmer spring temperatures in central Canada (Thompson and Wallace 2001, Sheridan 2003, Coulibaly 2006, Huang et al. 2006). I could not verify the relationship between local precipitation and NAOI values (due to the unavailability of local precipitation data).

Since the influence of NAOI and SOI is not limited to the Canadian prairies, the influence on timing of breeding in swallows may extend to wintering areas and migration routes. For example, swallows generally nested earlier in springs with positive NAOI values which correlates with warm wet conditions in the southeast U.S. (NOAA 2005a, 2005b, Coulibaly 2006). Swallows may be able to take advantage of favourable environmental conditions during migration (weather or food availability) and arrive at breeding areas earlier or in better condition. Females in poor condition are likely to initiate nesting later (Hipfner et al. 1999), lay smaller clutches (Goodburn 1991) and have fewer young fledge (Wendeln and Becker 1999). I was unable to evaluate female pre-laying body condition; female body mass was measured post-hatch and may not be indicative of arrival condition. However, if swallows are income breeders, as suggested by Winkler and Allen (1996), then conditions upon arrival at the breeding area may be more influential on reproductive output (Winkler and Allen 1996, Nooker et al. 2005).

Insect abundance. I found that insect biomass was negatively associated with initiation date; swallows nested earlier in years with higher insect biomass. This is consistent with Hussell and Quinney (1987) and Nooker et al. (2005) who also found aerial insect abundance correlated positively with swallow clutch size. Insect abundance was correlated with both local and regional variables. Insects were generally more abundant in springs with warmer temperatures (positive CIDTEMP, and negative spring SOI values) and cool wet winters (negative winter NAOI values). Surprisingly, wetland water levels had a relatively small influence on insect abundance. Local spring precipitation amounts may explain a larger amount of variation in insect abundance since wetland water levels can be influenced by precipitation and evaporation in previous seasons. NAOI was negatively correlated with insect abundance (Figure 2.6) and CID (Figure 2.6 and Table 2.6), suggesting that when the breeding area experienced cooler wet winters/springs (when NAOI values were low) subsequent spring insect abundance was higher but swallows nested relatively late (NAOI values had a stronger influence on BUG, see Figure 2.6). However, the climatic conditions simplified by the NAOI values are complicated by their predicted and actual relationship reported with temperature (see above and Chapter 4).

Female age. Female age had a negative effect on CID, suggesting earlier breeding by older females as reported by others (De Stevens 1978, Stutchbury and Robertson 1988, Winkler and Allen 1996, Robertson and Rendell 2001). Although female age influenced timing of breeding, female experience (e.g., comparing unbanded females with no previous experience with the NWA to recaptures from the area) may be more informative than age alone (Winkler and Allen 1996, Pyle et al. 1991). AGE correlated negatively with both DEPTH and spring SOI; younger breeding females were encountered more often in years with higher spring SOI values and deeper wetlands. More positive spring SOI values are associated with warmer dryer conditions in the winter areas, possibly increasing survival. Apparent annual survival of Yellow Warblers breeding in southern Manitoba correlated positively with SOI (Mazerolle et al. 2005). The negative relationship between DEPTH and AGE may be related to the previous year's wetland condition, and subsequent insect abundance and likelihood of offspring survival. This is not supported by the results from the reduced model that included BUG, which shows that insect abundance was higher during springs with lower water levels. The reduced AGE data set had some limitations (see methods); therefore these results should be considered cautiously.

2.5 CONCLUSIONS

Local and regional weather conditions had a strong effect on measures of reproductive performance in swallows nesting on the NWA. Annual and individual variation in timing of nesting were influenced by temperature and wetland conditions, and swallow clutch size and fledging success also varied with environmental conditions. Generally, annual CID advanced one day with each approximately one degree increase in mean minimum May temperature. For individual females, warmer local temperatures correlated with earlier clutch initiation dates. Regional climate indices and local temperature data also indicated that warmer conditions correlated with earlier swallow laying dates. Increases in both female age and local insect abundance also correlate with earlier CID. When insect abundance was included with environmental variables, clutches were generally initiated earlier in springs with deeper wetland water levels.

I found both local and regional environmental variables influenced swallow breeding. Higher spring temperatures and more frequent El Niño events are predicted by some climate models (Timmermann et al. 1999); this may result in earlier nesting but smaller clutches for swallows nesting in southern Saskatchewan. Furthermore, because of the unknown effects of continued local and regional climate change on swallow breeding, further study is needed to fully understand the importance of long-term climate variation. Swallows may use cues such as temperature and wetland condition to initiate nesting, given their influence on other factors such as insect abundance. I found correlations between variables, not cause and effect. Unfortunately, experiments manipulating ambient temperature, wetland condition and aerial insect abundance are logistically difficult. The relationships between aerial insect abundance, wetland condition (i.e., number of wetlands, pond depth) and weather variables need to be examined in greater detail, including possible lag effects from previous years. The use of other long-term data sets to explore similar questions would be an important first step in furthering our understanding of the role of climate in breeding success of migratory animals. These results begin to examine the complicated interplay between environmental variables at various scales and swallow breeding.

CHAPTER 3. EFFECTS OF HEATING NEST BOXES ON TIMING OF NESTING, REPRODUCTIVE INVESTMENT AND BREEDING SUCCESS OF TREE SWALLOWS

3.1 INTRODUCTION

There is growing interest in effects of climate change on wild animals and plants. Changes in seasonal patterns of warming and precipitation, and increases in the frequency of intense storms may seriously reduce survival and breeding success of wild plants and animals (see Hughes 2000). Timing of nesting by swallows varies with spring temperatures; females lay later in years with lower spring temperature (Dunn and Winkler 1999, Hussell 2003, Chapter 2). This delay may be due to low ambient temperatures increasing the costs of body maintenance at the expense of egg formation or, because flying arthropod abundance has been shown to be directly (Roeder 1953) and indirectly (Chapter 2) related to air temperature, food may be insufficient to allow body maintenance and egg formation, suggesting an energetic constraint on laying early (Perrins 1970).

Presumably due to the energy savings which acrued,Yom-Tov and Wright (1993) found that artificial night-time heating of nest boxes increased incubation consistency in Great Tits. Similarly Blue Tits had fewer laying interruptions (Bryan and Bryant 1999). Given that energy is likely limited during egg laying, I hypothesized that female swallows exposed to increased over-night nest box temperatures would lay earlier than females using unheated boxes. I also expected that nest-box heating would cause one or more of the following: larger clutch size, heavier eggs (due to energy savings), and lower fledging success (due to decreased food availability during fledgling period; mismatch hypothesis, e.g., Visser et al. 1998, Both et al. 2006). I applied two heating treatments, heat until the appearance of the first egg in the nest and until after the third egg was laid, to determine if heating would reduce laying interruptions. I expected that females nesting in boxes that were heated until after the laying of the third egg (i.e., females provided with energy savings during part of laying) would have the highest laying consistency compared to the other treatments (control, equipment control, and heated to first egg).

3.2 METHODS

3.2.1. Experimental heating

Nest box heating occurred during May 2003, prior to and during swallow laying on the NWA (Figure 1.1). Subsets of the available nest boxes were randomly allocated to 3 treatments: (1) warmed until first egg was laid (hereafter, H1: n = 35), (2) warmed until third egg was laid (hereafter, H3; n = 35) and (3) boxes equipped with the heating materials but not warmed (Equipment control (hereafter, EC), n = 15). Unmanipulated boxes served as controls (hereafter, control, n = 30). Based on average spring temperatures (Environment Canada 2003c), a swallow arrival date of 24 April 2003 and nest building progress, box heating started on 12 May. Due to predation and box use by other species, 30 swallow nests were available in H1, 29 were in H3, 15 were EC, and 27 were controls.

In treatment boxes, a layer of reflective foam insulation was stuck to the box bottom and covered by a heating pack (contained charcoal, iron power, vermiculite, salt, sawdust and moisture, Heat Factor Inc., Vista, CA.) placed between two sheets of 0.64 cm wire mesh. The reflective insulation helped to direct heat upward and the wire mesh allowed air flow, so heating packs could function. Swallows constructed nests directly on top of the wire mesh. In heated boxes (H1 & H3), heating packs were replaced daily during late afternoon to reduce disturbance to swallows, as nest building and egg laying generally occurs in the morning (Robertson et al. 1992). In EC boxes, used heating packs (i.e., packs that did not produce heat) were removed and immediately replaced in the same box to mimic the disturbance to heated boxes.

Temperature loggers (HOBO$_{tm}$ XT Temperature Logger, Onset Corp., Pocasset, MA) were tested to ensure consistent temperature readings (within 0.1 ^{o}C) and then placed nightly in randomly-selected nest boxes from heated (n = 2 /night) and unheated groups (control, n = 2/night; EC, n = 1/night). Loggers recorded temperature every 5 min. One thermister was placed within the nesting material at the same height as the bottom of the nest cup (within 2-3 cm the nest cup), and the second thermister was taped on the back wall, 2-3 cm above the nest cup centre. Temperature loggers were also placed 1.5 m above the ground at two locations in the study area to record ambient air temperature (hereafter, Ta).

Over-night box occupancy by females was recorded in 2002 and 2003. On one night during the nest building period (i.e., the experimental period in 2003), 53 (2002) and 23 (2003) randomly selected active boxes (evidence of nest building noted during previous afternoon's nest visit) were checked for female swallows.

3.2.2. Swallow reproductive investment and breeding success

Nest boxes were set up and heating equipment was installed in late April - early May, prior to the arrival of swallows. Nest boxes were checked every 2-3 days for activity. When nesting material appeared in approximately 10% of available nest boxes, all nest boxes were checked daily to determine laying dates. Swallows usually lay one egg per day early in the morning (Robertson et al. 1992), so clutch initiation dates were assigned to the day when the first egg was found. Laying dates were recorded for each egg, and eggs were weighed within 24 hrs of laying to determine fresh egg mass (nearest 0.01 g, using a Mettler PE 400 balance). Nests were checked daily until clutches were complete (no new eggs for 3 consecutive days). Laying rate was calculated for boxes that initiated during the heating experiment by dividing the total number of eggs by total number of days laying per female (see Wiebe and Martin 1995).

To reduce disturbance, nests were not visited during early and mid incubation. Nest visits recommenced just prior to hatch, 12 days after the last egg was laid (incubation period ranges 11 to 19 days at study area, 14 – year mean of 14.0 days ± 1.5 days, n = 1024). Since eggs usually hatch within 1 to 2 hr from when evidence of hatch is first present (i.e., eggs pipping; Robertson et al. 1992) nests were visited twice a day to determine hatch duration (within 15 hours).

Adults were captured in boxes shortly after hatching was complete (see Stutchbury and Robertson 1986). Unmarked adults were banded (using standard USFWS aluminium bands), sexed by the presence of a brood patch (female) or cloacal protuberance (male), and wing cord (nearest 0.1 cm, using a wing ruler), tarsus (nearest

0.01 mm, using dial calipers) and mass (nearest 1 g, using 100 g Pesola spring scale) were recorded.

Disturbing nestlings near the time of fledging (ranges from 15 to 22 days after hatch) can result in premature departure (Robertson et al. 1992), so banding and measuring (same as adults) occurred when the oldest nestling in each brood was 12 days old. Nest boxes were checked 20 days after hatch to determine how many nestlings had successfully fledged if no evidence of predation was present (e.g., disturbed nest material, blood, feathers, or dead nestlings). When no nestlings were present on day 20, it was assumed they had fledged; when nestlings were present, nests were checked every 3 days until fate was determined.

3.3.1. Statistical analysis

I tested for effects of nest box heating on clutch initiation date, laying rate, clutch size, total clutch mass, total brood mass (when the oldest nestling was 12 days old) as well as number of young fledged. Variation in clutch initiation date and clutch size due to treatment was analyzed using a G-test (PROC FREQ, SAS Institute Inc. 2001). I tested for effects of treatment on laying rate, total clutch mass and number of young fledged, accounting for possible effects of clutch initiation date and clutch size (laying rate only); Analysis of Variance (ANOVA) included interactions between treatment and clutch initiation date, and clutch initiation date and clutch size (Zar 1984, PROC GLM, SAS Institute Inc. 2001). I also evaluated differences in laying rate, clutch mass, total brood mass and number of young fledged between treatments using Multivariate Analysis of Variance (MANOVA; PROC GLM, SAS Institute Inc. 2001).

Analysis was restricted to those nests that were initiated during the heating experiment (i.e., did not include any clutches that were initiated after 29 May). Means and standard errors (±1 SE) are presented throughout unless indicated otherwise.

3.3 RESULTS

3.3.1. Experimental heating

Experimental heating began on 12 May; boxes were heated for 12 - 19 nights before laying started. During the heating period, swallows initiated 24 clutches in H1, 23 in H3, 9 in EC and 21 in control boxes.

Mean nightly (2200 - 0700) temperature recordings from the box side and nest bottom were significantly correlated in control (r^2 = 0.78, P = 0.003, n = 10) and EC (r^2 = 0.92, P < 0.001, n = 11) boxes. In heated boxes, mean nightly temperatures varied more between the two thermister locations (r^2 = 0.41, P = 0.41, n = 6); overall, nest bottoms (13.3 ± 7.1 SD °C, n = 11) were slightly warmer than sides (12.5 ± 4.6 SD °C, n = 6) but thermister location was not a significant predictor (F = 0.07, P = 0.80, n = 18). Since females often removed side thermisters from their original location during the night, I only used nest bottom temperatures in subsequent analysis.

Nest box temperature deviation from average nightly (2200 – 0700) Ta (average 5-minute temperature from two locations within study site) was calculated by subtracting mean Ta from mean nest box temperature (average 5-minute temperature by treatment). Heated nest box temperatures ranged from 5.3 to 20.4° C, control from 3.3 to 16.3 °C, and EC from 2.0 to 13.6 °C above ambient air temperature. Mean nightly nest temperature was significantly higher than ambient temperature in heated nests (6.1 ± 0.8 °C) when compared to control (1.7 ± 0.5 °C) and EC (0.5 ± 0.3 °C, Tukey's test, $P = 0.05$, see Figure 3.1 for an example).

3.3.2. Nest box occupancy

Approximately half of the nest boxes were occupied by a female over-night during the pre-laying period in 2002 (42%, 22/53, non-treatment year) and 2003 (48%, 11/23, heating experiment year). In 2002, 72.7% (16/22) of females were recaptured post-hatch in the same box, 22.7% (5/22) were recaptured in a different box, and 4.5% (1/22) were not recaptured later in the season. Similar results were found for 2003; 63.6% (7/11) were recaptured in the same box, 18.2% (2/11) were recaptured in a different box, and 18.2% (2/11) were not recaptured. Raw recapture rate was not related by year (Fisher's exact, $P = 0.69$).

In 2003, probability of recapture was weakly related to treatment group (Fisher's exact, $P = 0.06$); two of 11 females initially in heated boxes were recaptured in a different box, and two others were not recaptured later in the season. Pre-laying occupancy of boxes in 2003 did not differ between the four treatments (Fisher's exact, $P = 0.68$).

3.3.3. Clutch initiation date

A total of 101 boxes were available to swallows during the experiment; 82 females initiated nests during the heating experiment in all four groups. Five clutches were excluded from analysis due to eggs lost to predators (3/5), abandonment (1/5), or evidence of two or more females laying in the same box (1/5, see Quinny 1983). Of these five clutches, 3 were in heated boxes and two were in control. Since heating

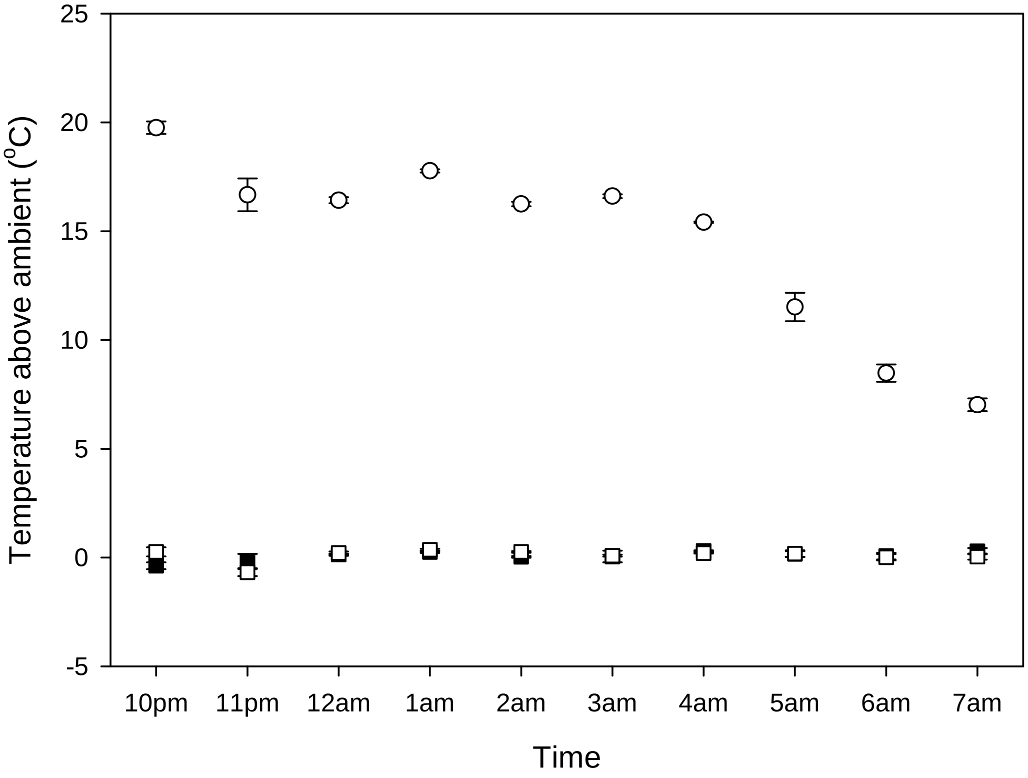

Figure 3.1 An example of mean hourly night temperatures (^{o}C ± SE; recorded in boxes during 16 – 17 May 2003) for experimentally heated (open circle, n = 2 boxes), equipment control (open square, n = 1 box), and control (closed square, n = 2 boxes) Tree Swallow (*Tachycineta bicolor*) nests on the St. Denis National Wildlife Area, Canada.

treatment (H1 & H3) did not differ prior to laying, heated nest boxes were combined for clutch initiation date analysis.

Of the available boxes (n=101), slightly more clutches were initiated in heated boxes (79.7 %, 47/59) than unheated (control and EC; 71.4%, 30/42), but this was not significant (Chi-square, $\chi^2 = 0.92$, P = 0.33, n = 101). There was no significant difference between number of nests initiated in control (77.8 %, 21/27), H1 (82.8 %, 24 /29), H3 (76.7 %, 23/29) and EC boxes (60.0 %, 9/15; Chi-square, $\chi^2 = 2.90$, P = 0.41, n = 101). Mean clutch initiation date for both heated (n = 47) and EC (n = 9) boxes was 27 May (range 23 to 29 May, 25 to 29 May, respectively). Control boxes (n = 21) had nests initiated on average one day earlier (26 May, range 24 to 29 May). Clutch initiation date was not advanced by nest box heating ($F_{2, 74} = 1.45$, P = 0.24) and initiation dates did not differ among the treatments (Tukey's, P > 0.05). Nest initiation for all treatments spanned a 6 day period; therefore, differences in variance of clutch initiation date were not evaluated.

3.3.4. Laying interruptions and rate

Ten laying interruptions occurred in nests that were initiated during the heating period (i.e., clutch was initiated before heating stopped). Duration of laying interruptions was one (n = 7) or two days (n = 3). One female had two, one-day laying interruptions. Half of the laying interruptions occurred on the night of 28 May (5/10), and all occurred between 27 and 31 May. Laying interruptions occurred in 12.5 % (3/24) of H1, 13.0 % (3/23) of H3, 11.1 % (1/9) of EC and 14.3 % (3/21) of control boxes. Of heated boxes, 85.7 % (6/7) of interruptions occurred after heating had finished (e.g., in H3 interruptions occurred after egg 3 was laid). The interruptions that occurred during nest box heating lasted for two nights (29 – 30 May). Laying rate was not associated with treatment ($F_{13, 52} = 0.16$, $P = 0.92$), after controlling for clutch initiation date and clutch size.

3.3.4. *Clutch size and egg mass*

Clutch size varied from 3 to 8 eggs. Due to small sample size, clutches of 3 and 4, and 7 and 8 were pooled for analysis. Average clutch size for each of the four treatments was 6, and was not affected by treatment group (G-test, $G_1 = 6.30$, $P = 0.71$, df = 9, Table 3.1). Fresh egg mass ranged from 1.18 to 2.30 g (n = 445). Accounting for variation in clutch initiation date, total clutch mass did not vary with treatment ($F_{4, 62} = 0.16$, $P = 0.92$, Figure 3.2). In heated nests, duration of box heating (12 to 16 days in H1, 13 to 19 days in H3), had no effect on total clutch mass ($F_{3, 38} = 1.13$, $P = 0.30$).

3.3.5. *Nestling mass and fledging success*

Hatching was asynchronous in boxes with all four treatments. Mean hatching time for control (n = 14) and EC (n = 7) was equal (1.3 ± 0.2 days). Nests heated until after the 3rd egg was laid took slightly longer to hatch; mean hatch time for H1 nests was 1.3 days ($\pm$ 0.2, n = 18 clutches) and for H3 nests was 1.7 days ($\pm$ 0.2, n = 18 clutches), but hatching duration was not associated with treatment ($F_{3, 53} = 1.28$, $P = 0.29$). I found a positive relationship between fresh egg mass and nestling mass at hatch in unheated (linear regression, $r^2 = 0.85$, $P = 0.03$, n = 5), and heated ($r^2 = 0.65$, $P = 0.001$, n = 13) nests. Total clutch nestling mass when oldest nestling in box was 12 days when nestling age varied from 10 to

Table 3.1 Average Tree Swallow (*Tachycineta bicolor*) clutch size in heated to first egg, heated to third egg, equipment control, and control nest boxes on the St. Denis National Wildlife Area, Canada, 2003.

		Clutch Size		
Treatment	n	Mean (mode)	Standard Error	Range
Heat to 1st egg	24	6.0 (6.0)	0.2	3 - 8
Heat to 3rd egg	23	6.0 (6.0)	0.1	4 - 7
Equipment Control	9	6.0 (6.0)	0.3	3 - 8
Control	21	6.0 (6.0)	0.2	5 - 7

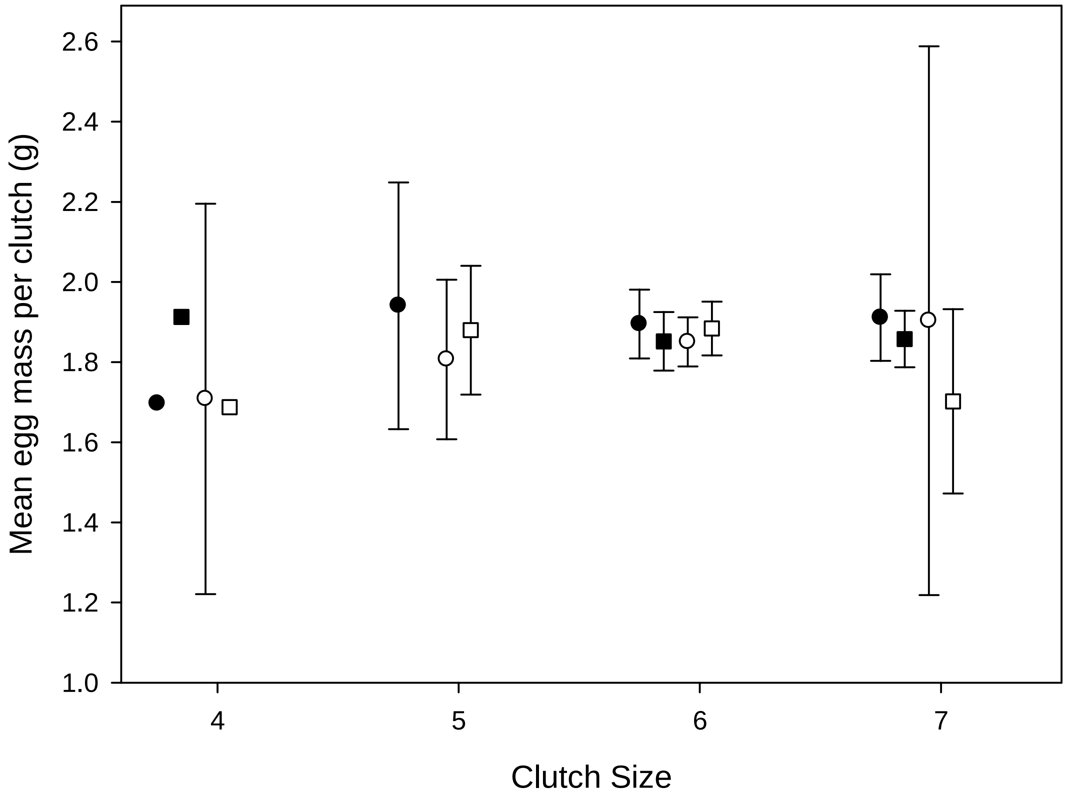

Figure 3.2 Mean fresh egg mass (± 95% confidence intervals) in Tree Swallow (*Tachycineta bicolor*) clutches of various sizes by treatment; control (closed circle), equipment control (closed square), heated to first egg (open circle), and heated to third egg (open square). Clutches laid on the St. Denis National Wildlife Area, Canada, 2003.

12 days old at time of banding) in successful boxes was 114.1 g (± 5, n = 16) for control, 114.5 g (± 7.3, n = 18) for H1 boxes, 111.7 g (± 5.6, n = 19) for H3 boxes, and 114.3 g (± 4, n = 5) for EC. Total brood mass in each successful box was not significantly related to treatment, regardless of clutch initiation date and clutch size ($F_{5, 52} = 0.15$, $P = 0.93$). Duration of nest heating, accounting for clutch initiation date, did not affect total clutch nestling mass at banding in heated boxes ($F_{3, 37} = 0.35$, $P = 0.56$). Fledging success (number of nestlings fledged/number of eggs laid per box) was not related to treatment, controlling for clutch initiation date and clutch size ($F_{13, 52} = 0.29$, $P = 0.83$). Mean fledging success for heated nest boxes was 0.74 ± 0.07 fledglings (H1) and 0.79 ± 0.06 fledglings (H3), and for unheated was 0.75 ± 0.09 fledglings (control) and 0.71 ± 0.11 fledglings (EC).

Similarly, results from the MANOVA analysis show that females nesting in warmed nests (H1 and H3 boxes) had the same laying rate (fewer laying interruptions), the same total clutch mass, total brood mass, and fledging success compared to females who nested in either control or EC boxes (MANOVA, Wilks' Lambda = 0.91, $P = 0.94$).

3.4 DISCUSSION

Warming boxes during the pre-laying period created a more consistent and warmer nest environment. I predicted females would redirect energy saved by staying over-night in heated boxes to advance laying date, increase clutch size, egg mass or take fewer laying interruptions. However, nest box heating did not advance laying date of swallows, had no observable effect on clutch size (Table 3.1) or mean fresh egg mass (Figure 3.2). Laying rates for females exposed to the four different treatments did not differ.

Swallows nested successfully in all four treatment boxes, with more nests initiated in control, H1 and H3 when compared to EC nests. This difference was not significant but may suggest a possible disturbance effect in these boxes that could have been mediated in the other treatment boxes by heating. A larger sample of EC nest would be needed to more fully examine this.

Nests heated until the laying of the 3rd egg took only slightly longer to hatch (i.e., were more asynchronous). Egg(s) in heated boxes were exposed to increased over-night temperatures prior to the onset of incubation which usually begins on the day the penultimate egg is laid (Robertson et al. 1992). This increased over-night temperature could cause egg development to begin prior to female incubation or it may have caused some females to begin incubation earlier. Ardia et al. (2006) found that females were more likely to begin incubating prior to clutch completion when temperatures were >26 °C and that clutches experiencing early incubation coupled with warmer temperatures were more likely to hatch asynchronously (+ 24 hours). Temperatures recorded in heated nests did exceed 26 °C during the experiment; however, since temperature was not recorded in each box on each night during the experiment, I could not determine if this was a factor.

During the study period, 8.2% (10/82) of breeding females had a laying interruption. Laying rate is not reported in many studies, however, swallows have been reported to interrupt laying up to 7 days (without egg viability loss; see Robertson et al. 1992). The laying rate of swallows' I recorded is lower than that of Blue Tits (20 – 40 %;

Nilsson and Svensson 1993, Yom-Tov and Wright 1993) and White-Tailed Ptarmigan (*Lagopus leucurus*), but similar to that found for Willow Ptarmigan (*L. lagopus;* Wiebe and Martin 1995). Half of all interruptions occurred on the same night (28 May), potentially meaning an effect of weather rather than individual females. Laying interruptions in Blue Tits correlated with low nightime temperature five days before the laying interruption occurred; however, when minimum temperature at night was warmer than 6 ^{o}C no interruptions occurred (Yom-Tov and Wright 1993). Wiebe and Martin (1995) found cooler temperatures and snowfall was a factor in decreased laying rates of white-tailed and willow Ptarmigan. Nilsson and Svensson (1999) found that female Blue Tits had fewer laying interruptions when they were supplied experimentally with extra food.

Heating of nest boxes used by swallows and other species modifies some breeding variables (Yom-Tov and Wright 1993, Bryan and Bryant 1999, Dawson et al. 2005b). Heating nest boxes increased the laying rate of Blue Tits (heated during the laying period, Yom-Tov and Wright 1993), the incubation consistency of Great Tits (heated during incubation period, Bryan and Bryant 1999) and the survival of swallow nestlings (heated during the nestling period, Dawson et al. 2005b). Heating was not conducted during the incubation or nestling period in this study. Yom-Tov and Wright (1993) found Blue Tits nesting in boxes heated during the laying period had fewer laying interruptions. The different responses of tits compared to the swallows may be due to different life history strategies. Blue Tits, like swallows, are cavity nesters with females building the nest, both sexes feed young, and rarely having two broods per season (Harrap and Quinn 1995, Snow and Perrins 1998). However, Blue Tits are non-migratory where these studies were conducted, have a more varied diet which includes insects but also spiders, seeds, nectar, and nuts and the males feed the females during laying and incubation (Harrap and Quinn 1995, Snow and Perrins 1998). These differences may allow tits to react to energy saving events.

Bryan and Bryant (1999) estimated that heating nest boxes over-night by an average of 6^{o} C saved female Blue Tits the equivalent of 35% of an egg in energetic terms. When compared to similar-sized birds that either are ground-foraging insectivores, picivores, or flycatchers, aerial foragers (hirundines) use 16 to 38% more energy during the nestling period (Williams 1988), and swallows have a higher field metabolic rate than Savannah Sparrows (*Passerculus sandwichensis*), a ground forager, even when sparrows were feeding one more nestling (Williams 1987, Williams 1988). If these results are indicative of energy use of pre-nesting and laying females, then swallows may have used any saved energy from the heated nest boxes to increase foraging time.

There is evidence that increasing spring temperatures may create a mismatch in timing of egg laying relative to food availability for nestlings, resulting in later-laying females producing fewer fledglings due to low food quality and quantity during the early stages of nestling growth (i.e., in the first 2 weeks post-hatching; Visser et al. 1998, Both et al. 2006). In order to test how a timing mismatch between nestling-rearing and food supply would affect swallow nestlings, the reproductive success of females with advanced laying dates would be compared to those in control boxes, accounting for variation in aerial insect abundance. The mismatch hypothesis predicts that nestling growth and survival will be poorer in experimentally advanced nests relative to controls during near normal and cooler spring weather (Visser et al. 1998). I was unable to test predictions of the mismatch hypothesis and examine the effects of advancement of laying on female productivity as there was no difference in timing of breeding between treatments.

There are several explanations for why the timing of breeding and breeding performance of female swallows did not differ from those using control boxes. Explanations may include insufficient heating in experimental boxes, low over-night nest box occupancy, use of other cues to determine when to initiate, use of 'saved' energy on variables not measured such as nest defence, or increased foraging.

The nest box heating systems warmed boxes over-night with mean over-night nest box temperatures of 6.1 ^{o}C ($\pm$ 0.8) above Ta. This amount of warming above Ta is similar to other studies (6 ^{o}C, Yom-Tov and Wright 1993; 6.15 + 0.92 ^{o}C, Bryan and Bryant 1999; 5.1 $\pm$ 0.81 ^{o}C laboratory control conditions, Dawson et al. 2005b). These studies reported increases in laying rate (Yom-Tov and Wright 1993), incubation consistency (Bryan and Bryant 1999) and enhanced survival, larger nestlings (Dawson et al. 2005b). Assuming that nest bottom temperature recordings are a reasonable index of box air temperature, then the heating equipment not only heated nest bottoms, but also increased the air temperature within heated boxes. The heating system performance was variable as in the other studies (Yom-Tov and Wright 1993, Bryan and Bryant 1999, Dawson et al. 2005b). Given the similar temperatures and consistency, it is reasonable to assume that the nest boxes in this study were heated sufficiently. However, swallows experience a wide variety of weather conditions during the pre-laying and laying period (Hussell 2003, Winkler et al. 2002, Chapter 2) and a increase of 6 ^{o}C over-night may be insufficient to alter investment in the clutch. Swallows nesting at Long Point Bird

Observatory, Ontario, Canada, experience pre-laying temperatures which vary by up to 10 ^{o}C between four sites and 1969 - 2001 median clutch initiation date was best predicted by maximum daily temperature (Hussell 2003), not over-night lows.

Female over-night nest attendance may have also reduced their exposure to increased roosting temperatures. Over-night nest box occupancy did not differ between years (2002 and 2003) or between the four treatments (2003), suggesting that swallows were not choosing to roost in heated or unheated boxes. Since over-night nest occupancy checks occurred only once, it is unknown for how much time and how many nights females spent in boxes during the over-night period. Therefore, I could not determine with certainty if females were exposed to sufficient heating to allow them to advance their clutch initiation, since it is unknown how many nights prior to laying each female spent in heated boxes, the nest temperature they experienced and the length of time spent in a box each night. Yom-Tov and Wright (1999) did not report nest attendance rates for laying Blue Tits in heated boxes; however Great Tits incubating in heated nest boxes increased their incubation period by an average of 55 minutes a day compared to unheated control incubating females (Bryan and Byrant 1999). Recent results show that pre-nesting female swallows may roost at great distances from their nest box (Dunn and Whittingham 2005, Stapleton and Robertson 2006). Dunn and Whittingham (2005) found that six radio-marked pre-laying female swallows roosted > 2 km away from their nest box. Similarly, Stapleton and Robertson (2006) found that four radio-marked pre-laying females roosted at locations that ranged from 0 m to > 2300 m from nest boxes. Both studies reported a large amount of individual variation. Females did roost in their nest box (Stapleton and Robertson 2006) and if they roosted away from their nest box, they often returned to them early in the morning (Dunn and Whittingham 2005). However, duration of time spent in their box during the morning was not reported (Dunn and Whittingham 2005). The results from both studies suggest that females roost at locations other than their nest box during the pre-laying period; this is consistent with the observation that swallows in my study did not always spend nights in the boxes and may explain the lack of an effect of over-night heating during the pre-laying period.

Winkler et al. (2002) suggested that changes in temperature affect later laying females, allowing them to lay earlier with increased clutch size but that early laying females do not change laying date or clutch size (shown by a decreased variation in warm years). Therefore, it is possible that the early nesting females in heated boxes could not advance their initiation date. This may be due to the use of photoperiod as a dominant cue (Rowan 1962), with other cues being used to 'fine tune' the timing of egg laying (Wingfield 1980).

In theory, female swallows should not be sensitive to the type of energy supplied or removed (e.g., changes in temperature or food supply), but should respond to the overall amount. If swallows did experience energy saving in heated nest boxes they may have used this energy on variables not measured, such as foraging activity, nest defence, and / or other body maintenance activities.

3.5 CONCLUSIONS

The inability of heating to advance laying date may be due to insufficient heating of boxes or low over-night nest box use by pre-laying females. Swallows may also be responding to other constraints or cues (such as food availability) to determine when to initiate laying (Hussell 2003, Nooker et al. 2005). If timing of nesting coincides with optimum conditions for raising nestlings, as Lack (1964) suggested, then swallows could be using environmental cues to optimize their reproductive output. However, swallows experience variation in environmental conditions between years and may depend on short term cues, such as temperature and food availability just prior to breeding, to determine when to lay (Nooker et al. 2005; see also Chapter 2: Discussion). Hussell (2003) found that swallow clutch initiation date correlated with prelaying temperature, but noted that temperature may only be a proximate cause of this relationship.

CHAPTER 4:SYNTHESIS AND RECOMENDATIONS

4.1 CLIMATE VARIABILITY, TIMING OF NESTING AND BRESSDING SUCCESS

Migratory birds may be sensitive to differences in local and regional climate as breeding and wintering areas may experience different climatic conditions. Some species may be incapable of alter timing of migration or laying dates and experience a mismatch between timing of nesting and peak insect availability for their nestlings. I investigated the influence of local conditions and regional climate indices on breeding performance of an insectivorous migrant songbird and tried to examine effects of a mismatch between the timing of breeding and food availability.

I found that annual variation in median clutch initiation date was best described by temperatures during the pre-laying period (early May). Larger clutches were laid in years with higher pond water levels (possibly an indication of increased insect availability) and under La Niña conditions. Fledging success tended to increase in years with higher temperatures during the fledging period (mid June); however, it was not substantially influenced by any explanatory variable. Individual variation in clutch initiation date was correlated with both local environmental variables and regional climate indices. Earlier nesting generally occurred in years when the breeding area experienced warmer early spring temperatures (warmer local May temperatures and more negative SOI values) and increased moisture (increased wetland water depth). Later initiation dates in years with negative NAOI values may be due to the cool dry conditions in the wintering areas, which may result in delayed timing of migration. If this occurs, then birds may arrive at breeding areas relatively late, and even with favourable conditions they may be unable to initiate clutches early relative to other years. Also, clutches were initiated earlier by older females and during springs with greater aerial insect abundance.

I compared timing of nesting, laying sequence, clutch size, egg mass and fledging success of birds that experienced experimentally heated boxes in the pre-laying period to those females in unheated control boxes. However, nest box heating failed to advance laying dates; therefore I was could not directly examine the predictions of the mismatch hypothesis. Although box heating increased nest temperatures an average of 6.1 ^{o}C (+ 0.8 SE) over controls, no increases in clutch size, egg mass or fledging success were detected between treatment and control nests. Females may not have spent sufficient time in experimentally heated boxes to alleviate energetic constraints of egg production. Alternatively, energy savings associated with box use may have been insufficient to overcome the influence of environmental conditions that influence energy expenditure and food availability for breeding swallows. My results suggest that both local and regional climate variation affect swallow clutch initiation dates, likely via effects on food supply.

4.2 IMPLICATIONS

It is clear that the effects of variable weather on the reproductive timing and performance of swallows cannot be easily explained. However, the fact that timing of clutch initiation correlates with changing local and regional weather suggests that climate warming may lead to earlier nesting of swallows and higher fledging success (Winkler and Allen 1991, Stutchbury and Robertson 1998, McCarty and Winkler 1999). As discussed in Chapter 3, swallows may be unable to shift their laying date due to limited phenotypic plasticity, especially if arrival on the breeding area is constrained by migration schedules and clutch initiation date is partly controlled by cues unchanged by varying climate (e.g., photoperiod) and/or has a genetic basis. If increasing spring temperatures lead to advances in aerial insect peak abundance, swallows, like some other species, may be unable to shift migration and breeding schedules and that find rapid climate change leads to population declines (Visser et al. 1998, Both et al. 2006).

Timing of nesting is an important variable in the context of avian reproductive success; breeding late in the season may incur high costs in terms of lower reproductive output, and decreased amount of time to accumulate energy reserves for molt and migration (DeSteven 1980), while early initiation typically increases annual fecundity (Bollmann et al. 1997). There is a relationship between climate variation and breeding parameters in other migratory aerial insectivores (Nott et al. 2002, Sillett et al. 2002, Mazerolle et al. 2005, Weatherhead 2005). Generally, local increases in temperature are correlated with advances in clutch initiation dates (Brown et al. 1999, Crick and Sparks 1999, Dunn and Winkler 1999, Hussell 2003), egg mass (Lessells et al. 2002), clutch size (Creswell and McCleery 2003), nestling growth rates (McCarty and Winkler 1999, McCarty 2001), and nestling survival (Tyler and Green 2004, Bolger et al. 2005). However, the relationship with regional climate indices is not so straight forward. One current climate model predicts that there will be increases in the El Niño phase of the

Southern Oscillation (Timmermann et al. 1999). If this is correct, then swallows may benefit with earlier clutch initiation dates but with reduced clutch sizes. The El Niño phase is positively correlated with improvements in breeding success in some species (Nott et al. 2002) but not in others (Sillett et al. 2000, Mazerolle et al. 2005); this may be due to different life history traits of the species or different climate variables may influence species differently. This could potentially create a trade-off between reproductive success and survival. For example, in swallows, an increased frequency of El Niño could result in earlier laying, leading to a greater number of successfully fledged young (Winkler and Allen 1991, Stutchbury and Robertson 1998, McCarty and Winkler 1999) which could in turn have higher recruitment (Shutler et al. 2006). However, these adults and nestlings could have decreased survival rates in the winter due to the wet cold conditions in the southern U.S. (i.e., winter El Niño conditions).

Climate indices have been linked to changes in stream flow (Coulibaly and Burn 2005) and ice break-up dates (Bonsal et al. 2006). Increases in clutch size and fledging success are negatively correlated with the timing of sea ice break-up in Common Eiders (*Somateria mollissima*, Lehikoinen et al. 2006) but has detrimental effects on available food resources for fulmars and puffins (Thompson and Ollason 2001, Gjerdrun et al. 2003). Changes in climate variables will influence many different taxa from advancing plant growing seasons and flowering dates to earlier hibernation termination dates and altered sex-ratios in mammals (see McCarty 2001 for review). Martin and Wiebe (2004) found delayed snow melt related to later laid clutches in alpine ptarmigan. This variation in influence complicates scientists' abilities to make long-term predictions about the implications of changes in such indices.

4.3 RECOMMENDATIONS

Recently, climate indices have been used to describe the effects of large-scale climate variability on many animals (birds, Nott et al. 2002, Sillett et al. 2002, Mazerolle et al. 2005, Weatherhead 2005; amphibians, Beebee 1995; red deer, Post et al. 1997). Climate indices, by definition, reduce complex space and time variability into a simpler unit (Stenseth et al. 2003). They not only correlate with temperature and precipitation, but have been linked to storm frequency and intensity (Hurrell and Van Loon 1997, Wang et al. 2006), and direction and intensity of wind (Hurrell et al. 2001, Sheridan 2003). Also, they allow for models of future climatic conditions to be developed which can be used to predict how animals may react to different climate scenarios. However, relationships between these indices and local weather vary geographically. Both Weatherhead (2005) and I found that NAOI correlated negatively with local temperatures, contradicting other reported relationships between the index and local conditions (Thompson and Wallace 2001, Huang et al. 2006). Given the contradictory results, other studies should exercise caution when using climate indices and, where possible, should use local data to better understand how these climate indices relate to local weather events and patterns. The need to use both climate indices and local weather conditions may help to clarify the complicated relationships between climate fluctuations and ecological patterns.

I found relationships between environmental variables and nesting of swallows; this is a relatively short time period in their annual life cycle. Using long-term data sets that include information about entire life cycles and cover a variety of geographic regions will provide a greater understanding of the relationships between climate indices, ecological effects and local weather. Also, expanding our focus beyond local conditions and regional variables to include both carryover effects on individuals (e.g., previous years reproductive success, previous year / season body condition) and the area (e.g., previous year's precipitation, wetland condition, insect abundance) where they are studied will enhance our understanding of climatic effects on avian life cycles.

Since swallows are a relatively easily studied species, using them as model organisms will help us to understand how climate change may affect other migratory insectivorous passerines. Understanding how large scale climate indices and local weather events affect migratory birds on their wintering grounds, during migration and on their breeding grounds, will lead to further understanding about how changes in climate impact all populations.

LITERATURE CITED

Ardia, D. R., Cooper, C. B., and A. A. Dhondt. 2006. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range. Journal of Avian Biology 37: 137–142.

Beebee, T. J. C. 1995. Tadpole growth: is there an interference effect in nature? Herpetological Journal 5: 204-205.

Blancher, P. J., and R. J. Robertson. 1987. Effect of food supply on the breeding biology of western kingbirds. Ecology 68: 723-732.

Blums, P., Mednis, A., and R. G. Clark. 1997. Effects of incubation body mass in reproductive success and survival of two European diving ducks: a test of the nutrient limitation hypothesis. Condor 99: 916-925.

Bollmann, K., Reyer, H-U., and P. A. Brodmann. 1997. Territory quality and reproductive success: can water pipits *Anthus spinoletta* assess the relationship reliably? Ardea 85: 83–98.

Bolger, D. T., Patten, M. A., and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia 142: 398–406.

Bonsal, B. R., Prowse, T. D., Duguay, C. R., and M. P. Lacroix. 2006. Impacts of large-scale teleconnections on freshwater-ice duration over Canada, Journal of Hydrology 330: 340-353.

Both, C., and M. E. Visser. 2005. The effects of climate change on the correlation between avian life-history traits. Global Change Biology 11: 1606-1613.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 396- 298.

Both, C., Bouwhuis, S., Lessells, C. M., and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441: 81-83.

Brewer, D., Diamond, A. W., Woodsworth, E. J., Collins, B. T., and E. H. Dunn. 2000. Canadian atlas of bird banding. Vol. 1: doves, cuckoos, and hummingbirds through passerines, 1921–1995. Canadian Wildlife Service, Ottawa, ON.

Brown, C. R., and M. B. Brown. 1999. Fitness components associated with clutch size in cliff swallows. Auk 116: 467-486.

Brown, J. L., Li, S. H., and N. Bhagabati. 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? Proceeding of the National Academy of Science 96: 5565-5569.

Bryan, S. M., and D. M. Bryant. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. Proceedings of the Royal Society of London Series B-Biological Sciences 266:157-162.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. New York: Springe-Verlag.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80: 272-287.

Creswell, W., and R. McCleery. 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. Journal of Animal Ecology 72: 356-366.

Crick, H. Q. P., Dudley, C., Glue, D. E., and D. L. Thomson. 1997. UK birds are laying eggs earlier. Nature 388: 526.

Crick, H. Q. P., and T. H. Sparks. 1999. Climate change related to egg-laying trends. Nature 399: 423.

Coulibaly, P. 2006. Spatial and temporal variability of Canadian seasonal precipitation (1900-2000). Advances in Water Resources 29: 1849-1865.

Coulibaly, P., and D.H. Burn. 2005. Spatial and temporal variability of Canadian seasonal streamflows. Journal of Climate 18: 191-210.

Dawson, A., King, V. M., Bentley, G. E., and G. F. Ball. 2001. Photoperiodic control of seasonality in birds. Journal of Biology Rhythms 16: 366-381.

Dawson, R. D., Hillen, K. K., and T. L. Whitworth. 2005a. Effects of experimental variation in temperature on larval densities of parasitic *Protocalliphora* (Diptera: Calliphoridae) in nests of tree swallows (Passeriformes: Hirundinidae). Environmental Entomology 34: 563-568.

Dawson, R. D., Lawrie, C. C., and E. L. O'Brien. 2005b. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity-nesting passerine. Oecologia 144: 499-507.

DeSteven, D. 1978. The influence of age on the breeding biology of the tree swallow *Iridoprocne bicolor*. Ibis 120: 516-523.

DeSteven, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (*Tachycineta bicolor*). Evolution 34: 278-291.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. Proceedings of the Royal Society of London Series B-Biological Sciences 266: 2487-2490.

Dunn, P. O., and L. A. Whittingham. 2005. Radio-tracking of female tree swallows prior to egg laying. Journal of Field Ornithology 76: 259-263.

Ellis, W. N., Donner J. H., and J. H. Kuchlein. 1997. Recent shifts in distribution of microlepidoptera in The Netherlands. Entomologische Berichten (Amsterdam) 57: 119-125.

Environment Canada. 2003a. Science of Climate change: 20th Century Trends in the Earth's Climate and BioPhysical system. Internet WWW page, at URL: <http://www.msc-smc.ec.gc.ca/education/scienceofclimatechange/understanding/trends/index_e.html> Version modified on 2003-06-16.

Environment Canada. 2003b. Science of Climate Change: Impacts of Climate Change. Internet WWW page, at URL: <http://www.msc-smc.ec.gc.ca/education/scienceofclimatechange/understanding/impacts_e.html> Version modified on 2003-06-16.

Environment Canada. 2003c. Climate Trends and Variations Bulletin: Temperature & Precipitation in Historical Perspective, Spring 2003. Internet WWW page, at URL: <http://www.msc.ec.gc.ca/ccrm/bulletin/spring03/national_e.cfm> Version modified on 2003-01-02.

Environment Canada. 2004. Hourly data report, Saskatoon, Saskatchewan <http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html> Version modified on 2004-01-21.

Forchhammer, M. C., Post, E., and N. C. Stenseth. 1998. Breeding phenology and climate. Nature 391: 29-30.

Geupel, G. R., and D. F. DeSante. 1990. Incidence and determinants of double brooding in wrentits. Condor 92: 67-75.

Goodburn, S. F. 1991. Territory quality or bird quality? Factors determining breeding success in the magpie *Pica pica*. Ibis 133: 67-78.

Gjerdrun, C., Vallee, A. M. J., St Clair, C. C., Bertram, D. F., Ryder, L. J., and G. S. Blackburn. 2003. Tufted puffin reproduction reveals ocean climate variability. Proceeding of the National Academy of Science 100: 9377 – 9382.

Grosbois, V., Henry, P-V., Blondel, J., Perret, P., Lebreton, J-D., Thomas, D. W., and M. M. Lambrechts. 2006. Climate impacts on Mediterranean blue tit survival: an investigation across seasons and spatial scales. Global Change Biology 12: 2235-2249.

Hammer, W. M. 1963. Diurnal rhythm and photoperiodism in testicular recrudescence of the house finch. Science 6: 1294-1295.

Hansen, J., Sato, M., Glascoe, J., and R. Ruedy. 1998. A common-sense climate index: Is climate changing noticeably? Proceeding of the National Academy of Science 95: 4113-4120.

Hansen, J., Ruedy, R., Sato, M., Imhoff, M., Lawrence, W., Easterling, D., Peterson, T., and T. Karl. 2001. A closer look at United States and global surface temperature change. Journal of Geophysical Research 106: 23947-23963.

Harrap, S., and D. Quinn. 1995. Chickadees, tits, nuthatches & treecreepers. Princeton, New Jersey: Princeton University Press.

Hatcher, L. 1998. A step-by-step approach to using the SAS system for factor analysis and structural equation modeling. Cary, NC: SAS Institute Inc.

Hipfner, J. M., Gaston, A. J., Martin, D. L., and I. L. Jones. 1999. Seasonal declines in replacement egg-laying in a long-lived, Arctic seabird: Costs of late breeding or variation in female quality? Journal of Animal Ecology 68: 988-998.

Huang, J. P., Ji, M. X., Higuchi, K., and A. Shabbar. 2006. Temporal structures of the North Atlantic Oscillation and its impacts on the regional climate. Advances in Atmospheric Science 23: 23-32.

Hughes, I. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15: 56-61.

Hurrell, J.W., Kushnir, Y., and M. Visbeck, 2001. The North Atlantic Oscillation. Science 291: 603-605.

Hurrell, J. W., and H. Van Loon. 1997. Decadal variation in climate associated with the North Atlantic Oscillation. Climate Change 36: 301-326.

Hurrell, J.W. 1995. Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. Science 269: 676-679.

Hussell, D. J. T. 2003. Climate change, spring temperatures, and timing of breeding of tree swallows (*Tachycineta bicolor*) in southern Ontario. Auk 120: 607-618.

Hussell, D. J. T. 1983. Age and plumage color in female tree swallows. Journal of Field Ornithology 54: 312-318.

Hussell, D. T. J., and T. E. Quinney. 1997. Food abundance and clutch size in tree swallows *Tachycineta bicolor*. Ibis 129: 243-258.

Immelman, K. 1971. Ecological aspects of periodic reproduction. In: *Avian Biology*, Volume I. Ed. D.S. Farner, J.R. King & K.C. Parkes. pp. 341-389. New York: Academic Press.

Johnson, A. L. 2000. Reproduction in the female. In: *Sturkie's Avian Physiology*, 5th Edition. Ed. G.C. Whittow. pp. 596-596. New York: Academic Press.

Lambrechts, M. M., Blondel, J., Maistre, M., and P. Perret. 1997. A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. Proceedings of the National Academy of Science 94: 5153-5155.

Lack, D. L. 1968. Ecological adaptation for breeding in birds. London: Methuen & Co. Ltd.

Lehikoinen, A., Kilpi, M., and M. Ost. 2006. Winter climate affects subsequent breeding success of common eiders. Global Change Biology 12: 1355-1365.

Lessells, C. M., Dingemanse, N. J., and C. Both. 2002. Egg weights, egg component weights, and laying gaps in great tits (*Parus major*) in relation to ambient temperature. Auk 119: 1091-1103.

Lindén, M., Gustafsson, L., and T. Pärt. 1992. Selection on fledging mass in the collard flycatcher and the great tit. Ecology 72: 336-343.

Lloyd, P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. Ibis 4: 637-643.

Magrath, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. Journal of Animal Ecology 60: 335-351.

Mazerolle, D.F., Dufour, K.W., Hobson, K.A., and H.E. de Haan. 2005. Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. Journal of Avian Biology 36: 155-163.

Martin, K., and K. L. Wiebe. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44: 177-185.

McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology 15: 320-331.

McCarty, J. P., and D. Winkler. 1999. Relative importance of environmental variables in determining the growth of nestling tree swallows. Ibis 141: 286-296.

McPhaden, M. J. 2002. El Niño and La Niña: Causes and global consequences. In: The Earth system: physical and chemical dimensions of global environmental change, Volume 1. Ed. M. C. MacCraken & J. S. Perry. pp 353-370. New York: John Wiley and Sons.

Meijer, T., Dann, S., and M. Hall. 1990. Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. Behaviour 114: 117-136.

Mitchell, R. J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. Functional Ecology 6: 123-129.

Morton, E. S. 1971. Nest predation affecting the breeding season of the clay-colored robin, a tropical song bird. Science 171: 920.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981-1991. Nature 386: 698-701.

Nager R. G., Ruegger, C., and A. J. VanNoordwijk. 1997. Nutrient or energy limitation on egg formation: a feeding experiment in great tits. Journal of Animal Ecology 66: 495-507.

Nager, R. F., and A. J. VanNoordwigk. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. American Naturalist 146: 454-474.

Nilsson, J. A., and E. Svensson. 1993. The frequency and timing of laying gaps. Ornis Scandinavica 24: 122-126.

NOAA. 2005a. The National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center: El Nino – Southern Oscillation (ENSO). Internet WWW page, at URL <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/enso.shtml> Version modified on 2005-12-12.

NOAA. 2005b. The National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center: Monitoring and Data, Northern Hemisphere Teleconnections Patterns, North Atlantic Oscillation (NAO). Internet WWW page, at URL < http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml > Version modified on 2005-05-23.

Nooker, J. K., Dunn, P. O., and L. A. Whittingham. 2005. Effects of food abundance, weather, and female condition on reproduction in Tree Swallows. Auk 122: 1225–1238.

Nott, M. P., Desante, D. F., Siegel, R. B., and P. Pyle. 2002. Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forest of the Pacific Northwest of North America. Global Ecology and Biogeography 11: 333-342.

Orians, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Monographs in Population Biology Number 14. Princeton, New Jersey: Princeton University Press.

Pap, P. L. 2002. Breeding time and sex-specific health status in the barn-swallow (*Hirundo rustica*). Canadian Journal of Zoology 80: 2090-2099.

Perrins, C. M. 1970. The timing of birds' breeding season. Ibis, 112: 242-255.

Pearce-Higgins, J. W., Yalden, D. W., and M. J. Whittingham. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). Oecologia 143: 470-476.

Post, E., Stenseth, N. C., Langvatn, R., and J-M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society of London Series B-Biological Sciences 264: 1317-1324.

Pyle, P., Spear, L. B., Sydeman, W. J., and D. G. Ainley. 1991. The effects of experience and age on the breeding performance of western gulls. Auk 108: 25-33.

Quinney, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100: 750-754.

Quinney, T. E., and C. D. Ankney. 1985. Prey size selection by tree swallows. Auk 102: 245-250.

Quinney, T. E., Hussell, D. J. T., and C. D. Ankney. 1986. Sources of variation in growth of Tree Swallows. Auk 103: 389-400.

Richner, H. 1989. The effect of extra food on fitness of breeding carrion crows. Ecology 73: 330-335.

Roeder, K. D. 1953. Insect physiology. New York: John Wiley and Sons.

Robertson, R. J., Stutchbury, B. J., and R. R. Cohen. 1992. Tree swallow. In: Poole A, Stettenheim P, Gill F, editors. The Birds of North America, No. 11. Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologist's Union.

Robertson, R. J., and W. B. Rendell. 2001. A long-term study of reproductive performance in tree swallows: the influence of age and senescence. Journal of Animal Ecology 70: 1014-1031.

Root, T., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Rowan, W. 1962. On photoperiodism, reproductive periodicity, and the annual migrations of certain birds and fishes. Proceedings of the Boston Society of Natural History 38: 147-189.

Saino, N., Romano, M., Ambrosini, R., Ferrari, R. P., and A. P. Møller. 2004. Timing of reproduction and egg quality covary with temperature in the insectivorous barn swallow, *Hirundo rustica*. Functional Ecology 18: 50-57.

SAS Institute Inc. 2001. SAS/STAT user's guide. Version 8. Cary, NC: SAS institute Inc.

Sheridan, S. C. 2003. North American weather-type frequency and teleconnection indices. International Journal of Climatology 23: 27-45.

Shutler, D., Clark, R. G., Fehr, C., and A. W. Diamond. 2006. Time and recruitment costs as currencies in manipulation studies on the costs of reproduction: evidence from tree swallows. Ecology 87: 2938-2946.

Shutler, D., and R. G. Clark. 2003. Causes and consequences of dispersal by tree swallows. Auk 120: 619-631.

Sillett, T. S., Holmes, R. T., and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040-2042.

Smith, R. J., and F. R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134: 325-331.

Snow, D.W., and C. M. Perrins (eds.). 1998. The birds of the Western Palearctic: Concise edition. Volume 2: Passerines. Oxford University Press, Oxford.

Stapleton, M. K., and R. J. Robertson. 2006. Female tree swallow home-range movements during their fertile period as revealed by radio-tracking. Wilson Journal of Ornithology 118: 502-507.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., Yoccoz, N. G., and B. Ǻdlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society of London Series B-Biological Sciences 270: 2087–2096.

Stocek, R. F. 1986. Spring weather and local movements of tree swallows, Tachycineta bicolor. Canadian Field Naturalist 100: 134-136.

Stutchbury, B. J., and R. J. Robertson. 1986. A simple trap for catching birds in nest boxes. Journal of Field Ornithology 57: 64-65.

Stutchbury, B. J., and R. J. Robertson. 1988. Within-season and age-related patterns of reproductive performance in female tree swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 66: 827-834.

Timmerman, A., Oberhuber, J., Blacher, A., Esch, M., Latif, M., and E. Roekner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 395: 694-696.

Thompson, D. W. J., and J. M. Wallace. 2001. Regional climate impacts of the Northern Hemisphere Annular Mode. Science 293: 85-89.

Thompson P. M., and J.C. Ollason. 2001. Lagged effects of ocean climate change on fulmar population dynamics. Nature 413: 417-420.

Tyler, G. A., and R. E. Green. 2004. Effects of weather on the survival and growth of Corncrake *Crex crec* chicks. Ibis 146: 69-76.

Visser M. E., VanNoordwijk, A. J., Tinbergen, J. M., and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society of London Series B-Biological Sciences 265: 1867-1870.

Visser, M. E., and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society of London Series B-Biological Sciences 268: 289-294.

Walther, G. R., Post, E., Convey, P., Manzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416: 389-395.

Wang, X. L., Wan, H., and V. R. Swail. 2006. Observed changes in cyclone activity in Canada and their relationships to major circulation regimes. Journal of climate 19: 896-915.

Wendeln, H., and P. H. Becker. 1999. Effects of parental quality and effort on the reproduction of common terns. Journal of Animal Ecology 68: 686-702.

Weatherhead, P. J. 2005. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. Oecologia 144: 167-175.

Wiebe, K. L., and K. Martin. 1995. Ecological and physiological effects on egg laying intervals in ptarmigan. Condor 97: 708-717.

Williams, J. B. 1987. Field metabolism and food consumption of savannah sparrows during the breeding season. Auk 104: 277-289.

Williams, J. B. 1988. Field metabolism of tree swallows during the breeding season. Auk 105: 706-714.

Wingfield, J. C. 1980. Fine temporal adjustment of reproductive functions. In Avian endocrinology. Ed. A. Epple & M. H. Stenson. Pp 367-389. New York: Academic Press.

Winkler, D. G., Dunn, P. O., and C. E. McCulloch. 2002. Predicting the effects of climate change on avian life-history traits. Proceeding of the National Academy of Science 99: 13595-13599.

Winkler, D. G., and P. E. Allen. 1996. Seasonal declines in tree swallow clutch size: physiological constraint or strategic adjustment? Ecology 77: 922-932.

Yom-Tov, Y., and J. Wright. 1993. Effect of heating nest boxes on egg-laying in the blue tit (*Parus caeruleus*). Auk 110: 95-99.

Zar, J. H. 1984. Biostatistical Analysis, 2nd edition. Englewood Cliffs: Prentice-Hall International, Inc.