Environmental determinants of reproductive success in cavity nesting songbirds of a semi-arid grassland in British Columbia

by

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BSc (Hons), University of Victoria, 2013

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE

MASTER OF SCIENCE

in

The Faculty of Science

(Environmental Science)

THOMPSON RIVERS UNIVERSITY

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Abstract

I investigated the influence of regional climate, local weather, and nest box features on the reproductive success of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*). I also evaluated the relative influence of local weather and parental care behaviour on mountain bluebird nestling growth and mortality. My results demonstrate that local weather can strongly influence the breeding performance of mountain bluebirds, with improved reproductive success during years of less rainfall. I conclude that this influence is likely exerted directly through acute nestling mortality rather than through nestling growth and prolonged nestling stress. As well, I show that regional climate plays an important role in tree swallow reproductive success, with improved tree swallow breeding performance during years of lower Southern Oscillation Index values (El Niño conditions). I suggest that the affect of regional climate on tree swallow reproductive success is likely due to influences that ENSO and regional climatic patterns may have on the aerial insect prey base of tree swallows in our study region near Kamloops, BC. For mountain bluebirds, I found the influence of weather on reproductive success is dependent on nest box features, including nest box entrance type. This study has implications for conservationists and managers of grassland passerines in British Columbia and beyond, especially in light of global climate change.

Keywords: Mountain bluebirds, tree swallows, reproductive success, grasslands, climate, weather, nest box, parental care

Abbreviated title: Environmental factors of breeding success in grassland songbirds

Preface

This work was funded by a research grant from NSERC (National Science and Engineering Research Council), a fellowship from the TRU Graduate Studies Office and a research grant from the North American Bluebird Society. This work was conducted under permit number BC-14-0025 granted by the Canadian Wildlife Service. The Thompson Rivers University Animal Care Committee approved this research, file number 10603, and no animals were harmed during the course of this study.

Table of Contents

List of Tables

List of Figures

Acknowledgements

I would like to acknowledge and thank my supervisor, Dr. Matthew Reudink, for all his support and guidance over the course of completing my MSc at Thompson Rivers University. Thank you for trusting me to complete this thesis remotely and for all the great feedback throughout this project. I would also like to thank my lab mates in the BEaC lab for your continued support despite our geographical differences. Special thanks to Jacob Bailey, Orri Greaves and Juliane Gaviraghi Mussoi for being such stellar field companions and nest video watchers.

Thank you to Stephen Joly for having much more patience for catching birds than I ever could. I am grateful for Dr. Nancy Flood and her many constructive comments and insights about this project, from beginning to end. Thank you to Dr. Mark Paetkau for all his support with the RFID and iButton systems, and for his unique perspectives. Many thanks to Dr. Ann McKellar for her incredible commitment and help with my thesis and manuscripts. Thank you as well to Dr. Scott Wilson for his valuable revisions to the thesis.

I am grateful for Glenn and Di Dreger for their support of my bluebird work and for welcoming me into their home and garden during the field seasons. I also thank Susan Weilandt and all of the fantastic volunteers at the Kamloops Naturalist Club for their enthusiasm for this project.

Thank you to my family for their continued support and reassurance. I would also like to thank Graham for his endless understanding and encouragement through the highs and lows of completing this thesis.

Chapter 1

Introduction

The drive to reproduce shapes the behaviour and life histories of individuals, as well as the demography and dynamics of bird populations and communities. Determining the influence of ecological and environmental factors on reproductive output is critical for understanding population dynamics (Shaffer 2004). Many environmental factors can contribute to the reproductive success of birds, including nest conditions, predation, parasitism, food availability, habitat conditions and land use, human activity, parental care behaviour, and weather (Best & Stauffer 1980, Lowe et al. 2014, Ludlow et al. 2014). Of particular interest to ornithologists is the study of how these factors interact, including connections among reproductive success, weather and parental care (e.g., Lack, 1947; Rotenberry & Wiens 1991; George et al. 1992; Tinbergen & Dietz 1994; Brinkhof & Cave 1997; Morrison & Bolger 2002; Weatherhead 2005; Dickey et al. 2008; Richmond et al. 2011; Winkler et al. 2013). In general, reproductive success is reduced when weather conditions are poor and when food supply and parental care is limited. For species that rear altricial young, parental care is especially important in contributing to nestling survivorship (Wright et al. 1998). Despite an extensive body of knowledge about weather and parental care individually, there is still considerable debate as to how exactly nestling survivorship and parental care are influenced by weather.

Weather conditions during the breeding season can directly or indirectly affect the reproductive success of birds, and disentangling these direct and indirect effects is no easy task. Weather can directly and acutely reduce nestling survival by affecting metabolic rates and thermoregulatory function during adverse (cold, wet) weather conditions (Broggi et al. 2004). Weather can also indirectly influence reproductive success over a more prolonged period, by influencing parental care (Tinbergen & Dietz 1994), food availability (Morrison & Bolger 2002), and predation risk (Schmidt et al. 2005). Of all the environmental factors that could affect nestling growth, food availability is thought to be the most influential (McCarty & Winkler 1999).

Lack (1947) was one of the first ornithologists to note the relationship between food availability, parental care and reproductive success, arguing that the ability of parents to feed their offspring limited the clutch sizes of altricial species. More recent research builds on this premise, suggesting that provisioning behaviour is not constrained by food abundance, but rather by food availability, which is mediated by variation in weather conditions (Dawson & Bortolotti 2000). That is, even though food may be in high abundance in an area, foraging is more difficult when weather conditions are poor, thus lowering the availability of food. Additionally, in a study of great tits (*Parus major*), parental energy expenditure was reduced as ambient temperature decreased (Tinbergen & Dietz 1994). Provisioning rates and provisioned prey biomass were also negatively affected by adverse weather in common Hoopoe (*Upupa epops*), an insectivorous farmland bird in the Swiss Alps (Arlettaz et al. 2010). Yet, in snow buntings (*Plectrophanx nivalis*) breeding in the high Arctic, parental feeding rates increased during periods of low temperatures (Hoset et al. 2004), presumably to meet the higher metabolic demands of their offspring when temperatures are lower. In general, researchers agree that weather conditions affect parental care, which influences food availability to nestlings and ultimately, nestling survival.

In addition to local weather conditions, regional climate can also influence the reproductive success of birds. In this thesis, I define regional climate as climatic patterns that operate over a broad geographic area, regardless ecosystem type; more specifically the Pacific Northwest or Cascadia region of North America, including all of British Columbia, Washington, and Oregon. Local weather refers to the weather patterns that operate over a smaller geographic area, including the semi-arid grasslands of the Thompson Nicola region of British Columbia. In western North America, a major driver of regional climate patterns is the El Niño South Oscillation (ENSO) cycle (Schonher & Nicholson 1989). While El Niño and La Niña events of the ENSO cycle do not directly influence the regional climate of Cascadia, they indirectly impact the weather of this region by affecting ocean temperature and global circulation patterns. Events like ENSO operate to influence climate over broad temporal and spatial scales, and this subsequently influences individuals through some change in the ecosystems.

For example, ENSO patterns have been shown to contribute to breeding bird performance on a regional scale through changes in rainfall, plant productivity, and, thus, food abundance (e.g., seeds, insects; DeSante & Geupel 1987, Chase et al. 2005). Regional climate can also play a role during the non-breeding season by affecting overwintering conditions that are carried-over through to the breeding season, such as winter food availability, body mass and condition, and timing of spring migration (Studds & Marr 2007). In ecosystems where weather and climate conditions can be quite variable seasonally, such as temperate grasslands, the influence of local weather and regional climate on breeding birds can be even more pronounced.

Temperate grasslands are one of the most threatened ecosystems in North America and represent the most significantly altered biome on the continent, with less than 20% of native grasslands intact (Samson & Knopf 1994). These ecosystems are expected to face additional challenges with global climate change, including changes in temperature and precipitation regimes, leading to changes in soil moisture, and frequency and severity of droughts (IPCC 2013). Weather during the breeding season in temperate grasslands is currently is characterized by periodic drought punctuated by heavy rainfall events, and often very hot temperatures exceeding 30°C. These weather conditions provide a unique challenge to breeding birds in grassland ecosystems. Grassland passerines are already under increasing pressure due to reductions of their breeding and foraging habitats from land-use changes and forest encroachment.

Research into how environmental factors, especially climate, influence grassland birds is essential for their conservation and management.

Study system

My research focuses on two grassland songbirds that occupy similar yet distinct ecological niches: the ground-foraging insectivorous mountain bluebird (*Sialia currucoides*) and the aerial-foraging insectivorous tree swallow (*Tachycineta bicolor*). Both species are obligate secondary cavity nesters that breed in the temperate grasslands of western North America from the end of April until early August, while tree swallows are also found across the continent. Both mountain bluebirds and tree swallows readily accept artificial nest boxes for breeding, which makes them ideal organisms for studying reproductive success and behaviour in passerines. Artificial nest boxes provide a simple and easy system in which to consistently and frequently monitor reproductive metrics over the course of a breeding season, and as such, they have been frequently used in studies of many aspects of ornithology, including reproductive behaviour, population dynamics, quantitative genetics, sexual selection, and several other fields (Møller 1989, Power & Lombardo 1996, Winkler et al. 2011). Here, I use long-term monitoring data for mountain bluebirds and tree swallows breeding in nest boxes to assess how environmental factors impact breeding performance in these two species.

Field sites

All monitoring data for mountain bluebird and tree swallow reproductive success used in Chapter 2 was derived from Kamloops Naturalist Club (KNC) records that spanned the years 1980 to 2014 and covered a wide geographic area surrounding Kamloops, British Columbia, Canada (50.68°N, 120.34°W). I obtained and digitized the KNC records in the summer of 2014, and nest box features were measured in the field during the fall of 2013. Field work for Chapter 3 was carried out in the grasslands of the Thompson Nicola Region south of Kamloops near Knutsford, British Columbia during the summers of 2013 and 2014. I monitored nest boxes along three KNC bluebird routes: Edith Lake (50°35'21"N; 120°21'08"W), Long Lake (50°35'43"N; 120°19'24"W),) and Jackson Road (50°33'43"N; 120°17'11"W).

Structure of thesis

The goal of this thesis is to quantify the effects of environmental factors on the reproductive success of mountain bluebirds and tree swallows. This thesis is organized into four chapters: the introduction, given here, two data chapters, and a concluding chapter. In Chapter 2, I report and interpret the results of statistical models that incorporate 35 years of reproductive success monitoring data and environmental factors to determine whether mountain bluebird and tree swallow breeding performance is influenced by local weather, regional climate and nest box features. In Chapter 3, I present the findings of a field observational study in which I quantified levels of parental care and nestling growth rates of mountain bluebirds to test whether local weather conditions or levels of parental care more heavily influence breeding performance and nestling growth. This thesis is concluded in Chapter 4, where I explore potential directions for future research and the implications that my findings have for managing grassland breeding birds.

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Chapter 2

Relative influence of environmental factors on the breeding performance of two grassland passerines

Abstract

Grasslands are among the most threatened ecosystems in North America, with less than 20% of native grasslands intact across the continent. They are expected to face additional challenges with global climate change, including alteration of temperature and precipitation regimes, leading to a loss of soil moisture and an increase in the frequency and severity of droughts. Grassland passerines are already under increasing pressure due to reduction of their breeding and foraging habitats from land-use changes and forest encroachment, and global climate change will no doubt provide further challenges to these species. Research into how environmental factors, especially climate, influence grassland birds is essential for their conservation and management.

Using long-term citizen-science based data, we asked how local weather, regional climate, and nest box features influenced the breeding performance of two grassland songbirds, mountain bluebirds and tree swallows, from 1980 to 2014. Locally high precipitation reduced the breeding performance (number of nestlings and fledglings) of mountain bluebirds, while higher mid-summer temperatures reduced the breeding performance (number of nestlings) of tree swallows. For bluebirds, lower reproductive success may be due to direct mortality of nestlings from chilling or due to an inability of parents to provision nestlings during heavy rainfall. For tree swallows, higher mid-summer temperatures may cause egg mortality from overheating. Tree swallow breeding performance (number of nestlings and hatching success) was also negatively associated with the El Niño Southern Oscillation: birds were more successful during warm, humid El Niño years.

Nest box features also influenced breeding performance for both species: mountain bluebirds had higher breeding performance (number of nestlings and fledglings) in hole-type nest boxes compared to boxes that had slot openings, and tree swallows had higher breeding performance (number of fledglings) in nest boxes attached to fences rather than trees. Our results suggest that local weather and regional climate differentially affect the reproductive success of mountain bluebirds and tree swallows, which is useful information for conservationists and managers of grassland species, especially in light of global climate change.

Introduction

Grasslands are among the most threatened ecosystems in North America and represent the most significantly altered biome on the continent (Samson & Knopf 1994). Grassland bird species have been particularly susceptible to habitat alteration and have declined more dramatically, consistently, and across a larger geographic area than any other group of birds in North America over the last three decades (Saab & Rich 1997, Krannitz & Rohner 1999, North American Bird Conservation Initiative, U.S. Committee 2014). These declines have resulted from of a number of factors that vary regionally, but are primarily due to habitat loss and fragmentation resulting from (1) agricultural development (Samson et al. 2004) and (2) forest invasion resulting from wildfire suppression (Krannitz & Rohner 1999). As well, intensification of agricultural practices and increased use of herbicides and pesticides have influenced grassland birds through changes in food quality and quantity (Benton et al. 2002). Furthermore, grassland birds are expected to face additional pressures due to climate change (North American Bird Conservation Initiative, U.S. Committee 2014). Temperate grasslands are predicted to experience increased precipitation and warming with climate change (IPCC 2013), and these weather changes are expected to intensify declines in grassland species that already have unstable populations (Sauer et al. 2013). An understanding of how weather influences the reproductive success and population dynamics of grassland birds is vital for understanding the effects of climate change on this avian group.

Individual reproductive success, which is a key component of population dynamics (Morrison 2001), is influenced by both intrinsic and extrinsic factors. Intrinsic factors include an individual's age, breeding experience, physiological condition, and hormone levels (Angelier et al. 2007). Extrinsic factors derive from the breeding environment and can be both biotic and abiotic. Biotic environmental factors, such as availability of food and nesting habitat, as well as competition, predation, and parasitism, often have direct impacts on reproductive success, but can also influence reproductive success indirectly (e.g., competition can reduce food availability). Abiotic factors, such as weather, can also influence reproductive success directly (e.g., chick/egg mortality due to freezing or overheating) or indirectly (e.g., reduced food availability due to poor foraging conditions, George et al. 1992, Ludlow et al. 2014). An understanding of how these factors influence reproductive success, and ultimately population dynamics, is important for successful management of bird populations.

Much research has focused on how weather conditions affect the breeding performance of birds by influencing breeding phenology (Dunn & Winkler 1999, Rodríguez & Bustamante 2003, Dickey et al. 2008, Charmantier & Geinapp 2013, Virkkala & Lehikonen 2014). However, weather can also influence other demographic factors, such as survival and performance throughout the breeding season (Morrison & Bolger 2002, Crick 2004). Weather can directly affect reproductive success by increasing the metabolic rates of birds (and thus stressing them) and the rates of nestling mortality through chilling/exposure (Morrison & Bolger 2002, Collister & Wilson 2007, Wilson et al. 2011). In addition, weather can act indirectly: nestling starvation may occur when heavy rainfall affects the ability of parents to collect food for and provision their young (Pipoly et al. 2013). Conversely, higher precipitation may increase reproductive success by increasing primary productivity and thus the availability of food items such as seeds and insects (Noy-Meir 1973, Cody 1981, Boag & Grant 1984). These contrasting effects make it difficult to discern the overall effect of weather on nestling mortality and breeding success in birds (Crick 2004).

The El Niño South Oscillation (ENSO) cycle is a major driver of large-scale regional climatic patterns in the north Pacific region (Schonher & Nicolson 1989, Chase et al. 2005) and has been associated with variation in the breeding performance of terrestrial birds in western North America (Sillett et al. 2000, Jonzén et al. 2002, Weatherhead 2005, Chase et al. 2005, Wilson et al. 2011). The ENSO cycle refers to the predictable and strong inter-annual variation in sea-surface temperatures of the equatorial Pacific that influence atmospheric circulation and the jet stream over western North America, resulting in El Niño or La Niña events (IPCC 2013). El Niño periods are characterized by increased precipitation in western North America throughout the year and occur, on average, every four years (Trenberth 1997).

El Niño events have been shown to increase the reproductive success of several songbird species due to enhanced plant productivity and food abundance during the breeding season (DeSante & Geupel 1987, Morrison & Bolger 2002, Nott et al. 2002, Chase et al. 2005). The effects of ENSO during the non-breeding season have also been found to influence breeding season performance due to carry-over effects of overwintering food availability, body mass, and spring departure timing of migration (Studds & Marra 2007). Because local weather can act more directly and acutely than regional climate on individual breeding performance and because both are important drivers of reproductive success in birds, the direct effects of local weather and the indirect effects of regional climate on breeding performance should be considered together (Weatherhead 2005). More specifically, the direct effects of local weather refer to temperature or precipitation directly affecting individuals through physiological costs. Regional climate effects refer to the longer term weather conditions of an area that have an effects on the resource base, the habitat, and/or the ecosystem, which then has an impact on individuals.

In addition to the influence of exposure and starvation on nestling mortality, weather conditions may also influence nestling survival by differentially affecting nesting microhabitats. This variability is especially strong in secondary cavity nesting species because competition for acceptable nesting cavities can be severe (Peterson & Gauthier 1985). Secondary cavity nesters preferentially select cavities with features that provide protection for their offspring from predation and poor weather (Cockle et al. 2015). For instance, some species experience improved breeding performance in cavities that are higher above ground (Cockle et al. 2015), have a smaller entrance diameter (van Balen et al. 1982), face a certain direction (Scott et al. 1980), or have a greater floor area (Rendell & Robertson 1989). This information is particularly relevant for secondary cavity nesters that are targets of conservation efforts such as artificial nest box programs; the construction and placement of these nest boxes can significantly influence the breeding performance of the birds that use them (Lambrechts et al. 2010). Artificial nest box programs, such as the bluebird trails across North America, provide a unique opportunity to examine long-term monitoring data for target species (Semel et al. 1988).

Here, we use a citizen science dataset spanning 35 years to investigate the relative influence of environmental factors on the reproductive success of two species of songbirds that occupy different yet overlapping ecological niches and nest in artificial cavities in the semi-arid grasslands of British Columbia, Canada. Specifically, we examine the influence of large-scale climate drivers (i.e., El Niño Southern Oscillation [ENSO] cycles), local weather, and nest box features on the reproductive success of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*). We predicted that: 1) conditions during warmer, more humid El Niño events would positively influence reproductive success due to an increase in food availability during the breeding season, 2) birds would experience higher breeding success when local weather conditions were warmer and drier, 3) nest boxes that provide better protection from the elements (e.g., have a smaller hole diameter) and better access to food resources (e.g., erected in open fields rather than wooded areas) would be associated with higher breeding success.

Materials and Methods

Study species

Mountain bluebirds are small thrushes that are obligate secondary cavity nesters which readily accept artificial nest boxes in open grassland areas. Conservation groups throughout North America have established "bluebird trails", series of nest boxes generally located 100 meters or more apart and often placed along fence lines in grasslands, to support populations of mountain bluebirds, western bluebirds (*Sialia mexicana*) and eastern bluebirds (*Sialia sialis*) (see North American Bluebird Society: www.nabluebirdsociety.org). These initiatives have stabilized and supported populations of mountain bluebirds across the continent (Power & Lombardo 1996). In North America, mountain bluebirds are listed as a species of least concern and their populations have been stable or slightly declining since 1970 (Power & Lombardo 1996). Canadian bluebird population trends are similar, with a slight decline in abundance since 1970; British Columbian populations appear to be stable (Pardieck et al. 2015). However, when considering Bird Conservation Regions as defined by the North American Bird Conservation Initiative (U.S. Committee 2000), mountain bluebirds have been in decline (-1.5% annually, Pardieck et al. 2015) since the 1970s in the Great Basin Region (Bird Conservation Region 9, where our study took place). This downward trend prompted the advent of bluebird trail establishment throughout the region during that decade.

Like mountain bluebirds, tree swallows are obligate secondary cavity nesters that also readily accept artificial nest boxes erected near open fields and meadows. Tree swallows often utilize bluebird boxes, although the boxes are not designed for them specifically. These medium-sized swallows are aerial insectivores that feed over areas of open ground or water where flying insects gather. Tree swallows are distributed across most of the continental US and in most southern provinces of Canada (Winkler et al. 2011). Although they are considered a species of least concern, their North American populations have been in decline (-0.8% annually, Pardieck et al. 2015) and they are part of the larger guild of aerial insectivores that is generally showing population declines across the continent (Nebel et al. 2010).

Field methods

Fieldwork for this project was conducted along bluebird trails, hereafter called routes, throughout the area around the confluence of the Thompson and North Thompson Rivers near Kamloops, British Columbia, Canada (50.68°N, 120.34°W) from 1980 to 2014. Volunteers from the Kamloops Naturalist Club monitored and recorded reproductive data for active nests along each route during the breeding season. Bluebird routes vary in the number of nest boxes erected along the route (2 to 70 boxes) and the length of the route (300m to 14km). Physical copies of bluebird route records for each year of the monitoring program were obtained from the Kamloops Naturalist Club and digitized in 2014. The protocol for bluebird volunteers was to check all nest boxes along their routes every 7-10 days throughout the breeding season (late April through early August).

Route specific data

The level of detail available in the monitoring records varied among routes. Summary data, hereafter termed “route specific data,” were available for all years and included the following for each species and each route: the number of clutches, number of first nests and second nests, number of eggs, number of nestlings, number of fledglings, total number of nest boxes, and number of boxes that were used for nesting. Other observations, such as evidence of predation, box conditions, and presence of breeding pairs were also noted. There were 26 routes with route specific data from 1980 to 2014.

Nest box specific data

We also had information for 15 routes for which there was detailed “nest box specific data” from 2001 to 2014. Box specific data collected by volunteers included information on breeding activity at each nest box along each bluebird route, such as: number of eggs in each nest box, number of nestlings, number of fledglings, and whether a nest was the first or second nesting attempt. In addition, in 2013 we recorded nest box specific features in the field for the above routes, including: aspect and bearing of nest box opening, type of nest box entrance (hole or slot opening, Appendix A), type of nest box attachment (tree or fence mounted), and nest box elevation. Nest box types were distributed randomly within routes.

Local weather

We obtained local weather information by accessing online Environment Canada weather station archives for the Kamloops A station, located at the Kamloops airport (50.70°N, 120.44°W). Mean monthly temperature and total monthly precipitation were calculated from daily records for April, May, June, and July for breeding season weather for the years 1980 to 2014. Kamloops A weather station data were not available for July 2013 nor for all of 2014, so temperature and precipitation data from the nearby Pratt Road station (50.60°N, 120.20°W) were used instead. Weather data from Kamloops A and Pratt Road stations were highly correlated for the years 1988 to 2013 for temperature ($r^2= 0.98$, $p < 0.01$) and precipitation ($r^2 = 0.70$, $p < 0.01$), and so, we felt justified in using Pratt Road data for July 2013 and all of 2014.

Regional climate

We used the standardized Southern Oscillation Index (SOI) to measure variation in regional climate, and we obtained monthly SOI values for all months from January 1980 to December 2014 from the U.S. National Oceanic and Atmospheric Administration (NOAA) online climate database. SOI is a measure of the fluctuations in air pressure between Tahiti and Darwin, Australia, and during El Niño and La Niña events, these air pressure differences affect the jetstream over western North American, influencing regional climatic patterns (Melack et al. 1997). Negative SOI values are associated with more warm, wet El Niño events in western North America, and positive values with cooler, dry La Niña events (Rasmusson & Wallace 1983, Melack et al. 1997). The El Niño Southern Oscillation (ENSO) cycle has an average periodicity of four years, but it has varied between two and seven years historically (Allan et al. 1996).

Statistical analyses

We constructed models that related local weather, regional climate, and nest box features to reproductive variables for route specific and box specific data separately. Reproductive variables used for route specific analyses included mean number of eggs per nest per route, mean number of nestlings per nest per route, mean number of fledglings per nest per route, and hatching success per nest per route (number of eggs hatched divided by number of eggs laid). To examine the effects of local weather and regional climate on breeding success at the route specific scale, we constructed generalized linear mixed effects models (GLMMs) that related reproductive variables to (1) local weather data (total monthly rainfall and mean monthly temperature for April, May, June and July), and (2) regional climate data (mean annual SOI). Poisson distribution was assumed for GLMMs for mean eggs, nestlings, and fledglings, and binomial distribution was assumed for hatching success GLMMs. We also included year in the GLMMs to allow for long-term trends in reproductive success (i.e., a single fixed effect parameter in the model). For route specific data, our analysis involved a total of 786 breeding season records for 26 routes from 1980 to 2014, including 401 records for mountain bluebirds and 385 records for tree swallows (routes that lacked complete data for all years were excluded from analyses).

For box specific data, reproductive variables included number of eggs per box, number of nestlings per box, and number of fledglings per box. Because data availability at the nest level was only available for some years (2001 to 2014), we constructed box specific models to include the more details nest-level data. To examine the effects of local weather, regional climate, and nest box features on breeding success at the box specific scale, we constructed GLMMs that related reproductive variables to (1) local weather data: total monthly rainfall and mean monthly temperature for April, May, June and July, (2) regional climate data: mean annual SOI, and (3) nest box feature data: aspect (in degrees) of the nest box opening, nest box elevation, nest box attachment type (fence or tree) and nest box entry type (slot or hole opening). However, because we recorded nest box specific features in 2013, we could not be confident that box entry type in 2013 was the same as in all previous years (i.e. boxes were occasionally replaced). Thus, for our box specific analysis that included all years (2001-2014), we did not include nest box entry type. We performed a subsequent analysis using only the years 2013 and 2014 (for which we could be confident of nest box entry type) that included the complete set of variables. Our initial box specific analysis included a total of 674 mountain bluebird records and 476 tree swallow records along 15 routes from 2001 to 2014. Our reduced box specific dataset that only included those years (2013 and 2014) for which we were confident we had correct data for nest box entry type included a total of 118 nest records, with 60 records for mountain bluebirds and 58 records for tree swallows.

To avoid problems of multicollinearity, we excluded weather variables that were highly correlated (correlation coefficient greater than 0.5) from the same model, while retaining one of the correlated variables for each model (i.e., April temperature and June temperature, April temperature and SOI, May temperature and May precipitation, June temperature and July temperature). We included route as a random effect in all models. We ranked all models with Akaike's Information Criterion (AIC) and considered models within four AIC units to be competitive (Burnham & Anderson 2002). We display only the top five models (or fewer) within four AIC units for clarity in the results, as there were often many more than five competitive models for each round of model selection. To complement the GLMM building and AIC model selection, we performed linear regression analyses (for continuous variables) between reproductive variables and those variables identified as important during the model selection step. As a final supplement to the above analyses, we used Welch's t-tests to examine whether there was a significant difference in reproductive success variables between categorical environmental variables such as nest box entry type and nest box attachment type.

Results

Route specific models

The mean proportion of nest boxes occupied per route decreased with time for mountain bluebirds ($r^2 = 0.13$, $t_{32} = -2.44$, $p = 0.02$; Figure 2.1a), but tree swallow nest box occupancy was stable over the study period ($r^2 = -0.02$, $t_{32} = -0.50$ $p = 0.62$; Figure 2.1a).

Eggs

The top model explaining variation in the mean number of eggs laid for mountain bluebirds included effects of April precipitation and year (Table 2.1). The other top models within 4 AICc units included the above effects as well as June temperature, July temperature, and SOI. For mean number of mountain bluebird eggs, confidence intervals for model-averaged parameter estimates for year did not overlap zero and parameter estimates were negative (-0.0082 (-0.016, -0.00097), Table 2.2), indicating a decrease in mean number of eggs over time ($r^2 = 0.12$, $t_{31} = -2.33$, $p = 0.03$; Figure 2.1b). The top model explaining variation in mean number of eggs for tree swallows included SOI, but confidence intervals overlapped zero. The next top four models for tree swallow eggs included effects of April precipitation, year, June temperature, and July temperature (Table 2.1).

Nestlings

The top model explaining variation in the mean number of mountain bluebird nestlings included May precipitation (Table 2.1). The other top models included April precipitation, May temperature, July temperature and year. Confidence intervals for model-averaged parameter estimates for May precipitation did not overlap zero and parameter estimates were negative (-0.0042 (-0.0095, -0.000015), Table 2.2), indicating a decrease in mean number of nestlings with increasing May rainfall. However, when considering annual mean number of nestlings totalled across all routes rather than each route individually, the relationship between nestlings and May precipitation was non-significant ($r^2 = 0.05$, $t_{31} = -1.67$, $p = 0.10$; Figure 2.2a).

The top model explaining variation in mean number of tree swallow nestlings included the effects of April temperature, year, and SOI (Table 2.1). Other top models included May temperature, June temperature, and June precipitation. Confidence intervals for model-averaged parameter estimates for April temperature (-0.1107709 (-0.22, -0.0094)) and SOI (-0.33, (-0.57, -0.092)) did not overlap zero and parameter estimates were negative (Table 2.2), indicating a decrease in mean number of tree swallow nestlings with increasing April temperature and increasing SOI values. Similarly, when considering annual mean number of nestlings across all routes, there was a significant association between number of tree swallow nestlings and SOI values ($r^2 = 0.20$, $t_{31} = -2.97$, $p = 0.006$; Figure 2.2b), indicating more nestlings were observed during warmer El Niño years for tree swallows. However, there was no significant effect of April temperature on number of tree swallow nestlings when considering mean annual nestlings across all routes ($r^2 = 0.02$, $t_{31} = -1.23$, $p = 0.23$; Figure 2.2c).

Fledglings

The top model for mean number of mountain bluebird fledglings included June precipitation and year, and other top models included April temperature, May temperature, May precipitation, and July precipitation (Table 2.1). For mean number of mountain bluebird fledglings, confidence intervals for model-averaged parameter estimates for year (-0.018 (-0.029, -0.0071)) and June precipitation (-0.0059 (-0.012, -0.00078)) did not overlap zero and parameter estimates were negative for both (Table 2.4), indicating a decrease in mean number of fledglings over time and with increasing June rainfall. Similarly, when considering annual mean number of fledglings across all routes, there was a significant decline over time ($r^2 = 0.13$, $t_{31} = -2.44$, $p = 0.02$; Figure 2.1c) and with June rainfall ($r^2 = 0.09$, $t_{31} = -2.06$, $p = 0.048$; Figure 2.2d).

The top model for mean number of tree swallow fledglings included the effects of April precipitation and May temperature (Table 2.1). Other top models also included April temperature, May precipitation, June precipitation and year. Confidence intervals for model-averaged parameter estimates for April precipitation did not overlap zero and parameter estimates were positive (0.014 (0.0054, 0.023), Table 2.2), indicating an increase in mean number of fledglings with increasing April rainfall. Linear regression analysis between annual mean number of fledglings across all routes and April precipitation approached significance ($r^2 = 0.09$, $t_{31} = 2.02$, $p = 0.052$; Figure 2.2e).

Hatching success

The top model explaining variation in tree swallow hatching success included June precipitation, July temperature, and SOI (Table 2.1). Other top models included April temperature, May precipitation, and July precipitation. Confidence intervals for model-averaged parameter estimates for July temperature (-0.93 (-2.69, -0.0064)) and SOI (-3.65 (-7.16, -046)) did not overlap zero and parameter estimates were negative (Table 2.2), indicating a decrease in hatching success with higher July temperatures and with higher SOI values. Similarly, when considering annual mean hatching success across all routes, a significant decline was noted in relation to both July temperature ($r^2 = 0.10$, $t_{31} = -2.13$, $p = 0.04$; Figure 2.2f) and SOI ($r^2 = 0.18$, $t_{31} = -2.81$, $p = 0.008$; Figure 2.2g). This indicates a lower hatching success for tree swallows during cooler, drier La Niña years. The top model explaining variation in mountain bluebird hatching success included May precipitation, but confidence intervals overlapped zero. Other top models included effects of SOI, May temperature, and June temperature (Table 2.1).

Box specific models, 2001-2014

Eggs

The top model explaining variation in mountain bluebird number of eggs was the null model (Table 2.3). The top model explaining variation in tree swallow number of eggs included April temperature, but confidence intervals overlapped zero. Other top models included effects of April precipitation, May precipitation, and May temperature (Table 2.3).

Nestlings

The top model explaining variation in number of mountain bluebird nestlings included April temperature, April precipitation and May precipitation (Table 2.3). Other top models included June precipitation, July temperature and box attachment type. For number of mountain bluebird nestlings, confidence intervals for model-averaged parameter estimates for April temperature and April precipitation did not overlap zero and parameter estimates were negative (Table 2.4), indicating a decrease in number of nestlings with increasing temperature and rainfall in April. However, when considering annual mean nestlings across all routes, these relationships were not significant for April precipitation ($r^2 = 0.09$, $t_{12} = -1.49$, $p = 0.16$; Figure 2.3a) nor April temperature ($r^2 = 0.12$, $t_{12} = -1.65$, $p = 0.12$; Figure 2.3b). The top model explaining variation in number of tree swallow nestlings included April precipitation, but confidence intervals overlapped zero. Other top models included effects of April temperature, June precipitation and box attachment type (Table 2.3).

Fledglings

The top model for number of mountain bluebird fledglings included April temperature, April precipitation and year, and the other top models included May temperature, May precipitation, July precipitation, and box attachment type (Table 2.3). Confidence intervals for model-averaged parameter estimates for April temperature, April precipitation and year did not overlap zero and parameter estimates were negative for all three (Table 2.4), indicating a decrease in number of fledglings with increasing temperature and rainfall in April, as well as over time. Similarly, the annual mean number of fledglings per nest across all routes significantly decreased with April precipitation ($r^2 = 0.39$, $t_{12} = -3.05$, $p = 0.01$; Figure 2.3c) but not with April temperature ($r^2 = 0.01$, $t_{12} = -1.09$, $p = 0.30$; Figure 2.3d) nor year ($r^2 = 0.05$, $t_{12} = -1.30$, $p = 0.22$; Figure 2.1d).

The top model explaining variation in number of tree swallow fledglings included June temperature, July temperature, and box attachment type, with other models including June precipitation, bearing of box opening, and elevation (Table 2.3). Confidence intervals for model-averaged parameter estimates for June temperature, July temperature, and box attachment type (tree) did not overlap zero and parameter estimates were negative (Table 2.4), indicating a decrease in number of fledglings with higher temperatures in June and July, and in nest boxes attached to trees rather than fences. However, when considering annual mean fledglings across all routes, these relationships were not significant for June temperature ($r^2 = 0.11$, $t_8 = -1.47$, $p = 0.18$; Figure 2.3e) nor July temperature ($r^2 = 0.22$, $t_8 = -1.90$, $p = 0.09$; Figure 2.3f).

Box specific models, 2013-2014

We conducted further analyses using the reduced box specific dataset containing data from 2013 and 2014 for which we could be certain that nest box opening type was correct. For mountain bluebird eggs, confidence intervals for all parameter estimates overlapped zero. Box opening type was the only variable in the top model for number of mountain bluebird nestlings and fledglings that had confidence intervals that did not overlap zero (Table 2.5). Other top models for nestlings included April precipitation and April temperature, similar to the results of the full 2001-2014 box specific dataset. Parameter estimates for slot boxes were negative for both mountain bluebird nestlings and fledglings (Table 2.4), indicating a lower number of nestlings and fledglings in slot type boxes than hole type. Similarly, when considering annual mean number of nestlings and fledglings across all routes for 2013 and 2014 separately, significantly more mountain bluebird nestlings per nest ($t_{49.68} = 3.20$, $p = 0.002$; Figure 2.4a) and fledglings per nest ($t_{51.43} = 2.57$, $p = 0.01$; Figure 2.4b) were produced in hole boxes than in slot boxes.

For tree swallow eggs, confidence intervals for all parameter estimates overlapped zero. The confidence intervals for April temperature and April precipitation did not overlap zero for tree swallow nestlings (Table 2.4), even though the top model included attachment type and April precipitation (Table 2.5). Other top models included April temperature and box type. For tree swallow fledglings, the top model included nest box attachment type (Table 2.5). Other top models included June temperature. However, confidence intervals for model-averaged parameter estimates for box opening type overlapped zero and there was no significant difference in annual mean number of fledglings between attachment types, although samples sizes were small for tree-attached boxes which may explain the lack of an effect ($n = 7$, $t_{6.39} = 1.59$, $p = 0.16$; Figure 2.4c).

Discussion

Based on citizen science data collected in the semi-arid grasslands of British Columbia, Canada, mountain bluebirds experienced reductions in nest box occupancy rates, clutch size, and number of fledglings over the past 35 years, while tree swallow occupancy rates and reproductive success remained relatively stable. Our results indicate that local weather is an important factor contributing to variation in mountain bluebird breeding success. Tree swallow breeding success also appears to be linked to local weather and, in addition, to regional climate cycles. Interestingly, nest box opening type also appeared to be important for mountain bluebirds, as birds nesting in hole-type boxes experienced higher breeding success than those nesting in slot-type boxes.

Mountain bluebird nest box occupancy decreased from approximately 58% in 1980 to 47% in 2014. Although this decline in box occupancy (-0.3% annually) is less than the Bird Conservation Region 9 average for population declines (-1.5% annually, Pardieck et al. 2015), the decline in bluebird occupancy is significant and may be due to a number of factors, including changes in population density or wintering, migration or breeding conditions. Because western bluebirds out-compete mountain bluebirds for nesting sites after mountain bluebird territories have been established, range expansion of western bluebirds in this area might result also in a reduction in the number of mountain bluebirds able to nest (Duckworth et al. 2015). However, western bluebirds were rare in the study area. (There were only 38 records of western bluebird box occupancy from 1980 to 2014.) A decline in the average number of mountain bluebird eggs and fledglings over time was detected, which could explain the decrease in box occupancy by mountain bluebirds. Tree swallow occupancy was generally stable over the study period, though tree swallows occupied fewer boxes than mountain bluebirds overall (approximately 42% of available boxes). This stable occupancy is consistent with previous studies showing steady or increasing tree swallow population densities in western North America (Shutler et al. 2012), in contrast to the declining populations of this species and other aerial insectivores in eastern North America (Nebel et al. 2010).

Local weather appeared to influence the breeding performance of mountain bluebirds more than tree swallows, with higher local precipitation associated with lower mountain bluebird breeding success. In particular, April (box specific data) and June (route specific data) precipitation were both negatively associated with number of fledglings, which suggests higher nestling mortality with greater rainfall during these months. The correlation between high June rainfall and low number of fledglings is consistent with previous studies of mountain bluebirds and suggests that cold rainy spells during the nesting period can lead to increased chick mortality (Power & Lombardo 1996). However, it is unclear whether high June rainfall directly or indirectly contributed to nestling mortality. One possibility is that direct mortality of nestlings occurred during heavy June rainfall, since being wet can reduce the thermoregulatory capabilities of nestlings (Gullett et al. 2015). Alternatively, or in addition, rainfall may reduce the provisioning rates of nestlings by bluebird parents (Møller et al. 2010), causing indirect mortality of nestlings due to starvation.

High rainfall in April may also indirectly influence nestling mortality by preventing effective foraging by both parents, which would lead to poorer body condition during the prelaying and egg laying stages (Lepage et al. 2000). Food supplementation experiments during the prelaying stage suggest a causal effect of parental body condition on reproductive success; individuals with improved body condition experience higher reproductive success (Daan et al. 1988, Korpimäki & Wiehn 1998, Lepage et al. 2000). Alternatively, higher rainfall in April might delay egg-laying (Dhondt & Eyckerman 1979, Meijer et al. 1999), which can also have negative consequences for reproductive success (Lack 1968, Dunn 2004). Thus, while we cannot discern the exact causal mechanism(s) linking April precipitation to number of mountain bluebird fledglings, our results are consistent with previous studies linking early breeding season rainfall with reproductive success.

For tree swallows, we found that higher July temperatures were associated with lower hatching success. This is contrary to the results of other studies, which have shown that warmer temperatures can improve hatching success (Martin 1987), as well as fledging success (Reid et al. 2000), nestling survival (Ardia et al. 2010) and post-fledging survival (Sankamethawee et al. 2009, Grüebler & Naef-Daenzer 2010). However, past a certain thermal threshold (usually around 36 – 39°C), organ failure and embryonic death can occur within an egg (Webb 1987). As the microclimate within artificial nest boxes can be up to 10°C warmer than the ambient temperature (McComb & Noble

1981), it could easily surpass 40°C within a nest box in the Kamloops grasslands in July (daily highs ranged from 26°C to 30°C, occasionally exceeding 35°C). Many tree swallows were still incubating their eggs in July in our study area (Author, unpublished data). The fact that a negative association between reproductive success and high temperatures was not seen in mountain bluebirds may be due to their earlier breeding phenology; most mountain bluebird nests were at the nestling stage in July, with some fledging as early as late July (Author, unpublished data). The lack of fine-scale phenological information is a limitation of this citizen science dataset, because volunteers collected nesting data only every 7-10 days.

Tree swallow reproductive success was also linked to large-scale climatic trends. Negative values of the Southern Oscillation Index were correlated with more tree swallow nestlings and higher hatching success, which suggests improved breeding performance during El Niño years (i.e., those with lower annual mean SOI values). El Niño events and lower SOI values have been linked to increased regional primary productivity (Barnston & Livezey 1987, Swetnam & Betancourt 2010) and increased insect prey abundance (Kemp et al. 1985, Swetnam & Lynch 1993) in northern latitudes of North America, which would improve tree swallow foraging throughout the breeding season, possibly contributing to improved breeding performance (Nott et al. 2002). This result is consistent with previous studies of other species: large-scale regional climate patterns such as ENSO have been shown to account for the majority of inter-annual variability in reproductive success for at least 10 other migratory bird species (Nott et al 2002).

However, we also observed a negative effect of April temperature on tree swallow nestlings, which is counter to the effect of negative effect of SOI on the same tree swallow metric. Yet, we did not observe this effect when considering all routes across all years. Additionally, the link between SOI and tree swallow reproductive success may also be driven by El Niño effects occurring outside the breeding season. Environmental conditions experienced throughout the annual cycle can influence both individuals (e.g., Saino et al. 2004, Reudink et al. 2009) and populations (e.g., Wilson et al. 2011, Pillar et al. 2014). In addition, carry-over effects of climate from one phase of the annual cycle to the next can also have differential effects on species that vary in migratory distance. Long-distance migrants may be more sensitive to environmental changes than short-distance migrants because of the energetic demands of longer migration journeys and the subsequent costs of reduced habitat quality at different stages of the annual cycle (Nebel et al. 2010). Based on range distribution maps, mountain bluebirds appear to have a shorter migratory distance than tree swallows (Power & Lombardo 1996, Winkler et al. 2011), which may explain why we observed an effect of SOI on tree swallows, but not mountain bluebirds on our study site. In addition, because the overwintering locations of mountain bluebirds (throughout southern US states and Midwest and northern to central Mexico, Power & Lombardo 1996) and tree swallows (southern edge of southern US states, throughout Mexico and eastern Central America to Costa Rica, Winkler et al. 2011) differ, regional climate may influence their overwintering locations differentially. Such species-specific differences have been noted elsewhere. For example, both breeding and wintering populations of black-throated warblers appear to be sensitive to ENSO cycle fluctuations (Sillett et al. 2000), while the breeding abundance of American redstarts is predicted by primary productivity on the wintering grounds in eastern, but not western populations (Wilson et al. 2011). As well, Bullock's orioles are sensitive to primary productivity on the breeding, but not wintering grounds (Pillar et al. 2014).

We also considered how nest box features, including box opening type (hole or slot) and box attachment type (fence or tree), might affect reproductive success in tree swallows and mountain bluebirds. The only nest box feature that we found to significantly predict breeding performance was nest box entrance type. Nest boxes with hole-shaped entrances had a higher number of mountain bluebird nestlings and fledglings than those with slot-shaped entrances. This is perhaps due to slot-shaped entrances being more exposed to the environment and/or being less effective at deterring predators. We are not aware of other studies that have shown differences in bird productivity between different next box types, but based on our data, we recommend that conservationists and naturalist clubs interested in improving their existing bluebird routes or in establishing new routes focus on building hole-type nest boxes for mountain bluebirds. We also observed a general improvement in tree swallow breeding performance when using nest boxes attached to fences rather than trees, although the power of our statistical analysis for this metric was low. This observation is consistent with previous studies of tree swallow nest box preference that showed swallows were more common in sites with long grass rather than in wooded areas, likely because there is more space for them to forage aerially (Winkler et al. 2011). It is important to note that we were unable to control for box type in our long-term analyses, although we are not aware of any changes in the frequency of different box types used over the study period.

As well, it should be noted that because this study focused on a population of mountain bluebirds and tree swallows occupying artificial nest boxes, some caution is needed when inferring that the patterns we observed are what would also be observed in a population breeding in natural cavities. There are several differences in populations studied in nest boxes, including: 1) possibly higher breeding densities, 2) nests along roadways which may or may not have an effect on food availability, productivity, disturbance, nest predation, behaviour, etc., and 3) different characteristic of the nest site. With respect to the latter, because we found differences in breeding success between nest box opening type, differences between artificial and natural cavities or differences among natural cavity opening types may also be observed.

In conclusion, we demonstrate that, over a 35-year period, mountain bluebirds in the grasslands of interior British Columbia exhibited a significant decline in nest box occupancy rates and reproductive success, and that reproductive success was associated with inter-annual variation in local weather patterns. We also found that although tree swallow reproductive success appeared to be linked to regional climatic patterns and local weather, occupancy rates and reproductive success of this species remained relatively stable in the Kamloops region. Future studies into the causal mechanisms driving the associations between local weather and regional climate and the reproductive success of grassland songbirds in British Columbia may demonstrate whether climatic conditions are acting directly or indirectly on breeding performance. On the basis of our results, we recommend that managers of artificial nest box programs for mountain bluebirds and tree swallows use boxes with of hole-shaped nest box entrances and mount nest boxes on fences rather than trees.

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Table 2.1 The AICc value, difference in AICc between the model and top model (ΔAICc), and model weights (w_i) for models explaining variation in reproductive success measures for mountain bluebirds and tree swallows using route specific data from 1980 to 2014. Route was included as a random effect in all models.

A April, *M* May, *J* June, *Jl* July, *Rn* total rainfall, *Tp* mean temperature (e.g., JRn = total June rainfall), *Yr* year, *SOI* annual mean SOI value

Model category	**Top models**	**AICc**	**ΔAICc**	**w_i**
Mountain bluebird mean eggs	ARn + Yr	866.3	0.00	0.03
	Yr	866.9	0.64	0.02
	ARn + Yr + JTp	867.8	1.51	0.01
	ARn + Yr + SOI	867.9	1.54	0.01
	ARn + Yr + JlTp	867.9	1.59	0.01
Tree swallow mean eggs	SOI	1111.6	0.00	0.02
	ARn + Yr	1112.3	0.71	0.02
	Yr + SOI	1112.3	0.74	0.02
	Yr	1112.6	1.04	0.01
	ARn + SOI	1112.9	1.36	0.01
Mountain bluebird mean nestlings	MRn	1041.6	0.00	0.03
	MRn + Yr	1042.8	1.19	0.02
	MRn + ARn	1043.2	1.52	0.02
	MRn + MTp	1043.5	1.85	0.01
	MRn + JlTp	1043.5	1.86	0.01
Tree swallow mean nestlings	ATp + Yr + SOI	1247.4	0.00	0.04
	ATp + Yr + SOI + JRn	1248.6	1.20	0.02
	ATp + Yr + SOI + JTp	1249.1	1.67	0.02
	ATp + Yr + SOI + MTp	1249.2	1.75	0.02
	ATp + Yr + SOI +ARn	1249.2	1.75	0.02

Mountain bluebird mean fledglings	JRn + Yr	1147.9	0.00	0.04
	JRn + Yr +MRn	1149.0	1.06	0.02
	JRn + Yr + ATp	1149.1	1.14	0.02
	JRn + Yr + MTp	1149.2	1.23	0.02
	JRn + Yr +JlRn	1149.2	1.32	0.02
Tree swallow mean fledglings	ARn + MTp	1283.7	0.00	0.01
	ARn + MRn + JRn	1284.1	0.45	0.01
	ARn + ATp + MRn + JRn	1284.4	0.72	0.01
	ARn + MRn	1284.4	0.76	0.01
	ARn	1284.5	0.78	0.01
Mountain bluebird hatch success	MRn	3318.6	0.00	0.03
	Null	3319.0	0.45	0.02
	MRn + SOI	3320.3	1.69	0.01
	MRn + MTp	3320.3	1.70	0.01
	MRn + JTp	3320.3	1.70	0.01
Tree swallow hatch success	JRn + JlTp + SOI	3274.3	0.00	0.03
	JRn + JlTp + SOI + ATp	3275.1	0.79	0.02
	JRn + JlTp + SOI + MRn	3275.7	1.45	0.01
	JRn + SOI + ATp + Yr	3275.9	1.63	0.01
	JRn + JlTp + JlRn + SOI	3276.0	1.75	0.01

Table 2.2 Model-averaged parameter estimates and 95% CI that did not overlap zero for variables included in the top-ranked models (<4 AICc units of best model) explaining variation in reproductive success measures for mountain bluebirds and tree swallows using route specific data from 1980 to 2014.

MOBL mountain bluebird, *TRSW* tree swallow, *nlgs* nestlings, *flgs* fledglings, see Table 2.1 for all other abbreviations

	MOBL eggs	MOBL nlgs	TRSW nlgs	MOBL flgs	TRSW flgs	TRSW hatch success
ATp			-0.1107709 (-0.22, -0.0094)			
ARn					0.014 (0.0054, 0.023)	
MRn		-0.0042 (-0.0095, -0.000015)				
JRn				-0.0059 (-0.012, -0.00078)		
JlTp						-0.93 (-2.69, -0.0064)
SOI			-0.33 (-0.57, -0.092)			-3.65 (-7.16, -046)
Yr	-0.0082 (-0.016, -0.00097)			-0.018 (-0.029, -0.0071)		

Table 2.3 The AICc value, difference in AICc between the model and top model (ΔAICc), and model weights (w_i) for models explaining variation in reproductive success measures for mountain bluebirds and tree swallows using box specific data from 2001 to 2014. Route was included as a random effect in all models.

El elevation of nest box, *Br* bearing of nest box opening, *At* attachment type of nest box (i.e., fence or tree), see Table 2.1 for all other abbreviations

Model category	Top models	AICc	ΔAICc	w_i
Mountain bluebird eggs	Null	2508.1	0.00	0.01
	El	2508.5	0.40	0.01
	El + Yr	2509.0	0.90	0.01
	Yr	2509.3	1.21	0.01
	ARn	2509.6	1.48	0.01
Tree swallow eggs	ATp	1865.7	0.00	0.01
	MRn	1866.2	0.46	0.01
	Null	1866.3	0.61	0.01
	ARn	1866.9	1.16	0.01
	MTp	1866.9	1.16	0.01
Mountain bluebird nestlings	ATp + ARn + MRn	2808.5	0.00	0.02
	ATp + ARn + MRn + At	2809.3	0.84	0.01
	ATp + ARn + MRn + JlTp	2809.6	1.11	0.01
	ATp + ARn + JRn	2810.1	1.58	0.01
	ATp + ARn + MRn + JRn	2810.2	1.76	0.01
Tree swallow nestlings	ARn	2222.1	0.00	0.01
	ATp	2222.1	0.07	0.01
	ATp + JRn	2222.8	0.74	0.01
	ARn + At	2222.9	0.87	0.01
Mountain bluebird fledglings	ATp + ARn + Yr	2988.9	0.00	0.07
	ATp + ARn + MTp + Yr	2989.8	0.90	0.04
	ATp + ARn + JlRn + Yr	2990.0	1.17	0.04

	ATp + ARn + MRn + Yr	2990.2	1.36	0.03
	ATp + ARn + Yr + At	2990.4	1.56	0.03
Tree swallow fledglings	JTp + JlTp + At	2311.1	0.00	0.01
	JTp + JlTp + At + Br	2312.1	1.07	0.01
	JTp + At	2312.2	1.13	0.01
	JTp + JlTp + At + El	2312.2	1.14	0.01
	JTp + JRn + JlTp + At	2312.8	1.72	0.01

Table 2.4 Model-averaged parameter estimates and 95% CI that did not overlap zero for variables included in the top-ranked models (<4 AICc units of best model) explaining variation in reproductive success measures for mountain bluebirds and tree swallows using box specific data from 2001 to 2014. Results for Bt (slot) box type are from the reduced box specific dataset from 2013 and 2014.

See Table 2.1 and 2.2 for abbreviations

	MOBL nlgs	**TRSW nlgs**	**MOBL flgs**	**TRSW flgs**
ATp	-0.034 (-0.087, -0.0029)	-0.044 (-0.26, -0.020)	-0.093 (-0.13, -0.052)	
ARn	-0.0031 (-0.0070, -0.00040)	0.006 (0.0013, 0.018)	-0.0066 (-0.011, -0.0025)	
JTp				-0.072 (-0.19, -0.031)
JITp				-0.027 (-0.15, -0.014)
At				-0.55 (-0.95, -0.15)
Yr			-0.033 (-0.035, -0.31)	
Bt (slot)	-0.36 (-0.55, -0.16)		-0.32 (-0.52, -0.12)	

Table 2.5 The AICc value, difference in AICc between the model and top model (ΔAICc), and model weights (w_i) for box specific models with box type and attachment type included (i.e., from 2013 and 2014 only). Route was included as a random effect in all models.

Bt nest box opening type (i.e., hole or slot), see Tables 2.1 and 2.2 for all other abbreviations

Model category	**Top models**	**AICc**	**ΔAICc**	**wi**
Mountain bluebird eggs	Null	224.8	0.00	0.22
	Bt	225.4	0.56	0.16
	At	227.0	2.22	0.07
	ARn	227.0	2.22	0.07
Tree swallow eggs	At	229.9	0.00	0.26
	Null	231.8	1.85	0.10
	At + ARn	231.9	2.00	0.09
	At + Arn + Atp	231.9	2.00	0.09
Mountain bluebird nestlings	Bt	1190.6	0.00	0.35
	Bt + ARn	1191.6	1.00	0.21
	Bt + ARn + ATp	1191.6	1.00	0.21
Tree swallow nestlings	At + ARn	284.3	0.00	0.12
	At	284.3	0.00	0.12
	At + Arn + Atp	284.3	0.00	0.12
	At + Arn + Bt	284.9	0.60	0.09
	At + Arn + Atp + Bt	284.9	0.60	0.09
Mountain bluebird fledglings	Bt	1234.9	0.00	0.25
	Bt+ Yr	1236.6	1.71	0.11
	Bt + ARn	1236.6	1.71	0.11
Tree swallow fledglings	At	1247.4	0.00	0.13
	At + JTp	1247.4	0.00	0.13
	Null	1249.0	1.61	0.06

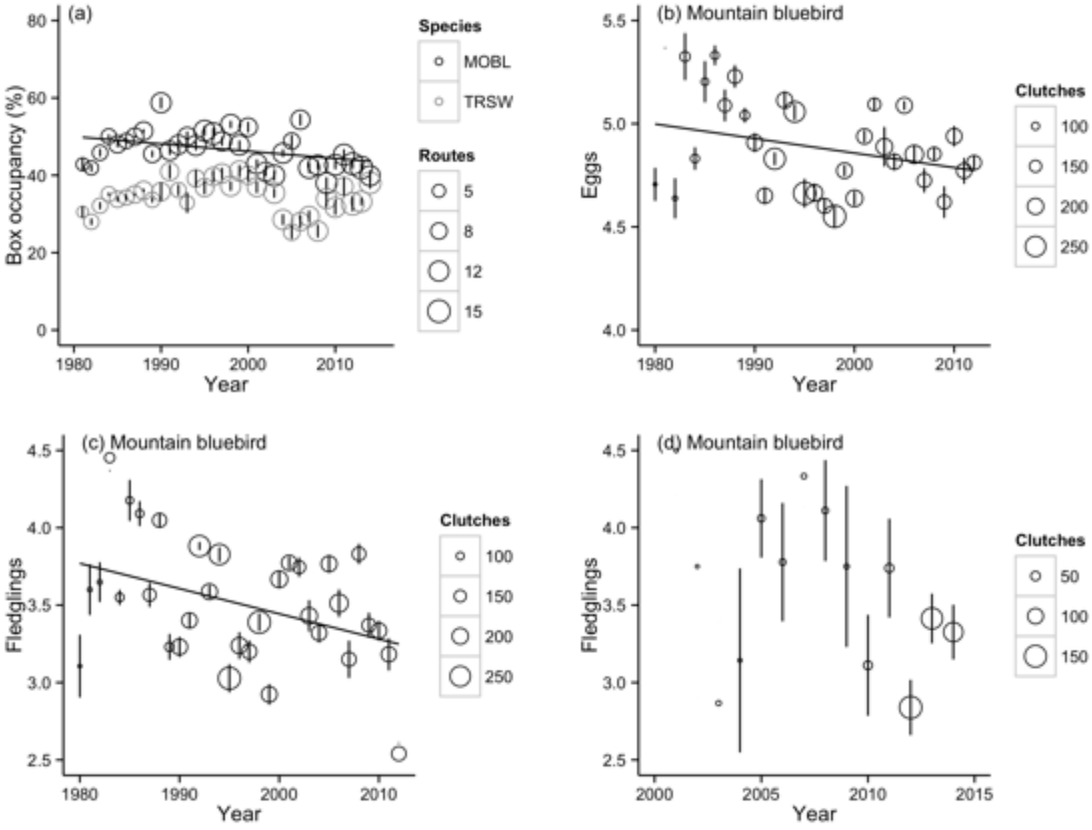

Figure 2.1 Year effects for route specific (a, b, c) and box specific (d) analyses for mountain bluebird and tree swallow reproductive success from 1980 to 2014. Nest box occupancy **(a)** for mountain bluebirds decreased over time. Mountain bluebird **(b)** mean number of eggs and **(c)** mean number of fledglings decreased over time. Mountain bluebird **(d)** mean number of fledglings did not significantly change over time. Data points are weighted by the annual number of routes (a) and clutches (b, c, d). Error bars represent standard error. *MOBL* mountain bluebird, *TRSW* tree swallow.

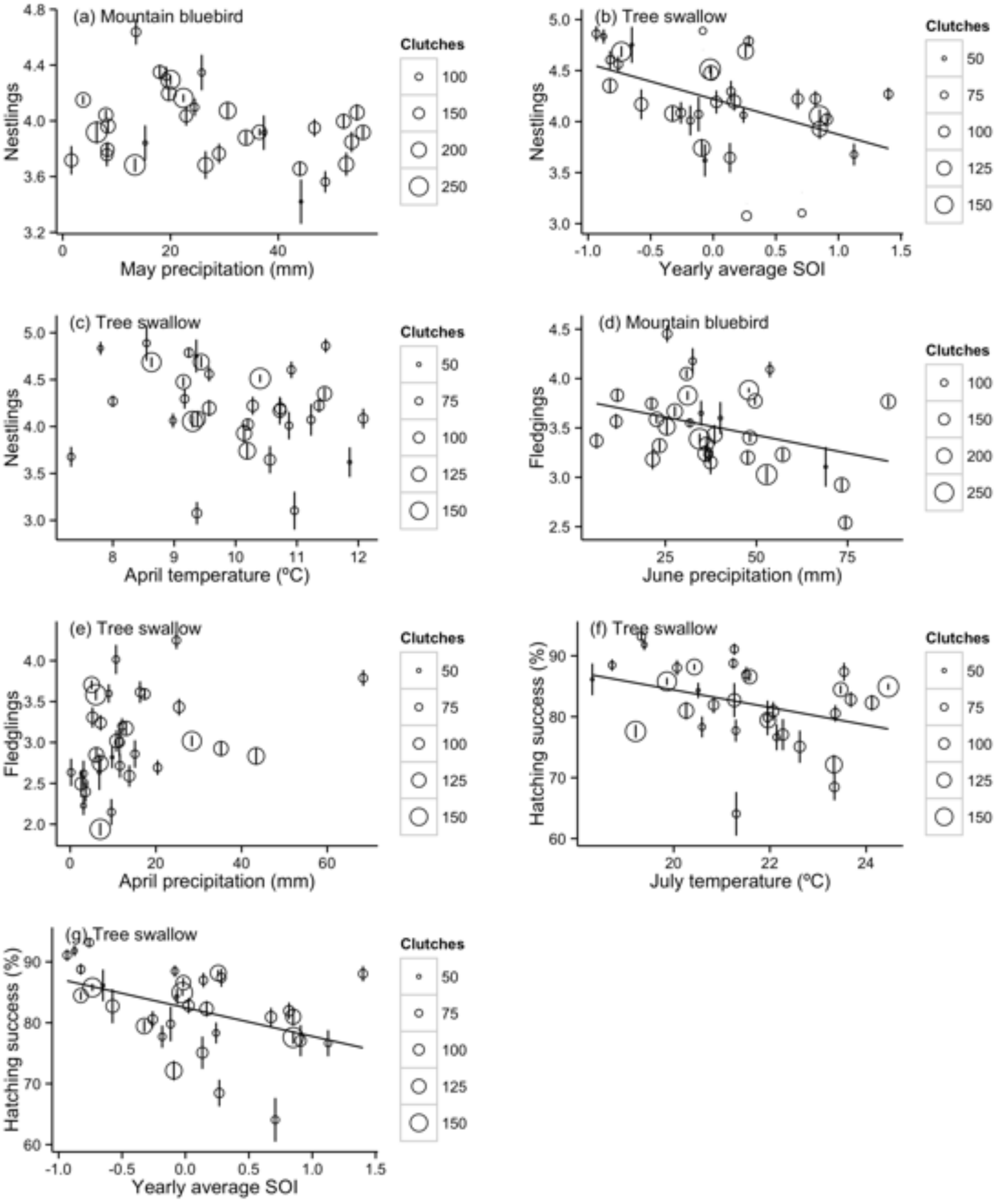

Figure 2.2 Weather and climate effects for route specific analyses of mountain bluebird and tree swallow reproductive success from 1980 to 2014. Mountain bluebird (a) mean number of nestlings did not significantly vary with total May precipitation. Tree swallow (b) mean number of nestlings decreased with Southern Oscillation Index (SOI) values but did not vary with (c) mean April temperature. Mountain bluebird (d) mean number of fledglings decreased with total June precipitation. Tree swallow (e) mean number of fledglings did not vary with mean April precipitation. Tree

swallow hatching success decreased with (f) mean July temperature and (g) SOI. Data points are weighted by the annual number of clutches. Error bars represent standard error.

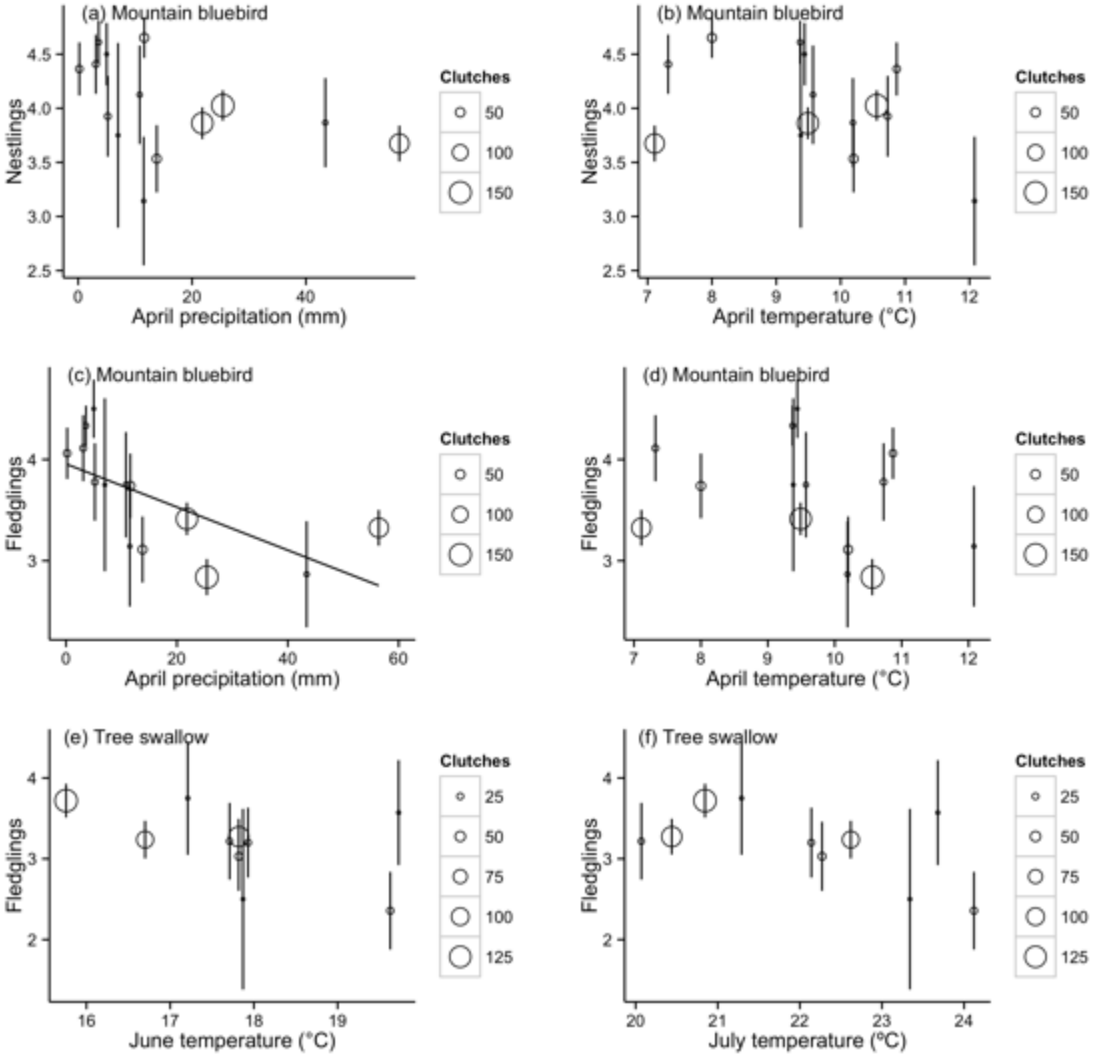

Figure 2.3 Weather effects for box specific data for mountain bluebird and tree swallow reproductive success from 2001 to 2014. Mountain bluebird mean number of fledglings per nest did not vary with (a) total April precipitation nor with (b) mean April temperature. Mountain bluebird mean number of fledglings per nest decreased with (c) total April precipitation but not with (d) mean April temperature. The mean number of tree swallow fledglings per nest did not vary with (e) June temperature nor (f) July temperature. Data points are weighted by the annual number of clutches. Error bars represent standard error.

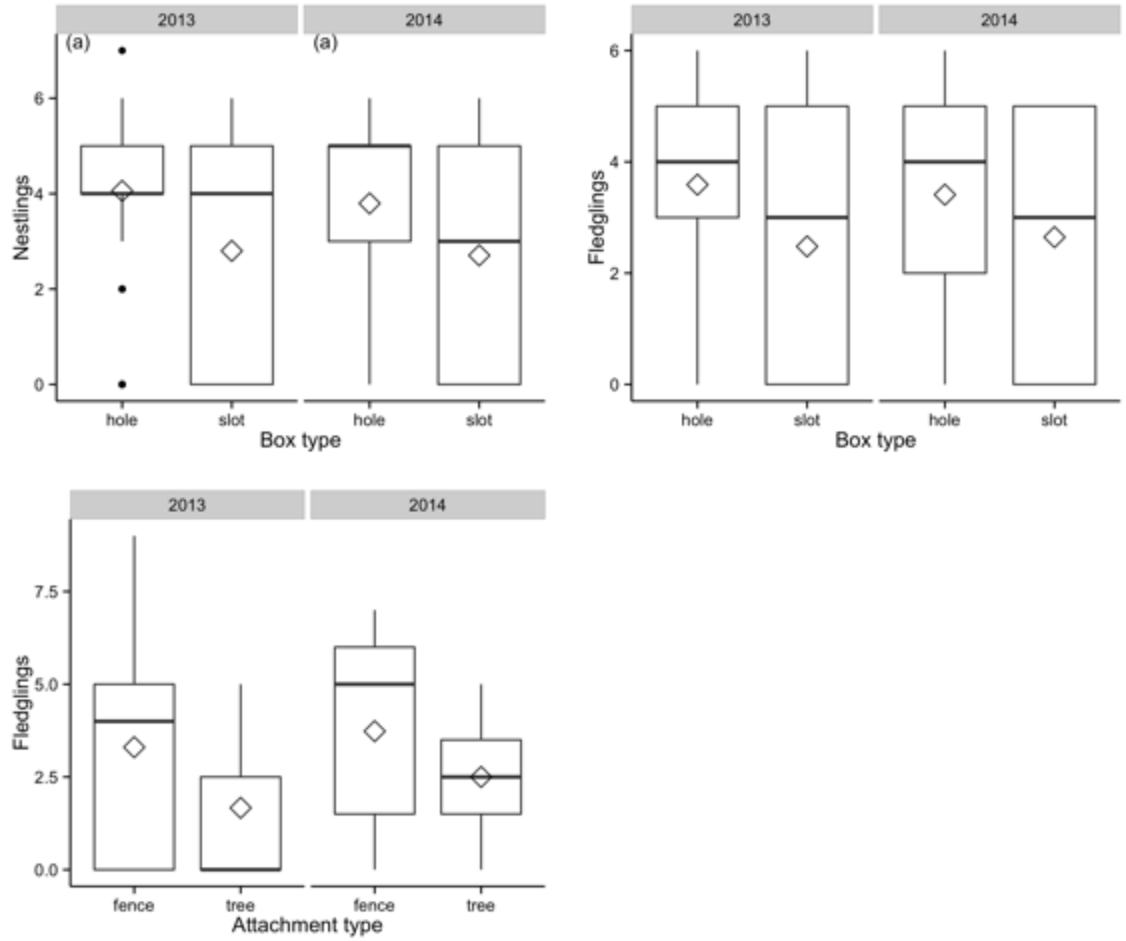

Figure 2.4 Nest box feature effects for the reduced dataset for 2013 and 2014. Mountain bluebird (a) mean number of nestlings and (b) mean number of fledglings were significantly higher for hole nest boxes for both years. Tree swallow (c) mean number of fledglings did not differ significantly between fence and tree nest box attachment types. Diamonds in boxes represent mean, the line across the boxes represent median.

Chapter 3

Relative impacts of weather and parental care on mountain bluebird reproductive success

Abstract

Both weather (e.g., precipitation, temperature) and parental care can influence avian reproductive success, yet few studies have investigated both factors concurrently. Here, we assess the relative influence of local weather and levels of parental provisioning on the breeding performance of mountain bluebirds (*Sialia currucoides*). Ambient temperature better predicted the number of fledglings than did rainfall or parental effort, but this finding was dependent on nest box entrance type. Reproductive success of individuals breeding in nest boxes with a slot-shaped entrance exhibited a stronger and positive association with ambient temperature, whereas success of individuals breeding in nest boxes with a hole-shaped entrance type exhibited a weak negative association with temperature. Boxes with hole-shaped entrances appeared to buffer against temperature shifts more effectively than slot boxes, which may help explain this pattern. We also found no association between weather conditions and rates of nestling growth, so we suggest that the relationship between temperature and bluebird reproductive success is likely an effect of a direct, acute nestling mortality rather than prolonged stress. Based on our results, the direct influence of weather on reproductive success appears to exert a greater effect on nestling survival than parental effort.

Introduction

Weather conditions during the breeding season can influence avian reproductive success in several ways. Hatching and fledging success may be directly influenced by extreme temperatures (Pipoly et al. 2013) or precipitation events (George et al. 1992, Grant et al. 2000). As well, weather can indirectly influence reproductive success through habitat changes (e.g., drought conditions; Ludlow et al. 2014) or changes in food availability and abundance (Grant et al. 2000). Weather may also indirectly affect reproductive success through changing levels of parental care and provisioning rates (Siikamäki 1998, Hoset et al. 2004).

Variation in parental investment in the form of offspring provisioning can have a major impact on the reproductive success of species that rear altricial young (Wright et al. 1998), where higher levels of parental care are associated with improved reproductive success (Rauter et al. 2000). Levels of parental care can affect nestling quality, influencing overall offspring condition (Lifjeld et al. 1998, Klug & Bonsall 2014), which, in turn, affects the reproductive success of parents. Additionally, the effort that parents expend provisioning their young can influence nestling growth rates; early nestling nutrition is linked to fledgling mass (Soma et al. 2006, Wilkin et al. 2009).

Weather can play an important role in influencing parental care behavior, and thus indirectly influence reproductive success. For example, in water pipits (*Anthus spinoletta*), females increase provisioning rates with decreasing ambient temperature (Rauter et al. 2000). This is also true for snow buntings (*Plectrophenax nivalis*) breeding in the Arctic, with the provisioning rates of both parents increasing during periods of low temperatures, likely to due to an increase in the metabolic demands of chicks in cool weather (Hoset et al. 2004). The availability of insect prey can also be mediated by weather conditions, which influences rates at which parents can provision their offspring (White 2008). Thus, while both weather and parental care can affect reproductive success, it is unclear as to the relative importance of these factors in determining overall reproductive success.

We studied a population of mountain bluebirds (*Sialia currucoides*) breeding in artificial nest boxes in a semi-arid grassland in the southern interior of British Columbia, Canada, to investigate the relative influence of weather and parental care in predicting reproductive success. Previous studies of mountain bluebirds in this region support the notion that weather conditions can negatively influence reproductive success (Author, Ch.2), however, it is not known whether this effect is acting directly (through nestling mortality) or indirectly (through a reduction in parental care behavior). We also asked if the effect of weather on reproductive success was acute (i.e., a direct impact via nestling mortality, with no effect on nestling growth) or if it acted over a prolonged period of time (i.e., if nestling growth rates changed over time with respect to weather).

Previous work on this population of mountain bluebirds has shown a difference in the effect of weather conditions on reproductive success between the opening type of the nest box occupied (i.e., nest boxes with a hole or slot opening; Author, Ch.2). At least 10 other species appear to prefer nest cavities with smaller entrance diameters (van Balen et al. 1982), though to our knowledge no studies have reported differences in reproductive success in relation to the form of the cavity entrance. The difference in reproductive success between box types in bluebirds may be because hole nest boxes have a smaller entrance diameter than slot nest boxes (Appendix A1) and may thus provide better insulation against the cold or better protection from the elements, predators, or nest competitors than slot boxes. To begin to address this question, we used temperature loggers to examine whether there was a difference in the internal temperature of hole and slot nest boxes.

Materials and Methods

Study species

Mountain bluebirds (*Sialia currucoides*) are small obligate secondary cavity-nesting thrushes that readily breed in artificial nest boxes throughout North America's grasslands. As predominantly ground-foraging insectivores during the breeding season, mountain bluebird diet consists mostly of Coleopera, Orthopera, Formicidae, Lepidoptera, Hymenoptera and Hemiptera (Power & Lombardo 1996). Both males and females provision offspring, but females tend to provision at higher rates (Power & Lombardo 1996).

Field methods

Fieldwork for this project was conducted on bluebird trails maintained by the Kamloops Naturalist Club in Knutsford, British Columbia, Canada (50.62°N, 120.33°W) from May-August 2011 to 2014. We recorded the number of eggs laid, number of nestlings, and number of fledglings for each nest box. Parents at each nest box were caught and banded with a unique aluminum Canadian Wildlife Service band and three colour bands.

Parental provisioning rates were quantified during the early nestling stage (3-5 days after hatching) and late nestling stage (14-16 days after hatching), as described in Morrison et al. 2014 and Evans et al. 2015. Parents at each nest were video recorded for 2 hour periods with a Sony Handycam DCR-SX45 (Sony, Toyko, Japan), a GoPro HD Hero2, or a GoPro HD Hero3+ (GoPro, San Mateo, CA). All recordings occurred between 06:20 and 13:00 once during each of the early and the late nestling stages (total: 4 hr/nest), and parental care was quantified as the number of trips to the nest per hour per chick for both male and female parents (Table A1).

Nestling growth data were collected during the 2014 breeding season by measuring length of P1 feathers (mm) on Day 5 and 13 of the nestling period. Average rate of nestling growth was then calculated as the mean difference in P1 length between Day 5 and Day 13 for all nestlings in each nest box.

Weather data

We obtained local weather information by accessing online Environment Canada weather station archives for the Kamloops Pratt Road station, located at 50.60°N, 120.20°W, approximately 10km from our study site. Mean monthly temperature and total monthly precipitation were calculated from daily records for April, May, June, and July for breeding season weather for the years 2011 to 2014. We then calculated the mean nestling period temperature and total nestling period precipitation for each nest box along each route for each year from 2011 to 2014. Nestling period is defined as the time period from the day eggs hatch to the day offspring fledge for each nest.

To assess whether there were differences in internal nest box temperatures between hole and slot nest boxes, iButton Thermochron® Temperature Data Loggers (Maxim Integrated, San Jose, CA) were deployed in five hole boxes and five slot boxes adjacent to one another in September 2015. One iButton was attached on the interior side of each nest box and one was placed on the exterior side of each nest box. Each iButton recorded temperature (sensitivity setting of 0.5°C) every 15 minutes for eleven days.

Statistical analyses

We used piecewise structural equation modelling (SEM) to investigate the correlations among reproductive success, weather conditions, and parental care. We created a path analysis diagram to visualize the decomposition of these relationships with each piecewise model in the structural equation (Figure 1). We constructed 16 models that related number of fledglings to the direct effects of mean nestling period temperature, total nestling period precipitation, and parental care, and to the combined effects of temperature and precipitation, temperature and parental care, precipitation and parental care, and temperature, precipitation and parental care. We also separated our models into hole and slot nest boxes. The fit of each model in the SEM was determined using D-separation tests, and models were compared using Akaike's Information Criterion adjusted for small sample size (AICc), estimated from D-separation tests (Shipley 2013).

To compare the thermal properties of nest box opening type, we assessed whether there was a significant difference for average daily mean, maximum, and minimum internal temperature between hole and slot boxes using Welch's t-test. As well, we used Welch's t-test to evaluate whether there was a significant difference for daily mean, maximum, and minimum difference between internal and external ambient temperatures for hole and slot boxes.

To evaluate the effect of weather conditions and parental care levels on nestling growth rates, we used simple linear regression models because our sample size for nestling growth rate was not large enough to perform path analyses (n = 22). We constructed 10 models that related mean wing growth rate to mean nestling period temperature, total nestling period precipitation, male and female provisioning rates, and total provisioning rates per chick per hour (combined male and female rates) for hole nest boxes and slot nest boxes. We also evaluated whether nestling mortality and mean nestling period temperature changed over the course of the breeding season. We used Welch's t-test to compare the mean number of nestlings that died, as well as the mean nestling period temperature in the early season to the means for these variables in the late season.

Results

For both hole and slot boxes, weather variables exerted the strongest effect on number of mountain bluebird fledglings (Figure 3.1). For hole boxes, temperature was a better predictor of, and explained more variance in, number of fledglings based on a comparison of model fit (P) and AICc (Table 3.1). However, when considering the SEM linear coefficients, this effect was weak and negative ($n = 82$, $\beta = -0.06$, $p < 0.01$, Table 3.2), indicating higher temperatures were weakly associated with fewer fledglings. For slot boxes, the best model that explained variance in number of fledglings included both temperature and precipitation (Table 3.1). The effect of temperature on number of fledglings was strong and positive ($n = 31$, $\beta = 0.34$, $p = 0.01$, Table 3.2), yet the effect of precipitation was weak, positive, and non-significant ($n = 31$, $\beta = 0.02$, $p = 0.11$, Table 3.2).

When comparing hole and slot boxes, the difference in temperature between internal and external daily maximums was significantly greater for hole type nest boxes ($\mathrm{maxdiff}_{hole} = 1.55$°C, $\mathrm{maxdiff}_{slot} = 0.79$ °C, $n = 110$, $t_{87.00} = 5.68$, $p < 0.01$, Figure 3.2). However, we found no difference in average daily mean ($n = 110$, $t_{107.87} = 0.37$, $p = 0.\ 71$), maximum ($n = 110$, $t_{107.02} = 0.43$, $p = 0.\ 67$), or minimum ($n = 110$, $t_{107.96} = 0.08$, $p = 0.\ 94$) internal temperature between hole and slot boxes (Table A2). Nor did we find a difference in average daily mean ($n = 110$, $t_{107.38} = -0.52$, $p = 0.\ 60$) or minimum ($n = 110$, $t_{94.33} = -1.62$, $p = 0.\ 11$) difference in internal and external temperature between hole and slot boxes (Table A1).

We found no association between nestling growth rates and weather conditions or provisioning rates. Mean wing growth rate was not correlated with mean nestling period temperature ($n = 22$, $r^2 = -0.04$, $t_{17} = -0.55$, $p = 0.59$) nor total nestling period precipitation ($n = 22$, $r^2 = -0.04$, $t_{17} = -0.55$, $p = 0.59$). Nestling growth was also not significantly influenced by male provisioning ($n = 22$, $r^2 = 0.0006$, $t_{16} = 1.01$, $p = 0.33$), female provisioning ($n =$

22, $r^2 = -0.06$, $t_{16} = 0.25$, $p = 0.81$), or parental provisioning rates combined ($n = 22$, $r^2 = 0.002$, $t_{16} = 1.01$, $p = 0.33$). We also did not observe a significant difference in nestling mortality ($n = 22$, $t_{59.5} = 0.33$, $p = 0.74$) nor mean nestling period temperature ($n = 22$, $t_{26.7} = -0.42$, $p = 0.68$) as the season progressed.

Discussion

While many studies have assessed the influence of local weather and parental care on reproductive success separately, few studies have concurrently evaluated the relative influence of these two factors on breeding performance (Öberg et al. 2015). Here, we assessed the relative influence of local weather and levels of parental care on the reproductive success of a population of mountain bluebirds breeding in a semi-arid grassland of interior British Columbia. We found that breeding season temperature was a better predictor of mountain bluebird reproductive success than breeding season rainfall or parental care. Reproductive success of mountain bluebirds was associated with breeding season temperature; however, the strength and direction of this association was dependent on nest box opening type.

For slot boxes, the number of mountain bluebird fledglings was positively associated with temperature, which may be due to improved hatching success (Martin 1987) or fledging success (Reid et al. 2000, Ardia et al. 2010) when weather is warmer. We also observed a weak positive relationship between breeding season rainfall and mountain bluebird reproductive success. This result is contradictory to previous work in other species such as northern wheatears (*Oenanthe oenanthe*), which reported strong evidence for reduced fledgling success with increased rainfall during the nestling period (Öberg et al. 2015).

In other arid regions, increased rainfall during the nestling period may actually improve reproductive success by reducing predation rates (Morrison & Bolger 2002). However, because predation rates for artificial nest boxes are lower than for natural cavities (Møller 1989) and because the size of the effect of rainfall on fledging success we observed was weakly positive and non-significant, it is likely that average nestling period rainfall does not exert an influence on mountain bluebird fledgling success in the Kamloops area.

The discrepancy between nest box types may be due to differences in insulative properties between hole and slot boxes–a trend we observed in our nest box temperature data. We observed a slight yet significant difference between hole boxes and slot boxes in daily maximum difference between internal nest box temperature and external ambient temperature. Though this difference between hole and slot box temperature differentials was not great (0.75°C), our results suggest that hole boxes may provide better insulation than slot boxes; other species, such as great tits (*Parus major*), have been shown to favour boxes with better insulation (Mertens 1977).

It is important to note that the temperature analysis was conducted on empty nest boxes, and the thermal properties of these boxes may be different during brooding when the female is present in the nest. Other studies have found that thermoregulatory stress experienced by nestlings within a nest box varied with internal cavity size (van Balen et al. 1982), indicating an influence of internal box temperature on nestling health. Other features of the nest boxes that may also contribute to variation in internal temperature and reproductive success include the cavity size, the thickness of the walls, the placement of the nest box and subsequent incoming solar radiation (insolation), as well as the type of wood used in construction and its water-holding capacities (McComb & Noble 1981). However, we suggest it is more likely that differences in protection from exposure (i.e., wind and rain entering the nest) contribute more to the differences in reproductive success that we observed between hole and slot boxes because the effect of temperature in hole boxes was so weak. Because the size of nest box entrances can determine how much protection a nest box offers to its occupants (Lambrechts et al. 2010), a hole nest box would presumably provide better protection from wind and rain than a slot box, thus contributing to maintaining the internal nest box temperature. Anecdotally, mortality appeared to be greatest during periods of cold weather following heavy rains – which should exert a stronger influence on nestlings in slot boxes if exposure is a major driver of mortality.

There was no effect of local weather or parental care on nestling growth rates for both hole and slot nest boxes. A lack of effect of weather on nestling growth suggests that the influence of temperature on fledging success was not a result of prolonged nestling stress, but rather more likely a result of acute, sudden changes in temperature (possibly coupled with a rainfall event) that led to rapid nestling mortality. Even though our results suggest hole boxes may provide better insulation than slot boxes, if temperatures exceed a certain thermal threshold, nestling mortality may occur regardless of nest box type (McComb & Noble 1981, Webb 1987). Given the high temperatures in the grasslands (>30°C), overheating could certainly be possible.

In conclusion, we demonstrate that breeding season weather, particularly for birds breeding in slot boxes, better predicts mountain bluebird reproductive success than levels of parental care. We suggest that the effects of weather on reproductive success are likely direct and acute, driven by nestling mortality that occurs over the course of one or a few days rather than prolonged exposure. These patterns were dependent on nest box entrance type, with a greater effect of weather on slot nest boxes compared to hole nest boxes. Hole boxes may provide improved thermal insulation and/or weather protection than slot boxes, and would thus be the recommended nest box type for managers of bluebird populations in our study area. Temperate grassland ecosystems experience wide variations in weather conditions during the summer months, and with global climate change, the frequency and severity of summer storms is expected to increase in grasslands (IPCC 2013). This could have negative impacts on mountain bluebird reproductive success and hence populations in grassland communities. Our results reinforce the need to consider the effects of weather on mountain bluebird reproduction if we want to understand or predict this species response to global climate change.

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Table 3.1 Candidate path models created using piecewise SEM path analysis to evaluate the effect of temperature, precipitation, and parental care levels on the number of mountain bluebird fledglings.

Temp mean monthly ambient temperature, *precip* total monthly rainfall, *Fit(P)* P-value indicating fit of model

		Hole boxes			**Slot boxes**		
Model	**Model**	**Fit (P)**	**K**	**AICc**	**Fit (P)**	**K**	**AICc**
1	Temp	**0.921**	**3**	**7.268**	0.33	3	11.56
2	Precip	0	3	199.328	0.067	3	15.74
3	Temp + precip	0.935	4	8.718	**0.803**	**4**	**10.107**
4	Parental care + temp	0.172	7	24.928	0.062	7	31.61
5	Parental care + precip	0.191	7	24.598	0.13	7	29.48
6	Parental care + temp + precip	0.134	8	25.513	0.068	8	32.299
7	Parental care	0.134	3	13.411	0.068	3	15.72
8	Null	0	2	224.341	0.181	2	13.322

Table 3.2 Linear coefficients from the structural equation model decomposing independent weather and parental care effects.

	Hole boxes			**Slot boxes**		
Predictor	**Estimate**	**Standard error**	**p-value**	**Estimate**	**Standard error**	**p-value**
Temperature	**-0.056**	**0.004**	**<0.01**	**0.335**	**0.135**	**0.013**
Precipitation	0.003	0.004	0.455	0.023	0.014	0.106
Parental care	0.010	0.064	0.873	0.014	0.186	0.942

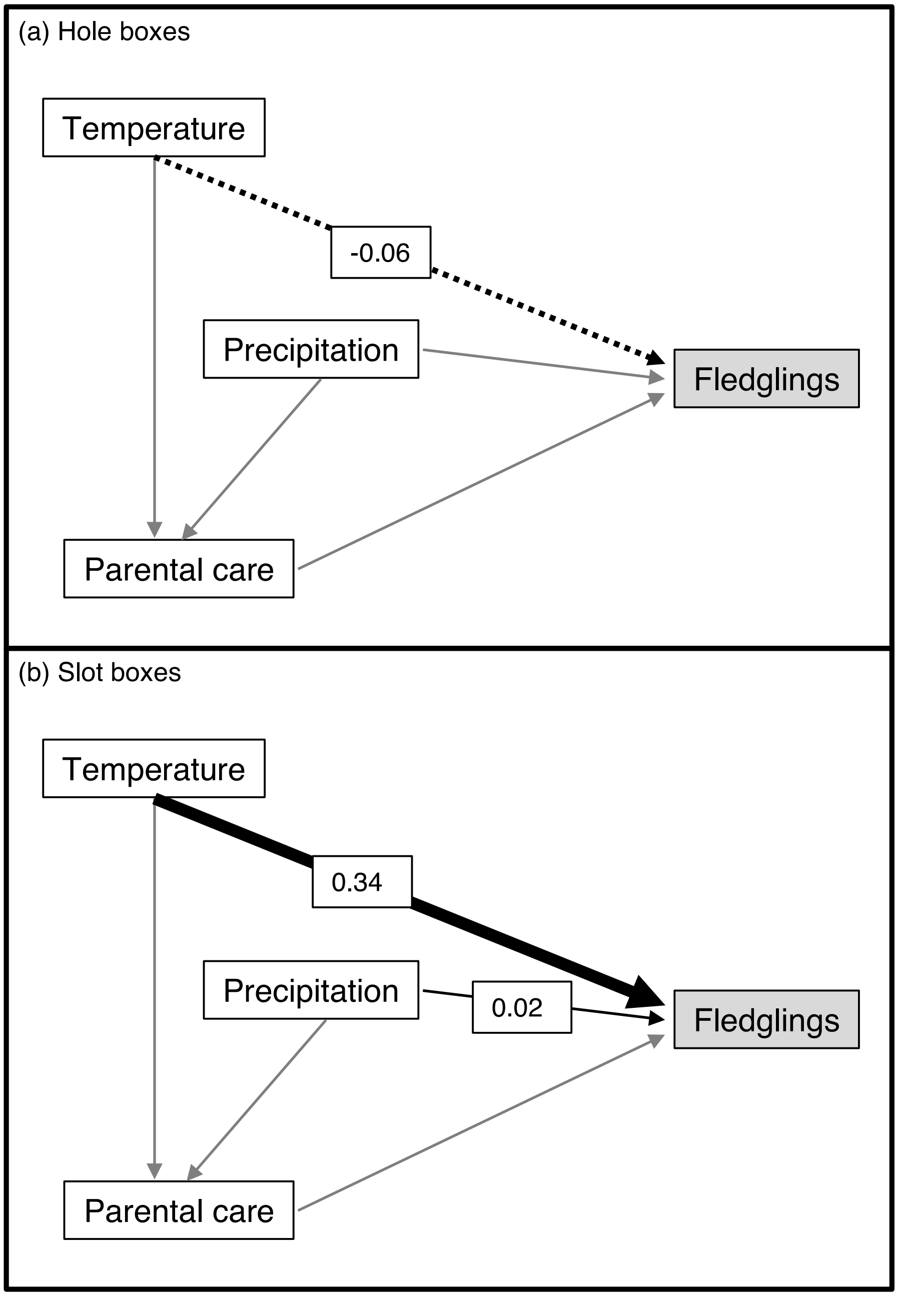

Figure 3.1 Path analysis of mean nestling period temperature, total nestling period precipitation, and total parental care on number of mountain bluebird fledglings for hole- and slot-opening type nest boxes. The thickness of the arrows represents the magnitude of the effect (ß) as well as the significance. A solid black arrow indicates a significant positive effect, a dotted black arrow indicates a significant negative effect, and a grey arrow indicates no significant effect.

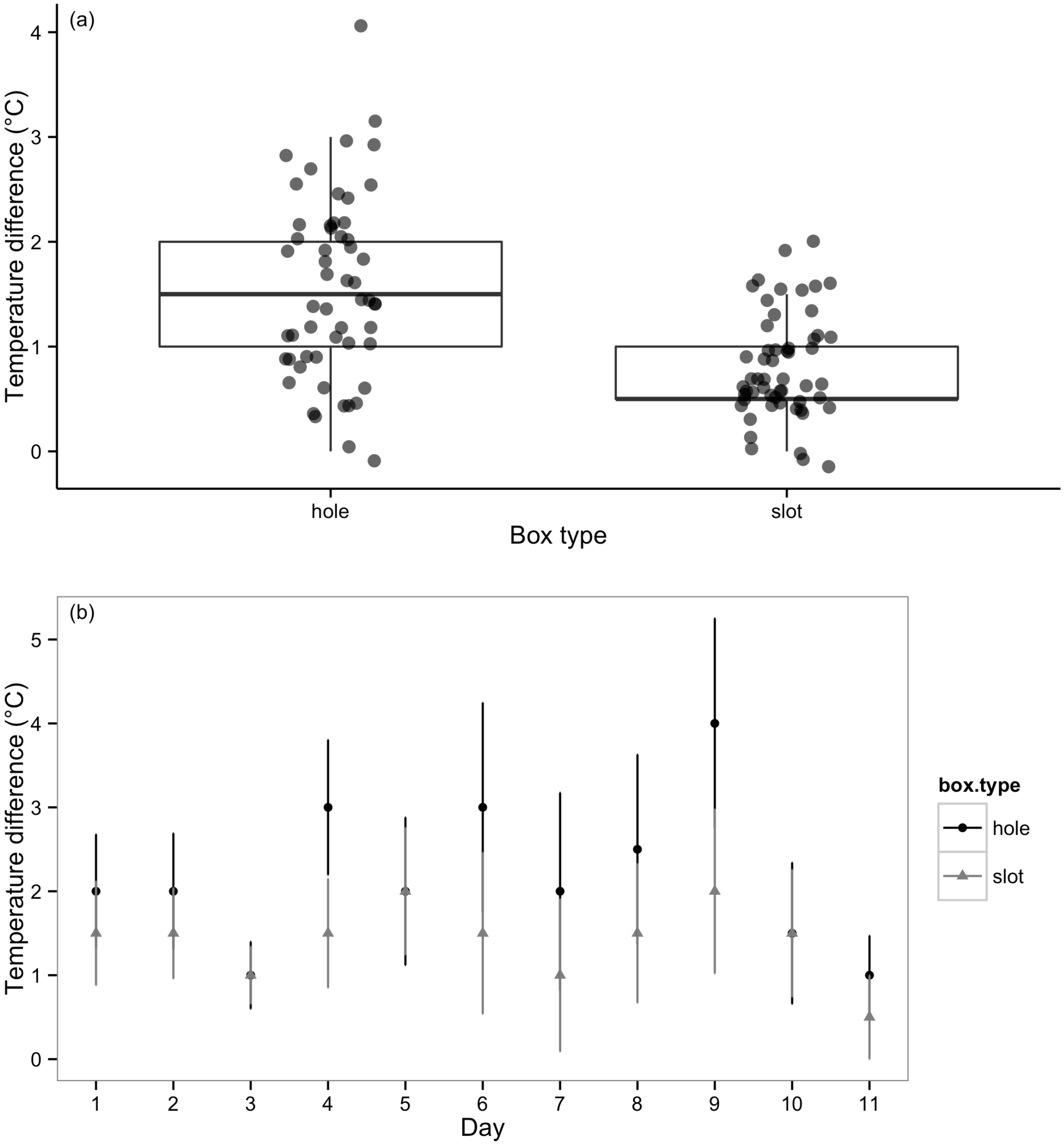

Figure 3.2 Difference in average daily maximum internal and external temperatures for hole and slot nest boxes over an 11-day period. Temperature differences were greater for hole boxes than for slot boxes. **(a)** Points show the average maximum daily temperature differences for each nest box (n=110). **(b)** Points show the mean maximum daily internal and external temperature difference and error bars are one standard deviation from the mean.

Chapter 4

Conclusion

The goal of this study was to evaluate the influence of regional climate, local weather, nest box features, and levels of parental care on the reproductive success of two grassland passerines: mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*). My results provide strong evidence to suggest that local weather plays an important role in mountain bluebird breeding performance, while for tree swallows, regional climate has a greater effect on breeding performance. I found that these associations were dependent on nest box features, most notably nest box entrance type (hole boxes were significantly more productive than slot boxes, and slot boxes were more sensitive to weather effects). This has allowed me to provide recommendations to conservationists and nest box monitoring program managers interested in more effectively supporting populations of nest box breeding grassland passerines. My data also indicate that the influence of weather on mountain bluebird reproductive success is likely a result of direct, acute nestling mortality during periods of poor weather.

Accurate projections for the ecological consequences of climate change depend on improved understanding of how large-scale climate phenomena and local weather conditions interact to influence individuals, populations, and communities. This is especially true for grassland songbird species because grasslands experience such variable climate and weather conditions; the severity of which is likely to only increase with global climate change. By considering the effects of regional climate and local weather in tandem, as well as with other environmental determinants of reproductive success, my research contributes to the body of knowledge that will help us predict how grassland songbirds may be affected by climate change in the future.

Based on predictions for alteration of spring and summer weather conditions in my study area with climate change, and the response of mountain bluebirds and tree swallows to temperature and precipitation, I predict that climate change may impact these species in the following ways: 1) increased spring rainfall will negatively influence mountain bluebird breeding performance through direct nestling mortality. Severity of rainfall events is expected to increase, which will likely contribute to an increase in mountain bluebird nestling mortality; 2) increased severity and frequency of droughts throughout the spring and summer will negatively influence tree swallow breeding success due to reductions in their aerial insect prey base. Increased drought conditions may reduce size and/or duration of ephemeral aquatic breeding habitat for aerial insects in temperate grasslands, thus reducing their numbers; and 3) hotter summer temperatures will negatively affect tree swallow breeding performance through nestling mortality due to overheating. Temperate grassland summer temperatures can often exceed the thermal threshold of organ failure in nestlings, and temperature extremes are expected to increase. Because tree swallow migration and breeding occurs later in the season than that of mountain bluebirds in my study region, tree swallows will likely experience a stronger effect of increased summer temperatures.

Future directions

Many biotic and abiotic factors contribute to reproductive performance of individuals during the breeding season. Considering these factors in isolation may contribute to a limited view of how environmental factors interact to influence reproductive success. A more comprehensive review of the environmental factors that contribute to the reproductive success of mountain bluebirds and tree swallows would provide a more complete picture of the influence of breeding environment on reproductive success. For example, considering the affect of weather on predation rates or levels of parasitism would increase our understanding of how weather can indirectly influence reproductive success of these species. Relatedly, studies into how weather and climate influence the predators and parasites that affect mountain bluebirds and tree swallows would shed more light onto how future climate change may impact these species. Additionally, further research into whether the affect of local weather and regional climate on reproductive success seem to have any perceptible influence on population demographics would provide insight into long-term effects of climate change on population dynamics in this system. For instance, years of high nestling mortality due to weather conditions (e.g., high rainfall years for mountain bluebirds) could affect recruitment levels and number of young birds entering into the population to reach breeding age after successful migration and overwintering. This type of study would provide further information about how global climate change may impact the populations of breeding birds in the Kamloops grasslands.

Climate change is expected to bring more extreme weather conditions to grasslands across the globe, likely with an increased frequency and severity of droughts and other precipitation events (IPCC 2013). As my results demonstrate that the effects of weather and climate on the breeding performance of bluebirds and tree swallows is likely acting directly through acute nestling mortality, it is probable that these effects occur during periods of extreme weather conditions. Future research into whether this is the case would provide an improved understanding of how these species may react to future changes in climate. For example, installing data loggers capable of recording temperature and humidity information (such as iButtons) within nest boxes and collecting weather data from within the nest box microenvironment throughout the breeding season, in combination with frequent nest visits to assess mortality, would allow for researchers to more decisively evaluate the direct effects of weather on nestling mortality.

The influence of nest box type and placement location on breeding performance of bluebirds and tree swallows will be of interest to managers of nest box programs in Kamloops and beyond. While my research provides tangible recommendations to nest box program managers, the results of the iButton box type experiment (Chapter 3) suggest only preliminary indications that insulation properties may differ between nest box types. Further research into the thermal properties of each nest box type would test these preliminary findings. As well, a natural experiment wherein all slot boxes along a bluebird route were replaced with hole boxes and the reproductive success of those boxes was compared to previous years would also solidify the premise that hole boxes better support reproductive success of mountain bluebirds than slot boxes. Additionally, future research into other aspects of the nest boxes that may be constraining reproductive success of mountain bluebirds would help determine why bluebirds perform better in hole boxes and how one might go about improving nest boxes and thus breeding performance of mountain bluebirds in all aspects of nest box construction and placement. Parallel studies into the reproductive success of mountain bluebirds nesting in natural cavities would be an interesting avenue to assess what it is about certain nest box physical attributes that contribute to improved breeding performance.

One limitation of this thesis was the relatively small sample size for nestling growth rates (Chapter 3). I collected a single breeding season of nestling growth data, which included only 22 nests. I would suggest continued monitoring of nestling growth and subsequent analysis of how weather and parental care levels may affect nestling growth rates in mountain bluebirds. This would provide more robust evidence to evaluate whether local weather acts directly and acutely on nestling mortality, while not affecting nestling growth rates.

Additionally, it should be noted that this study was focused on populations of mountain bluebirds and tree swallows breeding in artificial nest boxes, rather than natural cavities. I found different reproductive responses of mountain bluebirds to weather based on nest opening type of artificial boxes, which brings in to question the interpretation of this result in terms of the broader population of mountain bluebirds using natural cavities. Because there are many differences in the breeding conditions of artificial and natural cavities, I recommend caution when applying my results to the entire population of mountain bluebirds that breed in the Kamloops grasslands. Future research into reproductive differences in response to weather between artificial and natural cavities, or among different types of natural cavities, would allow more general population-level conclusions to be made.

To provide a more community-wide view of how grassland cavity nesting songbirds may respond to climate change, future studies should incorporate breeding information for all passerines that occupy grassland nest boxes during the breeding season. This would put the current study into a broader conservation context while providing valuable information about how grassland bird communities in British Columbia may be impacted by climate change. However, studies of individuals breeding in nest boxes may not be representative of the portion of the population breeding in natural cavities (Robertson & Rendell 1990, Purcell et al. 1997), so further research into mountain bluebirds, tree swallows and any other grassland passerines that utilize natural cavities would provide more holistic information about the population dynamics and reproductive success of these species.

Implications for management

Given the influence of weather and climate on the reproductive success of mountain bluebirds and tree swallow, both species face a potential threat to their populations from climate change. Although both mountain bluebirds and tree swallows are currently classified as species of least concern, the stability of their populations should not be taken for granted. There are other grassland species that are of special concern (vulnerable, or blue-listed) or threatened, endangered or extirpated (red-listed) in British Columbia, and the populations of these species are at risk, especially in light of global climate change. For example, the barn swallow (*Hirundo rustica*) is also an aerial insectivore that breeds in the grasslands of BC and is blue-listed in the province. Other grassland passerines of concern in the Kamloops area include the bobolink (*Dolichonyx oryzivorus*, blue-listed), Brewer's sparrow (*Spizella breweri breweri, breweri* subspecies red-listed), canyon wren (*Catherpes mexicanus*, blue-listed), grasshopper sparrow (*Ammodramus savannarum*, red-listed), lark sparrow (*Chondestes grammacus*, blue-listed), olive-sided flycatcher (*Contopus cooperi*, blue-listed), sage thrasher (*Oreoscoptes montanus*, red-listed), and yellow-breasted chat (*Icteria virens*, red-listed; B.C. Conservation Data Centre 2015). Impending global changes in climate, continued expansion of agricultural practices, and other land use changes in British Columbia's grasslands all pose risks for the future of our grassland passerines, especially species of concern.

In the Kamloops area, proposed mine developments near my study site are of special concern for the future of breeding birds. In particular, the controversial Ajax mine proposal may pose a direct risk to breeding birds in the vicinity. My research and the continued monitoring programs of the Kamloops Naturalist Club constitute part of the baseline knowledge required to assess future changes to grassland breeding birds if such a mine is developed. Thus, continued breeding and population monitoring of grassland songbirds will be necessary for detecting changes in reproductive behaviour and population size. I recommend that current monitoring programs continue and, where possible, additional grassland breeding bird monitoring programs be implemented, especially in areas of known future development, such as the Ajax mine site.

On the basis of my results, I recommend that bluebird nest box program managers in British Columbia's grasslands consider constructing all future nest boxes with hole type openings, as well as replacing current slot nest boxes with hole nest boxes. Additionally, if support of tree swallow populations is also of concern to nest box monitoring programs, I recommend placing new or existing nest boxes on fences in open grassland meadows, rather than on trees in more wooded areas.

It is important to note, however, that for continued success in future monitoring programs, continuity of nest box construction and placement is vital. Any changes in nest box construction or placement should be noted in robust monitoring databases. Additionally, database management should also be of primary concern to maintain the integrity and longevity of monitoring programs, and I recommend all field data, including notes and observations made by technicians and volunteers, be digitized within a master database that is maintained year to year.

In conclusion, this study has demonstrated that: 1) mountain bluebird reproductive success is impacted by local weather conditions during the breeding season, including temperature and rainfall, but this influence is nest box opening type specific (i.e., success is lower in slot nest boxes), 2) annual regional climate conditions better predict tree swallow reproductive success than local weather conditions, 3) local weather appears to influence mountain bluebird nestling mortality more strongly than levels of parental care and does so directly and acutely.

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Appendix A

Figure A1 Hole opening nest box (left) and slot opening nest box (right).

Table A1 Mean and standard deviation for provisioning rate (number of trips per hour per chick) for female and male mountain bluebird parents during early (Day 3-5) and late (Day 14-16) nest watches. Mean provisioning rates across all years are also displayed.

Avg mean, *StdDev* standard deviation

		Early Nest Watch				**Late Nest Watch**			
Year	**Nests**	**Avg Male**	**StdDev Male**	**Avg Female**	**StdDev Female**	**Avg Male**	**StdDev Male**	**Avg Female**	**StdDev Female**
2011	34	1.36	0.83	1.20	0.63	2.52	2.14	2.58	0.99
2012	24	1.26	0.87	1.90	1.49	2.48	1.56	2.76	2.38
2013	30	1.09	0.57	1.16	0.76	1.78	1.12	2.52	1.34
2014	22	1.32	0.77	1.28	0.75	1.95	1.51	2.43	1.66
Total avg		1.26	0.76	1.39	0.91	2.18	1.58	2.57	1.59

Table A2 Average daily mean and standard deviation, maximum, and minimum internal nest box temperature, average daily mean and standard deviation, maximum, and minimum external nest box temperature, and average daily mean and standard deviation, maximum, and minimum difference in internal and external temperatures over an 11-day period.

		Internal Temperature (°C)				**External Temperature (°C)**				**Temperature Difference (°C)**			
Box Type	**Day**	**Mean**	**Max**	**Min**	**Std. Dev.**	**Mean**	**Max**	**Min**	**Std. Dev.**	**Mean**	**Max**	**Min**	**Std. Dev.**
hole	1	8.9	19.5	0.5	5.3	8.8	18.5	0.5	5.2	-0.1	2.0	-2.5	0.7
hole	2	12.3	24.5	4.0	5.5	12.0	23.5	3.5	5.3	-0.3	2.0	-3.0	0.7
hole	3	12.0	21.5	9.0	3.1	11.6	21.5	8.5	3.1	-0.4	1.0	-1.5	0.4
hole	4	6.8	16.0	-0.5	4.4	6.5	15.0	-1.0	4.0	-0.3	3.0	-4.0	0.8
hole	5	6.6	19.0	-1.0	5.5	6.2	17.5	-0.5	4.9	-0.4	2.0	-4.0	0.9
hole	6	8.2	21.5	-2.0	6.8	7.3	19.0	-2.5	5.9	-0.9	3.0	-4.5	1.2
hole	7	9.9	23.0	0.0	6.7	9.0	21.5	-0.5	5.9	-0.9	2.0	-5.0	1.2
hole	8	11.5	25.5	1.0	6.7	10.6	23.5	0.5	6.0	-0.8	2.5	-5.5	1.1
hole	9	12.3	27.5	0.5	7.5	11.4	25.0	0.0	6.7	-0.8	4.0	-6.0	1.3
hole	10	9.7	27.0	4.0	3.7	9.3	22.5	3.0	3.2	-0.4	1.5	-4.5	0.8
hole	11	5.1	11.0	1.0	2.3	5.1	10.5	1.5	2.1	0.0	1.0	-1.5	0.5
slot	1	9.0	19.0	1.0	5.2	8.8	18.5	0.5	5.2	-0.2	1.5	-2.5	0.6
slot	2	12.1	24.0	3.5	5.3	12.0	23.5	3.0	5.3	-0.1	1.5	-2.5	0.5

slot	3	12.0	21.0	9.0	2.9	11.6	21.0	8.5	3.0	-0.4	1.0	-1.0	0.3
slot	4	6.8	15.5	-1.0	4.3	6.4	15.0	-1.5	4.0	-0.3	1.5	-3.0	0.6
slot	5	6.5	18.0	-0.5	5.1	6.1	16.0	-0.5	4.9	-0.4	2.0	-3.0	0.8
slot	6	7.7	20.0	-2.0	6.5	6.9	17.5	-2.0	5.9	-0.8	1.5	-3.5	1.0
slot	7	9.5	22.5	0.0	6.4	8.8	19.5	-0.5	5.9	-0.7	1.0	-3.5	0.9
slot	8	11.1	24.5	1.0	6.4	10.4	21.5	0.5	6.0	-0.7	1.5	-3.5	0.8
slot	9	11.9	25.5	0.5	7.4	11.2	23.5	0.5	6.8	-0.8	2.0	-3.5	1.0
slot	10	9.5	24.0	4.0	3.6	9.1	21.5	3.5	3.2	-0.4	1.5	-4.0	0.8
slot	11	5.2	12.0	1.0	2.4	5.0	11.0	1.0	2.1	-0.1	0.5	-2.0	0.5