

NESTLING DEVELOPMENT IN THE ALPINE: PREDATION RISK, PARENTAL CARE,  
AND ENVIRONMENTAL CONDITIONS ACROSS THE ANNUAL CYCLE

by

DEVIN RHYS DE ZWAAN

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The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the dissertation entitled:

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submitted by Devin R. de Zwaan in partial fulfillment of the requirements for  
the degree of Doctor of Philosophy  
in Forestry

**Examining Committee:**

Dr. Kathy Martin (Forestry)  
Supervisor

Dr. Scott Hinch (Forestry)  
Supervisory Committee Member

Dr. Scott Wilson (Environment and Climate Change Canada)  
Supervisory Committee Member

Dr. Jill Jankowski (Zoology)  
University Examiner

Dr. Dan Weary (Land and Food Systems)  
University Examiner

**Additional Supervisory Committee Members:**

Dr. Christa Beckmann (School of Science, Western Sydney University)  
Supervisory Committee Member

## Abstract

Offspring development is a critical life-history stage for altricial songbirds and a prime target for selection, as predation risk is high relative to other life-stages and environmental conditions can induce lasting consequences for life-time fitness. Nestling development rates vary widely among species, populations, and individuals. Rapid development is considered an evolved response to improve nest success given high predation risk at the species or population level. However, it is unclear what drives variation in development rate among individuals and whether offspring or parents have the adaptive capacity to respond to prevailing stressors.

I investigated the relative influence of multiple, interacting drivers from across the annual cycle on offspring developmental variation within an alpine breeding population of horned lark (*Eremophila alpestris*) by integrating ecological observations, behavioural experiments, physiology, and light-level geolocators to track migration. I demonstrated that rapid development was associated with a greater probability of nest success, confirming a selective advantage to fledging quickly. Cold ambient temperatures during the nestling period prolonged development, potentially due to resource constraints or thermoregulatory challenges, but females in better body condition were able to buffer offspring against harsh, early season conditions, enabling rapid development. With elevated predation risk, nestlings left the nest earlier by increasing wing growth. This effect was mediated by predator-specific glucocorticoid responses (stress biomarker) and parental provisioning behaviour. During spring migration, I showed that 59% of adults conducted extended stopovers (mean = 41 days) and subsequently had greater reproductive success during the breeding season. However, periods of extreme cold during stopover were correlated with prolonged offspring development, resulting in a lower probability of nest success.

My results demonstrate that: 1) nestlings have the adaptive ability to respond to elevated predation risk, 2) parental care can mediate offspring development in response to suboptimal conditions, and 3) prolonged stopovers may be key components of the annual cycle for alpine larks. By addressing within-population variation, I offer new insights into the eco-evolutionary drivers that shape offspring development across the annual cycle with implications for individual fitness and, ultimately, population-level responses to rapidly changing environments.

## **Lay summary**

The growth conditions of nestling songbirds can profoundly influence future survival and breeding success. I addressed how nestling growth responds to harsh, challenging weather and high predation risk in an alpine-breeding population of horned lark. I demonstrated that colder temperatures slow nestling growth, but high-quality females can buffer nestlings against poor conditions. In response to greater predation risk, nestlings grow longer wings and leave the nest earlier, potentially improving predator evasion. In spring, adult larks migrating north spend up to two months at a stopover site in the northern Columbia Plateau or Okanagan highlands. Adults that stopover for longer periods are more likely to successfully reproduce, particularly with warmer spring temperatures, highlighting the potential importance of this lower elevation region for alpine larks. Understanding what influences nestling growth and survival in unpredictable environments has important implications for the future of alpine songbirds under a rapidly changing environment.

## **Preface**

Beginning in 2003, Prof. Kathy Martin and previous grad students monitored the breeding parameters of an alpine population of horned lark. From these data, I developed a project investigating large within-year variation in nestling development time. Dr. Martin and I discussed how to maintain consistent methodology for the lark breeding ecology study while expanding data collection to address my questions. From 2015–2019, with the help of my field assistants, I monitored 358 nests, colour banded and measured 106 adults and 351 nestlings, and deployed 59 light-level geolocators to track migration.

All procedures herein were approved by the Animal Care Committee (ACC) at the University of British Columbia (UBC) in accordance with the Canadian Council on Animal Care’s national guidelines. Data were collected from 2003–2011 under the UBC IACUC protocols A03-0095, A07-0048, and A10-0128, and from 2015–2019 under A15-0027 and A19-0039, as well as, a Scientific Permit for Capture and Banding of Migratory Birds from Environment and Climate Change Canada (10365 DS and 10761 J).

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A version of chapter 4 has been published. de Zwaan, D. R., Wilson, S., Gow, E. A., and Martin, K. (2019). Sex-specific spatiotemporal variation and carry-over effects in a migratory alpine songbird. *Frontiers in Ecology and Evolution*, 7:285–297. I conceived the project with my co-authors. I led data collection, analysis and writing of the manuscript.

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## Dedication

*To my mother who instilled in me a love and curiosity for nature, and my grandpa who showed me how to explore it.*

*And to the larks. Nothing makes me happier than the song of a lark greeting the sunrise on a cold, snowy alpine morning.*

## **Chapter 1. Introduction and thesis overview**

Fundamental to ecology and evolution is understanding what drives variation in life-history traits among and within species. Across taxa, offspring growth and development rates are critical life-history traits that vary widely among species and along environmental gradients such as latitude or elevation (Lack 1968, Case 1978, Conover and Present 1990, Arendt 1997). Conditions that influence development are linked to life-time fitness metrics, including survival and fecundity (Lindström 1999), but juvenile mortality risk is often high compared to other life stages (Ricklefs 1969, Martin and Briskie 2009). Thus, offspring development is a prime target for selection.

Developing offspring must allocate limited available energy to either the growth of size traits or development of vital systems such as muscle coordination and thermoregulation in order to maximize stage-specific survival (Olson 1992, Roff 1992, Stearns 1992). This trade-off is exemplified by the precocial-altricial spectrum observed in birds and mammals. Precocial young are mobile and can thermoregulate at an early age, while altricial young are dependent on parents for food and warmth but exhibit faster growth rates (Ricklefs 1979, Hill 1992). The relative investment in size growth and vital systems is a strategy which ultimately determines the length of vulnerable developmental stages such as the nestling period in altricial birds (time from hatch to fledge; Arendt 1997, Cheng and Martin 2012, Martin 2015). Differences in adaptive histories and proximate environmental factors can produce considerable variation in development along a slow-fast continuum among- and within-species (Dunn 1975, Martin 1995), and even among individuals of the same population (Stodola et al. 2010, Freeman et al. 2019). Despite its importance to individual fitness, our understanding of variation in offspring development is restricted by issues of evolutionary scale (i.e., evolved versus proximate response), overlooked interactions among potential drivers, and limited data from historically understudied systems.

### *Potential drivers of offspring development*

For altricial birds, multiple hypotheses have been proposed to explain inter-specific differences in nestling development time, generally falling into two main categories: predation risk and resource availability. The probability of nest predation increases with time in the nest, and therefore rapid growth allows offspring to transition out of the vulnerable nestling stage (fledge) more quickly (Lack 1968, Martin et al. 2015). Inter-specific comparisons among habitats or nest types that vary in exposure to predators (i.e., cavity versus open-cup nest) have consistently demonstrated that greater predation risk is associated with shorter nestling development times (Bosque and Bosque 1995, Martin 1995, Remeš and Martin 2002, Martin et al. 2011). However, when environmental conditions or food availability are unpredictable, slower development may be adaptive because it reduces daily energy requirements and maximizes resource use efficiency (Martin 1987, Lambers and Poorter 1992, Arendt 1997). Whether development rate is an evolved or proximate response to environmental constraints is difficult to determine without considering individual responses to prevailing conditions.

For within-population variation, the relative influence of potential drivers is variable and more context-specific. Poor environmental conditions can constrain development by restricting resources or imposing thermoregulatory challenges that force investment in vital systems at the expense of growth (Stodola et al. 2010, Pérez et al. 2016). Greater predation risk can cause parents to reduce provisioning rate to avoid nest detection (Martin et al. 2000, Ghalambor and Martin 2001), disrupting food intake and prolonging development (Scheuerlein and Gwinner 2006). Nestlings able to develop rapidly to leave the nest earlier with larger size traits and greater mobility should gain an immediate survival advantage (Martin et al. 2018). However, even under ideal conditions, rapid development may be associated with poor quality growth, greater

oxidative stress, and ultimately reduced fitness (Lindström 1999, Mangel and Munch 2005, Monaghan 2008). Therefore, trade-offs exist between rapid and prolonged development to avoid predation while balancing resource constraints and fitness consequences.

Parental investment may be key to balancing the trade-offs that shape nestling development. Parents must partition resources between reproduction or self-maintenance (Williams 2012). Individuals in good body condition may invest more in parental care such as incubation, brooding, or provisioning nestlings, all of which can buffer offspring against environmental constraints and maximize development rate (Wendeln and Becker 1999, Dawson et al. 2005, Ardia et al. 2010, Sofaer et al. 2018). Resource-challenged adults may prioritize survival at the expense of nest attentiveness, leading to colder nest environments or disrupted provisioning rates that prolong development (Dunn et al. 2010, Nord and Nilsson 2011, Coe et al. 2015). Conditions prior to breeding can also influence parental investment through ‘maternal effects’ (Wolf and Wade 2009, Moore et al. 2019). For instance, stressed females may deposit high levels of glucocorticoids (i.e., stress biomarkers) into the egg yolk, resulting in smaller hatchlings and/or slower development rates (Love et al. 2005, Saino et al. 2005). The realization of an ‘optimal’ development strategy that balances survival trade-offs in response to prevailing conditions is likely dependent on parental condition prior-to and during reproduction.

### *Offspring development in fluctuating environments*

Predation risk and environmental conditions are variable through time, particularly in fluctuating or unpredictable environments like desert, arctic, or alpine habitats. In these environments, life-history traits like nestling development will have different optima depending on prevailing conditions and limitations on parental investment (Rollinson and Hutchings 2013, Chevin and

Hoffmann 2017, Kvalnes et al. 2018). Where and when a clutch is initiated will therefore drive differences in the environmental constraints experienced during development and promote within-population variation. Additionally, phenotypic flexibility is adaptive in unpredictable environments (Piersma and Drent 2003). For offspring development, this could entail accelerating growth rate in response to predation risk or following periods of disrupted development, sometimes referred to as compensatory growth (Criscuolo et al. 2011, Aldredge 2016). Fluctuating environments allow one to assess whether nestling development rate is simply a product of environmental constraints or represents adaptive responses to prevailing conditions.

Alpine habitats are characterized by cold, fluctuating temperatures, frequent storm events, and delayed snow-melt (Martin 2001, Bears et al. 2009, Martin et al. 2017). Breeding seasons are compressed, limiting the number of nesting opportunities (Badyaev 1997, Bears et al. 2009, Camfield et al. 2010). Alpine breeding birds often exhibit different life-history strategies or behavioural adaptations in comparison to low elevation populations, such as greater investment by both sexes in reproduction (Martin and Wiebe 2004, Sandercock et al. 2005, Bears et al. 2008, Wilson and Martin 2010, Boyle et al. 2015). Most species are also ground-nesters and may therefore experience greater predation risk (Martin 1993, Martin 1995), which can vary widely among- and within-seasons (MacDonald et al. 2016). Alpine habitats exemplify a challenging, fluctuating environment and are ideal for addressing within-population variation in life-history traits. Most studies on nestling development involve temperate populations at low elevations which may be relatively stable systems. Studies in extreme, stochastic environments will enhance our understanding of the adaptive capacity for nestling development to respond to variable conditions and perhaps identify stressors that exceed normal coping mechanisms.

### *Beyond the breeding season: a full annual cycle perspective*

Migratory songbirds spend up to 75% of the annual cycle in non-breeding habitat (Webster et al. 2002, Marra et al. 2015). Carry-over effects occur when environmental conditions at one stage of the annual cycle influence body condition or phenology at subsequent stages, resulting in altered behaviour or fitness (Norris 2005). For example, favourable conditions at winter or stopover sites can be associated with earlier clutch initiation and greater fecundity (Norris et al. 2003, Harrison et al. 2011). Poor conditions at critical non-breeding habitats can reduce resource uptake (Gill et al. 2001, Gunnarsson et al. 2005), resulting in depleted energy reserves or elevated corticosterone levels (Bêty et al. 2003, Sorenson et al. 2016). Energy-challenged adults arriving at the breeding site may invest less in breeding attempts (Descamps et al. 2011), highlighting the potential for non-breeding conditions to influence offspring development.

We are just beginning to understand the importance of non-breeding conditions in shaping life-history traits (Marra et al. 2015), particularly for alpine breeding birds where we lack data on migration behaviour and potential carry-over effects. In North America, > 90% of birds that breed at higher elevations are migratory (Boyle and Martin 2015), and breeding seasons are on average 42% shorter than at lower elevations (Boyle et al. 2015). Therefore, alpine breeding birds are dependent on multiple habitats throughout the annual cycle with potential implications for life-history strategies. Given energy limitations during harsh, early season conditions, carry-over effects may be more pronounced in the alpine (Harrison et al. 2013). Alternatively, birds that breed in highly seasonal habitats may be more flexible (Boelman et al. 2017) and might be able to overcome potential carry-over effects. Assessing the relative influence of multiple, interacting drivers across the annual cycle will advance our understanding of the eco-evolutionary dynamics that shape life-history traits such as nestling development.

## **Thesis objectives**

My research addressed the relative effects of multiple influential factors during the breeding and non-breeding season on within-population variation in offspring development for an alpine breeding population of horned lark (*Eremophila alpestris*). I also attempted to identify the time periods across the annual cycle that may be most critical to shaping offspring development rate. Finally, I assessed the fitness consequences of different development strategies in terms of hatching and fledging success across the breeding season.

My objectives were to:

- Address the relative effects of proximate weather, predation risk, and maternal condition on within-population variation in offspring development (Chapter 2);
- Investigate the capacity for offspring to adjust development in response to experimentally elevated predation risk and identify the underlying mechanisms (Chapter 3);
- Examine sex-specific variation in migration behaviour and the carry-over effects connecting migration strategies to reproductive success (Chapter 4);
- Assess the relative influence of non-breeding and breeding weather conditions on clutch initiation date and subsequent nestling development (Chapter 5).

## **Focal species**

The horned lark is an obligate ground-nesting songbird (28–40 g) that breeds in sparsely vegetated, open-country habitats such as short-grass prairies, semi-arid deserts, coastal sand dunes, and tundra (Beason 1995). Horned larks have the largest global range of the 92 species in the Alaudidae (lark) family and is the only species that breeds in alpine and arctic tundra (de

Juana et al. 2019). They have a Holarctic distribution, ranging throughout North America, Europe, and Asia, as well as, isolated populations in Morocco and Colombia (Donald and de Juana 2019). Horned larks are elevational generalists, breeding from sea level to over 4000 m above sea level (a.s.l.) in North America (Beason 1995), and up to 5400 m a.s.l. in the Himalayas (Donald and de Juana 2019). Within North America there are 21 subspecies with relatively distinct geographic ranges (Beason 1995). The pallid horned lark (*E. a. articola*) is an alpine breeding specialist with a range extending from Alaska and southern Yukon down through the Coastal and Rocky Mountains of British Columbia and Alberta (Behle 1942).

I studied an alpine population of *E. a. articola* in northern British Columbia, Canada from 2015 to 2019. This work was a continuation of a field project that collected data from 2003–2007, 2010, and 2011. Female larks are the primary care-giver, responsible for nest building, incubating and brooding without mate-feeding, and more than half of the nestling provisioning (Beason 1995, Goullaud et al. 2018). Alpine nests are generally built adjacent to short vegetation such as sedges or heather (*Cassiope mertensiana*, *Phyllodoce empetriformis*). Breeding pairs attempt 1 to 2 clutches per season in the alpine, with an average clutch size of 3.6 eggs (range: 2–5; Camfield et al. 2010). Nests are typically initiated mid- to late-May with all nest efforts completed by the end of July (Martin et al. 2017). Across North American populations, the incubation period has a relatively invariable duration (11–12 days; Pickwell 1931, Beason and Franks 1974, Cannings and Threlfall 1981). In contrast, the nestling development period ranges from 7–12 days (Beason 1995) and appears to be longer at higher elevations. Offspring fledged at 9–12 days post-hatch at 3200 m a.s.l. in Wyoming (Verbeek 1967), but 7–9 days at 1000 m a.s.l. in the Chilcotin, British Columbia (Cannings 1981), and 8–10 days in Newfoundland (Cannings and Threlfall 1981).

Horned lark populations throughout the United States are partially migratory or resident, while those in Canada are obligate migrants (Beason 1995). Wintering locations are predominantly below 49° latitude and extend as far south as the Chihuahuan grasslands in Mexico, although some individuals have been sighted as far north as 53.5° latitude in December and January (Sullivan et al. 2009). In spring, larks wintering farther south have been observed arriving in Canada as early as February (Cannings and Threlfall 1981). The migratory connectivity and phenology of alpine lark populations is unknown, but they are assumed to be at least altitudinal migrants (Beason 1995).

Horned larks have declined by 70% since 1970 which equates to an estimated loss of approximately 182 million individuals, the 2nd largest decline among avian species native to North America (Rosenberg et al. 2019). This trend is derived primarily from low elevation and lower latitude breeding populations as data are limited from less accessible northern grassland, arctic or alpine habitats. The alpine population on Hudson Bay Mountain was stable from 2003 to 2006 (Camfield et al. 2010), but it is unknown whether this is a unique or common occurrence among high elevation or latitude populations due to the paucity of population monitoring programs in these regions. Given data deficiencies and rapidly changing climates, there is a clear need to address how larks cope with multiple stressors, reproduce in unpredictable environments, and use non-breeding habitat to understand risk factors for alpine breeding populations.

## **Study area**

My study site exists entirely above tree-line (1650–2000 m a.s.l.) in ~3 km<sup>2</sup> of alpine tundra on Hudson Bay Mountain (HBM) near Smithers, British Columbia (54.8°N, 127.3°W; Figure 1.1). Vegetation is predominantly short alpine grasses and heathers that transition into scree at

approximately 1900 m a.s.l., interspersed with small patches of sedge and forbs in which larks may nest (Figure 1.2). HBM is on the boundary of the Coastal Mountain Heather and Boreal Altai Fescue Alpine zones (MacKenzie 2006), and as such is relatively wet, with several oligotrophic alpine lakes that persist throughout the season. This habitat is characterized by high winds and temperatures that can fluctuate from  $-5$  to  $+35$  °C in a single day (Camfield and Martin 2009). Nest predation rate is variable, ranging from 32.1 to 83.8% annually (average = 67.8%; MacDonald et al. 2016). Snowmelt fluctuates considerably among years and often extends into mid-June, resulting in compressed breeding seasons (41–57 days) that are ~57% shorter than low elevation populations (Camfield et al. 2010, Martin et al. 2017; Figure 1.3). During the breeding season (May–July), average monthly temperatures range from 3.69–7.31°C and total monthly precipitation varies from 99.0–237.0 mm across all years of the study, with May generally being the coldest and driest month (Table 1.1).

## **General methodology**

### *Field methods*

Consistent with data collected prior to 2015, I monitored territories from the time males arrived at the site until late July each year. I located nests by either systematically searching territories or through observation of behaviours such as nest building. Nests were typically located during the nest building or incubation phase and were monitored every 2–3 days to record clutch initiation date, clutch size, brood size, and nest fate (fledged, depredated, abandoned). If a nest was discovered during incubation, clutch initiation was estimated by back-calculating from hatch date using an average incubation period of 12 days and assuming incubation began the day the penultimate egg was laid (Camfield et al. 2010). Near expected hatch and fledge I switched to

daily nest visits to accurately determine age at fledging, calculated as the number of days from the day after hatch to fledging date (hatch date = 0 days). Nests were considered depredated if the contents of the nest were missing prior to predicted date of fledging, or after the predicted date if adults were not observed feeding fledglings. Nests without accurate estimates of hatching or fledging date ( $\pm 1$  day) and abandoned nests were removed from their respective analyses.

For banding and measurements, all nestlings were collected from the nest at once and were stored in a warm, dark bag to reduce stress while their siblings were being measured. I measured nestlings for body size and condition traits, including wing length ( $\pm 0.5$  mm), tarsus length ( $\pm 0.02$  mm), mass ( $\pm 0.01$  g), and furcular fat. I generally measured nestlings only once to avoid attracting predators to the nest. However, for 2015 and 2016 each nestling was measured at both 5- and 7-days post-hatch as a metric of growth rate over that period (see Chapter 3). At 5-days post-hatch, I used non-toxic markers to uniquely mark the tarsi of each nestling. At 7-days, each nestling was banded with one U.S. Geological Survey (USGS) numbered aluminum band and 2–3 plastic colour bands for subsequent identification. Since nestlings may fledge asynchronously, I recorded an individual-specific fledge date for each nestling based on their colour bands. For nestlings, the entire measurement process from removal to being returned to the nest typically took less than 10 minutes.

At approximately the same time (4–8 days post-hatch), I captured adults at the nest using a bownet trap that was triggered remotely when a bird entered to provision the nestlings (Camfield et al. 2010). Capture attempts were a maximum of 45 mins (average =  $17.5 \pm 1.3$  min) per day (max = 2 days). I observed no cases of premature fledging, and capture events likely did not prolong the nestling period because released larks returned to normal provisioning behaviour within 15 min (de Zwaan et al. 2018). Parents from the same nest were captured on separate days

to avoid undue stress on the nestlings. I measured all adults for the same size and condition traits as the nestlings and banded each with one USGS numbered aluminum band and three plastic colour bands. Adults were handled for less than 5 minutes from capture to release.

Since red fox (*Vulpes vulpes*) and common raven (*Corvus corax*) are likely the most significant nest predators at my site (Camfield 2008), I took precautions to limit scent and visual cues near the nest. Nests were marked using natural rock cairns placed 20 to 45 metres from the nest with distance and direction recorded for relocation. A cairn was used because ravens will investigate nests marked by coloured flags. I checked nests during the morning and limited my time in the vicinity of each nest so human scent would be less likely to remain for nocturnal predators. Nestlings and adults were measured at least 40 metres from the nest and out of sight.

### *Weather variables*

Precipitation and temperature variables at the breeding site were recorded using three HOBO weather stations (Onset Computer Co., Pocasset, MA, USA): a) a Micro Station Logger H21-002 from 2005 to 2007, 2) a U30-NRC station for 2010 to 2017, and 3) an RX3000 satellite station for 2018 and 2019. While the latter two stations were positioned ~1.2 km west of the original station, all three were located at 1,695 m a.s.l. and therefore weather data collected at both sites should be relatively comparable (Figure 1.1). The sensors were placed 1.5 and 3 m above ground, and less than 2.4 or 1.2 km from any nest for 2005–2007 and 2010–2019, respectively. Weather variables were recorded every 4 min and then averaged hourly.

Due to transitions to new equipment, precipitation and temperature values were missing for 2003, 2004, and parts of 2017. To estimate precipitation for these periods, I used values from the Smithers Regional Airport (522 m a.s.l.; ~8 km from study site). Daily precipitation varied

between the airport and study site, but consistently identified days with moderate precipitation ( $\geq 1$  mm) or storms ( $\geq 10$  mm; Martin et al. 2017). Therefore, to remain consistent, I classified each day as ‘precipitation day’ or ‘storm event’ as categorical precipitation variables, whether I was using precipitation data from the Smithers Airport or the weather station at the study site. For temperature gaps, I interpolated hourly estimates of air surface temperature from the 8 nearest grid points in the National Centers for Environmental Prediction (NCEP) R-1 dataset using the R package “RNCEP” (Kemp et al. 2012). To validate this method, I compared the interpolated estimates to measured temperature from our study site for all years with existing data. Estimates and true measurements were highly correlated ( $r_p = 0.91$ ), but the intercept differed, likely due to an elevation effect. I therefore subtracted the value of the intercept difference ( $1.78^\circ\text{C}$ ) from all interpolated estimates to better align them with true temperature measurements.

## **Thesis chapters**

In Chapter 2, I used path analysis to assess inclement weather, predation risk, and maternal condition as potential factors influencing offspring development time. I demonstrated that while rapid nestling development was associated with high predation risk, inclement weather and maternal condition were stronger drivers of within-population variation. Cold ambient temperatures late in the nestling period prolonged development, but females in good body condition were able to fledge offspring quickly under harsh, early season conditions. Given relatively high nest predation risk, I discuss the fitness benefits females accrue by promoting rapid nestling development despite harsh environmental conditions.

Since greater site-wide predation risk was linked to more rapid development (Chapter 2), in Chapter 3 I increased perceived predation risk at the nest experimentally to investigate if

nestlings can respond adaptively to direct detection of predation risk or whether development is simply constrained by changes in parental provisioning behaviour. I measured provisioning rate, nestling wing growth, and feather corticosterone as a metric of stress to assess changes in offspring growth and physiology. I found that nestlings suppressed corticosterone release and increased wing growth in response to greater predation risk, resulting in an earlier age at fledge. This association was driven both by a direct response that was predator-specific, and an indirect response that was dependent on parental provisioning rate. I discuss the potential for corticosterone as a mediator of the nestling growth response and the adaptive significance of faster wing growth in response to predation risk.

In Chapters 2 and 3, I demonstrated the influence of proximate breeding season factors on variation in nestling development, particularly the importance of parental care. The breeding season can represent < 25% of the annual cycle for migratory birds, and events that affect adult condition during the non-breeding season can carry-over to influence breeding parameters and ultimately offspring development. In Chapter 4, I tracked adult migration using light-level geolocators to identify key non-breeding habitats and migration timing for both males and females. I found that males tended to spend more time farther north and arrived an average of 6 days earlier at the breeding site in spring, while females were more flexible in their migration speed and use of stopovers. In spring, both sexes used staging areas for extended periods (average = 41 days), with birds that demonstrated this behaviour experiencing greater reproductive success during the breeding season. I discuss the importance of sex differences in non-breeding habitat use given different reproductive roles and how staging areas could be key components of the annual cycle.

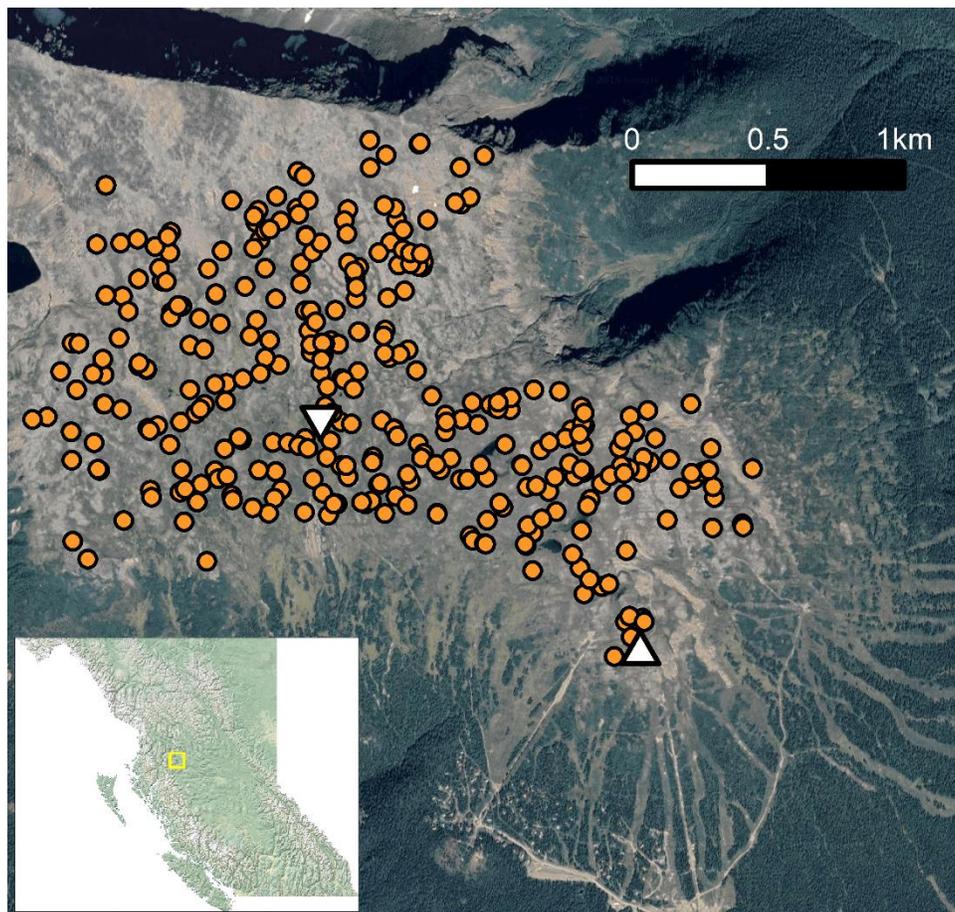
In Chapter 5, I used the spatial and temporal estimates of non-breeding habitat use (Chapter 4) to address potential carry-over effects on variation in clutch initiation date and nestling development time among years. I found that harsher winters and colder spring temperatures at the breeding site delayed clutch initiation date, while periods of extreme cold at the spring staging site prolonged nestling development, independent of any effects on clutch initiation date. I discuss the potential mechanisms for the observed carry-over effects on breeding phenology, as well as, the individual fitness consequences for late clutch initiation and prolonged nestling development time.

In Chapter 6, I integrated the results of the four previous data chapters to highlight how addressing within-population variation in life-history traits and multiple potential drivers simultaneously can complement and advance our understanding of life-history. I further outlined significant scope for future research, particularly on the long-term consequences of different development strategies and the mechanisms underlying carry-over effects. I conclude by discussing what the results from this dissertation may suggest for the future of alpine nesting songbirds that rely on both high elevation breeding sites and low elevation non-breeding habitat under the escalating pressures of climate and land-use change. This dissertation delves into the factors that shape offspring development across the annual cycle and offers insights into life-history theory for songbirds in rapidly changing environments.

**Table 1.1.** Average temperature and precipitation for the breeding season (May to June) across all years of the study. Precipitation values in bold were measured at the Smithers Airport and thus are only approximations of the total precipitation at the alpine study site.

Year	Temperature (°C)				Precipitation (mm)			
	May	June	July	Average	May	June	July	Total
2003	0.68	7.53	10.22	6.14	<b>20.4</b>	<b>69.0</b>	<b>55.6</b>	145.0
2004	1.83	9.82	9.92	7.19	<b>15.8</b>	<b>74.2</b>	<b>39.8</b>	129.8
2005	3.89	6.84	6.18	5.64	41.0	56.0	48.6	145.6
2006	1.76	8.46	10.16	6.79	82.9	17.4	33.8	134.1
2007	0.74	5.44	9.32	5.17	51.7	80.0	38.4	170.1
2010	1.15	4.45	8.43	4.68	47.4	50.6	22.0	120.0
2011	1.12	4.54	5.40	3.69	89.6	41.8	106.4	237.8
2015	4.82	7.75	9.35	7.31	29.6	23.8	45.6	99.0
2016	3.29	6.37	8.66	6.11	19.8	93.6	<b>82.8</b>	196.2
2017	1.95	5.13	7.71	4.93	<b>90.2</b>	<b>57.2</b>	<b>31.0</b>	178.4
2018	4.31	5.29	10.84	6.81	23.2	27.4	22.4	73.0
2019	5.36	5.81	8.35	6.51	26.6	50.2	114.0	190.8
Average	2.58	6.45	8.71	5.91	44.9	53.4	53.4	151.7

**Figure 1.1.** Map of the study site on Hudson Bay Mountain near Smithers, British Columbia, Canada. The orange points represent nest locations from 2015 to 2019 to visualize the extent of the study area. The pyramid indicates the location of the original weather station (2005–2007), while the inverted pyramid is the position of the two later weather stations (2010–2019). The yellow square in the inset depicting B.C. is centered on the study site. The top of the map is North. The topography layer for the inset was downloaded from Natural Earth Data © 2019 and the satellite image is a product of Google Imagery © 2019.



**Figure 1.2.** A typical alpine horned lark nest with heather substrate. Photo credit: Devin R. de Zwaan.



**Figure 1.3.** Photos from the highest point of the study site looking southeast and demonstrating how quickly conditions change from early season conditions in mid-May when nest initiation begins to mid- to late-June when the majority of first nesting efforts have been completed. Photo credit: Devin R. de Zwaan.



## **Chapter 2. Variation in offspring development is driven more by weather and maternal condition than predation risk**

### **Introduction**

Offspring development is a critical life-stage for vertebrates, as conditions during development have lasting effects on life-time fitness (Arendt 1997, Lindström 1999, Metcalfe and Monaghan 2001, Monaghan 2008). Life-history theory predicts that variation in offspring development rates along a slow-fast continuum stems from constraints on resource allocation between offspring growth versus development of thermoregulation and other vital systems (Stearns 1992). Two antagonistic constraints potentially place the development characteristics of a species along this continuum: predation risk and inclement weather. Greater predation risk should select for faster maturation, particularly of mobility traits, to improve predator evasion (Coslovsky and Richner 2011, Cheng and Martin 2012), while stochastic environmental conditions may constrain development by restricting food intake and/or increasing thermoregulatory costs (Stodola et al. 2010; Pérez et al. 2016). Development speed and resource allocation have implications for both immediate and future fitness: greater mobility of juveniles can improve predator evasion (Dial et al. 2006) but may have long-term effects if oxidative stress experienced during rapid development affects reproductive success as adults (Monaghan 2008). Understanding the relative importance of environmental constraints on developmental traits provides critical insight into how species and populations may respond to rapidly changing environmental conditions.

For songbirds, comparisons among species have established predation risk as a predominant extrinsic constraint on offspring development rates (Bosque and Bosque 1995). A critical life-stage transition for songbirds is the date of fledging, when offspring leave the nest

and become more exposed to the surrounding environment. Rapid development (earlier fledging) has evolved in species experiencing high nest predation rates, reducing the risk of losing all offspring simultaneously given that the cumulative risk of predation increases with time in the nest (Remeš and Martin 2002). Species experiencing low predation risk tend to prolong offspring development, potentially to maximize post-fledging survival (Martin et al. 2018) and minimize the negative long-term fitness consequences of oxidative stress associated with rapid development (Lee et al. 2013). Studies addressing among- and within-population variation have provided support for additional influential drivers of offspring development duration, including: inclement weather (Pérez et al. 2016), microclimate temperature (Dawson et al. 2005, Sofaer et al. 2018), and food availability (Stodola et al. 2010, Tuero et al. 2018). Variation in influential factors across populations challenge the generality of predation risk as the predominant driver. This discrepancy may be explained by individual responses to environmental constraints that are lost when considering only mean species or population responses. For example, adult birds may mediate nest predation risk through camouflage (Albrecht and Klvaňa 2004) or predator avoidance behaviours (Peluc et al. 2008) and compensate for inclement weather by investing in brooding rather than self-maintenance activities like foraging (Wiebe and Elchuk 2003).

Additional variation in offspring development may stem from carry-over effects between non-independent developmental stages. Avian offspring development is a two-stage process along a single developmental trajectory, but incubation and the nestling period have historically been considered separately. Incubation duration results from a trade-off between embryo development and parental self-maintenance (Conway and Martin 2000). Thus, we might expect the duration of development stages to be correlated because inclement conditions that deplete parental energy reserves and reduce nest attentiveness during the incubation period may ‘carry-

over' to prolong the nestling period, either through deleterious physiological processes stemming from frequent embryo cooling or by influencing parental investment (Webb 1987, Nord and Nilsson 2011). Inter-specific comparisons find incubation duration in birds is decoupled from nestling period duration ( $r = 0.13$ ; Martin et al. 2015), similar to other taxa (e.g., intertidal fish; Thia et al. 2018), suggesting development stages are susceptible to different extrinsic drivers. However, within-population research indicates greater ambient temperatures or greater nest attentiveness during incubation decreases incubation duration and directly translates into increased nestling growth rates (Dawson et al. 2005, Ospina et al. 2018), providing support for developmental carry-over effects.

Variation in offspring development is likely shaped by multiple, interacting extrinsic and intrinsic drivers, yet many studies address influential factors in isolation. A comprehensive approach incorporating multiple effects simultaneously allows assessment of the relative importance of each factor and their subsequent fitness effects. Variable environments are valuable systems for testing multiple effects because trade-offs among life-history strategies may be more pronounced (Piersma and Drent 2003). Alpine habitats are cold, with short breeding seasons and extreme weather events (Martin et al. 2017). Ground-nesting, open-cup species in these habitats may be most constrained by the environment given frequent exposure to ambient conditions and predation risk (Martin and Ghalambor 1999, de Zwaan and Martin 2018). We studied an alpine population of a ground-nesting songbird, the horned lark, which can experience daily temperature fluctuations up to 30 °C (Camfield and Martin 2009) and nest predation rates that vary by up to 250% across years (MacDonald et al. 2016). Females incubate without mate-feeding (Beason 1995), strengthening the potential relationship between maternal condition and

offspring development. Thus, conditions are ideal to address multiple drivers of offspring development simultaneously in a highly variable environment.

Using path analysis on a 7-year dataset, I addressed the relative effects of weather, predation risk, and maternal condition on variation in offspring development (incubation, nestling period). I predicted inclement weather such as cold ambient temperatures and heavy precipitation would prolong offspring development (later fledging), while elevated predation risk would reduce development duration to expedite fledging. I expected females would mediate these effects and reduce the time offspring remain within the nest, either directly by increasing incubation attentiveness and provisioning rate, or indirectly, through the carry-over effects of incubation behaviour on nestling development. I further quantified the probability of nest loss as an immediate consequence of prolonged time in the nest for each of the incubation and nestling periods. Addressing offspring development patterns in a highly variable environment will provide a more comprehensive understanding of the natural variation in this trait and its significance for individual fitness and life-history evolution.

## **Methods**

### *Parameter definitions*

*Weather*—Daily temperature and precipitation recordings were gathered for the breeding season from 2003–2007 and 2010–2011 (see *Chapter 1: General methodology*). To reflect the relative influence of different environmental intensities, I calculated two metrics of precipitation: 1) precipitation days (> 1 mm), and 2) storm events (> 10 mm; Martin et al. 2017). I also derived three temperature metrics: 1) average daily temperature, 2) days < 5 °C, and 3) days < 10 °C. Days < 5 °C and < 10 °C indicate periods of extreme and ecologically relevant periods of cold,

respectively, both of which can create food availability or thermoregulatory challenges. For larks at this site, 10 °C acts as a threshold, below which females increase nest attentiveness during the incubation period (MacDonald et al. 2014).

To calculate a unique climate profile for each nest, weather variables were extracted at 3 temporal scales: 1) stage-specific (incubation, nestling period), 2) early nestling period, and 3) late nestling period. I could then determine if offspring development was most influenced by overall weather patterns or fine-scale weather events at sensitive stages of development.

The nestling period was divided into two developmental phases to reflect different susceptibilities to ambient environmental conditions: 1) ‘Early’—nestlings are essentially ectothermic and unable to thermoregulate (0–4 days post-hatching), and 2) ‘Late’—after endothermy has been achieved ( $\geq 5$  days post-hatching to fledging). The age of endothermy for horned larks is unknown. However, alpine skylark (*Alauda arvensis*) nestlings reach effective endothermy at 4–5 days post-hatching (Verbeek 1988), while nestlings of the ecologically similar Lapland longspur (*Calcarius lapponicus*) achieve endothermy at  $\sim 0.69$  of their asymptotic mass (Maher 1964); a threshold that horned larks reach at 4–5 days post-hatching (see Chapter 3). In summary, I associated 5 weather variables with the incubation period (3 temperature; 2 precipitation) and 15 with the nestling period (5 weather variables; 3 temporal scales – overall, early, and late nestling period) for each nest.

*Predation risk*—Annual predator population densities were not monitored, so I calculated a proxy of perceived predation risk as one minus the site-wide average daily nest survival ( $1 - \text{DNS}$ ) using the Mayfield method (Mayfield 1975). In this population, DNS increases later in the breeding season (MacDonald et al. 2016), so I calculated different predation risk values for nests

in which offspring development primarily occurred in each of May (early), June (mid), and July (late). I assumed: 1) greater predation risk reflects either greater predator abundance or more active predators, and 2) regardless of the mechanism, it operated evenly across the study site such that perceived predation risk was comparable among nests for a given time period.

*Maternal condition*—I estimated maternal condition using the residuals from a mass-wing regression (Jakob et al. 1996). Positive values reflect females in good condition and negative values indicate poor condition, or females that are lighter than average for a given body size. Maternal condition estimates were restricted to the nesting attempt during which the female was captured. I acknowledge that maternal condition was measured during the nestling stage and may change over the course of offspring development. However, nestling age on the day a female was captured did not bias maternal condition estimates (linear model:  $t = 0.92$ ,  $P = 0.36$ ).

## **Statistical analysis**

### *Candidate weather variables*

Since I collected 20 weather variables per nest (2 precipitation and 3 temperature variables; 4 temporal scales—incubation, and early, late, and overall nestling stage), I used Akaike Information Criterion (AIC) to select the most relevant candidate variables for inclusion in the final models (Anderson et al. 2001). I built a series of linear mixed-effects models (LMMs) describing variation in both the incubation and nestling period using the R package ‘lme4’ (Bates et al. 2015). This series included single models with one weather variable, as well as, additive and interaction models with two weather variables (one temperature and one precipitation). For the nestling period, I also fit models including both early and late temperature variables (see

Appendix 1: Table A1.1). Each model contained date as a fixed effect and year as a random effect. I used  $\Delta\text{AIC} \leq 6$  as the threshold to designate the top models for use in further analysis because it corresponded with a cumulative Akaike weight of  $\geq 0.90$ .

### *Path analysis*

I used piecewise path analysis to address the proximate drivers of variation in offspring development, as well as indirect carry-over effects from incubation to the nestling period. Path analysis is a particularly strong tool for evaluating complex relationships because it can calculate the relative strength of indirect and direct effects of proximate factors in a causal network structure (Shipley 2009). Each causal pathway represents a direct effect with an associated partial regression coefficient. Indirect effects are the product of all one-way path coefficients connecting the explanatory variable of interest to the response variable. Piecewise path analysis involves fitting multiple individual LMMs independently prior to integration, allowing the use of different model distributions and smaller sample sizes (Lefcheck 2016).

Since I did not have maternal condition data for all nests, I built two path models, testing: 1) predation risk and weather effects only ('extrinsic model'), and 2) the addition of maternal condition ('complete model'). Each path model consisted of two sub-models, describing: 1) the incubation period using direct drivers (weather, predation risk, maternal condition), and 2) the nestling period with incubation duration (indirect effects), as well as direct drivers. For the complete model, I included a date by maternal condition interaction for the nestling period to test the ability of females to consistently facilitate rapid nestling development early in the season (harsh, cold) and later in the season (mild, warm). For both models, year was included as a random effect. Explanatory variables were standardized and considered significant at  $\alpha = 0.05$ .

I used D-separation tests and Akaike's information criterion (AIC) to identify the most parsimonious path structure for both the extrinsic and complete models (Shipley 2013). First, I calculated the Fisher's C statistic for the a priori path structure to evaluate whether the model fit the data well and determine if any major pathways were missing (Shipley 2013). I then tested the importance of each individual pathway by step-wise removal and evaluated the change in model fit with  $\Delta$ AIC (Flockhart et al. 2016, Woodworth et al. 2017). Paths were retained if their removal increased AIC by more than 2. Model selection began with the incubation period, followed by the nestling period sub-model. Following Woodworth et al (2017), the order of term removal within each sub-model was decided by first comparing all models where one term was removed using AIC, and then removing each term in a step-wise fashion, starting with the weakest effect and ending with the strongest. The final path model used in further analysis was chosen based on the smallest combined Fisher's C statistic and AIC.

Once the final path structure was selected, I used a Markov chain Monte Carlo (MCMC) approach to evaluate the explanatory power of each path model to detect a significant effect. Probability distributions for each variable were created by randomly sampling 10,000 points. The path models were then boot-strapped with 1000 iterations, restricting the number of samples to the observed sample size for each model (extrinsic  $n = 102$ , complete  $n = 50$ ). The original path model and iterative model were compared using AIC and RMSEA (Root Mean Square Error of Approximation) to evaluate sample size adequacy.

### *Fitness consequences*

I estimated daily nest survival (DNS) separately for both the incubation and nestling period using a discrete proportional hazards model with exposure days as an offset. Date of clutch initiation

was included as an explanatory variable to account for differences in nest survival over the season. I then calculated the average daily probability of nest predation ( $1 - \text{DNS}$ ) for each day beyond the population average for hatching and fledging, allowing me to evaluate the fitness consequences of extended development time for each stage.

Analyses were conducted in R version 3.6.1 (R Development Core Team 2018). I used package ‘lme4’ (Bates et al. 2015) to fit mixed-effects models, ‘piecewiseSEM’ (Lefcheck 2016) for path analysis, and ‘simsem’ (Jorgensen et al. 2018) for MCMC iterations of the path model.

## **Results**

Over 7 field seasons, 255 nests were monitored, 102 of which survived to and had accurate estimates of date of fledging. Of the successful nests, 50 were associated with measurements of maternal condition. Most females only produced a single brood, with an average of 7.7% of females attempting a double brood each year. In 2007, the few nests that successfully fledged did not have accurate estimates of date of hatching or fledging ( $n = 4$  nests), so these nests were included in the survival analysis only and not in the path analysis. Average incubation period was  $12.0 \pm 0.1$  days (mean  $\pm$  se; range: 10–14 d) and nestling period was  $9.4 \pm 0.1$  days (range: 7–13 d). Generally, 2003, 2004, and 2006 were mild to warm years with moderate to low precipitation, while 2005, 2007, 2010, and 2011 were cold, with extended snow cover, and heavy precipitation (see Appendix 1: Table A1.2).

### *Model selection and fit*

When determining which weather variables to include in the path model, AIC model selection retained days  $< 10$  °C and precipitation days ( $> 1$  mm) as the most influential temperature and

precipitation variables for both the incubation and nestling period (Table 2.1). For the nestling period, a precipitation by temperature interaction was retained in the extrinsic, but not complete model (Table 2.1). After D-separation and AIC selection, brood size (extrinsic and complete model) and precipitation days (complete model only) were dropped from the a priori path model because their exclusion significantly improved model support. Both final path models had a robust fit (Extrinsic – Fisher’s  $C = 10.8$ ,  $P = 0.55$ ; Complete – Fisher’s  $C = 13.03$ ,  $P = 0.22$ ), with an adequate sample size as validated by MCMC iterations (Extrinsic – AIC:  $P = 1.00$ , RMSEA:  $P = 1.00$ ; Complete – AIC:  $P = 0.92$ , RMSEA:  $P = 0.29$ ).

### *Inclement weather*

Periods of cold weather (days  $< 10$  °C) during the incubation stage delayed hatching date and prolonged incubation duration, while a greater number of mild precipitation days ( $> 1$  mm) decreased incubation duration (Figure 2.1A, Figure 2.2A). Cold weather late in nestling development ( $\geq 5$  days post-hatch) prolonged the nestling period, contrasting with temperatures early in development ( $< 5$  days post-hatch) which had no effect (Figure 2.1A, Figure 2.2B). I also found support for a precipitation by temperature interaction late in the nestling period, such that more precipitation days promoted rapid development during warm temperatures, but prolonged development during cold periods (Figure 2.1A).

### *Predation risk*

Predation risk did not influence incubation duration. However, nestling development was more rapid during months with greater predation risk after controlling for date (Figure 2.1A).

Although significant, the effect size of predation risk was at least 2.7 times less than temperature

or precipitation indicating that weather is the predominant driver of offspring development in our system.

### *Maternal condition*

The proportion of explained variance for the incubation period was relatively low in both path analyses ( $R^2 = 0.15$ ; Figure 2.1). However, including maternal condition accounted for an additional 17% of the observed variation in nestling period duration, increasing the proportion of explained variance from 0.56 (extrinsic model;  $n = 102$  nests; Figure 2.1A) to 0.73 (complete model;  $n = 50$ ; Figure 2.1B). Maternal condition was negatively associated with both the incubation and nestling periods, such that females in good condition produced offspring with shorter development times (Figure 2.1B). Additionally, a date by maternal condition interaction for the nestling period indicated that females in good condition were able to fledge nestlings more rapidly earlier in the season when conditions were harsh, compared to females in poor condition (Figure 2.1B, Figure 2.3). When maternal condition was included in the path model, precipitation did not factor into the model for either incubation or the nestling period (Figure 2.1). However, precipitation and maternal condition were uncorrelated ( $r = 0.15$ ), suggesting this result did not stem from a confounding relationship. Finally, maternal condition predominantly influenced nestling period duration directly, rather than through indirect developmental carry-over effects, as incubation period length did not influence nestling development time.

### *Cost of extended development time*

Average daily nest survival (DNS) for the incubation period was  $0.983 \pm 0.024$  (mean  $\pm$  SE), translating into an average  $81.4 \pm 1.2\%$  probability of surviving to the date of hatching based on

12 days of incubation. DNS for the nestling period was lower overall at  $0.968 \pm 0.007$ , giving a fledging success of  $74.6 \pm 1.7\%$  for a 9-day nestling period. DNS was consistent within development periods such that extended time within the nest was not associated with greater or lesser predation risk than the background rate (incubation:  $z = -1.27$ ,  $P = 0.20$ ; nestling:  $z = 0.37$ ,  $P = 0.71$ ). Delayed hatching increased the risk of predation by 1.4%/day, while delayed fledging increased risk by 2.3%/day (Table 2.2). Thus, nestlings fledged at 7 days were on average 13.8% more likely to fledge than those delaying to 13 days given that they hatched. The magnitude of the cost of delayed hatching or fledging varied significantly among years, ranging from 0.0–2.6%/day for hatching and 1.0–3.4%/day for fledging (Table 2.2).

## **Discussion**

For an alpine songbird, nestling period duration varied by nearly 100% (7–13 days) and incubation duration by 40% (10–14 days). Since the length of the nestling period is strongly correlated with average growth rate across altricial species ( $r = -0.92$ ; Martin et al. 2011), this indicates significant within-population variation in both the rate of nestling size growth and development of critical traits like mobility (Martin et al. 2018). Rapid offspring growth may have long-term negative fitness consequences, such as decreased longevity (Metcalf and Monaghan 2001), but under high predation risk conditions the short-term benefits of rapid maturation of mobility traits to facilitate predator evasion should be prioritized (Coslovsky and Richner 2011). While I identified predation risk as an influential factor, inclement weather and maternal condition had stronger effects on within-population variation. Additionally, an interaction between date and maternal condition demonstrated that females in good condition consistently created a nest environment that promoted rapid nestling development compared to females in

poor condition, regardless of environmental conditions. Overall, although offspring development was responsive to environmental drivers like weather and predation risk, females in good condition appear able to buffer offspring against environmental constraints.

Weather conditions can prolong offspring development and the timing of weather events may be critical. Colder ambient conditions are associated with reduced egg temperatures and prolonged incubation periods (Martin et al. 2007), particularly in cold adapted species (Ton and Martin 2017), while experimentally heating tree swallow (*Tachycineta bicolor*) nests during the nestling period promotes rapid development (Dawson et al. 2005). I found colder temperatures prolonged the incubation period, as well as, the nestling period, but only when occurring during the late nestling stage. Since the ability for nestlings to thermoregulate does not develop immediately, females brood more frequently early in the nestling period and likely can buffer offspring against colder ambient temperatures (Wendeln and Becker 1999). During colder conditions later in development, nestlings may have to direct limited energetic resources to thermoregulation rather than structural growth, effectively extending development (Wingfield et al. 2017). We also identified an interaction between precipitation and ambient temperature on nestling development, potentially reflecting food availability. Warm, wet weather promotes greater resources for insectivores (Tuero et al. 2018), facilitating rapid development, while cold storms likely severely depress resource availability (Martin et al. 2017). ‘Cold storms’, like other ecological extremes, have potentially disproportionate effects on fitness and are increasing in frequency with climate change (Wingfield et al. 2017). Our results support the association between extreme weather events and non-lethal effects on life-history traits that increase susceptibility to fitness loss, such as a higher probability of nest predation.

Predation is the greatest source of nest loss for songbirds (Ricklefs 1969) and thus greater predation risk should drive an increase in offspring development rates to improve the probability of evading predators (Coslovsky and Richner 2011). Yet, poor weather conditions may set limits on this relationship (Stodola et al. 2010). Although I found that periods of greater predation risk promoted more rapid nestling development, I demonstrate that the effect size of ambient temperature on the rate of offspring development was greater than predation risk in this system. It is important to note however, that the relative strength of each driver may be habitat or condition-dependent (Wilson et al. 2018). For example, weather may be most influential in harsh, stochastic environments like alpine, arctic or desert habitats compared to predation risk in habitats with more benign conditions. The effect of predation risk on nestling period duration may reflect a flexible response in nestling development to prevailing conditions, and/or a by-product of only rapidly developing nestlings surviving to the date of fledging under high predation risk. Regardless of the mechanism, during periods of high predation risk rapid offspring development should be favoured when weather conditions allow.

Since the probability of nest success declines with prolonged offspring development, the capacity to shorten development time carries distinct fitness benefits. For the female, per offspring energy expenditure is influenced by variation in environmental conditions or reproductive costs (Stodola et al. 2010), and in turn, is mediated by female condition or the capacity for greater reproductive investment (van Noordwijk and de Jong 1986, Jablonszky et al. 2018). The developmental benefits of greater reproductive investment compared to self-maintenance have been demonstrated in tree swallows, where greater nest attentiveness during incubation relative to time away from the nest was linked to higher egg temperatures and thus reduced incubation periods (Coe et al. 2015). For larks, females in good condition consistently

maintained nest environments that facilitated rapid development times throughout the season. In contrast, females in poor condition were associated with prolonged offspring development early in the season when energy limitation is a greater constraint, but achieved more rapid development with benign, late season conditions. Thus, females in good condition likely have a greater capacity to invest in either incubation or brooding despite suboptimal conditions, while females in poor condition may be more energy limited, requiring frequent or extended off-bouts in inclement weather.

I did not find support for an indirect influence of maternal condition on nestling development time acting through developmental carry-over effects of incubation duration. This contrasts with expectations from experimental studies where cooled embryos and prolonged incubation reduced nestling growth and development rate (Nord and Nilsson 2011, Ospina et al. 2018). It is likely that both physiological maternal effects which act through steroid hormones (i.e., glucocorticoids; Weber et al. 2018), as well as more direct behavioural adjustments contributed to the strong influence of ‘maternal condition’ on nestling development, but due to the nature of this variable I could not separate direct and indirect effects. Since I lacked data on multiple nests per female, I was unable to address whether offspring development was a flexible trait among nesting attempts of an individual female. In more variable environments like the alpine, flexible life-history traits are advantageous (Piersma and Drent 2003). The benefits of rapid offspring development are potentially limited due to deleterious long-term fitness consequences (Monaghan 2008). Therefore, being able to fledge offspring rapidly during periods of high predation risk, but prolonging development during more benign conditions, may carry a selective advantage that has not previously been addressed.

In an alpine songbird population, I found extraordinary variation in nestling development duration (7–13 days) with consequences for nest success. Overall, I identified pronounced effects of inclement weather, maternal condition, and predation risk on offspring development. It seems feasible that greater environmental stochasticity with climate change may have disproportionately negative effects on populations by reducing reproductive success in combination with daily predation risk rates, or by increasing fitness disparities between females in good and poor condition which may make populations less robust to disturbance. In this context, flexible life-history strategies are necessary for individuals to respond to climate change (Forcada et al. 2008). Importantly, my models accounted for significantly less variation in incubation duration than nestling development, suggesting that variation in incubation may be driven more by intrinsic constraints than responses to environmental factors, and thus may be more susceptible to changing climates. By addressing multiple proximate drivers, I identified nuanced associations between offspring development and the environment, providing important implications for our understanding of life-history theory under changing environmental conditions.

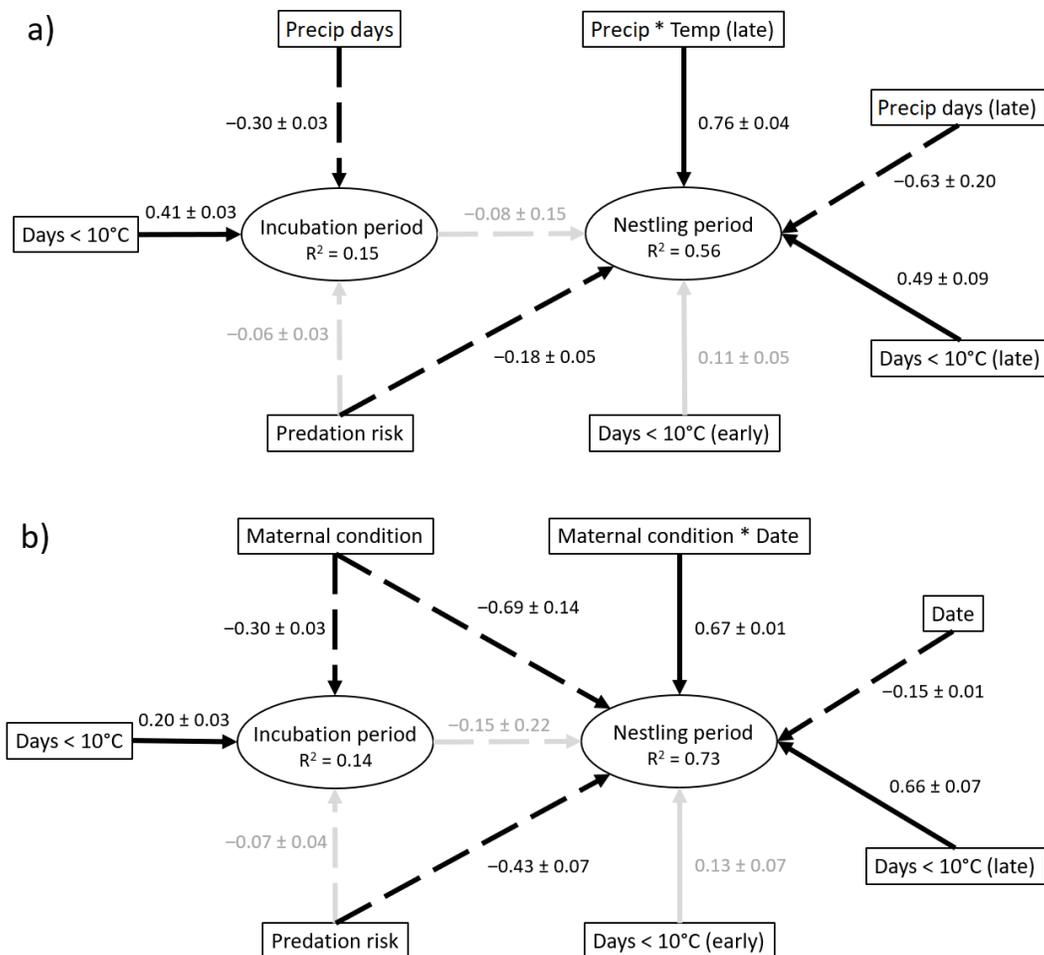
**Table 2.1.** Most relevant environmental variables based on the top models for the incubation (I) and nestling (N) period for an alpine population of horned larks. Models are presented for (a) the extrinsic dataset (without maternal condition), and (b) the complete dataset (with maternal condition). For maximum parsimony, only variables from models with a cumulative Akaike weight ( $w$ ) of 0.90 ( $\Delta\text{AICc} < 6$ ) were included in the path analysis. Terms in brackets designate the temporal scale for each variable (overall, early, or late nestling stage).

Models	Df	LogLik	$\Delta\text{AICc}$	$w$	Cumulative $w$
<b>(a) Extrinsic (n = 102)</b>					
<i>Incubation period</i>					
I < 10 °C (overall)	5	-132.6	0.0	0.63	0.63
I < 10 °C (overall) * precipitation days (overall)	7	-131.6	2.4	0.19	0.82
I < 10 °C (overall) + precipitation days (overall)	6	-133.4	3.8	0.09	0.91
I < 10 °C (overall) + storms (overall)	6	-133.6	4.1	0.08	0.99
<i>Nestling period</i>					
N < 10 °C (early) + < 10 °C (late)	7	-126.2	0.0	0.82	0.82
N < 10 °C (early) + < 10 °C (late) * precipitation days (late)	9	-126.5	5.4	0.05	0.87
N < 10 °C (early) + < 10 °C (late) + precipitation days (early)	8	-127.7	5.5	0.05	0.92
N < 10 °C (early) + < 10 °C (late) + precipitation days (late)	8	-127.9	5.8	0.05	0.97
<b>(b) Complete (n = 50)</b>					
<i>Incubation period</i>					
I < 10 °C (overall) + precipitation days (overall)	5	-24.6	0.0	0.41	0.41
I < 10 °C (overall)	4	-26.7	1.6	0.19	0.60
I precipitation days (overall)	4	-27.0	2.3	0.13	0.73
I < 10 °C (overall) * precipitation days (overall)	6	-24.6	2.5	0.12	0.85
I avg temperature (overall)	4	-27.5	3.2	0.08	0.93
I < 5 °C (overall)	4	-27.6	3.4	0.07	1.00
<i>Nestling period</i>					
N < 10 °C (early) + < 10 °C (late)	9	-68.8	0.0	0.76	0.76

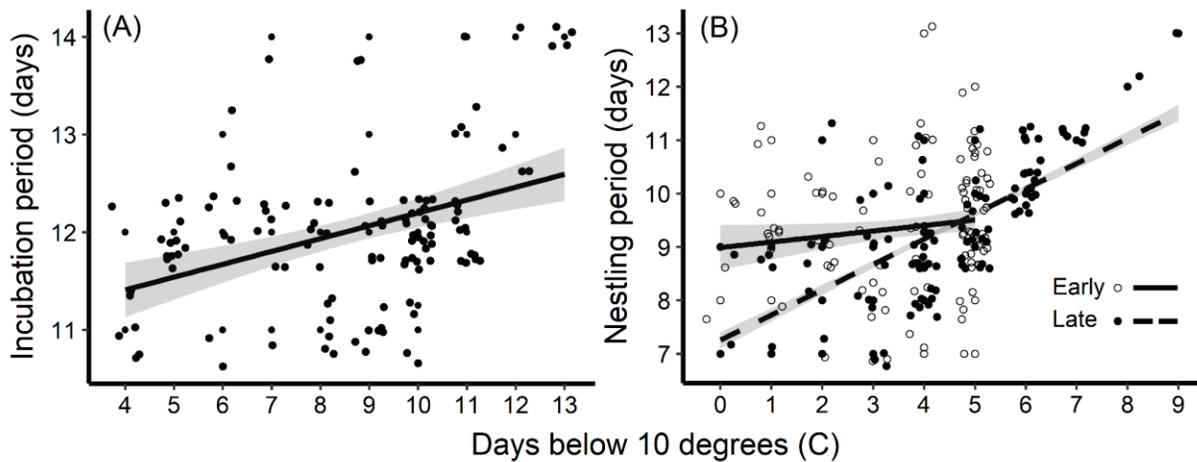
**Table 2.2.** Average daily nest survival (DNS) and nest success (%) per year for each development stage (incubation and nestling period). The predicted nest success is based on an average development time of 12 and 9 days for the incubation and nestling stage, respectively. Delayed costs indicate the decreased daily probability (%/day) of successfully hatching or fledging beyond the mean date of hatching and fledging, respectively.

Year	Incubation		Nestling stage		Delayed cost of hatching	Delayed cost of fledging
	DNS	%	DNS	%	%/day	%/day
2003	1.000	100.0	0.939	56.8	0.0	-3.2
2004	0.997	96.5	0.989	90.5	-0.3	-1.0
2005	0.992	90.8	0.982	84.9	-0.7	-1.5
2006	0.980	78.5	0.981	84.1	-1.4	-1.8
2007	0.982	80.4	0.904	40.3	-1.4	-3.4
2010	0.974	72.9	0.934	54.1	-1.8	-3.2
2011	0.946	51.4	0.964	71.9	-2.6	-2.5
Average	0.983	81.4	0.968	74.6	-1.4	-2.3

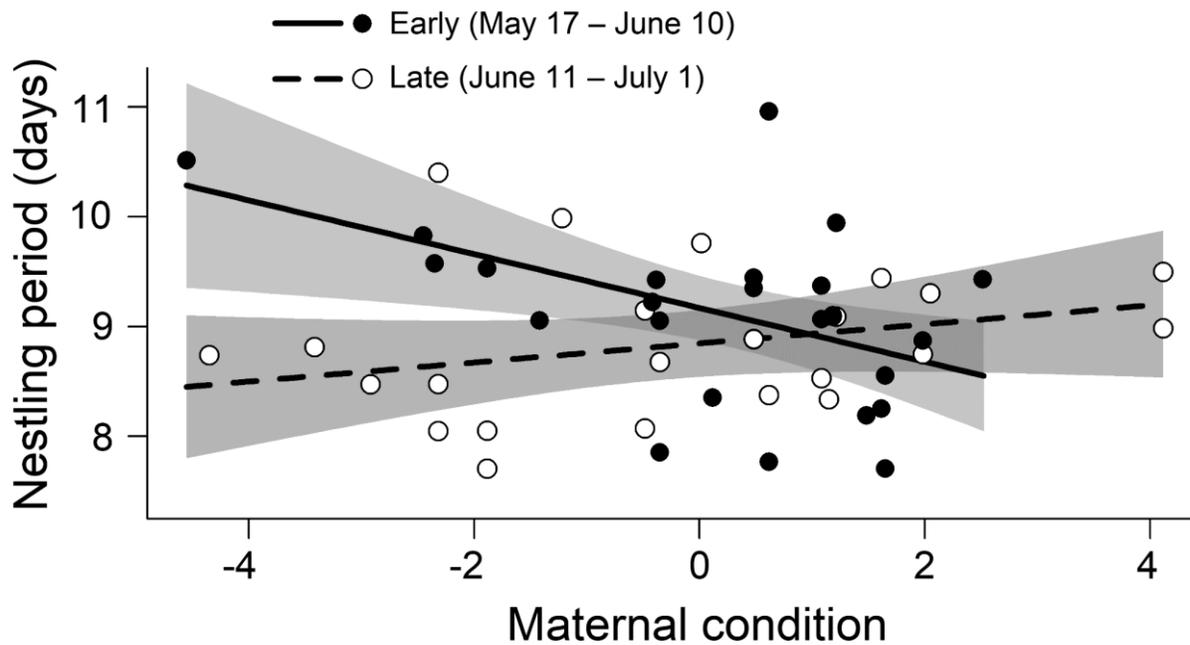
**Figure 2.1.** Path models for (a) the extrinsic dataset without maternal condition, and (b) the complete dataset including maternal condition, for an alpine breeding population of horned lark. Values next to the arrows are the standardized effect sizes ( $\pm$  SE). Solid arrows depict positive effects and dashed arrows are negative effects. Grey lines are non-significant.  $R^2$  is the proportion of variance for each of the incubation and nestling period described by the models. Ovals encompass the two response variables, while rectangular boxes depict drivers of offspring development. Sample sizes per year for each model (extrinsic/complete) are: 2003 = 5/0, 2004 = 15/12, 2005 = 30/19, 2006 = 36/18, 2010 = 9/1, 2011 = 7/0).



**Figure 2.2.** Relationship between the length of a development period and the number of cold days ( $< 10^{\circ}\text{C}$ ) during the A) incubation and B) nestling period. The nestling period is further subdivided into early (0–4 days post-hatching) and late ( $\geq 5$  days post-hatching to fledging). These relationships are derived from the incubation and nestling period sub-models in the path analysis using the extrinsic dataset ( $n = 102$  nests). The shaded band depicts the predicted 95% confidence intervals.



**Figure 2.3.** The influence of a maternal condition by date interaction on nestling period duration. Positive values of maternal condition indicate females that are heavier for a given wing size (good condition), while negative values are lighter (poor condition). Early and late periods were based on natural peaks in nest initiation. The trends represent best fit regression lines and the shaded bands depict 95% confidence intervals of the partial residuals.



## **Chapter 3. Hierarchical fear: parental behaviour and corticosterone mediate nestling growth in response to predation risk**

### **Introduction**

Predation risk is a fundamental driver of ecological and evolutionary processes in the animal kingdom, eliciting responses in individual life-history strategies and avoidance behaviours with consequences for fitness and ultimately population dynamics (Lima and Dill 1990, Creel and Christianson 2008, Sheriff et al. 2010). In fact, by reducing individual fitness, the non-consumptive effects of predator presence can equal or exceed the strength of consumptive effects on population growth (Preisser et al. 2005, Zanette et al. 2011). Nestling development in altricial songbirds is a vulnerable life-history stage, with nest predation making up 70–95% of all reproductive mortality (Martin and Briskie 2009). When resources are uncertain, slower development may be adaptive because it reduces daily per nestling energy requirements (Arendt 1997). However, high predation risk may select for accelerated development, as nest predation is a cumulative risk that increases with time in the nest (Martin 1995). Thus, nestling development rates occur along a slow-fast continuum, where rapid development is associated with greater predation risk among species (Bosque and Bosque 1995, Remeš and Martin 2002, Martin et al. 2011) and within populations (Hua et al. 2014, Chapter 2).

Differential growth, the process of allocating resources to the development of traits that improve survival at the expense of less critical traits, has been hypothesized as a mechanism to prioritize wing growth in response to greater predation risk (Coslovsky and Richner 2011, Cheng and Martin 2012, Martin 2015, LaManna and Martin 2016). Immediately upon leaving the nest (fledging), altricial offspring have limited mobility and are highly vulnerable to predation

(Sullivan 1989, Both et al. 1999). Within the first two weeks of fledging, survival of altricial songbirds ranges from 23–87% and increases with offspring size (Cox et al. 2014). Offspring with longer wings at fledge generally have greater mobility, and thus have a greater capacity to evade predators and improve post-fledging survival (Dial et al. 2006, Morrison et al. 2009, Martin et al. 2018). Therefore, rapid growth within the nest to promote fledging at an earlier age with longer wings is an adaptive response to elevated predation risk with immediate survival benefits (Martin 2014).

Nest predation risk represents a hierarchical form of risk, composed of both indirect and direct effects on nestling growth (Figure 3.1). Parents may respond to predator presence by reducing provisioning rate to avoid nest detection (Martin et al. 2000, Eggers et al. 2005). Reduced provisioning rate may in-turn constrain resource availability for nestlings which can negatively impact growth and the development of flight capabilities (*indirect effect*; Dunn et al. 2010, Criscuolo et al. 2011). This resource constraint may not be experienced equally by all nestlings. As a form of brood reduction, adults may provision larger nestlings preferentially in order to fledge a partial brood of the largest nestlings quickly rather than losing the entire brood (Wagner et al. 2019). Additionally, nestlings may be able to detect predator presence and respond adaptively, such as by reducing begging upon hearing a predator (*direct effect*; Magrath et al. 2010). Both resource availability and behavioural responses to predation risk can induce physiological changes which have the potential to trigger differential growth or shifts in development rate (Sapolsky et al. 2000).

Corticosterone (CORT) is a glucocorticoid released in large quantities in response to unpredictable stressors to initiate emergency behaviours that improve immediate survival (Wingfield et al. 2017, Creel 2018). Glucocorticoids are also involved in regulating internal

systems such as homeostasis and metabolism (Wingfield et al. 1998, Romero 2004), and thus CORT has been suggested as a possible mediator of nestling developmental responses to predation risk (Coslovsky and Richner 2011). Chin et al (2008) found that nestlings with experimentally elevated CORT had longer wings and larger pectoral muscles supporting a potential investment in flight capabilities. However, this experimental result is inconsistent with empirical field studies where greater concentrations of CORT in blood and tissue are often correlated with reduced nestling growth (Wingfield and Sapolsky 2003, Spencer and Verhulst 2007, Wada and Breuner 2008). While predator cues tend to increase corticosterone levels in nestlings (Fridinger et al. 2007, Tilgar et al. 2010, Crino et al. 2011), periods of restricted resources and reduced provisioning rates can also trigger corticosterone release (Rensel et al. 2010, Will et al. 2014, Lamb et al. 2016). Therefore, whether predation risk influences nestling growth indirectly or directly, and whether corticosterone may mediate this response remains unclear, requiring a comprehensive framework that simultaneously addresses all potential linkages to understand the component effects.

In Chapter 2, I demonstrated that greater site-wide predation risk was linked to more rapid development (earlier age at fledge) among and within years for an alpine population of horned lark in northern British Columbia, Canada. Here, I experimentally increased perceived predation risk at the nest to investigate the underlying mechanisms for this result by assessing the relative indirect and direct effects on nestling growth. Specifically, I addressed whether: (1) wing length is a limiting growth factor that determines age at fledging, and (2) perceived predation risk influences wing growth, and if so, if this relationship acts indirectly through parental behaviour or is a direct response by nestlings independent of the parents. In addition, I (3) addressed the association between wing growth and feather corticosterone levels in nestlings to

assess support for corticosterone as a potential physiological mechanism underlying indirect and direct predation risk effects. Finally, parents may employ brood reduction strategies to successfully fledge a partial brood at an earlier age. Thus, I (4) investigated whether predation risk influenced within-nest variance in wing length and corticosterone and, in turn, whether larger nestlings from nests with greater size disparities fledged at an earlier age.

## **Methods**

See *Chapter 1* for general details on the study system and field methodology.

### *Experimental methodology*

I used predator presentations at the nest to experimentally manipulate perceived predation risk with three treatment levels: 1) red fox *Vulpes vulpes*, 2) common raven *Corvus corax*, and 3) savannah sparrow *Passerculus sandwichensis* as a control. The fox presentation involved a decoy and represents a scent-oriented, terrestrial predator, while the raven included a decoy with audio playback and represents a visually-oriented, aerial predator. I also used audio playback for the non-competitive, sympatric breeding savannah sparrow (hereafter ‘control’) to produce an audio disturbance near the nest that did not represent a threat. Raven calls and savannah sparrow songs were retrieved as band-pass filtered audio from an online library (Xeno-Canto Foundation 2014) and were originally recorded in the general region of the study site. For both the control and raven, recordings were combined into a 30 min loop and programmed to play in 6 min segments of 5 min of sound and 1 min of silence. These recordings were projected through TDK A33 speakers (TDK Corporation, Tokyo, Japan). During predator presentations, the decoys were

placed ~8 m in front of the nest and moved freely in the wind, which helps prevent habituation when combined with sound (Ghalambor and Martin 2000, 2001).

Predator presentations were conducted once per day between 0600 and 1300 h PDT over 2 consecutive days for each nest (5- and 6-days post-hatch). Nestlings fully open their eyes at about 4-days post-hatch and become aware of their surroundings as evidenced by behaviours such as suppressed begging or crouching when observers approach (personal observation). Therefore, nestlings may be more responsive to perceived predation risk during this stage of development. Treatment type was randomly assigned to each nest and remained consistent for both days of the experiment. Canon VIXIA HF-R500 camcorders (Canon Inc., Tokyo, Japan) were mounted on tripods and placed ~15 m from the nest to record parental provisioning rates. Each day, recording began with 30 min of silence (no visual or audio cues) to establish a baseline for provisioning behaviour, followed by a 1-hour predation risk treatment for a total of 3 hours per nest over the 2 days. Provisioning rate did not differ between the 30 min pre-treatment period and the savannah sparrow treatment (Goullaud et al. 2018), indicating that the savannah sparrow represents a valid control and that larks do not simply respond to the speaker.

Nestling size and condition traits were measured prior to the experiment at 5-days post-hatch and following the experiment at 7-days to quantify nestling growth (*Chapter 1: General methodology*). For changes in corticosterone, I measured feather CORT, a minimally invasive measurement of the stress response which is particularly useful for assessing the accumulation of CORT over an extended period (Romero and Fairhurst 2016) and can allow coarse differentiation of CORT concentrations over time as it deposits along a growing feather (Fairhurst et al. 2011, Jenni-Eiermann et al. 2015). At 5-days post-hatch (pre-experiment), I measured the length of 10 dorsal tract feathers on each nestling to determine an average feather

length, and then removed 6–10 feathers from the same region at 7-days (post-experiment). I later cut each feather using the average pre-experiment length for each nestling to approximately separate feather material grown prior-to and during the experiment, allowing me to address differences in corticosterone accumulation (see *Feather corticosterone* for extraction details).

### *Feather corticosterone*

To analyze feather corticosterone, I chose two nestlings per nest; the largest and third largest nestling based on mass at 7 days post-hatch. Corticosterone was extracted from the feather samples using a methanol-based technique and following the protocol described in Bortolotti et al. (2008). All samples were extracted in duplicate batches, such that each nestling sample was analyzed twice. The recovery efficiency was calculated by including three feather samples spiked with approximately 5000 CPM of  $^3\text{H}$ -corticosterone in each extraction batch (see Bortolotti et al. 2008, Supplementary Appendix S1). More than 96% of the radioactivity was recovered in each batch. The dried methanol extracts were reconstituted with 600  $\mu\text{l}$  of phosphate-buffered saline (0.05 M and pH 7.6) and kept frozen at  $-20^\circ\text{C}$  until corticosterone was analyzed by radioimmunoassay. Feather extract samples were analyzed randomly in duplicate in six different radio-immunoassays. Anti-serum (C8784; lot 092M4784) and purified CORT (C2505, Lot 22K1439) for standards were purchased from Sigma-Aldrich (St. Louise, Missouri, USA) and [ $^3\text{H}$ ] CORT from Amersham Bioscience (Piscataway, New Jersey, USA). The assay variability was determined as the percentage of coefficient of variation (CV) resulting from repeated measurement of six samples spiked with a known amount of corticosterone in each assay. Intra- and inter-assay CV were 7.4% and 8.4% respectively and the limit of detection (ED  $80 \pm \text{SD}$ ) average was  $15.37 (\pm 3.47)$  pg per tube. I expressed feather corticosterone values as a

function of feather length (pg/mm; Bortolotti et al. 2008, 2009, Jenni-Eiermann et al. 2015).

Hormone analyses were performed in the Department of Biology, University of Saskatchewan (Canada).

### *Temperature data*

Daily temperature recordings were gathered for the breeding seasons (*Chapter 1: General methodology*). Extended periods of cold (days < 10 °C) prolongs nestling development time (Chapter 2). Therefore, I calculated the number of days with an average temperature below 10 °C prior to the experiment (0–4 d post-hatch) and during the experiment (5–7 d) to control for the influence of ambient temperature on different stages of development.

### **Statistical analysis**

Each nestling was associated with a unique set of size trait measurements (wing length, tarsus length, mass, wing load), feather CORT concentrations (pg/mm) at 5- and 7-days post-hatch, and an age at fledging. Wing load was estimated as the residuals from a wing by mass regression such that nestlings with positive values have longer wings and negative values have shorter wings for a given mass. Prior to assessing predation risk effects on nestling development, I investigated which size traits were most predictive of age at fledging to validate whether wing length limits when a nestling leaves the nest (*Objective 1*). I fit separate linear mixed effects models (LMMs) for each size trait with age at fledging as the response, clutch initiation date and brood size as covariates, and nest ID as the random effect. Only 3 nests had fledging ages  $\geq 12$  days, so I combined these with 11 days to form an 11+ group for this analysis.

## *Path analysis*

I used piecewise path analysis to address the hierarchical effects of predation risk on nestling wing growth and feather corticosterone. See *Chapter 2: Path analysis* for more details.

To identify the direct and indirect effects of predation risk on nestling growth (*Objective 2*), I included both predation risk (direct effect) and  $\Delta$  provisioning rate (indirect effect) as fixed effects in models explaining wing length (7 d) and feather CORT. I also included a sub-model with wing length at 5-days as a predictor of wing length at 7-days to control for variation in nestling size prior to the predation risk treatment and to understand how early development conditions influence later growth dynamics. Predation risk was included as a three-level categorical predictor (raven, fox, control). Adult larks respond to perceived predation risk by reducing nest visits, but the extent of this response varies among individuals (Goullaud et al. 2018). Therefore, I calculated  $\Delta$  provisioning rate as the difference between the number of nest visits/10 min during the 30 min pre-treatment controls and the 1 hr treatment for each of the two days. Parents that responded strongly to predator presentations had larger and positive  $\Delta$  values, and those who did not respond had small  $\Delta$  values. Clutch initiation date, brood size, and days < 10 °C were included as covariates and nest ID as a random effect in each sub-model. Finally, since my data included both first nests and re-nests, I tested an interaction between date and feather CORT with wing length (7 d) as the response variable to account for potentially different mediating effects of CORT between early and late season broods. I acknowledge that not all possible predictors were measured, and therefore unmeasured variance in the model is denoted with a ' $\mu$ '. All path coefficients were standardized and considered significant at  $\alpha = 0.05$ .

I fit two alternative structures for the relationship between CORT (7 d) and nestling wing length (7 d). First, wing length and feather CORT were both treated as correlated response

variables (non-directional association; hereafter “correlational model”). In the second model, wing length at 7-days was treated as the sole response variable, with feather CORT as a causal predictor of wing length (hereafter “causal model”). Comparing the fit of these path structures allowed me to test whether CORT and wing length are simply correlated responses to predation risk, or whether CORT is a potential mediator of nestling growth response to perceived risk (*Objective 3*). For the full hypothesized path structures, see Appendix 2: Figure A2.1.

I used D-separation tests and Akaike’s information criterion (AIC) to identify the most parsimonious path model (Shibley 2013). First, I compared support for the causal and correlational model using AIC and calculated the Fisher’s C statistic for each to determine if any major pathways were missing (Shibley 2013). Once a single global model was selected, I then used step-wise removal and  $\Delta$ AIC to evaluate the change in model fit, retaining paths if their removal increased AIC by  $> 2$  (Flockhart et al. 2016, Woodworth et al. 2017). Model selection began with the wing length (5 d) sub-model, followed by provisioning rate, CORT (7 d), and wing length (7 d). Finally, I used a Markov chain Monte Carlo (MCMC) approach to evaluate explanatory power for the final path model. See *Chapter 2: Model selection and fit* for full details on both model selection and power analysis. Model selection results can be found in Appendix 2: Table A2.1 and A2.2.

From the final path model, I predicted the total effect of predation risk on nestling wing growth. The total effect is the sum of all direct and indirect pathways and thus a predicted response can be calculated by multiplying the s.d. of the explanatory variable by the total effect and then converting the predicted s.d. value to raw units (Bart and Earnst 1999, Norris et al. 2003). In my data, both clutch initiation date (Julian date; range: 143 – 178; s.d. = 12.4 days) and  $\Delta$  provisioning rate (range: 0.0 – 2.9 less nest visits/10 min; s.d. = 0.8) varied among nests. Time

of year can influence nestling growth dynamics (Naef-Daenzer and Keller 1999), and parents can vary in their ability to fledge offspring quickly during harsh, early season conditions (Chapter 2). Therefore, I predicted the total effect of predation risk on nestling wing growth using the range of observed parental provisioning responses to predation risk at intervals of 1 s.d. (4 total), as well as, across three time periods (average clutch initiation, 1 s.d. earlier, and 1 s.d. later; hereafter ‘average’, ‘early’, and ‘late’ season).

### *Compensation for early development*

The path model controls for the influence of early development conditions by incorporating the sub-model with wing length at 5-days as a predictor of wing length at 7-days post-hatch. However, if poor conditions early in development result in shorter wing length at 5-days, it is possible nestlings may accelerate growth during the experimental period independent of predation risk (i.e., compensatory growth; Criscuolo et al. 2011, Aldredge 2016). To test for compensatory growth, I fit an LMM that predicted the change in wing length between 5- and 7-days post-hatch ( $\Delta$  wing length) with wing length at 5-days as the explanatory variable, clutch initiation date as a covariate, and nest ID as the random intercept. I also included experimental treatment as a control for the indirect and direct predation risk effects I tested with the path analysis. Compensatory growth would be evident if smaller nestlings at 5-days post-hatch were associated with a larger  $\Delta$  wing length, or a greater than average growth rate.

### *Within-nest variance*

To test the influence of predation risk on differences among nestlings of the same nest (i.e., brood reduction; *Objective 4*), I calculated the within-nest variance for wing length and feather

CORT for each nest at both 5- and 7-days post-hatch. I then fit LMMs to test the effect of predator treatment on within-nest variance at 7 days post-hatch. To further understand the within-nest dynamics that influence age at fledging, I also tested the effect of within-nest variance in wing length on age at fledging. In both cases, brood size, clutch initiation date, and days < 10 °C were included as covariates and nest ID as a random effect.

## Results

I conducted predator presentation experiments on 87 nests consisting of 26 Fox, 29 Raven, and 32 control treatments. From the 56 nests that survived to fledge (Fox = 18, Raven = 16, control = 22), I measured size traits at 5- and 7-days post-hatch for 188 nestlings and extracted feather corticosterone for 112 nestlings (n = 2 per nest). At 7-days post-hatch, the average wing length was 37.3% of expected adult size compared to 88.6% and 60.0% for tarsus and mass, respectively. Between 5- and 7-days post-hatch, the average nestling increased its wing length by  $13.8 \pm 0.2$  mm (mean  $\pm$  SE), tarsus length by  $3.31 \pm 0.08$  mm, and mass by  $3.99 \pm 0.19$  g, corresponding to 35.3%, 16.7% and 19.5% of the total size growth over 7 days, respectively.

### *Age at fledge*

The average age at fledge across treatments was  $9.2 \pm 0.2$  days (mean  $\pm$  SE; range = 7–12 days). Nestlings predominantly fledged synchronously within nests, as in only three of 56 nests (5.4%) did a single nestling leave the nest a day later than its siblings. Greater wing length at 7-days post-hatch was associated with an earlier age at fledge, compared to tarsus length and mass which were unrelated (Figure 3.2). Wing load, a measure of wing growth relative to mass development, was negatively associated with fledge age, although with greater variation among

nestlings compared to wing length alone (Figure 3.2B). Therefore, while wing and tarsus length are correlated ( $r = 0.89$ ), age at fledge is better predicted by wing length.

### *Path model selection and fit*

D-separation tests and AIC indicated that the causal wing model, where feather CORT predicts wing length, fit the data better than the correlational model where wing length and CORT are non-directionally associated responses to predation risk (Appendix 2: Table A2.1). The final causal path model had a robust fit (Fisher's  $C = 15.4$ ,  $P = 0.95$ , d.f. = 26) and MCMC iterations validated that the sample size carried adequate explanatory power ( $\chi^2$ :  $P = 0.37$ , RMSEA:  $P = 0.35$ ). The model explained most of the observed variation among nestlings in wing length at both 5-days ( $R^2 = 0.76$ ) and 7-days post-hatch ( $R^2 = 0.95$ ), but there were significant sources of unexplained variation in feather CORT accumulated during the experiment ( $R^2 = 0.18$ ).

### *Nestling wing growth*

The response of wing growth to increased predation risk was mediated by corticosterone concentrations, both directly as a nestling response, and indirectly through parental behaviour. Nestlings responded directly to greater predation risk by decreasing feather CORT which was in turn associated with greater wing length (Figure 3.3). This association was strongest in response to raven compared to fox treatments (Figure 3.3). As an indirect pathway, parents responded to both raven and fox presentations by reducing provisioning rate relative to the control period (Figure 3.3). Parental provisioning rate did not influence nestling wing growth directly. Rather, nestlings of parents with greater reductions in provisioning rate had higher CORT concentrations, and subsequently, reduced wing growth (Figure 3.3). Interestingly, a feather

CORT by date interaction revealed that nestlings with below average CORT exhibited more rapid wing growth early in the season, but this benefit disappeared later in the season during re-nests (Figure 3.3; Figure 3.4).

Parental provisioning behaviour varied markedly in response to predation risk. Summing the indirect and direct effects of predation risk across the observed range of parental responses revealed that wing growth declined more strongly with larger reductions in parental provisioning compared to the control (Figure 3.5). In contrast, nestling wing growth increased when parents demonstrated a limited response to predation risk (Figure 3.5). This relationship was most distinct in response to raven (Figure 3.5A) compared to fox presentations (Figure 3.5B) because of the positive and direct relationship between raven presentation and nestling wing growth. The overall effect tended to be greater wing growth in response to raven presentations and reduced wing growth in response to fox presentations (Figure 3.5). Additionally, because the strength of the association between feather CORT and wing length changes over the season, the effect of predation risk on wing growth is greatest early in the season and essentially disappears later in the season, regardless of the parental provisioning response (Figure 3.5).

### *Early development conditions and compensatory growth*

Growth dynamics prior to the experiment also carried over to influence wing growth during the experiment. Wing length at 5 days post-hatch was shorter with an increasing number of cold days (< 10 °C) and with greater concentrations of feather CORT (Figure 3.3). In turn, early wing growth was strongly and positively associated with wing length at 7-days post-hatch (Figure 3.3). Consequently, for every day below 10 °C prior to the experiment, average wing length at 7-days post-hatch was reduced by 2.6 mm. Early conditions influenced wing length at 7-days post-

hatch because nestlings did not exhibit compensatory growth. Wing length at 5-days post-hatch was not associated with  $\Delta$  wing length ( $\beta = 0.06$ ,  $t = 1.1$ ,  $P = 0.28$ ), indicating that on average nestlings did not accelerate growth following poor early development conditions (Figure 3.6).

### *Within-nest variation*

Within nests, the average difference in wing length between the largest and smallest nestling was  $8.9 \pm 0.7$  mm (mean  $\pm$  SE; range = 0.5 to 22.3 mm), while differences in feather corticosterone concentrations averaged  $4.41 \pm 0.53$  pg/mm (range = 0.08 to 14.01 pg/mm). I did not find evidence for brood reduction behaviour, as neither predation risk treatment nor parental provisioning response influenced within-nest variation in wing length or feather CORT (Table 3.1). Despite often large size disparities among siblings, within-nest variance was not associated with age at fledging ( $t = 0.27$ ,  $P = 0.79$ , d.f. = 43).

## **Discussion**

I demonstrate that nestling wing growth responds directly to the presence of a predator and indirectly through changes in parental provisioning rate. I further show that both pathways are intrinsically linked to physiological changes in nestling corticosterone levels. While predation risk influences nestling growth or corticosterone concentrations in many systems, the direction of these associations often varies and the mechanism by which offspring respond to risk has remained unclear (Clinchy et al. 2013, Ibáñez-Álamo et al. 2015). Under greater predation risk, rapid development and differential growth of mobility traits should be prioritized (Coslovsky and Richner 2011, Martin 2015). Nestling horned larks responded to greater predation risk by increasing wing growth, particularly in response to the presence of ravens. Given that longer

wing length is linked to earlier fledging and improves post-fledging survival through greater predator evasion capabilities (Dial et al. 2006, Martin et al. 2018), my results provide evidence for an adaptive response to predation risk over a relatively short period of time.

### *Indirect predation risk effects*

Adults decreased provisioning rates in response to greater predation risk which had subsequent negative impacts on nestling wing growth. Reduced provisioning rate in the presence of predators may help avoid nest detection (Martin et al. 2000), but the resulting resource limitations can constrain nestling growth (Dunn et al. 2010, Sofaer et al. 2018). Interestingly, provisioning rate did not directly influence nestling growth but instead was associated with wing length through a corticosterone response. This implies that direct food limitation was either not prolonged enough to directly constrain growth or that parents were able to compensate after the predation risk was removed by increasing provisioning rate above background levels (Eggers et al. 2005). Regardless, variable resource availability can induce a stress response with downstream growth effects (Lindström 1999, Monaghan 2008, Criscuolo et al. 2011), potentially explaining the importance of corticosterone in the provisioning rate—wing length pathway.

Adults with a limited response to predation risk fledged larger offspring compared to those with strong reductions in provisioning rate, but this benefit disappeared later in the season. Despite increased nestling growth, the realized reproductive benefit of maintaining provisioning rates in the presence of a predator is unclear considering that activity near the nest may increase the likelihood of nest predation (Martin et al. 2000). Instead, variation in parental response may indicate individual differences in investment. Parents that respond strongly to experimental predation risk may be more likely to reduce parental care in response to stressors in general, such

as poor weather conditions; effectively prioritizing self-maintenance over reproductive investment. Early nesting alpine birds must contend with challenging environmental conditions and energy limitations (Martin et al. 2017), likely differentiating parents in good or poor condition (Descamps et al. 2016). This agrees with my findings that female larks with better body condition fledge nestlings more rapidly early in the season (Chapter 2). Therefore, some larks may be able to mediate the negative impacts of predation risk on nestling development, with benefits apparent when resources are limiting.

### *Direct predation risk effects*

The direct, positive association between predation risk and nestling wing growth was nearly double the strength of the indirect, negative effect through the parental provisioning response. Nestlings can respond to parental alarm calls by suppressing begging and crouching in the nest (Magrath et al. 2006, Johnson et al. 2008, Magrath et al. 2010), and may directly assess risk by recognizing specific predators (Magrath et al. 2007, Haff and Magrath 2010). Low corticosterone levels have been proposed as a mechanism to suppress begging (Kitaysky et al. 2001, Loiseau et al. 2008, Ibáñez-Álamo et al. 2011) and may allow for rapid growth (Saino et al. 2005, Lamb et al. 2016), offering a potential explanation for our observed direct pathway. Nestling age likely influences the strength of the direct effect of predation risk as nestlings may not respond until their senses have properly developed (Khayutin 1985, Magrath et al. 2010). My results may therefore have been different if I had conducted the experiment earlier in development. However, I provide strong evidence that near expected fledged altricial offspring can respond pro-actively to predation risk and are not simply responding to changes in parental provisioning behaviour.

Nestling growth was most responsive to the presence of a raven, resulting in generally longer wings compared to the fox treatment. This occurred at the nestling level, as parental provisioning response does not differ between predator treatments (Goullaud et al. 2018). Predator-specific responses have been observed in nestlings of other species, particularly in response to alarm calls (Platzen and Magrath 2005, Suzuki 2011). Nestlings in enclosed nests respond to terrestrial and not aerial predators, but switch closer to fledging age, potentially because the offspring are only vulnerable to aerial predators after leaving the nest (Magrath et al. 2006). For highly exposed, open-cup lark nests, sight-oriented ravens may represent a significant threat both in the nest and post-fledging. Therefore, adaptive responses to corvids may be critical, particularly those that reduce detectability in the nest or improve predator evasion post-fledge. Unfortunately, I do not have data on predator identity to determine whether corvid or mammalian predators represent a greater threat which could highlight the adaptive significance of a predator-specific response in this system. I also cannot rule out the possibility that raven presentations represented a more intense stressor because it was accompanied by sound while the fox was silent, even though parents consistently made alarm calls during both treatments (unpublished data). Therefore, I highlight potential predator-specific selective pressures, but further experiments across different risk intensities are required.

### *Corticosterone as a physiological mediator*

Corticosterone was involved in both the direct and indirect pathways, highlighting its potential importance in mediating adaptive responses to predation risk. While the benefits of CORT for nestling development have been proposed (Chin et al. 2008, Coslovsky and Richner 2011), empirical evidence is highly mixed with respect to the influence of risk on nestling

corticosterone levels and subsequent growth (Ibanez-Alamo et al. 2015, Crino and Breuner 2015). Feather CORT provides a measurement of corticosterone release over longer time-periods than plasma or fecal CORT (Bortolotti et al. 2008), which is critical considering that the stress response is cumulative and can reach thresholds that result in adaptive or deleterious effects (Wingfield et al. 2017). While caution is required when interpreting results based on feather CORT (Romero and Fairhurst 2016), experiments like the one conducted here are necessary to better understand feather CORT dynamics and its relationship with environmental variables like weather and predation risk (Harris et al. 2016). Importantly, while I only addressed the influence of corticosterone, multiple steroid hormones may be involved in growth prioritization (e.g., testosterone; Coslovsky et al. 2012). Therefore, I provide support for corticosterone as an underlying mechanism in the nestling growth response to predation risk but encourage future research on multiple physiological parameters using a similar framework.

I observed pronounced within-nest variation in nestling size which surprisingly did not influence fledging age. Given high fledging synchrony in this population, this suggests that some nestlings leave the nest at a serious size disadvantage which can impact survival within the first week post-fledge (Cox et al. 2014). Intriguingly, I also found that ambient temperature and corticosterone levels accumulated from 0–5 days post-hatch strongly influenced wing length at 7-days due to a general lack of compensatory growth later in development. I acknowledge that I did not measure nestling size at hatch, nor pre-natal corticosterone levels, both of which may constitute ‘maternal effects’ which are responsible for significant variability in offspring morphology, growth dynamics, and reactivity to stressors (Love and Williams 2008, Moore et al. 2019). These are important considerations when addressing nestling growth, and for this reason I included wing length at 5-days post-hatch in the path model as a control. In combination, these

results and caveats highlight the potential importance of early development conditions on growth dynamics closer to fledge. How conditions during different stages of development influence future survival and fitness merits further study.

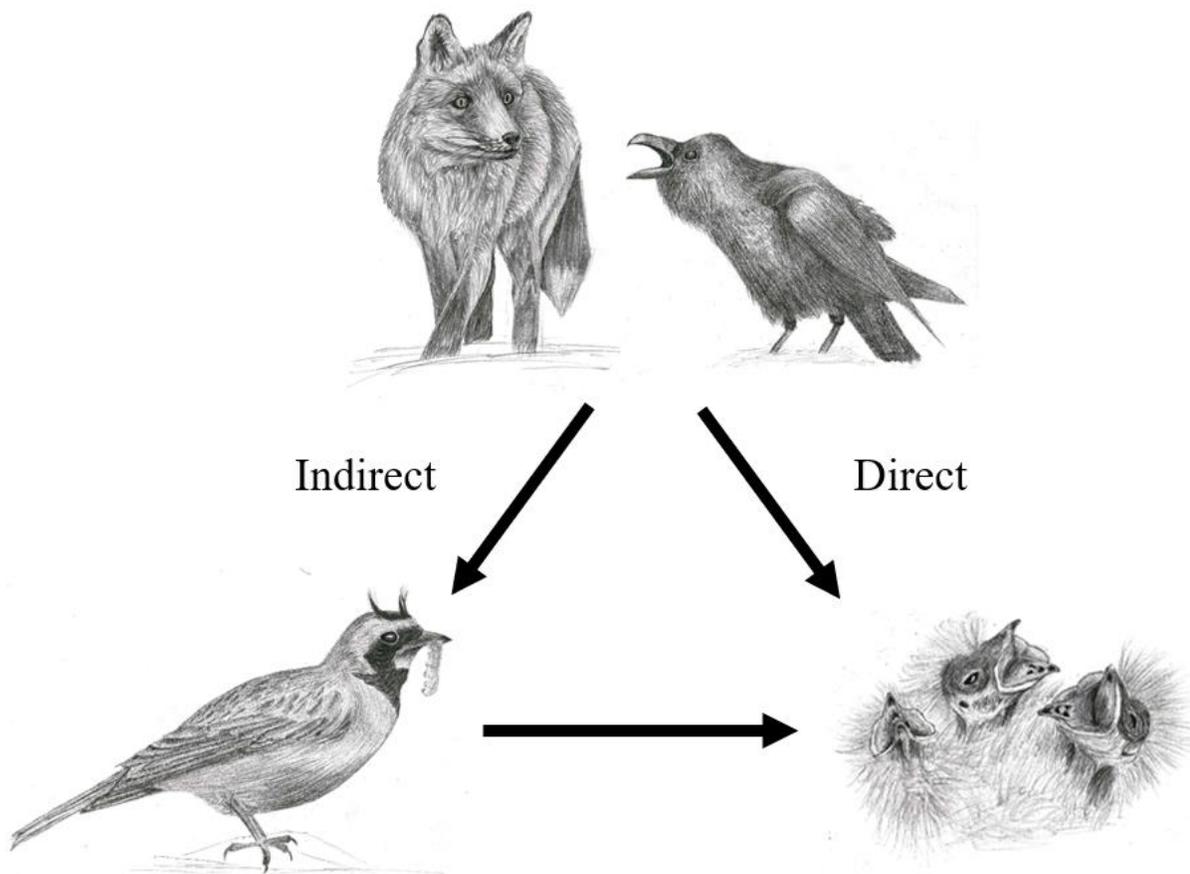
## **Conclusion**

I present the first study to separate the direct and indirect effects of predation risk on nestling development in a causal, hierarchical framework that incorporates corticosterone as a potential underlying mechanism within both response pathways. Research on predation risk dynamics typically involves temperate lowland habitats or nest-box studies (Ibáñez-Álamo et al. 2015). However, the non-consumptive effects of predation risk may be more pronounced in stochastic environments like the alpine (Preisser et al. 2009), and thus provide opportunities to advance our understanding of predator-prey interactions. With climate change and habitat modification, predation risk from generalist meso-predators like corvids is expected to increase (Legagneux et al. 2014). Overall, my results indicate that nestling development can respond adaptively to elevated predation risk given the right conditions, with potential immediate survival benefits during a vulnerable life-history stage.

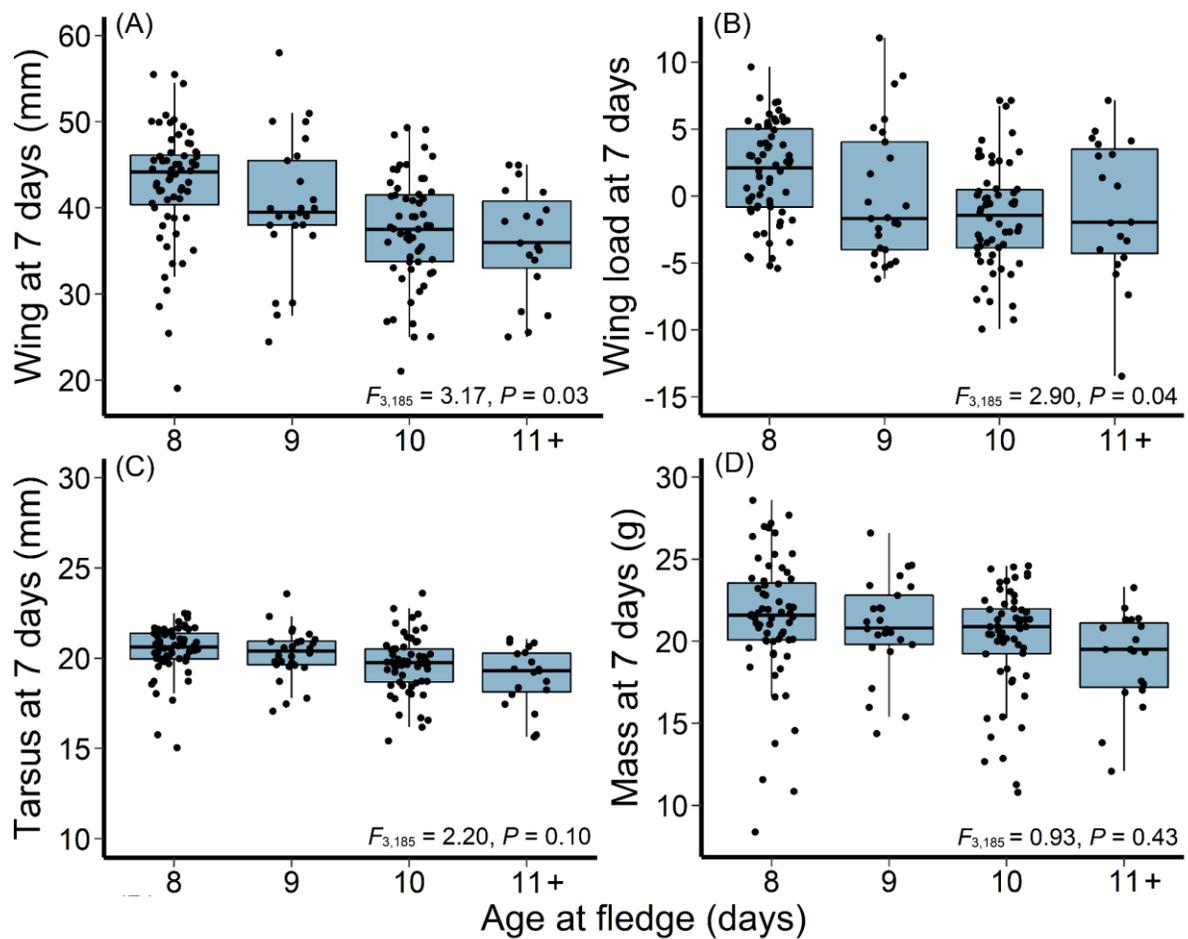
**Table 3.1.** Results for models addressing within-nest variance in wing length and feather corticosterone (CORT). Treatment levels (Fox, Raven) are relative to the control treatment, ‘Age 5 d’ is the within-nest variance measured at 5 days post-hatch, and ‘Brood size’ is the number of nestlings within a nest. Clutch initiation date was not significant and was removed from the table for brevity. Values represent t-statistics and P values. Positive test statistics are associated with greater within-nest variance, and those in bold are considered significant at  $\alpha = 0.05$ .  $R^2$  is the proportion of observed variance explained by the model.

Variance	Treatment		$\Delta$ Prov. rate	Age 5 d	Brood size	$R^2$
	Fox	Raven				
<i>Wing length</i> (mm)	-1.12 P = 0.27	-1.00 P = 0.32	0.90 P = 0.37	<b>7.33</b> P < 0.001	0.08 P = 0.94	0.67
<i>CORT</i> (pg/mm)	0.84 P = 0.40	-0.46 P = 0.65	-0.05 P = 0.96	<b>2.26</b> P = 0.03	-0.31 P = 0.76	0.16

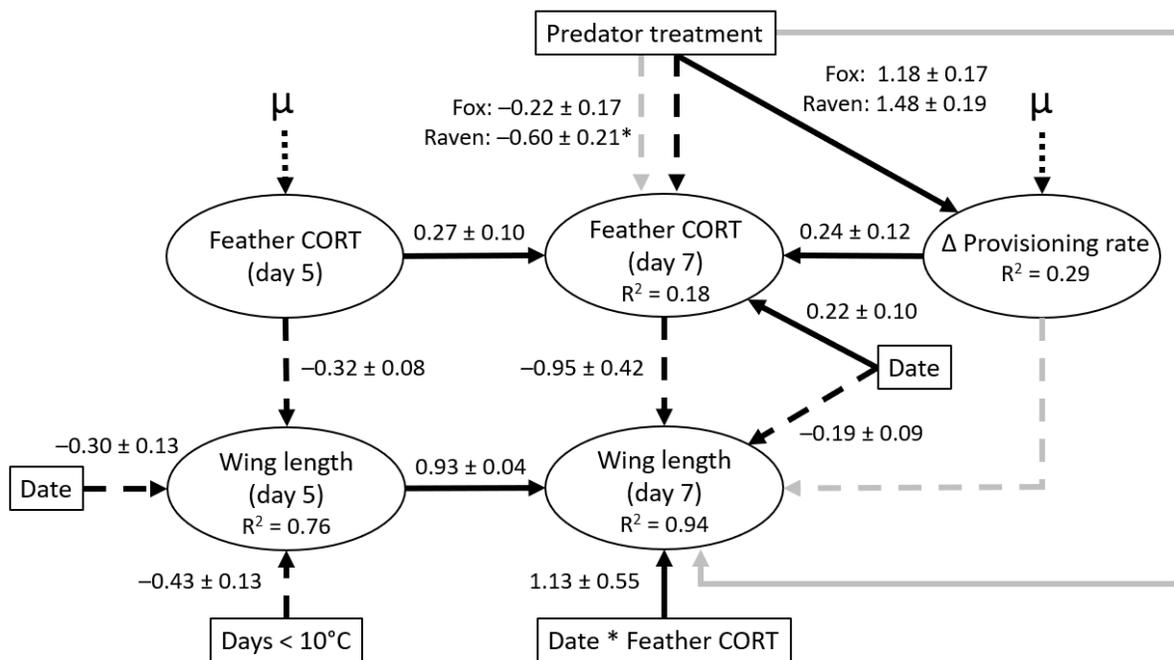
**Figure 3.1.** Hypothesized hierarchical structure of predation risk on nestlings. Indirectly, predation risk may cause adults to avoid the nest as a risk aversion behaviour, consequently reducing provisioning rate and resource availability for the nestlings. Additionally, if made aware of predator presence, either by predator vocalization or parental alarm calls, nestlings may respond directly to predation risk. These direct and indirect pathways may be additive, synergistic, or antagonistic, and both may produce similar growth or physiological responses in the nestlings, requiring a variance partitioning approach. Artistic credit: Sunny Tseng.



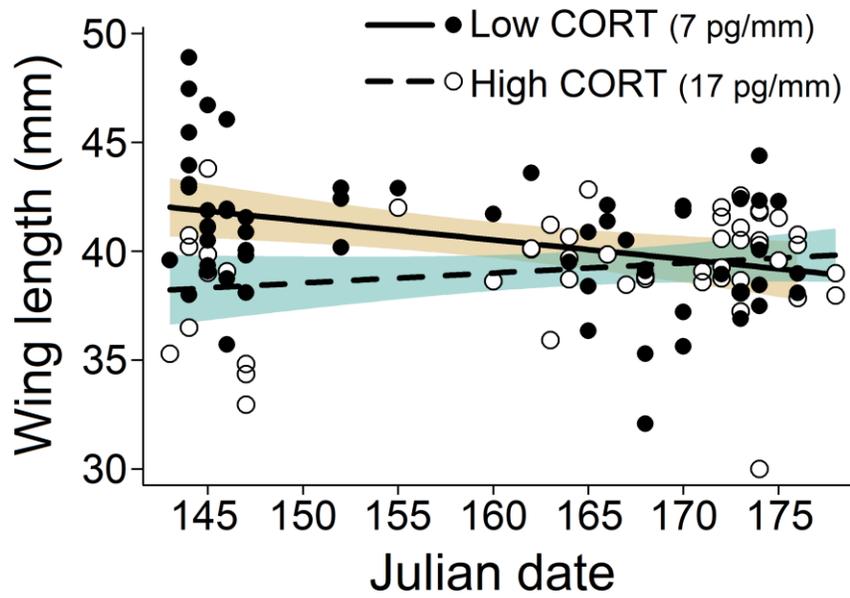
**Figure 3.2.** Relationship between nestling age at fledgling and average (A) wing length, (B) wing load, (C) tarsus length, and (D) mass measured at 7-days post-hatch for an alpine population of horned lark. Points depict the raw data. Boxplots indicate the median (line within the box), first and third quartiles (box ends), and 1.5 \* inter-quartile range (whiskers). Model results included at the bottom indicate the overall relationship between age at fledge and the respective size trait.



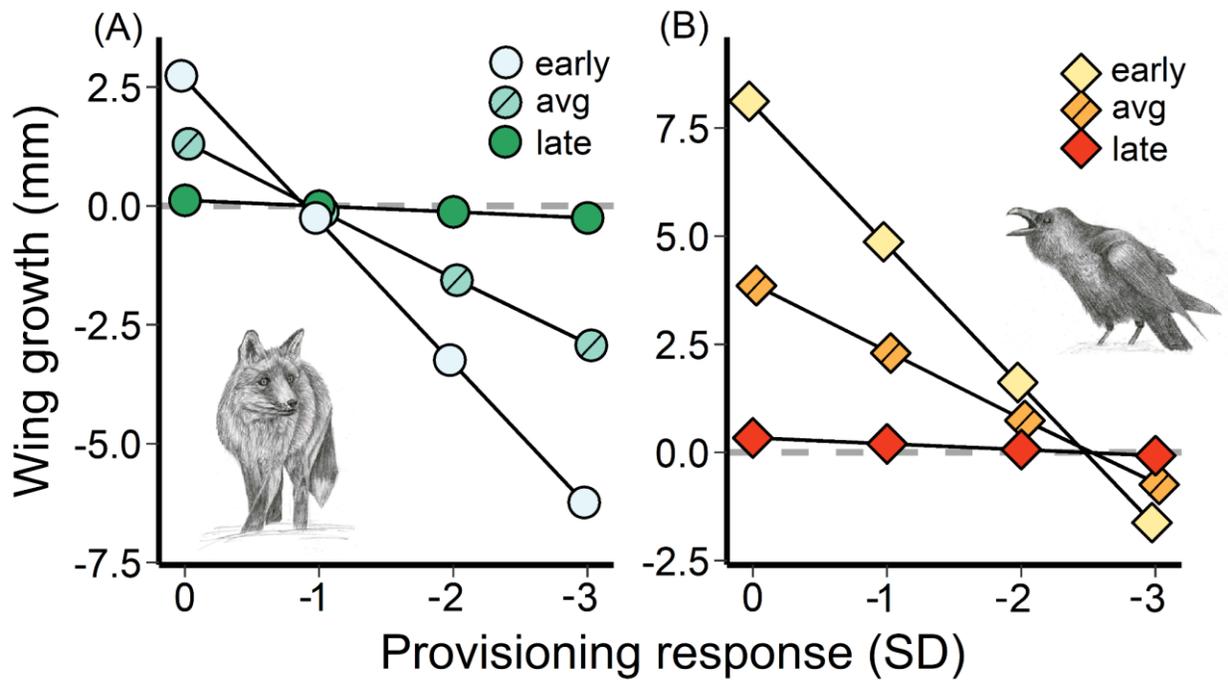
**Figure 3.3.** Path model for nestling wing growth in an alpine breeding population of horned lark. Ovals depict response variables and boxes are measured or experimentally manipulated drivers. Solid arrows indicate positive effects and dashed arrows are negative effects. Grey arrows are non-significant and were removed during model selection. Values next to the arrows are the standardized effect sizes ( $\pm$  SE).  $R^2$  indicates the proportion of variance explained by the combined fixed and random effects for each sub-model and ‘ $\mu$ ’ indicates unmeasured variance. The asterisk indicates that the effect of the Raven treatment was significant while the Fox treatment was not. The sample size consists of 112 nestlings across 56 nests.



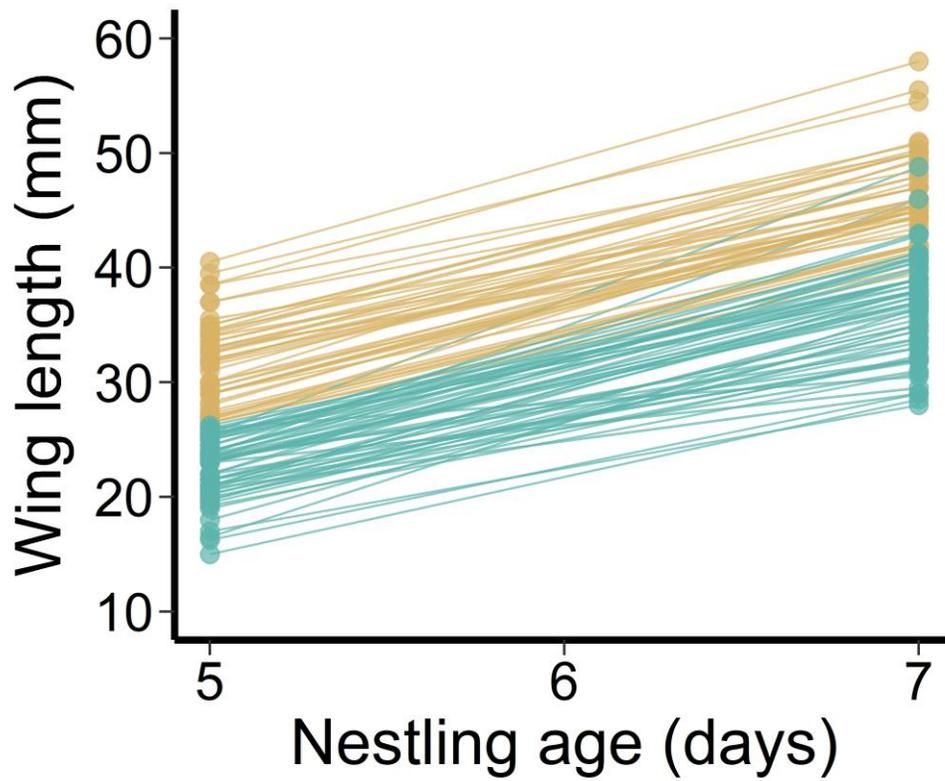
**Figure 3.4.** The interaction between feather corticosterone and time of season (date) on wing length at 7-days post-hatch. The values for low and high CORT concentrations were chosen because they represent 1 s.d. below and above the average value across all nestlings. Most first nests are initiated prior to June 10<sup>th</sup> (160), while those initiated afterwards represent re-nests or second broods. Trend lines represent best fit regression lines and the shaded bands depict 95% confidence intervals of the partial residuals. Julian date 145 = May 25.



**Figure 3.5.** The predicted total effect of (A) Fox and (B) Raven predation risk treatments on nestling wing growth across the observed distribution of parental provisioning responses. The relationship is further separated temporally as early-, average-, and late-initiated nests based on the interaction between feather CORT and date on wing length (see Fig. 3.4). I chose early, average, and late dates as  $-1$  s.d., mean, and  $+1$  s.d. of the observed clutch initiation dates, representing a span of  $\sim 1$  month. A provisioning response of zero indicates no difference between control and predator treatment provisioning rates, while negative values represent reductions in provisioning rate under predation risk. Note the position of the dashed, grey line which indicates average wing growth between 5- and 7-days post-hatch.



**Figure 3.6.** Nestling wing length at 5- and 7-days post-hatch. Each point and associated line represent a nestling. Colours indicate nestlings that had larger (tan) or smaller than average wing length at 5-days post-hatch (green). Generally, the differences in wing length among nestlings at 5-days are maintained at 7-days indicating a lack of compensatory growth following poor early development conditions.



## **Chapter 4. Sex-specific spatiotemporal variation and carry-over effects in a migratory alpine songbird**

### **Introduction**

Migratory birds can spend up to 75% of the annual cycle away from the breeding site (Webster et al. 2002), often using multiple habitats in different locations and for variable time periods (Marra et al. 1998, Briedis et al. 2018). How individuals disperse spatially across the landscape and the timing of migration events can have important consequences for both individual fitness and population dynamics (Legagneux et al. 2012, Møller et al. 2008, Runge et al. 2014, Wilson et al. 2018). Migratory strategies can vary among populations (Gilroy et al. 2016, Knight et al. 2018, Gow et al. 2019), in response to inclement weather (Morganti et al. 2011, Schmaljohann et al. 2017), and among individuals of different age or sex classes (Tøttrup et al. 2012, McKinnon et al. 2014, Woodworth et al. 2016, Briedis et al. 2019). Understanding drivers of within-population variation in migratory strategies and how differences are linked across seasons is critical to understanding the ecological and evolutionary processes shaping life-history dynamics throughout the full-annual cycle (Marra et al. 2015, Paxton and Moore 2017).

Spatial and temporal segregation of the sexes during the non-breeding season occur in avian populations, but the drivers of these patterns are not well understood (McKinnon and Love 2018). For sexually dimorphic species, the larger sex (often male) may winter farther north or closer to the breeding site (Cristol et al. 1999, MacDonald et al. 2015) and exhibit protandry (i.e., earlier spring arrival for males; Morbey and Ydenberg 2001). Non-mutually exclusive hypotheses such as the ‘body size’, ‘arrival time’, and ‘social dominance’ hypotheses, all predict that larger individuals can withstand harsher winter conditions that enable them to remain closer

to the breeding site (Ketterson and Nolan Jr 1976, Gauthreaux Jr 1978) and better monitor environmental cues to match breeding site arrival with optimal weather conditions (Saino et al. 2010). The selective advantage of an earlier arrival includes improved territory and mate acquisition (Kokko 1999, Reudink et al. 2009) and reproductive success (Norris et al. 2003, Smith and Moore 2005, Gienapp and Bregnballe 2012), and is most apparent for the more territorial sex (Møller 2004, Kokko et al. 2006). Thus, the reproductive roles of each sex can produce spatial and temporal differences among individuals during the non-breeding season (Gow and Wiebe 2014, Meissner 2015), and consequently may lead to sex-specific fitness consequences of variation in migration behaviours (Saino et al. 2017).

The annual cycle is partitioned into specific life-history stages that are linked across seasons and conditions that influence energy reserves in one season can ‘carry-over’ to influence subsequent stages (Marra et al. 1998). Conditions during the non-breeding season can influence breeding site arrival and success (Norris et al. 2003, Norris 2005, Harrison et al. 2011). Similarly, breeding success may affect autumn departure date (Stutchbury et al. 2011, Meissner 2015, van Wijk et al. 2017) which in-turn can influence stopover ecology and arrival at the winter site (Briedis et al. 2016, Gow et al. 2019). Thus, carry-over effects can cascade through temporally-linked phases of the annual cycle during both autumn and spring migration (Piersma 1987). Behavioural adjustments such as altering stopover duration can allow individuals to buffer cascading effects, but the ability to adjust behaviour may be condition-dependent (Gómez et al. 2017). Thus, during autumn migration (post-breeding), individuals that invested more in reproduction may have a reduced capacity for flexible migration behaviour, consequently exhibiting greater delays in arrival at non-breeding sites. Similarly, energy-constrained individuals that delay spring migration and arrive late to the breeding site may delay clutch

initiation or experience reduced breeding success. Given differences in reproductive investment, males and females may have differing abilities to compensate for delayed migration events.

Variation in migratory strategies among individuals in response to reproductive effort and timing is a type of phenotypic flexibility, or the capacity to reversibly alter phenotypic traits (i.e., behaviour) in response to prevailing conditions (Piersma and Drent 2003). Populations may differ in their capacity for flexible migration behaviour based on the breeding and non-breeding habitat to which they are adapted. For example, short-distance migrants exhibit greater flexibility in phenology, potentially by monitoring environmental conditions near the breeding site (Usui et al. 2017, Lehikoinen et al. 2019). Additionally, phenotypic flexibility should be adaptive in stochastic conditions (Piersma and Drent 2003), and as such birds that breed in highly variable environments, like alpine or arctic habitats, may be more likely to demonstrate and benefit from flexible migration behaviours. Recent studies from far northern latitudes indicate strong potential flexibility in migration timing and stopover behaviour (e.g., Krause et al. 2016, Schmaljohann et al. 2017). Addressing within-population variation of migration behaviours for alpine birds will advance our understanding of sex-specific flexibility in migratory traits and thus the capacity for populations to respond to rapidly changing environments (Shaw 2016, Beever et al. 2017).

In this study, I examined sex-specific variation in migration behaviour and the carry-over effects between reproductive output and migration strategies for an alpine breeding population of horned larks. Specifically, I tested four predictions involving spatial and temporal differences between sexes across the full-annual cycle. First, since larks are sexually dimorphic (Beason 1995) I predicted spatial sex segregation during the non-breeding season such that the larger males would remain closer to the breeding site. Second, I expected that males would depart and arrive at the breeding site earlier than females, demonstrating protandry. Third, I predicted

greater nesting effort or success would influence departure dates from the breeding site, and that a later departure would influence subsequent arrival at non-breeding sites. I expected breeding effort to more strongly influence female migration timing because female larks invest more in reproduction, being solely responsible for nest building, incubation, and half of offspring provisioning (Beason 1995). Finally, I predicted that migration distance and departure date from the non-breeding site would influence spring arrival date and subsequent breeding success. I expected this inter-dependency to be most pronounced in males due to the territorial advantage of arriving early at the breeding site (Reudink et al. 2009).

## **Methods**

See *Chapter 1* for a description of the study system and current understanding of lark migration.

### *Light-level geolocator deployment*

From 2015–2017, I fit 37 males and 22 females with Intigeo-P65B1-11 light-level geolocators (Migrate Technology Inc.). The geolocators were attached using a leg-loop harness (Rappole and Tipton 1990) tied using 45 lb test nylon string (Lee Valley Tools Ltd., Ottawa, Canada), allowing the fit of each harness to be adjusted for individuals in the field. The string was double knotted and glued with epoxy to prevent geolocator loss. The total weight of the geolocator (0.77 g) plus harness (0.20 g) was 0.97 g which, on an average lark for this population (35.1 g; Camfield et al. 2010), is 2.8% of body mass and thus is below the generally accepted 3% threshold. Tracking devices weighing less than 3% body mass limit negative effects on survival and reproductive success, particularly for species like larks that predominantly forage terrestrially (Barron et al. 2010, Bodey et al. 2018). All birds were captured on fair-weather days

and released in under 12 min. I monitored individuals for ~15 min after release to ensure there were no immediate effects of the geolocator. The following year, returning individuals with geolocators were captured at the nest during the nestling stage (males) or the incubation stage (females) using a noose-line trap surrounding the nest (de Zwaan et al. 2018). I removed the geolocator from recaptured birds, measured body size traits, and released them in under 5 min.

### *Geolocator analysis*

All analyses were performed in R version 3.5.1 (R Development Core Team 2018). Due to significant trap avoidance in the first season, I only retrieved 17 geolocators (8 males, 9 females) from 35 individuals that were re-sighted. Pre-processing of drift-adjusted ‘.lux’ files and calibration were conducted using package ‘GeoLight’ (Lisovski and Hahn 2013). I used a light level threshold of 1 to estimate twilights and removed outliers if they differed by more than 30 min from adjacent twilight estimates. To calibrate the data, I used the ‘Hill-Ekstrom method’ which estimates the zenith angle based on the lowest amount of variance in latitude estimates during stationary periods (Hill and Braun 2001, Ekstrom 2004). This method provides more accurate location estimates than both ‘roof-top’ and ‘on-the-bird’ calibration when a lengthy stationary period occurs near an equinox (Lisovski et al. 2012). I identified likely stationary periods (> 10 days) during the non-breeding season using the ‘changeLight’ function. Stationary periods were distinguished from movement based on high probability changes in twilight times, where a change point probability greater than the 90<sup>th</sup> percentile of all probabilities calculated within the entire migration period indicated movement. I then estimated the zenith angle based on the longest stationary period in the non-breeding season.

Location estimates were derived using package ‘SGAT’ (Sumner et al. 2009) which allows prior distribution knowledge and bird behaviour to be incorporated into a Bayesian framework and tends to more accurately estimate locations than ‘GeoLight’ (Lisovski et al. 2019). ‘SGAT’ uses the curve method to estimate locations based on the difference between twilight times, in combination with movement behaviour priors which apply constraints to the estimates. I identified likely stopover locations where the bird was stationary for  $\geq 3$  days within a distance threshold of 150 km. I then created a prior movement model of flight speeds for each day of the migration period with most speeds from 0 to 40 km/h but allowing for speeds up to 80 km/h with rapidly diminishing likelihood. This allows travel distances of 200 km per 5 hr flight to be common, up to a maximum of 400 km, which is comparable to migration estimates for other songbirds (Hall-Karlsson and Fransson 2008, MacDonald et al. 2015, Wright et al. 2018).

I also developed a land mask to restrict the locations of individuals to suitable habitats. I used a 1 km\*1 km landcover database from Tuanmu and Jetz (2014) which classifies the globe into 12 landcover categories based on a consensus from multiple remote-sensing sources. Since horned larks are obligate open-country birds that avoid forested areas, I used ‘herbaceous vegetation or grassland’ and ‘barren’ (often alpine) landcover categories as identified by a remote-sensing consensus of greater than 25%. Agricultural fields are also potential non-breeding habitat (Beason 1995), and therefore I included the category ‘cultivated or managed vegetation’ which includes fallow fields and rangeland. Birds were restricted to stopping in these habitat types but could move freely between stopover sites over any landcover, including water.

I fit a group Estelle model incorporating the behaviour model and land mask to estimate locations of stationary and movement periods with a multivariate normal error distribution. The

model was trained using 1000 initial iterations with a 20 iteration burn-in, followed by MCMC chains including 10 rounds of 300 iterations each. The final model was run with 2000 iterations.

The average geolocator error based on location estimates from a known location—the breeding site—was  $59 \pm 56$  (s.d.) km (range: 3 – 224 km) in latitude and  $57 \pm 50$  km (1 – 185 km) in longitude. Similarly, the average 95% credible interval for point estimates of non-breeding stationary periods (unknown locations) was 58 km (range: 30 – 101 km) for latitude and 61 km (range: 34 – 122 km) for longitude. As a result, I defined the non-breeding season as beginning when an individual moved  $> 150$  km from the breeding site in a consistent direction. Similarly, I considered estimated stopover locations to be distinct if they were separated by at least 150 km, otherwise they were grouped by calculating the centroid weighted by the number of days at each location. Location estimates indicating large latitudinal fluctuations 2 weeks prior-to and after an equinox were removed because at this time estimates of latitude can be inaccurate, although longitude is still relevant (Hill 1994, Ekstrom 2004). As a result, if a bird arrived or departed from a stationary point during an equinox period, the arrival and departure times were approximated based on longitudinal shifts and when the longitude stabilized to match the stationary site. Normally, estimates of departure and arrival dates are accurate to  $\pm 2$  days. However, when estimating phenology during an equinox period based on longitudinal shifts, I assumed accuracy to be  $\pm 5$  days. This inaccuracy predominately occurred when estimating arrival at prolonged stopovers during autumn migration.

### *Migration terminology*

Following location estimation, I calculated several migration traits that require definition:

*Winter site* – The non-breeding site farthest to the south and with the longest duration of stay.

*Stopover* – Any stationary period  $\geq 3$  days between the breeding and winter site. Due to location estimate error, stopovers represent general but distinct regions within which an individual may use several locations.

*Spring staging area* – Stopovers during northward migration where a bird remained stationary for  $> 20$  days. The length was chosen to be consistent with other examples in the literature (Renfrew et al. 2013, Gow et al. 2019) and to account for error in location estimates. I acknowledge that staging areas can be considered alternative wintering locations, similar to observations for Neotropical migrants like purple martin (*Progne subis*; Stutchbury et al. 2016) and veery (*Catharus fuscescens*; Heckscher et al. 2011). However, since they generally occurred on the migration route between the wintering and breeding site, it is reasonable to treat these locations as staging areas (Warnock 2010, Bayly et al. 2018).

*Absolute distance* – Calculated as the linear distance between the breeding and winter site using the Vincenty ellipsoid method to account for curvature in the earth (Vincenty 1975).

*Route distance* – Absolute distance does not account for route variation. Therefore, I also calculated the one-way sum of the linear distances between the breeding site, stopovers, and winter site for both southward and northward migration as a measure of realized distance.

*Staging distance* – The linear distance between the staging area (or winter site if an individual did not demonstrate staging behaviour) and the breeding site. This allowed us to address proximity to the breeding site and spring phenology in a manner that is comparable among larks who did or did not exhibit staging behaviour.

*Migration speed* – The route distance divided by the duration, and thus incorporates flight speed and stopover duration. Due to error in location estimates, distance and speed variables should be considered relative for comparison among individuals and not exact differences.

## Statistical analysis

To test sex-specific differences in spatial distribution and phenology, I used four separate one-way Analysis of Variance (ANOVA) tests with sex as the explanatory variable and absolute distance, staging distance, breeding site departure, or breeding site arrival date as the response variables. Separate ANOVAs were necessary because each response variable reflects different migration events that are distinct in time and space.

I fit simple linear models to address: 1) the influence of breeding success on departure date, 2) subsequent effects of departure date on autumn migration speed, stopover use, and non-breeding arrival dates, and 3) effects of using spring staging areas and breeding site arrival date on breeding success. Breeding success was calculated as the proportion of nests that successfully fledged offspring in a season. Total nesting attempts ranged from 1–3 but most individuals attempted two nests (12/17 birds; 5 males, 7 females). For autumn stopover behaviour, I fit a logistic regression where an individual either did (1) or did not (0) remain stationary at a prolonged stopover for > 20 days. Since several individuals migrated during part of the autumn equinox, identifying extended stationary periods was more reliable than the total number of stopovers. All other response variables were fit to a Gaussian distribution. For effects of spring migration behaviour on breeding parameters, I addressed two response variables: 1) nest success, and 2) the total number of fledglings in a season.

For all migration behaviour associations, I fit separate models for males and females. If neither were significant, I combined the data from both sexes and reported the association from a model with sex as an additive term. I used this process because I was specifically interested in sex-specific differences in flexible migration behaviours. An  $R^2$  was calculated for each model to indicate the strength of the association.

Finally, I assessed the potential effects of geolocators on fitness both during the year of application and the following year by comparing birds with geolocators applied to those that were just colour banded. I used Generalized Linear Mixed-effects Models with tracking status (geocator, no geocator) and sex as explanatory variables and year of capture as a random effect. For the first year, I modelled: (1) nest success of the current attempt, and (2) probability of re-nesting. For the following year, I tested: (1) probability of returning, (2) clutch initiation date, and (3) probability of successfully fledging at least one nest. For nest success, I fit a discrete proportional hazard model with a complementary log-log link and exposure days as an offset. For all other probability response variables, I fit a binomial distribution with a logit link, and for clutch initiation date I fit a Gaussian distribution.

## **Results**

Horned larks from an alpine breeding population in northern British Columbia, Canada wintered predominantly east of the Cascade mountain range in Washington and Oregon, USA, with one female overwintering in southeast Idaho (Figure 4.1). Most males and females exhibited ‘loop’ migrations, traveling southward at higher elevations along the Coast Mountains to the northern Columbia Plateau region before dispersing farther south or east (Figure 4.1A). Northward migration tended to be at lower elevation through the Thompson-Okanagan and up through the Central Interior Plateau of British Columbia (Figure 4.1B). Individuals departed the breeding grounds within a span of 31 days from early August to early September and arrived at the wintering grounds over a span of 81 days (Table 4.1), subsequently spending an average of 170 d or 5.5 months at the wintering site (range: 56–242 days). Both sexes demonstrated faster spring than autumn migration speeds (Table 4.1).

During autumn migration, at least 11 individuals (~65%) appeared to remain stationary at a prolonged stopover site prior to continuing south. However, because this period tended to occur at least partially within the fall equinox, I could not accurately estimate arrival date, although it was usually possible to estimate departure date. During spring migration, both males (5/8; 63%) and females (5/9; 56%) stopped at staging areas on their northward route, predominantly within the Thompson-Okanagan or northern Columbia Plateau regions (Figure 4.2). Individuals remained at staging areas for periods of 21 to 66 days (Table 4.1).

### *Spatial and phenological segregation of the sexes*

The mean winter coordinates for males ( $46.8 \pm 1.5^\circ\text{N}$ ,  $-120.1 \pm 0.9^\circ\text{W}$ ; mean  $\pm$  SD) tended to be farther north than for females ( $45.8 \pm 1.3^\circ\text{N}$ ,  $-119.6 \pm 1.6^\circ\text{W}$ ), although the average distance between the breeding and wintering sites did not differ between sexes (Table 4.2). However, when considering the spring staging area, the spatial segregation between males ( $48.4 \pm 1.3^\circ\text{N}$ ,  $-120.0 \pm 0.6^\circ\text{W}$ ) and females ( $46.9 \pm 1.3^\circ\text{N}$ ,  $-119.8 \pm 0.9^\circ\text{W}$ ) was more distinct (Figure 4.2). Thus, males spent less time at their winter sites and significantly more time closer to the breeding site (Table 4.2). Autumn departure dates from the breeding grounds were similar for males and females (Table 4.2). During spring migration, males arrived at the breeding grounds an average of 6 days earlier than females (Table 4.2).

### *Effects of reproductive success on autumn migration behaviour*

Reproductively successful females departed earlier from the breeding site ( $t = -2.4$ ,  $P = 0.04$ ,  $R^2 = 0.46$ ), while males did not exhibit an association ( $t = 0.1$ ,  $P = 0.90$ ,  $R^2 = 0.00$ ; Figure 4.3A). Departure date was positively associated with arrival at the first prolonged stationary site (i.e.,

stopover > 20 d or wintering site) for males ( $t = 3.2$ ,  $P = 0.02$ ,  $R^2 = 0.63$ ), but not for females ( $t = 1.2$ ,  $P = 0.26$ ,  $R^2 = 0.17$ ; Figure 4.3B). However, when just the winter site was considered, arrival was not associated with departure from the breeding site for either sex ( $t = -1.5$ ,  $P = 0.16$ ,  $R^2 = 0.15$ ; Figure 4.3B), likely due to variable stopover use. Later departing females increased migration speed to the first stopover site ( $t = 2.4$ ,  $P = 0.05$ ,  $R^2 = 0.45$ ; Figure 4.3C), and were less likely to exhibit prolonged stopover behaviour ( $t = -5.3$ ,  $P < 0.01$ ,  $R^2 = 0.82$ ; Figure 4.3D). In contrast, regardless of departure date, males maintained migration speed ( $t = 0.2$ ,  $P = 0.83$ ,  $R^2 = 0.01$ ; Figure 4.3C) and stopover use ( $t = 0.0$ ,  $P = 1.00$ ,  $R^2 = 0.00$ ; Figure 4.3D).

### *Effects of spring migration behaviour on breeding success*

While breeding season arrival date was positively associated with departure date from the last prolonged stationary site (i.e., staging area or wintering site) for both sexes ( $t = 4.6$ ,  $P < 0.01$ ,  $R^2 = 0.69$ ; Figure 4.4A), arrival date did not correlate with clutch initiation date (Pearson's product-moment correlation:  $r_p = 0.32$ ,  $t = 1.3$ , d.f. = 15,  $P = 0.21$ ). However, larks that stopped at staging areas while travelling northward demonstrated greater breeding success ( $t = 2.7$ ,  $P = 0.02$ ,  $R^2 = 0.39$ ; Figure 4.4B) and consequently produced more fledglings than those that stopped farther south or migrated directly from the winter site ( $t = 2.4$ ,  $P = 0.03$ ,  $R^2 = 0.30$ ). On average, larks that stopped at staging areas farther north produced 1.8 more fledglings over the season ( $2.2 \pm 0.6$ ; mean + SE;  $n = 10$ ) than individuals that remained farther south ( $0.4 \pm 0.4$ ;  $n = 7$ ).

### *Consequences of geolocator application*

Nest success for the current nest at capture did not differ between birds with and without geolocators ( $z = -0.13$ ,  $P = 0.90$ ), nor did the likelihood of re-nesting ( $z = 0.60$ ,  $P = 0.55$ ). Based

on re-sights, the average return rate for geolocator birds was 59.3% (35 of 59 tagged birds) versus 68.2% and was not significantly different ( $z = -0.33$ ,  $P = 0.74$ ). For the following year, the probability of fledging a single nest did not differ between larks with and without geolocators ( $z = 0.40$ ,  $P = 0.70$ ). However, larks with geolocators were more likely to initiate clutches later the following year ( $t = 3.35$ ,  $P < 0.01$ ). On average, males with geolocators initiated  $4.2 \pm 2.4$  days (mean  $\pm$  SE) later and females  $9.0 \pm 1.6$  days later.

## **Discussion**

### *Sex-specific differences in spatial distribution and phenology*

In an alpine breeding population of horned larks, males spent a significantly longer time farther north and closer to the breeding site than females. In contrast to expectations for a short-distance migrant, males arrived on the breeding grounds an average of 6 days earlier, demonstrating relatively minor protandry. Short-distance migrants often exhibit greater protandry (~2 weeks) compared to long-distance migrants (2–8 days; Tøttrup and Thorup 2008, Briedis et al. 2019). Closer proximity to the breeding site should allow individuals to monitor environmental cues (Ouwehand and Both 2017, Lehikoinen et al. 2019) to arrive as early as possible and gain territorial benefits (Reudink et al. 2009). However, the competitive advantage of arriving early is balanced with the cost of arriving too early when harsher weather may limit available resources and deplete energy reserves (Kokko et al. 2006, Coppack and Pulido 2009). In a stochastic alpine habitat, the cost-to-benefit ratio of arriving early may be greater than in a less seasonal and more environmentally consistent low elevation habitat. At this alpine site, daytime temperatures often remain at or below zero degrees Celsius throughout the first half of May, with frequent storms

and high wind speeds (Camfield and Martin 2009, Martin et al. 2017). Therefore, both males and females may experience stabilizing selection to arrive at similar times.

I did not find a relationship between breeding site arrival and clutch initiation date, which contradicts patterns observed in migrating songbirds breeding at low elevation (Norris et al. 2003, Woodworth et al. 2016). A selective advantage for early spring arrival is predicated on expected high-quality territory acquisition and subsequent benefits for breeding success (Morbey and Ydenberg 2001). In the alpine, regardless of arrival date, ground-nests cannot be initiated until late May due to extensive snow cover. Even after onset of snowmelt, the higher probability of severe and cold early-season storms that lead to nest failure can limit the fitness benefits of breeding early (Martin et al. 2017). Alpine and arctic birds likely have greater flexibility to respond to proximate environmental conditions to advance or delay both breeding site arrival and clutch initiation date (Bears et al. 2009, Boelman et al. 2017). As a result, a relationship between arrival and clutch initiation date is likely moderated by variable environmental conditions, regardless of any potential competitive advantage to arriving early.

### *Cascading effects of breeding success on autumn migration*

Breeding effort and success showed sex-specific associations with autumn migration behaviour, indicating potentially different mechanisms driving the timing of autumn migration, and subsequently different migration strategies. During autumn migration, breeding site departure date was delayed with reduced breeding success for females but not males. Since females will re-nest multiple times following failed attempts, this suggests greater energy investment during the breeding season can influence timing of autumn migration. Although similar evidence is limited, individuals that invest more in reproduction may be energetically constrained to depart later

(Wojczulanis-Jakubas et al. 2013). For example, dunlin (*Calidris alpina*) delay breeding site departure following greater breeding success (Meissner 2015), and wood thrush (*Hylocichla mustelina*) in low body condition at the end of the breeding season tend to remain farther north for longer, potentially because these individuals have delayed moulting behaviour (Stutchbury et al. 2011). Horned larks moult at the breeding site before departing (Beason 1995), and thus moult could exacerbate departure delays for females considering the substantial energy investment required when late reproduction and moult coincide (Flinks et al. 2008, Borowske et al. 2017). Regardless of the mechanism, our results indicate that greater breeding effort has the potential to delay departure from the breeding site.

Males and females commonly differ in their capacity for flexibility across a wide range of behaviours (Nakagawa et al. 2007), including migration strategies (Both et al. 2016). I demonstrated sex-specific abilities to compensate for delayed departure during autumn migration, or to buffer cascading constraints so they did not carry over indefinitely (Conklin and Battley 2012, Senner et al. 2014). Termed ‘reversible state effects’, conditions that influence energy reserves in one stage of the annual cycle can produce temporary constraints that influence subsequent stages but are corrected over time (Senner et al. 2015). While males maintained consistent stopover behaviour, later departing females increased migration speed and decreased stopover use, providing some support for reversible state effects. Short-distance migrants likely have a greater capacity for flexible stopover behaviour (Schmaljohann and Both 2017), which can compensate for a late departure (Stutchbury et al. 2011). Speeding up migration implies an urgency to arrive at a destination and this selective pressure is thought to be greater in spring than autumn (Horton et al. 2016). It is unclear why female larks speed up autumn migration, but one possibility is that poor weather conditions at northern stopovers later in autumn may mean

less territorial individuals, like females, continue migrating south (Stutchbury et al. 2016, Schmaljohann et al. 2017).

### *Spring staging behaviour*

I observed exceptionally prolonged staging behaviour during spring migration, with some individuals remaining at northern staging areas for up to 2 months. The traditional expectation for stopovers is that their duration should be minimized, such that birds stay just long enough to refuel (Alerstam et al. 2003). While evidence for staging in songbirds originally stemmed from long-distance migrants preparing to cross major landscape features (e.g., the Sahara; Arlt et al. 2015), recent observations indicate this behaviour may be more prevalent in songbirds than once thought (Bayly et al. 2018). For example, bobolink (*Dolichonyx oryzivorus*) may stop for more than 20 days during both southward and northward migration (Renfrew et al. 2013), while rusty blackbirds (*Euphagus carolinus*) exhibited average stationary periods of 25.5 days (max = 62 d) prior to arriving at the breeding site (Wright et al. 2018). Interestingly, staging behaviour is most commonly observed in capital breeders like snow goose (*Anser caerulescens*) when preparing to arrive at unpredictable, high latitude breeding sites (Bêty et al. 2004). While songbirds are income breeders, staging behaviour may allow larks to improve fat reserves to respond to variable, early season conditions upon arriving in the alpine.

For larks, staging areas may be key components of the annual cycle (Pledger et al. 2009), particularly because individuals that exhibited staging behaviour farther north demonstrated greater reproductive success. The use of a specific staging area may have intrinsic value that carries over to reproduction. For example, high-quality individuals may be able to move earlier to northern staging areas to maximize limited resources in a harsher environment and thus be in a

better position to arrive at the breeding site at an optimal time to acquire high-quality territories and mates. This may explain why two males remained in the region for the entire non-breeding season. In support of this mechanism, black-and-white warblers (*Mniotilta varia*) that arrive early at stopovers close to the breeding grounds remain longer and accumulate more fat than later arriving birds (Paxton and Moore 2017). Future research that addresses the habitat quality of staging areas, as well as, the body condition of individuals that remain at these sites for prolonged periods of time would help identify the drivers of this behaviour in an alpine population of horned larks.

### *Potential fitness consequences of geolocator application*

Many inferences are drawn from geolocator data, yet it is unclear whether the observed behaviour is representative of birds without tracking devices. Although data are limited, the extra weight or aerodynamic drag of geolocators may impact individual survival, breeding success, or investment in parental care (Bodey et al. 2017, Geen et al. 2019). I found that the return rate of larks with geolocators was within the expected range for those without geolocators, indicating minimal effects on annual survival for this species. Particularly females with geolocators tended to delay clutch initiation the following year. While I found no overall effects of geolocator application on reproductive success, delayed clutch initiation can lead to reduced nest success or offspring survival (Perrins 1970, Visser et al. 2015, Raquel et al. 2019). Delayed phenology can also lead to mismatches between nestling development and resource peaks (Visser et al. 2006), with subsequent effects on growth and survival that I did not address. Future research should assess the effects of tracking devices beyond simple metrics of survival to better inform field techniques and validate whether inferences are representative of natural systems.

## **Conclusion**

I report sex differences in spatial distribution during the non-breeding season and flexibility in migration behaviour. Since the sample size was modest, with 17 individuals over 3 years, I acknowledge that my results, although intriguing, may not capture the full range of variability in certain parameters measured in this study (e.g., departure date, nest success). Nevertheless, the sex-specific patterns I observed indicate the potential importance of flexible migration behaviours in shaping individual life-history strategies and fitness, with implications for population dynamics. If individuals from one sex are more constrained to specific migration behaviours or non-breeding sites, they may be more susceptible to changing environmental and land-use conditions which may influence sex-biased mortality or dispersal rates. As a result, identifying critical non-breeding sites, as well as, within-population variation in how these locations are used is an important step in the conservation of declining open-country birds (Cohen et al. 2017). To this end, I observed striking spring staging behaviour and its potential influence on subsequent breeding success, suggesting staging areas in the Thompson-Okanagan and Columbia Plateau may be critical components of the annual cycle. Staging behaviour is difficult to recognize and poorly understood among songbirds owing to their small size and often greater dispersion across the landscape, but future studies like this will improve our ability to identify staging areas and the factors influencing this behaviour.

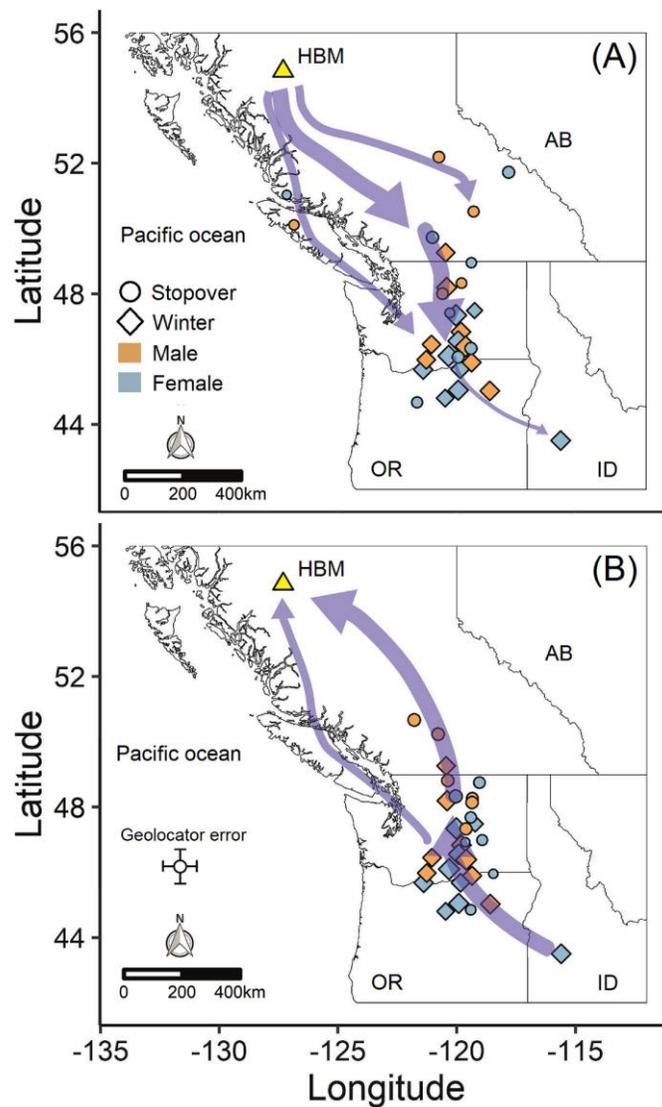
**Table 4.1.** Migration behaviour for an alpine breeding population of horned larks in northern British Columbia for both autumn and spring migration. Top values are the mean  $\pm$  SD, while those in brackets depict the range. The location that departure and arrival refer to depends on the migration season. For example, departure in autumn is from the breeding site, but in spring it is from the winter site. Duration refers to the staging area in spring, often in the Thompson-Okanagan or northern Columbia Plateau regions.

	Timing (d)		Route distance (km)	Speed (km/d)	Duration (d)
	Departure	Arrival			
<i>Autumn</i>					
Overall	Aug 23 $\pm$ 9 (Aug 9, Sep 9)	Oct 12 $\pm$ 25 (Sep 9, Nov 29)	1314 $\pm$ 248 (908, 1637)	43 $\pm$ 49 (14, 217)	– –
Male	Aug 22 $\pm$ 6 (Aug 9, Sep 1)	Oct 8 $\pm$ 21 (Sep 9, Nov 3)	1232 $\pm$ 259 (908, 1623)	28 $\pm$ 7 (18, 39)	–
Female	Aug 24 $\pm$ 11 (Aug 11, Sep 9)	Oct 15 $\pm$ 30 (Sep 14, Nov 29)	1387 $\pm$ 227 (1039, 1637)	58 $\pm$ 65 (14, 217)	
<i>Spring</i>					
Overall	Mar 29 $\pm$ 35 (Jan 24, May 18)	May 10 $\pm$ 7 (Apr 26, May 21)	1200 $\pm$ 308 (699, 2086)	107 $\pm$ 136 (15, 475)	41 $\pm$ 14 (21, 66)
Male	Mar 28 $\pm$ 24 (Mar 6, May 1)	May 7 $\pm$ 6 (Apr 26, May 15)	1062 $\pm$ 167 (698, 1257)	85 $\pm$ 120 (17, 349)	47 $\pm$ 6 (39, 54)
Female	Mar 30 $\pm$ 44 (Jan 24, May 18)	May 13 $\pm$ 6 (May 6, May 21)	1323 $\pm$ 360 (950, 2086)	126 $\pm$ 154 (15, 475)	34 $\pm$ 18 (21, 66)

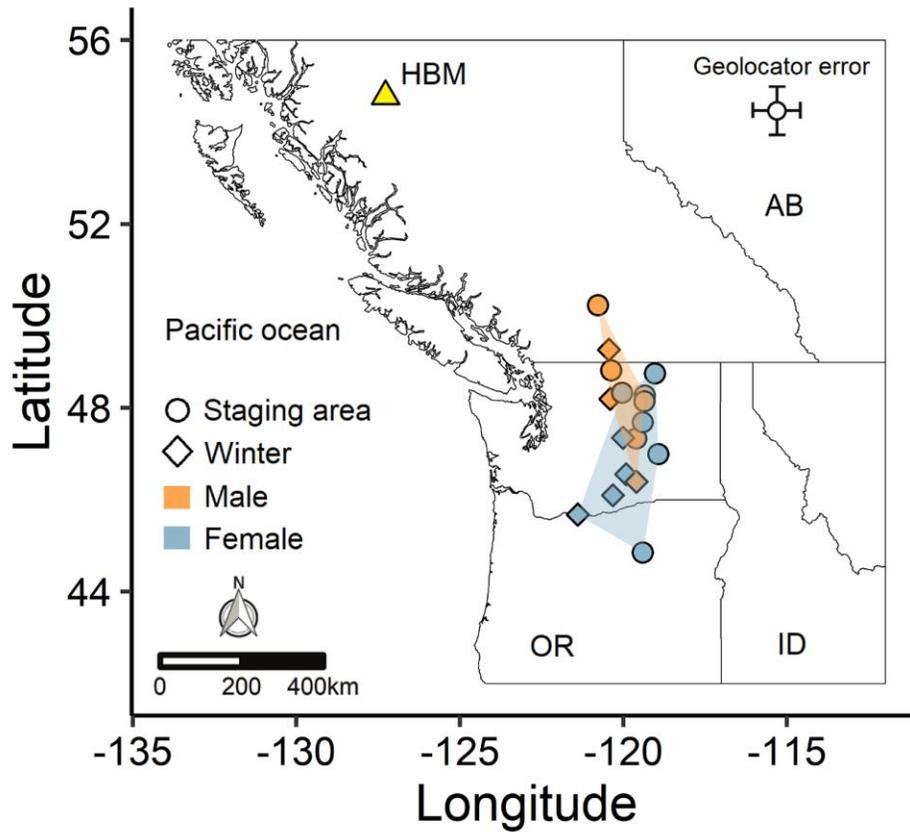
**Table 4.2.** Analysis of Variance (ANOVA) results for sex-specific differences in spatial distribution and phenology during the non-breeding season. Absolute distance is the linear distance between two points rather than route distance to facilitate comparison of spatial segregation. Staging distance is the distance between the breeding site and the staging area (or winter site if the individual did not exhibit staging behaviour). Departure and arrival dates refer to the breeding season only. Values in brackets depict the range. An asterisk indicates significance at the  $\alpha = 0.05$  level.

Spatiotemporal variables	Males	Females	F <sub>(1,15)</sub>	P
Absolute distance (km)	1020 ± 59 (698, 1250)	1140 ± 59 (970, 1512)	2.2	0.16
Staging distance (km)	870 ± 49 (672, 1079)	1023 ± 39 (876, 1240)	6.2	0.03*
Autumn departure (days)	Aug 22 ± 2 (Aug 9, Sep 1)	Aug 24 ± 4 (Aug 11, Sep 9)	0.2	0.69
Spring arrival (days)	May 7 ± 2 (Apr 26, May 15)	May 13 ± 2 (May 6, May 21)	4.2	0.06

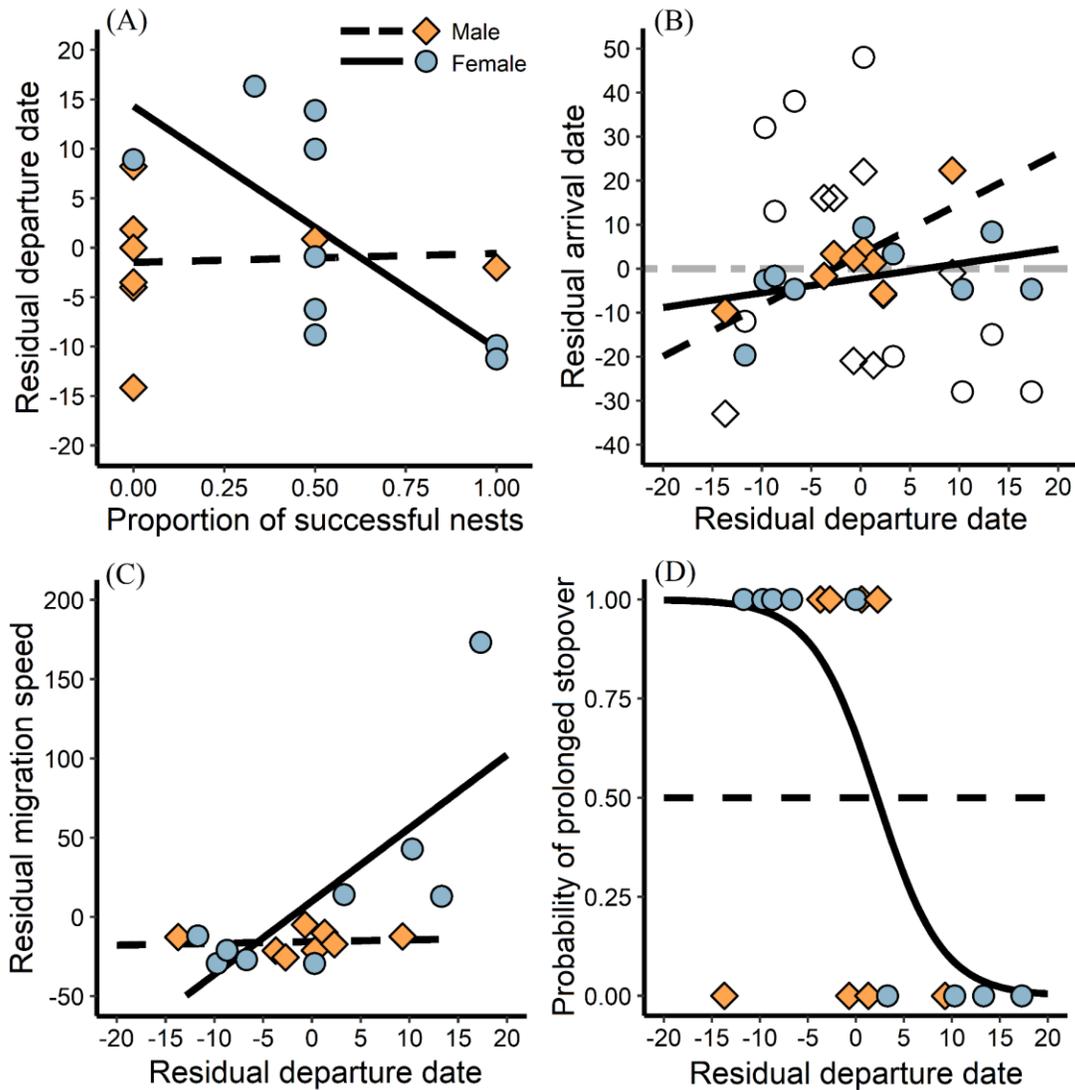
**Figure 4.1.** Migration routes between the breeding site (HBM) and winter sites for (A) autumn and (B) spring migration. The purple arrows are weighted to depict the most common migration routes. Points indicate winter sites (diamonds) and stopovers > 14 days long (circles) and are weighted by the number of days at each site. Stopovers < 14 days long are not shown for the sake of clarity. Each individual is represented by at least one winter site and up to one or two stopover sites (n = 17 birds).



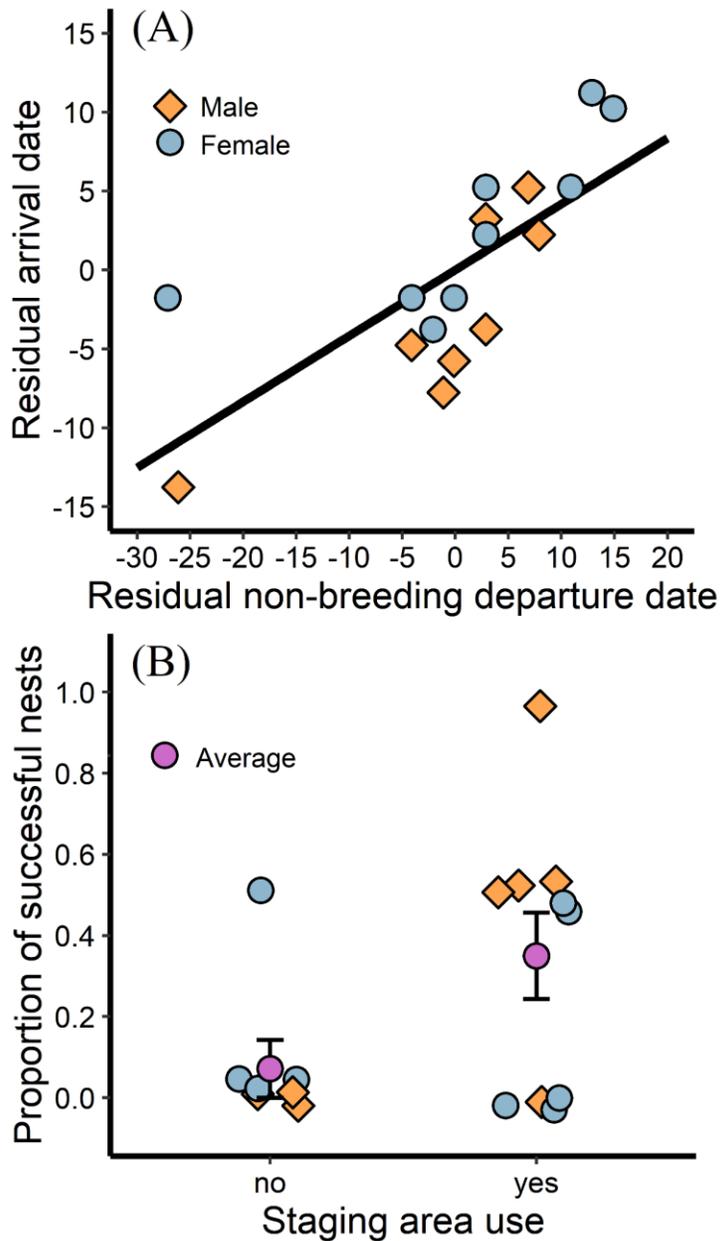
**Figure 4.2.** Spatial segregation of male and female non-breeding areas for an alpine population of horned lark. Points indicate the last prolonged stationary period for each individual prior to migrating back to the breeding site (HBM), based on whether the individual used a staging area (circle) or travelled straight from the winter site (diamond). Shaded regions depict the minimum convex polygons for each sex.



**Figure 4.3.** The association between (A) breeding success and timing of departure from the breeding site, and (B) the subsequent association between departure date and arrival at the first prolonged non-breeding site (black lines) and winter site (dashed grey line). The grey line depicts the relationship for both males and females because there were no sex differences, but the empty points indicate males and females separately for comparison. Additionally, (C) late departing females increased migration speed to the first stopover, and (D) reduced use of prolonged stopovers following delayed departure. Residuals were calculated by subtracting from the mean such that positive is greater and negative is less than average.



**Figure 4.4.** The association between spring migration behaviour and breeding success: (A) individuals that depart the last stationary site (i.e., staging area or winter site) later arrive late to the breeding site, and (B) individuals that use staging areas in the northern Columbia Plateau region en route to the breeding site have greater breeding success. Positive residual values are later than average and negative are earlier.



## **Chapter 5. Harsh winter and spring stopover conditions reduce nest success by delaying clutch initiation and prolonging offspring development**

### **Introduction**

Carry-over effects stem from conditions at one stage of the annual cycle that alter the state of an individual in subsequent stages, potentially influencing behavioural decisions and fitness (Norris 2005, Norris and Marra 2007). Carry-over effects may be time- or energy-based (Harrison et al. 2011). Delays in phenology at one point can cascade across temporally-linked stages (Piersma 1987, Gow et al. 2019), while environmental factors that affect resource acquisition may reduce individual body condition and energy availability for reproduction or survival at subsequent stages (Gill et al. 2001, Paxton and Moore 2015, Rockwell et al. 2017). While time- and energy-based effects are related, the former involves individuals prioritizing resource acquisition and survival over timing, resulting in delayed phenology. The latter may occur if timing is critical to breeding success, forcing individuals to maintain phenology even with sub-optimal energy levels (Descamps et al. 2011, Harrison et al. 2011). Migratory songbirds, which spend up to 75% of the annual cycle away from their breeding site, may be particularly susceptible to carry-over effects (Runge et al. 2014, Marra et al. 2015). Linking breeding phenology and reproductive success to non-breeding habitat conditions allows us to identify critical periods in space or time throughout the annual cycle that have the greatest influence on individual fitness.

Carry-over effects are commonly observed as altered breeding phenology. Winter habitat quality or weather conditions can influence the arrival of individuals at the breeding site and subsequently clutch initiation (Marra et al. 1998, Norris et al. 2003, Gunnarsson et al. 2005). In addition to the winter site, songbirds may use spatially-distinct stopover habitats for varying

periods of time to accumulate the resources necessary for migration and breeding (Bayly et al. 2018, Briedis et al. 2018). Time-delays or energy-limitations have the potential to arise at each location, such that where and when songbirds use non-breeding habitats can influence the relative strength of carry-over effects (Marra et al. 2015). Nesting earlier is often linked to greater nesting success (Perrins 1970, Raquel et al. 2019), and fledging offspring with greater recruitment potential (Visser et al. 2015, Alves et al. 2019). Therefore, there should be strong selection for early clutch initiation (Lepage et al. 2000), and suboptimal conditions at any point in the annual cycle can theoretically produce negative fitness consequences through delayed breeding phenology.

For birds breeding in seasonal environments like the alpine or arctic, timing of migration and reproductive events may be particularly critical to individual fitness (Bauer et al. 2016). Since breeding seasons are more compressed, with limited opportunities to reproduce successfully, earlier nesting may be disproportionately beneficial (Martin and Wiebe 2004). However, stochastic habitats with frequent winter-like storms early in the season may deplete energy reserves and lead to decisions that prioritize survival over reproductive investment (i.e., nest abandonment; Martin et al. 2017, Wingfield et al. 2017). Under these conditions, selection on clutch initiation should be more stabilizing (Coppack and Pulido 2009). While earlier clutch initiation can be risky, individuals that arrive at the breeding site in better condition may be able to invest more in parental care and benefit from early breeding even if conditions deteriorate (Bêty et al. 2003, Descamps et al. 2011). Energy-based carry-over effects may therefore influence clutch initiation date in unpredictable environments, but it is unclear whether non-breeding conditions can mitigate or compound the effects of harsh, early season conditions at the breeding site.

Offspring development is a potential link between clutch initiation and reproductive success. Nestling development—the period from hatch to fledge—is a critical, but vulnerable life-stage for altricial songbirds, where predation is the major source of fecundity loss and risk accumulates with time in the nest (Martin 1995, Martin and Briskie 2009). Nestlings that develop quickly can fledge earlier and potentially at a larger size, improving probability of survival in the first week outside of the nest when most post-fledging mortality occurs (Cox et al. 2014, Martin et al. 2018). Rapid development may be constrained by early season storm events, prolonging time in the nest by restricting food availability and challenging thermoregulation (Stodola et al. 2010, Pérez et al. 2016). The ability for parents to act as a buffer to these constraints and invest in maintaining nestling development rates likely depends on individual body condition (Chapter 2). Carry-over effects may influence offspring development and subsequently nest success either through clutch initiation decisions or parental energy availability.

In an alpine population of horned lark in northern British Columbia, Canada, age at fledging ranges from 7 to 13 days (mean = 9.2) and is influenced by temperature, predation risk, and importantly, female body condition (Chapter 2). Larks from this population are short-distance migrants (mean distance = 1080 km), yet some individuals exhibit prolonged staging behaviour during spring migration (mean = 41 days; Chapter 4). Therefore, spatially-structured environmental conditions during different time windows have the potential to produce carry-over effects on breeding parameters. Few studies assess the combined influence of weather conditions across non-breeding and breeding habitats (Mazerolle et al. 2011, Ockendon et al. 2013, Finch et al. 2014, Drake et al. 2014). Therefore, the nature of carry-over effects stemming from different stages of the annual cycle and the critical time windows to which individuals respond are poorly understood, particularly for alpine songbirds.

Using 12 years of breeding data and 3 years of non-breeding location estimates from light-level geolocators, I assessed the influence of non-breeding and breeding weather conditions on subsequent clutch initiation and nestling development time. Specifically, I investigated: (i) the critical time windows over which temperature and precipitation variables may influence breeding phenology from three distinct regions (winter, stopover, and breeding site), and (ii) whether non-breeding conditions influence nestling development rate, either through their effects on clutch initiation (time-based) or independent of phenology (energy-based carry-over effect). Finally, (iii) I quantified the combined effects of shifting clutch initiation dates and nestling development rates on nest success. Due to the unpredictability of early season weather in alpine habitats, I expected stopover and breeding site conditions to influence reproductive decisions more than winter site conditions because they are closer in time and space. Additionally, given that nest predation risk is cumulative, I predicted that females able to fledge offspring at a younger age and earlier than the average clutch initiation date would benefit from greater nest success.

## **Methods**

For 12 years (2003–2007, 2010, 2011, and 2015–2019), clutch initiation date, brood size, age at fledge, and nest success were recorded for each nest. For full details on the study system and field methods see *Chapter 1*.

Larks from this population are short-distance migrants that spend the winter east of the Cascade mountains in the south Columbia Plateau and the northern extent of the Great Basin region (Chapter 4). During spring migration, they pass through the northern Columbia Plateau and Okanagan Highlands, with some individuals stopping for extended periods of time from late-February to mid-April (average: 41 days, range = 21 – 66 days). Typical arrival date at the breeding site ranges between late-April and mid-May (Chapter 4).

### *Local weather variables*

For the breeding site, I calculated daily average, minimum and maximum temperature, freeze days (days  $\leq 0^{\circ}\text{C}$ ), and precipitation days ( $\geq 1 \text{ mm/m}^2$ ). See *Chapter 1: Weather variables* for full details on weather data from Hudson Bay Mountain (HBM).

I retrieved snow depth data for 2009–2019 from the HBM ski resort’s historical record. From 2003–2007, I extracted data from the two nearest weather stations involved in the automated snow weather station array of the Provincial Snow Survey Network (B.C. Ministry of Environment and Climate Change Strategy 2019). The closest station (Tsai creek station; 27.3 km west; 1360 m a.s.l.) performed moderately when compared to HBM data from 2009–2019 (Pearson’s correlation:  $r = 0.72$ ). However, the Sherdin Creek station (120.5 km north; 1480 a.s.l.) correlated strongly with HBM snow depth data ( $r = 0.90$ ). Therefore, I used Sherdin Creek data as a proxy of snow depth at our study site from 2003–2007. I evaluated snow depth on April 15<sup>th</sup> because this is the latest date with consistent data across years and, being just prior to when larks arrive in the alpine, is likely to influence breeding decisions (Chapter 4).

### *Non-breeding weather variables*

Using location estimates derived from 17 individual geolocators in Chapter 4, I created kernel density plots to quantify regions with at least 75% of the locations for both the winter and stopover sites (Figure 5.1). Most of the location estimates could be classified into two distinct areas: 1) winter region (Latitudinal range:  $44^{\circ}\text{N} - 47^{\circ}\text{N}$ ; Longitudinal range:  $121.5^{\circ}\text{W} - 119^{\circ}\text{W}$ ), and 2) stopover region ( $47^{\circ}\text{N} - 49^{\circ}\text{N}$ ;  $120.5^{\circ}\text{W} - 118.5^{\circ}\text{W}$ ). While some overlap existed, explicitly separating the stopover and winter locations allowed me to test if conditions closer to the breeding site, both in time and space, may influence breeding parameters.

I gathered separate temperature and precipitation data for both the winter and stopover areas. Within each region, I laid out a grid of points spaced at 50 km intervals. I then interpolated surface air temperature ('air.sig995') and precipitation rate ('prate.sfc') from the NCEP R-1 database to each point four times daily (midnight, 0600, 1200, and 1800) from December 1 – May 1 at the winter site, and from February 15 – May 1 at the stopover site for all 12 years of the study. These time periods captured when individuals were most likely to be at the winter and stopover site (Chapter 4). The average, min, and max temperatures were calculated per point and then averaged within a region for each day. If the regional average daily temperature was  $\leq 0^{\circ}$  C, I denoted this as a 'freeze day'. Similarly, I converted the point estimate precipitation rate to total mm/m<sup>2</sup> per day and averaged within each region for a mean daily precipitation. Therefore, for both the stopover and winter regions the weather variables consisted of average daily, minimum and maximum temperatures, freeze days, and average daily precipitation (mm/m<sup>2</sup>).

## **Statistical analysis**

### *Weather variable selection and model fitting*

I assessed the influence of spatially-explicit weather conditions on clutch initiation and age at fledging for first nests only. For each response variable, I used a sliding window approach with the R package 'climwin' (Bailey and van de Pol 2015) to identify the most influential weather variables and associated time windows for each of the winter region, stopover region, and breeding site. This systematic approach tests the influence of specified weather variables across all possible time windows within the designated date range on the response variable and then ranks each model with Akaike Information Criterion (AIC; van de Pol et al. 2016). I then extracted the top time windows for each weather variable to build a global candidate model and

used model averaging to estimate effect size and variable importance. All analyses were performed using R version 3.6.1 (R Development Core Team 2018).

I constructed a sliding window that spanned different but overlapping time windows for each of the three regions of interest based on prior knowledge of when individual larks arrive and depart from each region. These time windows consisted of December 1 to May 1, February 15 to May 1, and April 15 to June 1 (clutch initiation) or June 12 (age at fledging) for the winter, stopover, and breeding sites, respectively. June 1 and June 12 were chosen as reference points as they represent the average clutch initiation and hatch date for first nests across all years. I constrained the minimum time window to 21 days for winter and stopover conditions, and 7 days for the breeding site, with the maximum window size allowable being the entire time window. The minimum non-breeding time windows were chosen to better reflect weather patterns rather than anomalies and to avoid spurious correlations with short time periods that do not make biological sense. A minimum window of 7 days was selected for the breeding site to allow time for female larks to exhibit a physiological response (i.e., ova development) and make reproductive decisions based on prevailing weather conditions (Williams et al. 2015).

All possible time windows were ranked with AIC relative to the null model (year as the only predictor) and the ‘best’ time window was chosen based on the lowest AIC. Multiple comparisons can lead to spurious results, so I used the built-in randomization procedure in ‘climwin’ to determine the likelihood of selecting the same top model by chance (Type 1 error). Each model was run on 100 randomized datasets and the  $\Delta$ AIC of the observed data was compared to the  $\Delta$ AIC of each of the randomizations. Weather variables where the observed results were significantly different ( $P < 0.05$ ) from the randomization results, and that were within  $\Delta$ AIC  $< 2$  of the top performing weather variables were selected as candidate variables.

Since larks from this population are short-distance migrants, temperature and precipitation values for different regions (winter, stopover, breeding site) and time periods may be spatially or temporally autocorrelated (Legendre and Fortin 1989). I used Pearson's product-moment correlations and Variance Inflation Factors (VIF) to test for possible multicollinearity among candidate weather variables. For clutch initiation, winter temperature and precipitation were highly correlated ( $r = -0.80$ ; Figure A3.1). Therefore, I excluded models containing both variables from consideration when conducting AIC model selection and averaging (see below). For age at fledging, winter and stopover freeze days were highly correlated ( $r = 0.87$ ; Figure A3.2). These variables represented similar time windows (winter = Mar 27 – Apr 17; stopover = Apr 1 – Apr 22) and were likely capturing the same weather pattern. Therefore, I chose to only include stopover freeze days because it had the greatest effect size and lowest AIC relative to the null during sliding window selection (stopover  $\Delta AIC = -7.4$ ; winter  $\Delta AIC = -4.5$ ). Following these steps, all predictor variables of both clutch initiation and age at fledging had a subsequent  $VIF < 1.9$ , indicating no multicollinearity (recommended  $< 4.0$ ; Belsley and Welsch 1980). The final candidate set included 5 weather variables for clutch initiation and 2 for development time.

I built global models for both clutch initiation and age at fledging which included the selected candidate weather variables and additional biologically relevant explanatory variables. For clutch initiation date, I included snow depth as an explanatory variable. For age at fledging, I included clutch initiation date and brood size to control for potential effects on development rate. All variables were standardized and centered to allow comparison of relative effect sizes. I broke each global model into all possible subset models (clutch initiation:  $n = 64$ ; age at fledge:  $n = 16$ ) and ranked each with AIC. As mentioned above, clutch initiation sub-models that included both winter temperature and precipitation were not considered, allowing us to determine which winter

weather variable best fit the data. Each sub-model was bootstrapped 1000 times and models with Akaike weights summing to  $> 0.99$  were model-averaged to produce the final coefficients (Burnham and Anderson 2002; see Appendix 3: Table A3.1 and A3.2 for top models).

Bootstrapped means and 95% confidence intervals were used to evaluate parameter strength and significance. I also report variable importance (VI) for the averaged model to indicate the proportion of model weight attributable to each variable, ranging from 0 (unimportant) to 1 (very important; Burnham and Anderson 2002).

### *Fitness effects*

I assessed the influence of advanced or delayed clutch initiation relative to the annual mean on daily nest survival (DNS). I centered clutch initiation within year such that negative values were earlier than average and positive values were later. I fit a mixed effects discrete logistic exposure model with a complementary log-log link to model the probability of successfully fledging offspring while accounting for exposure days. Year was included as the random effect and relative clutch initiation as the only fixed effect. I fit two separate models, with clutch initiation as a linear and quadratic term. A linear relationship would be expected if nest survival was highest early in the season and declined with greater predator activity as the season progressed. Conversely, nest survival could increase with time because less snow cover means more searchable nesting habitat, decreasing the likelihood of predators locating a nest (Martin and Roper 1988, Chalfoun and Martin 2009). A quadratic relationship would occur if nest survival was highest for early and late nests because predators were targeting nests during peak nesting activity at some middle date. Support for both models was compared with AIC.

## Results

Over 12 years, 382 first nests were monitored. Average clutch initiation date was June 1, spanning only 11 days across years from May 28 to June 8 (Figure 5.2A). Variation among first nests of the same year ranged from 10 to 26 days (mean = 17.3 days). For age at fledging, I could only use 10 years of data, as 2007 had no successful first nests and 2010 had one (see Table A3.4 for annual sample sizes). For 118 nests, age at fledging ranged from 7 to 13 days. Average age at fledging across all years was  $9.2 \pm 0.1$  (SE) days, with a minimum of 8.4 and maximum of 10.2 days (Figure 5.2B).

### *Clutch initiation date*

Sliding window analysis identified winter temperature (best window: Dec 2 – Mar 10), winter precipitation (Feb 10 – Apr 10), and stopover precipitation (Feb 21 – Apr 9) as the most likely non-breeding predictors of clutch initiation date. Local temperature (May 1 – May 22) and precipitation (May 1 – May 9) were selected as the best breeding site correlates.

After model selection, winter precipitation was a better predictor of clutch initiation than winter temperature, which did not factor into any of the top models (Table A3.1). Model averaged estimates indicated that greater winter precipitation delayed clutch initiation ( $\beta = 0.28$ ; Figure 5.3A; Figure 5.4A). For every 0.5 mm/m<sup>2</sup> increase in average daily winter precipitation, clutch initiation date was delayed by 4.5 days. At the breeding site, higher temperatures prior to breeding were linked to earlier egg laying dates ( $\beta = -0.38$ ; Figure 5.3A; Figure 5.4B). For every 1°C increase in average temperature during the month of May at the breeding site, clutch initiation date advanced by 1.5 days. Stopover and local precipitation, as well as, snow depth failed to influence clutch initiation date (Figure 5.3A; Table A3.3).

### *Age at fledging*

Stopover freeze days (best window: Apr 1 – Apr 22) and local precipitation (May 7 – May 15) were the only weather variables selected with the sliding window approach for age at fledge. After model averaging, a greater proportion of freeze days at the stopover location was associated with prolonged nestling development (older age at fledging;  $\beta = 0.29$ ; Figure 5.3B; Figure 5.5). For every 2 days below 0°C in April, age at fledging increased by 0.15 days. Neither local precipitation, average clutch initiation date nor brood size influenced age at fledge (Figure 5.3B; Table A3.3).

### *Fitness consequences*

The linear and quadratic daily nest survival (DNS) models did not differ ( $\Delta AIC \leq 2$ ) and therefore I selected the linear relationship as the most parsimonious. For a mean clutch initiation date, the average estimated DNS across years was  $0.967 \pm 0.002$  ( $\pm$  SE), corresponding to a  $44.2 \pm 1.2\%$  probability of successfully fledging over a 24-day nest cycle. This ranged from a low of  $0.492 \pm 0.281$  in 2007 to a high of  $0.997 \pm 0.002$  in 2004 (Table A3.4).

Within years, DNS declined with later clutch initiation ( $z = -2.85$ ,  $P < 0.01$ ). For the earliest observed clutch initiation (13 days earlier than average), the predicted DNS was  $0.986 \pm 0.003$  or  $71.0 \pm 3.8\%$  nest success, compared to  $0.940 \pm 0.017$  or a  $22.8 \pm 4.8\%$  nest success for the latest observed clutch initiation (14 days later than average). The fitness consequences of nestling development time were dependent on clutch initiation date. For an average clutch initiation, prolonged development times (13 days) had a predicted 14.6% lower probability of success than rapid development (7 days; Figure 5.6). For early nests, the predicted cost of

delayed fledge was minimal (−6.9%), but as the season progressed, the cost became more apparent (−20.1%; Figure 5.6).

## **Discussion**

I demonstrate that among year variation in clutch initiation date and nestling development time is influenced by spatially- and temporally-explicit weather conditions at both the non-breeding and breeding sites. Despite the expectation that shifts in clutch initiation date would have subsequent effects on age at fledging, periods of extreme cold at spring stopover sites prolonged nestling development time independent of clutch initiation. Given this independence and that arrival date at the breeding site does not influence clutch initiation in this population (Chapter 4), my results align most with expectations for energy-based rather than time-related carry-over effects (Harrison et al. 2011). In addition, while later clutch initiation is often linked to reduced nest success and fecundity (e.g., Rockwell et al. 2012, Imlay et al. 2018), I show that delayed clutch initiation and prolonged offspring development combine synergistically to reduce nest success. Therefore, suboptimal conditions at critical points in the non-breeding season can influence individual fitness through carry-over effects on both clutch initiation and nestling development.

### *Clutch initiation*

Colder, early season temperatures at the breeding site, but not snow depth, delayed clutch initiation. Larks are early breeders and can build nests as soon as small patches of ground are snow-free (Beason 1995). Snow depth may therefore only influence clutch initiation at a more localized scale because topography and temperature can combine to drive heterogeneity in snow-melt, exposing nesting habitat independent of average snow depth (Niittynen et al. 2018). Even without snow as a constraint, synchronizing hatch date with resource availability can be critical

to nest success (Visser et al. 2006). Warmer spring temperatures at the breeding site are often associated with earlier clutch initiation (Bowers et al. 2016, Imlay et al. 2018), including in arctic habitats (Liebezeit et al. 2014, Ram et al. 2018). In seasonal environments, timing of foliage leaf-out is linked to both snow depth and spring temperatures (Cooper 2014), and the window of greatest insect abundance may be relatively short (Tulp and Schekkerman 2008). Therefore, postponing clutch initiation with colder early-season temperatures may also represent resource tracking by female larks, although this decision likely depends on individual condition and predation risk costs as the season progresses (Chapter 2).

While greater than average precipitation at the winter site delayed clutch initiation, colder temperature and greater precipitation were highly correlated, indicating that this result may indicate the effects of harsher winter conditions on breeding phenology. Carry-over effects stemming from winter habitat conditions can represent cascading time delays or energy-based state effects (Harrison et al. 2011). Short-distance migrants that breed in naturally variable alpine or arctic habitats are expected to be more flexible in their breeding phenology than long-distance migrants (Boelman et al. 2017, Mizel et al. 2017), and therefore time-based carry-over effects may be less pronounced (Briedis et al. 2018, Gow et al. 2019). Instead, harsh winter conditions may disrupt resource acquisition and influence the body condition of individuals upon arrival at the breeding site, requiring females to recover energy stores prior to breeding (Bêty et al. 2003, 2004). In alpine habitats, challenging early season conditions may compound the effects of harsher winters, prolonging the time needed to invest in self-maintenance (Harrison et al. 2013). However, given the strength of local versus non-breeding effects, my results demonstrate it may also be possible for more favourable breeding site conditions to moderate the influence of poor winter conditions (Descamps et al. 2011).

## *Age at fledge*

Periods of sub-zero temperatures at the stopover region in April increased average age at fledge. A similar relationship was not observed for average temperature, suggesting that only severely sub-optimal conditions can induce cross-seasonal effects on nestling development. While most individuals pass through the stopover region during northward migration, I acknowledge that time spent in the area can range from days to months (Chapter 4) and therefore the exposure to stopover conditions varies among individuals. However, 59% of tracked larks remained in this stopover region  $\geq 21$  days and enjoyed improved reproductive success, producing an average of 1.8 more fledglings than individuals that did not stopover for an extended period (Chapter 4). Therefore, given the prolonged duration of stay and the association with both reproductive success and nestling development rate, the northern Columbia Plateau stopover region, particularly during the April time window, could be an important component of the annual cycle.

Stopover conditions did not influence clutch initiation, indicating that prolonged development time is not a result of cascading time-dependencies. Instead, periods of extreme cold may induce changes in female physiology or body condition shortly before breeding (Sorenson et al. 2016). Corticosterone (CORT) is a glucocorticoid hormone that regulates homeostasis and is released in large quantities in response to stressors (Wingfield et al. 2017). Stressed females can deposit CORT into egg yolk, promoting maternal effects like slower nestling development (Love et al. 2005, Saino et al. 2005). Poor body condition prior to breeding can reduce investment in parental care behaviours such as incubation and offspring provisioning relative to self-maintenance (Williams 2012). Resource-challenged females may limit incubation bouts, leading to cooled embryos (MacDonald et al. 2013, Coe et al. 2015) and reduced nestling development rates (Nord and Nilsson 2011). While female condition time-series and tests for

maternal effects are necessary to determine the mechanism, I demonstrate that stopover conditions can influence offspring development independent of clutch initiation.

### *Fitness effects*

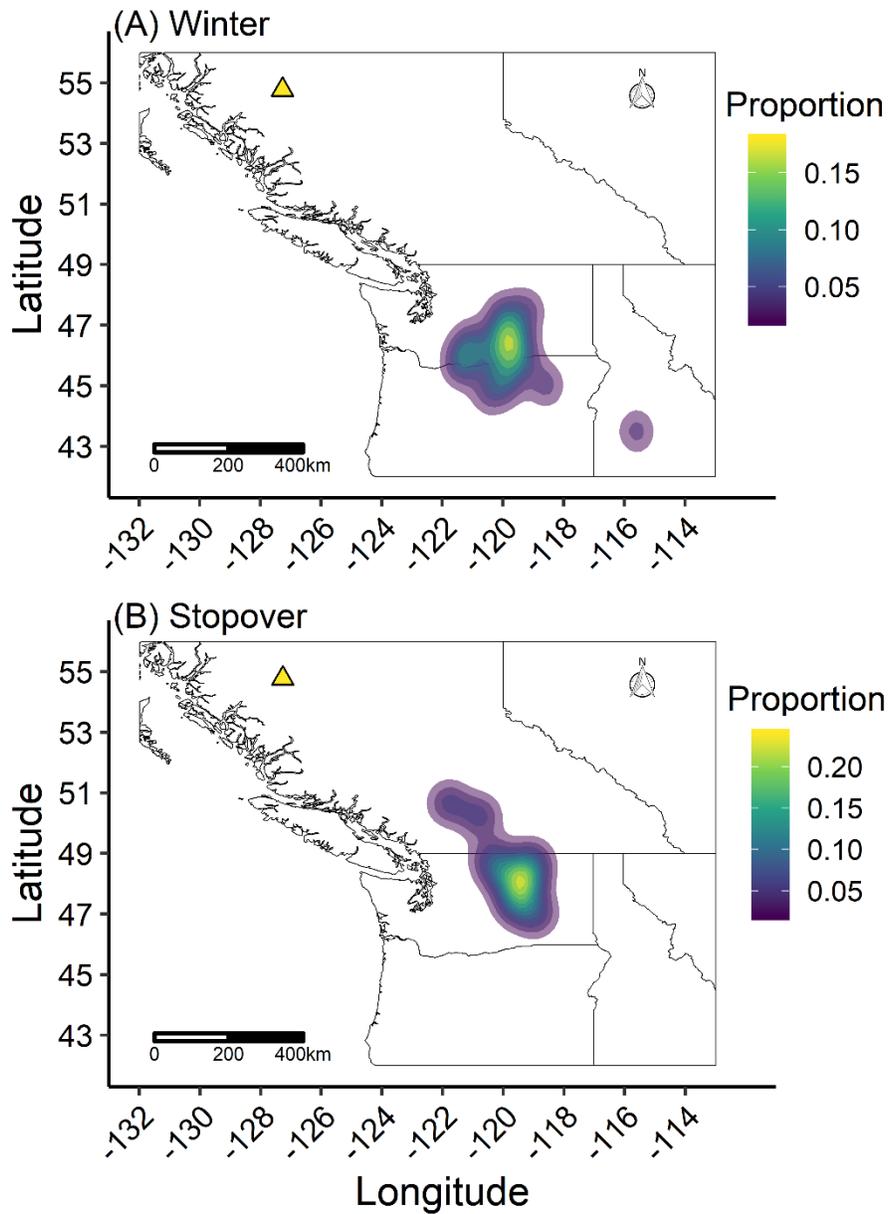
Carry-over effects stemming from different points in the annual cycle that influence clutch initiation and nestling development can combine synergistically to impact individual fitness. Nest survival of first nests declined linearly with time of season. Prolonged development time had minimal negative consequences for early nests, but drastically reduced success of later nests. Notably, slower development is hypothesized to be adaptive in unpredictable conditions (Arendt 1997), with rapid development potentially leading to reduced fitness later in life (Monaghan 2008, Criscuolo et al. 2011). Therefore, females able to initiate clutches earlier may benefit from disproportionately greater fitness through a combination of reduced nest predation risk and longer offspring development periods that may result in higher quality offspring. Early clutch initiation is frequently linked to greater reproductive success, but the underlying mechanisms are often unclear (Morrison et al. 2019). I propose that offspring development is an integral component of this association.

### **Conclusion**

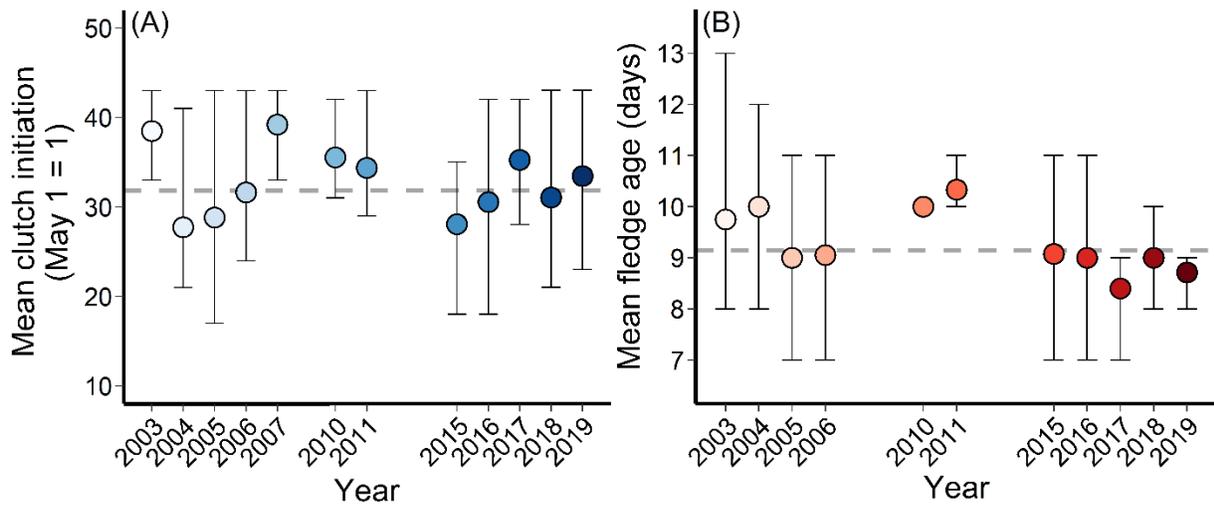
Early clutch initiation and rapid offspring development can be adaptive, but environmental conditions throughout the annual cycle may constrain the ability for phenological advancement. For an alpine population of larks, I demonstrate that both non-breeding carry-over effects and breeding site conditions can influence reproductive phenology, as well as, nestling development rate with direct fitness consequences. I also highlight that carry-over effects may be particularly

pronounced for birds breeding in stochastic habitats like the alpine where early season conditions and resource availability is unpredictable and short breeding seasons limit reproductive opportunities. The climate is changing at different rates across latitude and elevation (IPCC 2018), potentially decoupling conditions between non-breeding and breeding habitats and limiting the capacity for phenotypic flexibility in breeding phenology (Charmantier and Gienapp 2014, Senner et al. 2018). By addressing the influence of conditions across the annual cycle, we can better understand the mechanisms driving breeding decisions in stochastic habitats and make predictions about future individual- and population-level responses to climate change.

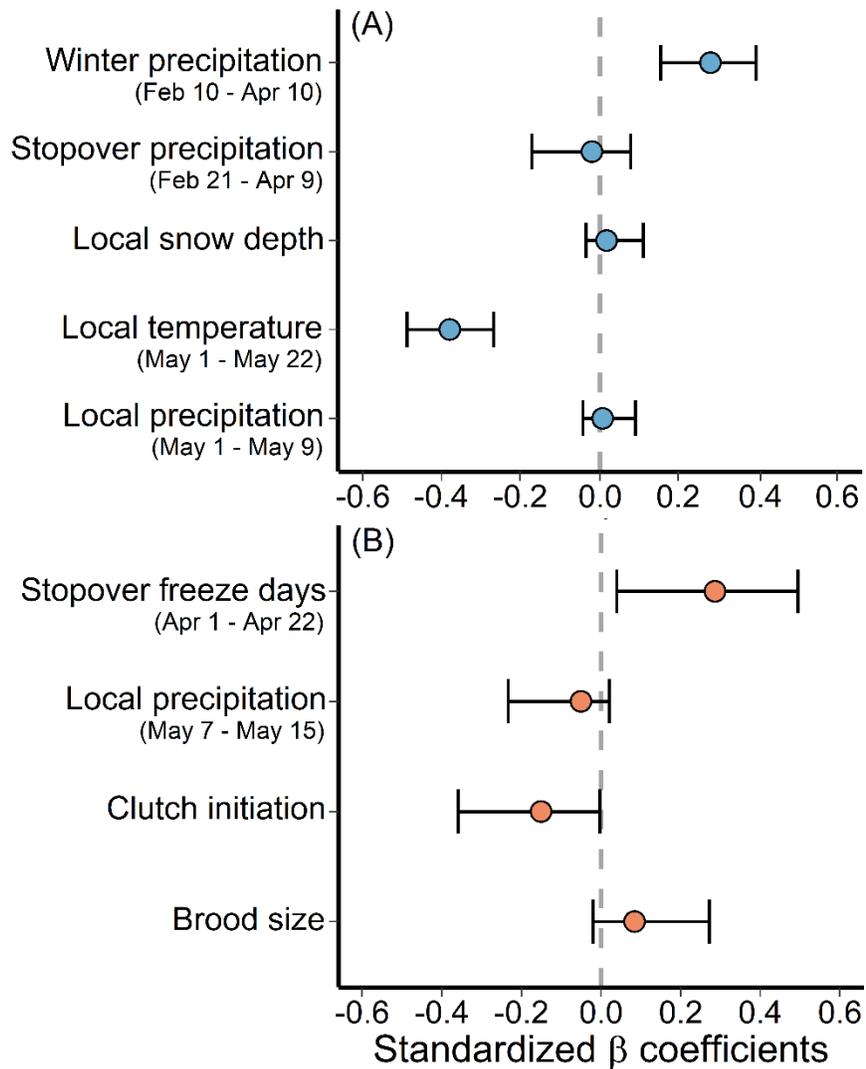
**Figure 5.1.** Kernel density plot showing the proportion of horned lark location estimates from Chapter 4 within the winter (A) and spring stopover (B) regions. Areas that contained at least 75% of the stage-specific location estimates were selected to differentiate the two regions such that the areas did not overlap. The yellow triangle denotes the breeding site.



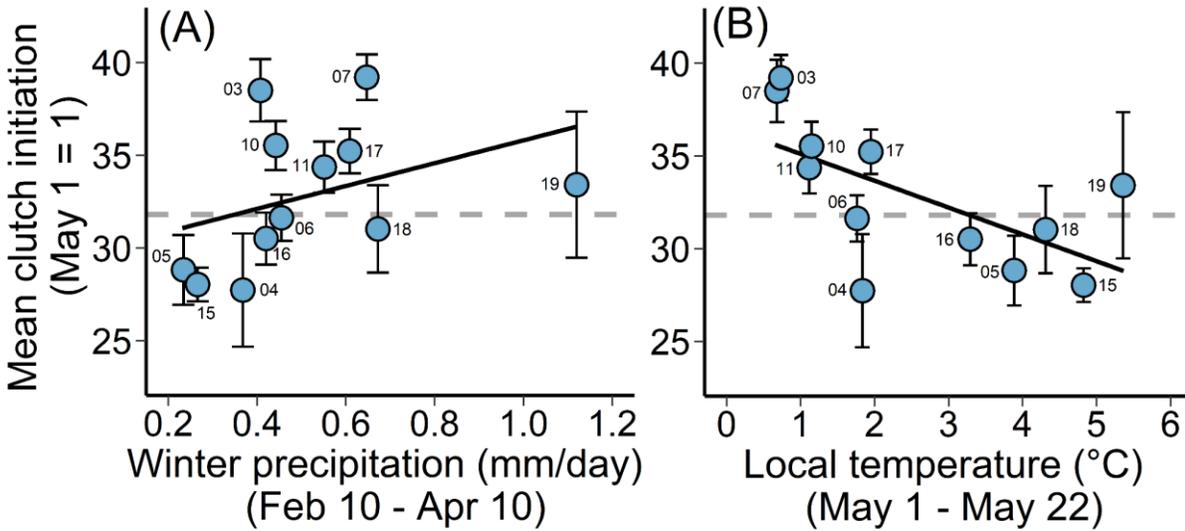
**Figure 5.2.** Within-year averages of (A) clutch initiation date and (B) age at fledge for an alpine breeding population of horned lark in northern British Columbia, Canada. Error bars depict the range of values (min, max) and the dashed grey line is the among-year average. In (B), 2010 represents only one nest and thus was not included in analysis but is depicted here for visualization purposes. The colour gradients are simply used to visualize progression over time.



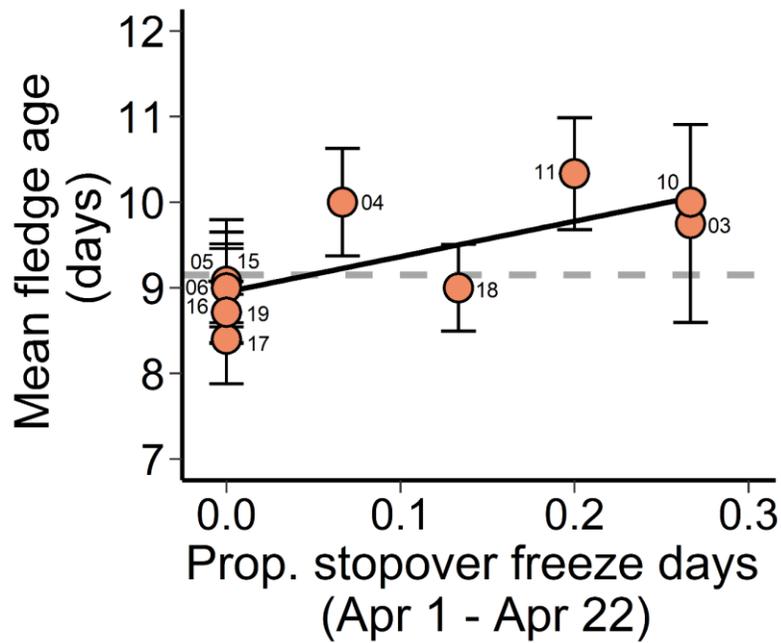
**Figure 5.3.** Standardized  $\beta$ -coefficients and 95% confidence intervals as estimated from model averaging and 1000 bootstraps for (A) clutch initiation and (B) age at fledge. The points depict the bootstrapped mean and the error bars are the 95% credible intervals. Variables are considered significant if their 95% CI does not include zero (the grey dashed line). Local refers to the breeding site.



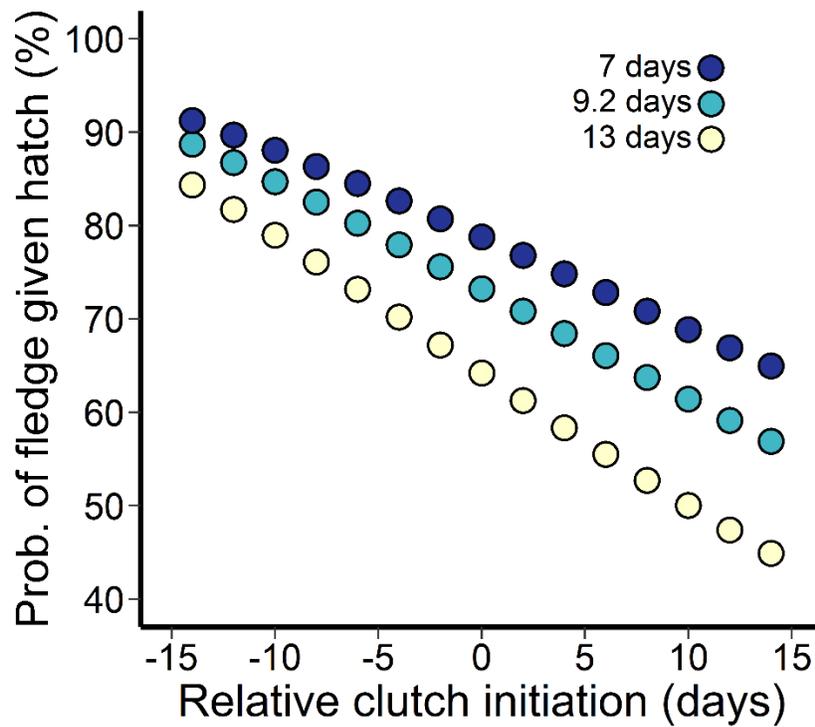
**Figure 5.4.** The influence of (A) winter precipitation and (B) local temperature on average clutch initiation date among years. The dashed grey line represents the average across all years, while the points are the within-year averages labelled by year (last two digits). The trend lines and 95% confidence intervals (error bars) were derived from the bootstrapped models.



**Figure 5.5.** The relationship between the proportion of stopover freeze days (days  $\leq 0^{\circ}\text{C}$ ) and average age at fledge. The dashed grey line represents the average across all years, while the points are the within-year averages labelled by year (last two digits). The trend lines and the 95% confidence intervals (error bars) were derived from the bootstrapped models. For 2010, a point is included for reference, but the data were not involved in the analysis due to a low sample size ( $n = 1$ ) and thus it does not influence the trend line.



**Figure 5.6.** The association between clutch initiation date and probability of fledging given hatch (i.e., nestling survival) across minimum (7 days), average (9.2 days), and maximum (13 days) observed nestling development times. These values are predicted from the relationship between clutch initiation and average daily nest survival (DNS). Relative clutch initiation was calculated per year, such that zero is the within-year average. Points depict probability of survival at 2-day intervals starting 14 days prior-to and ending 14 days after the within-year average for clutch initiation date to cover the observed range across years.



## Chapter 6. Discussion and synthesis

### *Overview*

When comparing life-history traits among species or across large geographic scales, we often consider local adaptations with a focus on adult traits like basal metabolic rate or thermal tolerance (e.g., Wiersma et al. 2007). However, in many cases the selective pressures that filter adult phenotypes act first on juveniles as their critical size and functional traits are developing (Ricklefs et al. 1994). In challenging environments, adult traits may be less variable because of strong early-life selection (Conklin et al. 2017). Therefore, the same selective pressures can induce different responses or fitness consequences depending on the life-stage.

In this dissertation, I focused on early-life conditions and trade-offs to understand what factors promote or constrain offspring development in the context of life-history theory. I demonstrated that temperature during specific periods across the annual cycle was the strongest predictor of offspring development rate (Chapters 2 and 5), but that nestlings have the adaptive capacity to increase wing growth, or potential mobility, in response to elevated predation risk (Chapter 3). I further demonstrated that some females may be capable of buffering offspring against harsh, early season conditions and mediating growth responses to predators (Chapters 2 and 3). These results agree with the expectation that abiotic factors are more influential drivers of local adaptation than biotic interactions at high latitudes or elevations (Terborgh 1971, Boyle et al. 2015, Runquist et al. 2019), but also demonstrate that abiotic and biotic factors can form critical trade-offs in which the realization of an ‘optimal strategy’ may depend on parental investment. By addressing within-population variation in life-history traits and considering multiple potential drivers simultaneously, I provide insights into life-history theory that can not be derived from inter-specific comparisons.

### *The value of individual differences in life-history traits*

In comparative studies, identifying whether an observed life-history trait is an evolved or proximate response is difficult because species and populations differ in their underlying genetic structure and selective pressures (Conover and Present 1990, Martin 2004). For example, lark nestlings grow slower in arid than mesic habitats (Tieleman et al. 2004), but it is unclear whether this is an evolved trait that reduces per nestling resource requirements in harsher environments (Arendt 1997), or a proximate response to resource disruptions that constrain growth (Searcy et al. 2004, Bize et al. 2006). Investigating within-population variation in nestling development ensured that individuals were operating under similar selective pressures, allowing me to assess the relative strength of proximate drivers and critical trade-offs such as the antagonism between predation risk and cold temperatures (Chapter 2). Inter- or intra-specific comparisons along environmental gradients can identify important life-history trade-offs operating over evolutionary time (Badyaev and Ghalambor 2001, Sandercock et al. 2005), but within-population studies are critical for understanding the eco-evolutionary dynamics that shape life-history traits.

Variation in maternal condition (Chapter 2) and parental responses to predation risk (Chapter 3) highlighted a mediating effect of parental investment on nestling development. Adults must partition resources between self-maintenance and parental care (Williams 1966). As such, energetically-compromised individuals may reduce investment in critical behaviours like brooding or provisioning offspring in favour of self-preservation tactics such as foraging (Patterson et al. 2011). Female larks vary in their resilience to harsh or stressful conditions. Extreme cold can cause some, but not all, females to abandon their nest (MacDonald et al. 2013), while some females show only minor reductions in provisioning rate in response to predation risk (Goullaud et al. 2018). This variability may reflect differences in available resources or risk

aversion among females, allowing some to prioritize investment in parental care even in suboptimal conditions (Reid et al. 2000, Ghalambor and Martin 2001, Descamps et al. 2011, Ruffino et al. 2014). Maintaining high levels of investment may facilitate rapid offspring development (Chapters 2 and 3), and subsequently greater nest success (Chapters 2 and 5). My research suggests parental investment is critical in harsh, unpredictable environments like the alpine and demonstrates that, depending on individual state, females may be able to buffer offspring against challenging conditions by maintaining a nest environment that promotes offspring development.

Flexibility is adaptive in fluctuating environments like the alpine (Piersma and Drent 2003), but it is unclear if nestling development can respond adaptively to prevailing conditions. Cold temperatures early in development did not prolong time in the nest (Chapter 2), which could be due to compensatory growth later in development (Hector and Nakagawa 2012). However, in Chapter 3, I demonstrated that rapid wing growth did not occur between 5- and 7-days post-hatch to compensate for poor early development conditions. Instead, nestlings adaptively accelerated wing growth in response to elevated predation risk (Chapter 3). Predation risk has been hypothesized to induce rapid growth of mobility traits like wing length to promote early fledging (Coslovsky and Richner 2011), but empirical evidence has been lacking. Rapid growth can be associated with delayed negative fitness effects (Monaghan 2008) which might limit accelerated growth following poor early development conditions, but the short-term benefits of avoiding an imminent threat like predation may be worth the long-term cost. By addressing variation within a stochastic, alpine habitat I highlighted the adaptive capacity for nestling development to respond to unpredictable stressors.

### *Multiple drivers across the annual cycle*

Assessing the relative importance of multiple influential factors can reveal hidden synergisms that influence life-history decisions (Côté et al. 2016). For example, horned larks are resilient to breeding season temperatures or precipitation in isolation, but ‘cold storms’ increase nest abandonment (Martin et al. 2017). Multiple stressors can also accumulate across different annual- or life-stages of an individual, altering energy allocation and life-history strategies (Wingfield et al. 2017). Termed ‘carry-over effects’, events at spatially or temporally separated stages of the annual cycle are linked, as the state of an individual at one stage can influence behaviour and fitness parameters in subsequent stages (Harrison et al. 2011). Despite the non-breeding season making up a large portion of the annual cycle, research across taxa is highly biased towards the breeding season (Marra et al. 2015). A central component of my research is incorporating multiple potential drivers of nestling development across the annual cycle. In doing so, I identified the importance of maternal condition or parental care (Chapters 2 and 3) which forms a plausible link with conditions during the non-breeding season.

A key finding that stemmed from considering the annual cycle was prolonged spring stopover behaviour. Individuals of both sexes remained in the northern Columbia Plateau for up to 2 months (Chapter 4), suggesting this stopover may be a critical component of the annual cycle (Pledger et al. 2009). In fact, individuals that stopped over for an extended period were more likely to successfully fledge offspring in the subsequent breeding season (Chapter 4), and extremely cold periods during April carried over to prolong nestling development (Chapter 5). Theoretically, songbirds should minimize time spent in potentially risky, unfamiliar stopover habitat and depart after acquiring the necessary resources to continue migration (Alerstam and Lindström 1990). Yet, accumulating evidence suggests prolonged stopovers may be more

common for songbirds than once thought (Bayly et al. 2018, Wright et al. 2018). For larks, the links between prolonged stopover use and breeding parameters require further study and could help highlight why some songbirds conduct extended stopovers and others do not.

Prolonged stopover behaviour and the potential link to subsequent breeding parameters raises the question: are alpine breeding larks income or capital breeders? To invest in reproduction, income breeders continuously acquire resources while capital breeders rely on stored energy reserves (i.e., fat; Drent and Daan 1980). While originally considered to be a dichotomous strategy, modern interpretations allow for hybrid strategies along an income-capital spectrum (Meijer and Drent 1999). Larks arrive at the breeding site when environmental conditions are challenging and resources may be unreliable (Martin et al. 2017); conditions that select for capital strategies (Jönsson 1997, Sainmont et al. 2014). Females arriving with greater energy reserves may be able to invest in reproduction sooner and possibly enjoy an adaptive advantage since early breeding is linked to greater nest success (Chapter 5). In the arctic, the reproductive success of capital breeding snow geese (*Chen caerulescens*) depends on stopover conditions (Bêty et al. 2003). However, whether prolonged stopover behaviour is a viable strategy for songbirds, shared among populations breeding in unpredictable environments, has not been assessed. While alpine larks are clearly not true capital breeders, a hybrid strategy could improve their capacity to breed in harsh, early season conditions, especially considering that opportunities for reproduction are limited in a highly compressed breeding season.

## **Limitations and future directions**

In this dissertation, I identified potential drivers of variation in nestling development from across the annual cycle, as well as, the short-term fitness consequences on nest success. In the process,

several additional questions were raised that highlight avenues for future research and have the potential to continue expanding our understanding of offspring development in variable habitats.

### *Delving into maternal condition*

I demonstrated that female condition strongly influenced nestling development time (Chapter 2). This result could stem in part from ‘maternal effects’, where the environment experienced by the female causally affects offspring development (Wolf and Wade 2009). Maternal effects can take many forms and can be passive or adaptive. Stressed females may deposit high levels of corticosterone into the egg yolk, resulting in slower nestling growth (*passive*; Love et al. 2005, Saino et al. 2005). Females may also lay larger eggs that promote greater nestling size (Mousseau and Fox 1998), or deposit androgens and glucocorticoids into egg yolk at levels that either promote faster growth (Coslovsky et al. 2012, Weber et al. 2018) or stimulate greater developmental plasticity (*adaptive*; Love and Williams 2008). Maternal effects may be particularly important in fluctuating environments (Proulx et al. 2019), especially if they prepare offspring for variable development conditions.

To avoid attracting predators, I only measured nestlings at 5- and 7-days post-hatch. Therefore, I did not measure propagule size (e.g., egg volume) which could explain nestling size variation within nests. I also did not measure corticosterone in females or egg yolk, both of which could have contributed to nestling feather corticosterone, as well as, variation in responses to predation risk (Hausmann et al. 2011). Potentially as a result, my models explained only a small proportion of the variance in feather corticosterone (Chapter 3). While maternal effects are often addressed in lab experiments, research on free-living birds is needed to understand corticosterone dynamics, preparatory effects, and fitness consequences in variable environments

(Love and Williams 2008, Harris et al. 2016). For larks, addressing interactions between conditions prior-to and during offspring development could determine the relative influence of maternal effects compared to parental care and link maternal condition more explicitly to nestling development.

Given the association between female condition and offspring development, a better understanding of carry-over effects on reproductive success is warranted. The northern Columbia Plateau is clearly an important stopover site that can influence subsequent fecundity (Chapter 4) and nestling development (Chapter 5). However, I only had location estimates for 9 females, of which 5 exhibited prolonged stopover behaviour (Chapter 4). Thus, females spend varying amounts of time at both the winter and spring stopover sites and likely experience different environmental conditions, potentially diluting the strength of the observed carry-over effects.

To assess the importance of spring stopover habitat, I would propose expanding the Motus Wildlife Tracking System (Birds Canada; <https://motus.org/>) through the South Okanagan and northern Columbia Plateau to track individuals using automated radio telemetry. By deploying Motus radio tags at the stopover site, it would be possible to address: (1) changes in body condition or stress biomarkers over time, (2) short-distance movement patterns and resource use within the stopover region, and (3) what conditions stimulate departure. For example, Motus tags revealed that rusty blackbirds (*Euphagus carolinus*) make long repositioning flights within stopover regions (up to 35 km) and individuals in poor condition stopover longer (Wright et al. 2018). By investigating inter-individual differences in stopover use for larks, as well as, associations among stopover conditions, body condition, and subsequent investment in reproduction, one could better understand the mechanisms underlying the observed carry-over effects on breeding parameters.

### *Predation risk: a classic 'whodunnit'*

Rapid nestling development was associated with greater predation risk (Chapter 2) and accelerated nestling wing growth was predator-specific, with stronger responses to raven than fox decoys (Chapter 3). While fox and raven are both expected to be influential nest predators, I did not measure the relative frequencies of predation by each species. This is notable because nestlings may respond differently to specific predators based on the relative threat (Platzen and Magrath 2005, Suzuki 2011). If rapid development is costly, nestlings may not have the adaptive capacity to respond to predator cues that indicate an unreliable or inconsistent threat. Diurnal predators like ravens may actively search for ground nests by sight or by observing parental activity, while the more nocturnal, scent-oriented fox may prey upon nests incidentally. Thus, foraging theory predicts that ravens pose the greatest threat to exposed alpine nests based on hunting strategy (Schmidt 1999), potentially selecting for a greater nestling response.

The nestling development response to predator cues may also vary across years depending on fluctuations in predation risk. For example, juvenile snowshoe hare (*Lepus americanus*) exhibit reduced or elevated stress responses following periods of low and high Canadian lynx (*Lynx canadensis*) densities, respectively (Sheriff et al. 2010). Predation pressure on one prey species may increase following crashes of a preferred prey due to prey-switching (Angelstram et al. 1984, Holt and Kotler 1987). For instance, in an arctic habitat, low lemming (*Lemmus* sp.) densities induced greater predation rates for artificial shorebird nests, particularly in areas with high snow goose densities (McKinnon et al. 2013). Brown lemmings (*Lemmus trimucronatus*) at Hudson Bay Mountain are frequently targeted by predators but were essentially absent in years with the greatest nest predation rates (personal observation). Whether predation risk varied across years because of changing predator abundance or prey-switching, if

this variation is predictable, the strength of nestling and parental responses to predator presence may shift accordingly. Future research employing camera traps or track boards to estimate the abundance of predators and alternative prey, as well as, nest predation activity would address fluctuations in predation risk across years and elucidate the basis for predator-specific development responses.

### *Downstream fitness effects*

Rapid nestling development is associated with greater nest success (Chapters 2 and 5), and accelerated growth of mobility traits may improve predator evasion post-fledge (Martin et al. 2018). However, the short-term fitness benefits of rapid growth may be balanced by negative long-term consequences for endurance, reproduction, and longevity (Monaghan 2008, Grace et al. 2017, Hsu et al. 2017). For example, zebra finch (*Taeniopygia guttata*) nestlings that undergo compensatory growth following periods of restricted resources demonstrate reduced flight endurance as adults (Criscuolo et al. 2011). In this dissertation, I focused on the short-term benefits of rapid nestling development in alpine larks. However, I was able to collect data on the breeding success of returning offspring for multiple consecutive years. As a result, I plan to address the impacts of offspring development rates on apparent first-year survival, as well as, reproductive investment and annual fecundity as adults. Studies investigating long-term consequences of different growth dynamics are rare outside of a lab setting, but necessary to determine if fitness consequences are more pronounced under stochastic conditions.

Understanding both the drivers and consequences of different development rates is key to predicting optimal development strategies across a range of climate conditions, with implications for individual and, ultimately, population-level responses to a changing climate.

## **Conclusion**

The importance of multiple stressors across the annual cycle on offspring development and reproductive success has broader significance for the future of alpine lark populations. In North America, horned larks at low elevation have experienced the second largest absolute decline in numbers among avian species since 1970 (Rosenberg et al. 2019). Alpine habitats may appear to be a refugia for larks (Camfield et al. 2010), as the intensity of habitat loss is greatest at low elevation (Scott et al. 2001). However, I demonstrate that alpine larks spend only about 29% of the annual cycle at their high elevation breeding site, with the remainder of the year spent at lower elevation non-breeding habitat. Coupled with the potential importance of stopover habitat for reproductive success, alpine larks are likely susceptible to habitat degradation at low elevation along migration routes. Additionally, while I demonstrate that nestling development and parental behaviour have some adaptive capacity to respond to fluctuating stressors, environmental stochasticity during the breeding season will continue to increase (IPCC 2018). The effects of climate change are occurring more rapidly in alpine and arctic habitats (IPCC 2018), potentially decoupling breeding and non-breeding conditions and exacerbating carry-over effects on nestling development. Whether flexible life-history strategies will continue to be a feasible coping mechanism is an open but critical question for the long-term prospects of alpine lark populations. This dissertation offers new insights into the multiple, nuanced associations that shape offspring development across the annual cycle and provides important context to understand life-history theory for songbirds in rapidly changing environments.

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## Appendices

### Appendix 1. Supplementary material for Chapter 2.

**Table A1.1.** Candidate weather models for the incubation and nestling period, organized by the complexity of the model (single variable, 2-variable additive models, and 2-variable interaction models). All models include clutch initiation date as a fixed effect and year as a random effect, but they are not included in this table for simplicity.

Model	Model terms
<b>Incubation period</b>	
<i>Single models</i>	
1	~ days < 5°C
2	~ days < 10°C
3	~ average temperature
4	~ precipitation days
5	~ storms
<i>Additive models</i>	
6	~ days < 5°C + precipitation days
7	~ days < 5°C + storms
8	~ days < 10°C + precipitation days
9	~ days < 10°C + storms
10	~ average temperature + precipitation days
11	~ average temperature + storms
<i>Interaction models</i>	
12	~ days < 5°C * precipitation days
13	~ days < 5°C * storms
14	~ days < 10°C * precipitation days
15	~ days < 10°C * storms
16	~ average temperature * precipitation days
17	~ average temperature * storms
<b>Nestling period</b>	
<i>Single models</i>	
1	~ days < 5°C <sub>(entire)</sub>
2	~ days < 10°C <sub>(entire)</sub>
3	~ average temperature <sub>(entire)</sub>
4	~ precipitation days <sub>(entire)</sub>
5	~ storms <sub>(entire)</sub>
6	~ days < 5°C <sub>(early)</sub>
7	~ days < 10°C <sub>(early)</sub>
8	~ average temperature <sub>(early)</sub>
9	~ precipitation days <sub>(early)</sub>
10	~ storms <sub>(early)</sub>
11	~ days < 5°C <sub>(late)</sub>

Model	Model terms
12	~ days < 10°C <sub>(late)</sub>
13	~ average temperature <sub>(late)</sub>
14	~ precipitation days <sub>(late)</sub>
15	~ storms <sub>(late)</sub>
<i>Additive models</i>	
16	~ days < 5°C <sub>(entire)</sub> + precipitation days <sub>(entire)</sub>
17	~ days < 5°C <sub>(entire)</sub> + storms <sub>(entire)</sub>
18	~ days < 10°C <sub>(entire)</sub> + precipitation days <sub>(entire)</sub>
19	~ days < 10°C <sub>(entire)</sub> + storms <sub>(entire)</sub>
20	~ average temperature <sub>(entire)</sub> + precipitation days <sub>(entire)</sub>
21	~ average temperature <sub>(entire)</sub> + storms <sub>(entire)</sub>
22	~ days < 5°C <sub>(early)</sub> + precipitation days <sub>(early)</sub>
23	~ days < 5°C <sub>(early)</sub> + storms <sub>(early)</sub>
24	~ days < 10°C <sub>(early)</sub> + precipitation days <sub>(early)</sub>
25	~ days < 10°C <sub>(early)</sub> + storms <sub>(early)</sub>
26	~ average temperature <sub>(early)</sub> + precipitation days <sub>(early)</sub>
27	~ average temperature <sub>(early)</sub> + storms <sub>(early)</sub>
28	~ days < 5°C <sub>(late)</sub> + precipitation days <sub>(late)</sub>
29	~ days < 5°C <sub>(late)</sub> + storms <sub>(late)</sub>
30	~ days < 10°C <sub>(late)</sub> + precipitation days <sub>(late)</sub>
31	~ days < 10°C <sub>(late)</sub> + storms <sub>(late)</sub>
32	~ average temperature <sub>(late)</sub> + precipitation days <sub>(late)</sub>
33	~ average temperature <sub>(late)</sub> + storms <sub>(late)</sub>
34	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub>
35	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub>
36	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + precipitation days <sub>(entire)</sub>
37	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + precipitation days <sub>(early)</sub>
38	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + precipitation days <sub>(late)</sub>
39	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + storms <sub>(entire)</sub>
40	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + storms <sub>(early)</sub>
41	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> + storms <sub>(late)</sub>
42	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + precipitation days <sub>(entire)</sub>
43	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + precipitation days <sub>(early)</sub>
44	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + precipitation days <sub>(late)</sub>
45	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + storms <sub>(entire)</sub>
46	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + storms <sub>(early)</sub>
47	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> + storms <sub>(late)</sub>
48	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub>
49	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 5°C <sub>(entire)</sub>
50	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 10°C <sub>(entire)</sub>
51	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + average temperature <sub>(entire)</sub>
52	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 5°C <sub>(early)</sub>
53	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 5°C <sub>(late)</sub>
54	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 10°C <sub>(early)</sub>
55	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> + days < 10°C <sub>(late)</sub>
<i>Interaction models</i>	
56	~ days < 5°C <sub>(entire)</sub> * precipitation days <sub>(entire)</sub>
57	~ days < 5°C <sub>(entire)</sub> * storms <sub>(entire)</sub>

Model	Model terms
58	~ days < 10°C <sub>(entire)</sub> * precipitation days <sub>(entire)</sub>
59	~ days < 10°C <sub>(entire)</sub> * storms <sub>(entire)</sub>
60	~ average temperature <sub>(entire)</sub> * precipitation days <sub>(entire)</sub>
61	~ average temperature <sub>(entire)</sub> * storms <sub>(entire)</sub>
62	~ days < 5°C <sub>(early)</sub> * precipitation days <sub>(early)</sub>
63	~ days < 5°C <sub>(early)</sub> * storms <sub>(early)</sub>
64	~ days < 10°C <sub>(early)</sub> * precipitation days <sub>(early)</sub>
65	~ days < 10°C <sub>(early)</sub> * storms <sub>(early)</sub>
66	~ average temperature <sub>(early)</sub> * precipitation days <sub>(early)</sub>
67	~ average temperature <sub>(early)</sub> * storms <sub>(early)</sub>
68	~ days < 5°C <sub>(late)</sub> * precipitation days <sub>(late)</sub>
69	~ days < 5°C <sub>(late)</sub> * storms <sub>(late)</sub>
70	~ days < 10°C <sub>(late)</sub> * precipitation days <sub>(late)</sub>
71	~ days < 10°C <sub>(late)</sub> * storms <sub>(late)</sub>
72	~ average temperature <sub>(late)</sub> * precipitation days <sub>(late)</sub>
73	~ average temperature <sub>(late)</sub> * storms <sub>(late)</sub>
74	~ days < 5°C <sub>(early)</sub> * precipitation days <sub>(early)</sub> + days < 5°C <sub>(late)</sub>
75	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> * precipitation days <sub>(late)</sub>
76	~ days < 5°C <sub>(early)</sub> * storms <sub>(early)</sub> + days < 5°C <sub>(late)</sub>
77	~ days < 5°C <sub>(early)</sub> + days < 5°C <sub>(late)</sub> * storms <sub>(late)</sub>
78	~ days < 10°C <sub>(early)</sub> * precipitation days <sub>(early)</sub> + days < 10°C <sub>(late)</sub>
79	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> * precipitation days <sub>(late)</sub>
80	~ days < 10°C <sub>(early)</sub> * storms <sub>(early)</sub> + days < 10°C <sub>(late)</sub>
81	~ days < 10°C <sub>(early)</sub> + days < 10°C <sub>(late)</sub> * storms <sub>(late)</sub>
82	~ precipitation days <sub>(early)</sub> * days < 5°C <sub>(early)</sub> + precipitation days <sub>(late)</sub>
83	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> * days < 5°C <sub>(late)</sub>
84	~ precipitation days <sub>(early)</sub> * days < 10°C <sub>(early)</sub> + precipitation days <sub>(late)</sub>
85	~ precipitation days <sub>(early)</sub> + precipitation days <sub>(late)</sub> * days < 10°C <sub>(late)</sub>

**Table A1.2.** Weather variables experienced by an alpine population of horned larks in northern British Columbia, Canada in each month of the study period (2003-2007 and 2010-2011). Daily temperature is the average, while precipitation days and storm events are total counts. May variables are calculated from May 15<sup>th</sup> (just prior to the earliest nest initiation) to the end of the month. June and July depict averages and totals for the entire month. ‘Category’ is based on temperature and precipitation values for June, the critical month during which an average of 74.2% of nests per breeding season have nestlings (range = 60.0 – 91.7%).

Year	Month	Daily temperature	% Days		Precipitation days (> 1mm)	Storms events (> 10 mm)	Category
			< 5°C	< 10°C			
2003	May	3.02	69.2	100.0	3	0	Mild-Dry
	June	7.53	33.3	76.7	9	1	
	July	10.22	6.5	61.3	11	1	
2004	May	3.41	84.6	100.0	4	0	Warm-Dry
	June	9.81	23.3	56.7	9	3	
	July	9.92	9.7	54.8	12	0	
2005	May	6.78	46.2	69.2	3	1	Mild-Wet
	June	6.84	23.3	90.0	12	1	
	July	6.61	25.8	93.5	12	0	
2006	May	4.97	53.8	100.0	6	0	Warm-Dry
	June	8.46	30.0	70.0	4	1	
	July	9.93	6.5	64.5	8	1	
2007	May	3.54	69.2	100.0	2	0	Cold-Wet
	June	5.44	56.7	90.0	16	2	
	July	9.32	6.5	64.5	8	1	
2010	May	1.15	83.9	100.0	8	1	Cold-Wet
	June	4.45	63.3	100.0	13	0	
	July	8.43	25.8	61.3	8	0	
2011	May	1.12	83.9	100.0	14	4	Cold-Wet
	June	4.54	60.0	100.0	9	1	
	July	5.40	51.6	93.5	16	3	

## Appendix 2. Supplementary material for Chapter 3.

**Table A2.1.** D-separation and AIC results for the global causal and correlational model. The ‘ $\sim$ ’ symbol indicates a non-directional correlation. The causal wing model (bold) was chosen as the global model to proceed with analysis based on the combination of a low Fisher’s C value and a similar AIC.

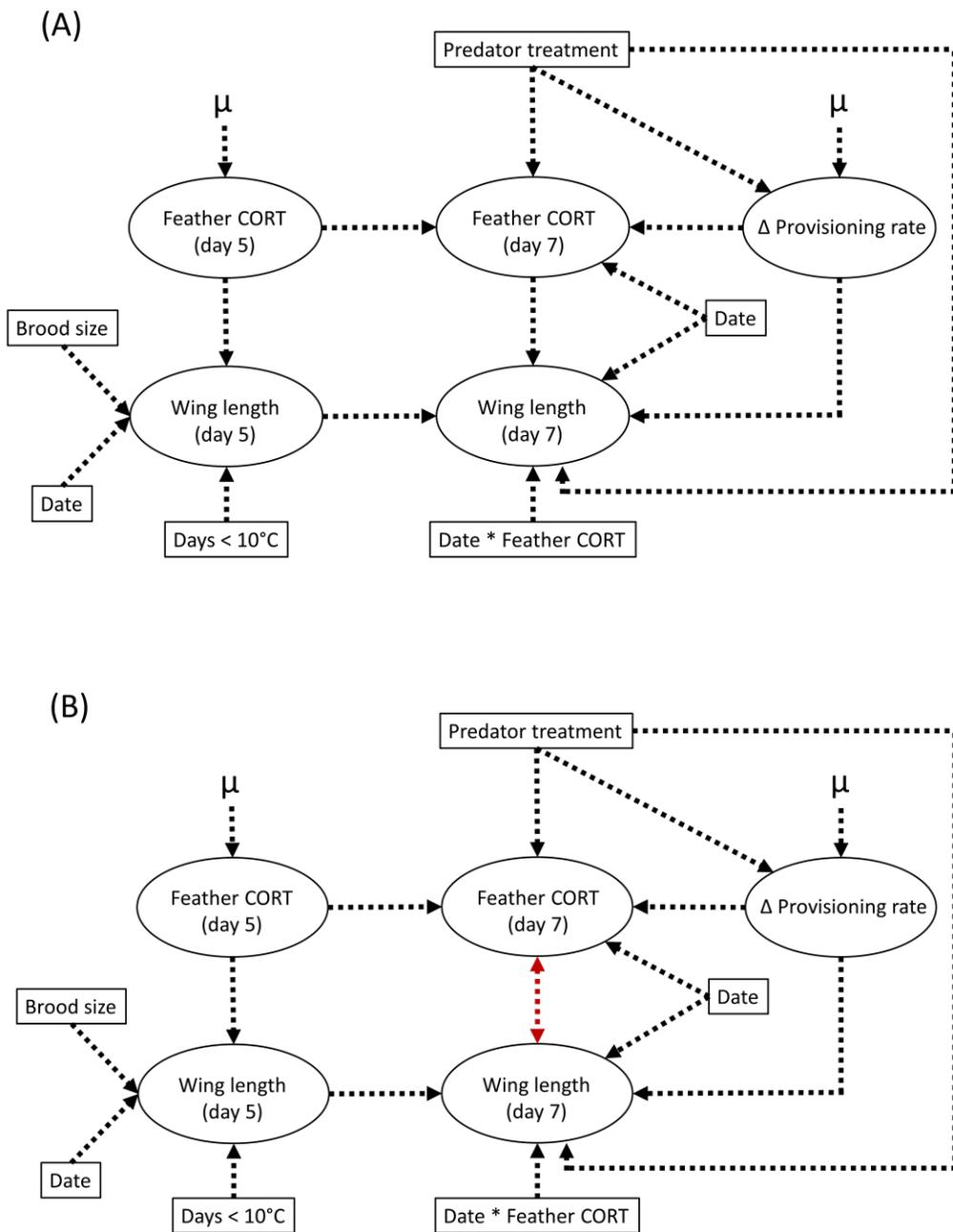
Model structure	d.f.	Fisher’s C	AIC	$\Delta$ AIC
<i>Causal model</i>				
Wing (5 d) $\sim$ date + temp + brood size + CORT (5 d)	<b>21</b>	<b>12.48</b>	<b>68.48</b>	<b>1.68</b>
Wing (7 d) $\sim$ wing (5 d) + CORT (7 d) + date + CORT (7 d) * date + $\Delta$ provisioning rate + treatment				
$\Delta$ Provisioning rate $\sim$ treatment				
CORT (7 d) $\sim$ CORT (5 d) + $\Delta$ provisioning rate + treatment + date				
<i>Correlational model</i>				
Wing (5 d) $\sim$ date + temp + brood size + CORT (5 d)	17	20.80	66.80	0.00
Wing (7 d) $\sim \sim$ CORT (7 d)				
Wing (7 d) $\sim$ wing (5 d) + date + $\Delta$ provisioning rate + treatment				
$\Delta$ Provisioning rate $\sim$ treatment				
CORT (7 d) $\sim$ CORT (5 d) + $\Delta$ provisioning rate + treatment + date				

**Table A2.2.** D-separation and AIC results for the causal wing path model (global and sub-models). The first model is the original a priori path model and represents the entire path structure. The following models indicate the changes made to create a sub-model with a (–) indicating path removal. The model highlighted in bold is the final model selected based on a combination of low AIC and Fisher’s C.

Model structure	d.f.	Fisher’s C	AIC	ΔAIC
Wing (5 d) ~ date + temp + brood size + CORT (5 d)	21	12.48	68.48	3.04
Wing (7 d) ~ wing (5 d) + CORT (7 d) + date + CORT (7 d) * date + Δ provisioning rate + treatment				
Δ Provisioning rate ~ treatment				
CORT (7 d) ~ CORT (5 d) + Δ provisioning rate + treatment + date				
Wing (5 d) ~ – brood size	22	13.62	69.14	3.70
Wing (5 d) ~ – CORT (5 d)	22	21.22	75.22	9.78
CORT (7 d) ~ – CORT (5 d)	22	15.92	69.92	4.48
Wing (5 d) ~ – CORT (5 d)	40	63.91	123.91	58.47
CORT (7 d) ~ – CORT (5 d)				
Wing (7 d) ~ – wing (5 d)	22	161.84	215.84	150.40
Wing (7 d) ~ – CORT (7 d) * date	24	26.40	76.40	10.96
Wing (7 d) ~ – CORT (7 d)	22	17.65	69.65	4.21
Wing (7 d) ~ – date	22	20.48	72.48	7.04

Model structure	d.f.	Fisher's C	AIC	$\Delta$ AIC
Wing (7 d) ~ - $\Delta$ provisioning rate	22	14.19	68.19	2.75
<b>Wing (7 d) ~ - <math>\Delta</math> provisioning rate - treatment</b>	<b>26</b>	<b>15.44</b>	<b>65.44</b>	<b>0.00</b>
CORT (7 d) ~ - $\Delta$ provisioning rate	22	26.14	80.14	14.70
Wing (7 d) ~ - treatment	26	27.17	77.17	11.73
CORT (7 d) ~ - $\Delta$ provisioning rate				
Wing (7 d) ~ - $\Delta$ provisioning rate - treatment	28	33.57	81.57	16.13
CORT (7 d) ~ - $\Delta$ provisioning rate				
CORT (7 d) ~ - treatment	24	17.18	69.18	3.74
Wing (7 d) ~ - treatment	28	18.33	66.33	0.89
CORT (7 d) ~ - treatment				
Wing (7 d) ~ - $\Delta$ provisioning rate - treatment	30	20.61	66.61	1.17
CORT (7 d) ~ - treatment				
Wing (7 d) ~ - $\Delta$ provisioning rate - treatment	36	55.59	103.59	38.15
$\Delta$ Provisioning rate ~ - treatment				
Wing (7 d) ~ - $\Delta$ provisioning rate - treatment	28	20.80	66.80	1.36
Wing (7 d) ~ ~ CORT (7 d)				

**Figure A2.1.** A priori path structures for the (A) causal and (B) correlational model with the difference in structure highlighted in red. The correlational model predicts that corticosterone and wing length are two separate responses to predation risk, whereas the causal model predicts that predation risk influences wing length with a corticosterone mediator. All arrows are dotted to represent that we did not predict the direction of the association.



### Appendix 3. Supplementary material for Chapter 5.

**Table A3.1.** Top models for clutch initiation date ranked by AIC prior to bootstrapping and model averaging. ‘Local temp’ and ‘Local precip’ refers to temperature and precipitation for the breeding site. Of the total 64 models, only those with Akaike weights that sum to  $\geq 0.99$  are displayed. Values below the model terms are the standardized  $\beta$  coefficients.

Winter precip	Stopover precip	Snow depth	Local temp	Local precip	df	AIC	$\Delta$ AIC	Akaike weight
0.26	–	–	–0.38	–	4	985.10	0.00	0.35
0.27	–	0.03	–0.38	–	5	986.69	1.59	0.16
0.28	–0.04	–	–0.39	–	5	986.71	1.61	0.16
0.26	–	–	–0.38	0.00	5	987.10	2.00	0.13
0.28	–0.02	0.02	–0.38	–	6	988.56	3.46	0.06
0.27	–	0.03	–0.37	0.02	6	988.60	3.50	0.06
0.28	–0.04	–	–0.39	0.01	6	988.68	3.58	0.06

**Table A3.2.** Top models for age at fledging ranked by AIC prior to bootstrapping and model averaging. ‘Local precip’ refers to precipitation recorded at the breeding site. Of the total 16 models, only those with Akaike weights that sum to  $\geq 0.99$  are displayed. Values below the model terms are the standardized  $\beta$  coefficients.

Stopover freeze days	Local precip	Clutch initiation date	Brood size	df	AIC	$\Delta$ AIC	Akaike weight
0.31	–	–0.18	–	4	328.72	0.00	0.23
0.31	–	–0.20	0.12	5	328.89	0.18	0.21
0.29	–0.09	–0.15	–	5	329.87	1.15	0.13
0.24	–0.15	–	0.11	4	330.24	1.52	0.11
0.29	–0.08	–0.17	–	6	330.24	1.53	0.11
0.27	–	–	0.09	3	330.84	2.12	0.08
0.24	–0.14	–	0.09	5	331.28	2.56	0.06
0.27	–	–	–	4	331.80	3.08	0.05
–	–0.20	–	0.09	3	335.29	6.57	0.01
–	–0.19	–	–	4	336.23	7.51	0.01

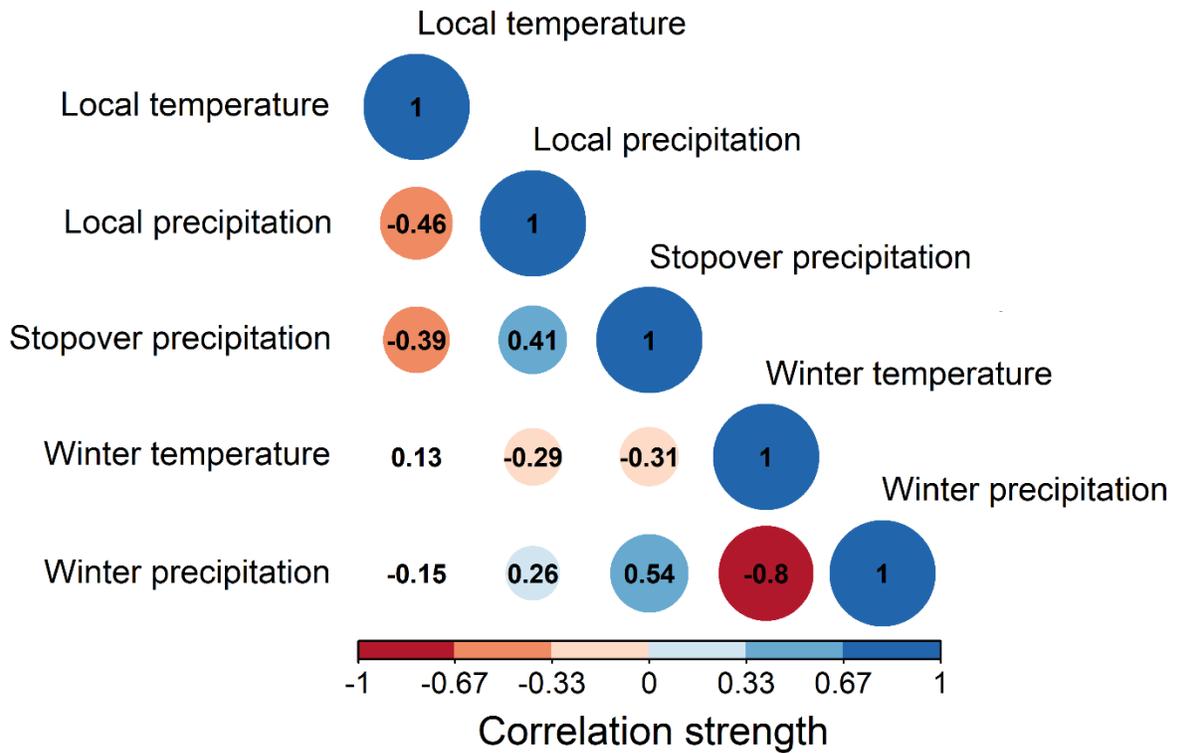
**Table A3.3.** Model outputs for clutch initiation and age at fledging depicting the mean bootstrapped standardized coefficients, standard error (SE), and 95% credible intervals (CI). Variable importance (VI) is the sum of the Akaike weights for all models that include that parameter. Significant predictors (95% CI does not include zero) are in bold.

	Mean $\beta$ -coefficient	SE	Lower CI	Upper CI	VI
<i>Clutch initiation</i>					
<b>Winter precipitation</b>	0.28	0.06	0.16	0.39	1.00
Stopover precipitation	-0.02	0.07	-0.17	0.07	0.30
Snow depth	0.02	0.04	-0.03	0.10	0.31
<b>Local temperature</b>	-0.38	0.06	-0.48	-0.27	1.00
Local precipitation	0.01	0.04	-0.04	0.09	0.27
<i>Age at fledging</i>					
<b>Stopover freeze days</b>	0.29	0.12	0.04	0.50	0.97
Local precipitation	-0.05	0.09	-0.23	0.02	0.43
Clutch initiation	-0.15	0.12	-0.36	0.01	0.68
Brood size	0.08	0.10	-0.02	0.27	0.44

**Table A3.4.** Annual sample sizes for the clutch initiation date and age at fledging analysis. Due to low sample size, 2007 and 2010 were removed from consideration for age at fledge. Predicted daily nest survival (DNS) and survival estimates ( $\pm$  SE) are for first nests only. Survival is based on a 24-day nesting cycle (first egg to fledge). The standard error was estimated by bootstrapping the predictions 1000 times.

Year	Clutch initiation (n)	Age at fledging (n)	DNS	Survival (%)
2003	14	8	0.987 $\pm$ 0.003	72.8 $\pm$ 3.7
2004	15	13	0.997 $\pm$ 0.002	93.6 $\pm$ 3.0
2005	45	24	0.993 $\pm$ 0.001	84.1 $\pm$ 1.8
2006	55	19	0.978 $\pm$ 0.001	58.8 $\pm$ 1.5
2007	19	0	0.492 $\pm$ 0.281	00.0 $\pm$ 2.5
2010	21	1	0.898 $\pm$ 0.002	07.7 $\pm$ 0.4
2011	25	3	0.950 $\pm$ 0.002	29.4 $\pm$ 1.4
2015	56	13	0.952 $\pm$ 0.001	30.9 $\pm$ 0.8
2016	53	14	0.956 $\pm$ 0.001	34.4 $\pm$ 0.9
2017	35	10	0.968 $\pm$ 0.001	45.6 $\pm$ 1.3
2018	32	6	0.947 $\pm$ 0.001	27.3 $\pm$ 0.7
2019	12	7	0.991 $\pm$ 0.002	80.6 $\pm$ 3.7
Total	382	118	0.967 $\pm$ 0.002	44.2 $\pm$ 1.2

**Figure A3.1.** Pearson’s correlation matrix among the candidate climate variables for clutch initiation date. Correlations were considered significant when  $P < 0.005$  to correct for multiple comparisons. Larger, darker circles indicate stronger correlations, while correlations without a circle are non-significant.



**Figure A3.2.** Pearson’s correlation matrix among the candidate climate variables for age at fledging. Clutch initiation was included to test for potential multi-collinearity with the climate variables. Larger, darker circles indicate stronger correlations, while correlations without a circle are non-significant.

