

**SONGBIRD INCUBATION DILEMMAS IN THE ALPINE: MANAGING  
PARENT-OFFSPRING TRADE-OFFS IN A VARIABLE THERMAL  
ENVIRONMENT**

by

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## ABSTRACT

Small-bodied bird species exhibiting single-sex incubation must expend energy to create a buffered thermal environment for their eggs, while also meeting their own energetic requirements. The resultant trade-off between incubation and foraging is intensified in cold environments like the alpine, where energetic constraints are high. Ambient temperature influences incubation behaviour, with variable relationships across species, habitats and populations. I examined incubation rhythms of an alpine population of Horned Larks (*Eremophila alpestris*) in British Columbia across four years with different thermal regimes (2005 = moderate, 2006 = warm, 2010 = cold overnight, 2011 = cold during day) to determine whether incubating larks exhibited variable relationships between attentivity and temperature under different thermal conditions and how this related to management of the parent-offspring trade-off.

Early in the morning, females had to leave their nest to forage to reduce their energy deficit following 7 h of night incubation in near freezing conditions. Since temperatures at this time were still  $< 5^{\circ}\text{C}$ , embryos were at a high risk of potentially lethal chilling when females left the nest. From 06:00 to 08:00, incubating larks reduced attentiveness to 75% from 94% overnight. However, during this time period, females in 2010 spent more time off the nest as temperatures warmed than in other years. Throughout the study, adults took occasional “extended recesses” (incubation breaks lasting  $\geq 59$  min). These recesses were longer and more frequent in cold years, particularly 2011, and appeared to be largely related to harsh weather events. There are potential fitness consequences associated with these extended recesses, as egg hatching rate dropped to 81% in 2011 from 94% in the other years, and the incubation period was lengthened in two nests that engaged in multiple extended recesses.

Overall, this work demonstrated that incubating larks favour themselves when coping with difficult thermal conditions. Lark embryos appeared more tolerant to long periods of considerable cooling than previously thought, although, the reduced hatching rate in one cold year suggested there may be a limit to their cold tolerance.

## **PREFACE**

This research was conducted in collaboration with my supervisors, Drs. Kathy Martin and Jill Jankowski (UBC) as well as Dr. Alaine Camfield (Environment Canada). I carried out data collection in 2010 and 2011 and Dr. Camfield provided data from 2005 and 2006. I have conducted all analyses and written both manuscripts with input from my co-authors.

The protocols outlined in this thesis have been approved by the University of British Columbia Animal Care Committee (AUP numbers A07-0048 and A10-0128). Chapters 2 and 3 have been prepared as individual manuscripts, versions of which will be submitted for publication.

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## CHAPTER 1 – GENERAL INTRODUCTION AND THESIS OVERVIEW

### INTRODUCTION

Extreme and stochastic weather coupled with a short growing season make the alpine a challenging place to live for vertebrate homeotherms (Martin 2001). Alpine wildlife are faced with daily temperature fluctuations of up to 40°C, high winds, high UVB light, prolonged snow cover and year-round storms (Martin 2001, Camfield and Martin 2009). Some wildlife, known as alpine specialists, live and/or breed exclusively at high elevation, while alpine generalist species breed across a range of elevations. In order to be successful, these high elevation species and populations are equipped with a suite of morphological, physiological and/or behavioural adaptations to cope with the harsh and unpredictable conditions of their environment (Martin and Wiebe 2004).

Some alpine populations adopt different life history strategies than their lowland counterparts. Specifically, with increasing elevation, vertebrates tend to shift from a high reproductive life history strategy to a high survival life history strategy (Dobson 1992, Sandercock et al 2005, Bears et al 2009). This pattern of reduced fecundity and increased adult survival at high elevation has been observed among related species of Ptarmigan (*Lagopus* spp.; Sandercock et al 2005, Wilson and Martin 2011) and in passerines such as Savannah Sparrows (*Passerculus sandwichensis*; Martin et al 2009) and Dark-eyed Juncos (*Junco hyemalis*; Bears et al 2009). Camfield et al (2010) conducted the first demographic study comparing life history strategies of two subspecies of Horned Larks (*Eremophila alpestris*) at different elevations. The high elevation population (the same population on which I have conducted my study) adopted this “survivor” life history strategy, with high apparent adult survival and a larger body size; however, unexpectedly, fecundity was also higher than at low elevation (Camfield et al 2010). During their study, Camfield et al (2010) found that 35% of nests, on average, were depredated at high elevation and there was a 35% chance that a nest would fledge at least one chick (compared to a 45% nest predation and 23% nest survival rate at the low elevation site). In my two years of study, however, nest predation rates were much higher and overall nest survival was much lower (Table 1.1). Consequently, the high fecundity Camfield and others observed may not occur in every year. The combination of these studies

demonstrate the unpredictable nature of alpine systems; not all years may be successful for breeding (Martin et al 2000, Bears et al 2009) and a high survival strategy is likely important for long-term viability. This strategy, evident in demographic studies, may also be reflected in the behaviour of breeding adults.

Adult survival affects how parent-offspring trade-offs are managed. If adult mortality is low, there can be greater fitness benefits to further reducing the risk of adult mortality than increasing investment in reproduction (Martin 2002, Wilson and Martin 2010). For birds, incubation can be energetically expensive (Williams 1996). Parent and offspring needs are often in direct conflict, as incubation and foraging are mutually exclusive behaviours (Williams 1996, Conway and Martin 2000a). The resultant trade-off is intensified in cold environments like the alpine, where energetic constraints are high (Carey 2002, Creswell et al 2004). How a bird manages this trade-off in a cold and unpredictable environment such as the alpine should relate to their value of future versus current reproduction (Ghalambor and Martin 2001, Martin 2002, Tieleman et al 2004). The high survival life history strategy characteristic of high elevation populations suggests an alpine bird would shift investment towards self-maintenance (rather than towards reproduction) when faced with severe energetic constraints.

Behavioural responses to changing energetic constraints may be one area to observe the shift from investment in reproduction towards self-maintenance. Incubation behaviour is affected by ambient temperature (Conway and Martin 2000a), and how an incubating parent alters behaviour with changing temperature should reflect how they manage this trade-off. Camfield and Martin (2009) found a non-linear relationship between time spent incubating and ambient temperature in alpine Horned Larks; larks decreased time on the nest as temperatures warmed to 12-13°C, at which point they slightly increased time on the nest as temperatures continued to warm. Incubating larks generally maintained high attentivity and appeared to favour their offspring at cold temperatures; however, there was substantial variation in the response Camfield and Martin reported, particularly at lower temperatures. This pattern seemed to warrant an examination of finer-scale responses, during an ecologically relevant time period, to

determine what might drive this variation, and whether parents always favour their eggs in energetically stressful conditions.

My objectives for this study were to gain further understanding of the behavioural mechanisms an alpine-breeding songbird uses to manage the parent-offspring trade-off experienced during incubation. Motivated by the variation observed by Camfield and Martin, I examined how the relationship between ambient temperature and incubation rhythms differed in this population when faced with variable environmental conditions. Focusing on the period of potentially greatest parent-offspring conflict (06:00-08:00), I determined 1) whether Horned Larks breeding in an alpine habitat displayed variable patterns in how they altered incubation behaviour in relation to ambient temperature among years with different thermal regimes and 2) what their behaviours under different thermal conditions revealed about their management of this parent-offspring trade-off. Specifically, were they responding to different thermal regimes or were they compensating for or anticipating critical thermal conditions?

## **STUDY SPECIES**

Horned Larks (*Eremophila alpestris*) are widely distributed across North America and Eurasia and are found in isolated populations in Columbia and Morocco (Beason 1995). They are small (25-40 g), ground-nesting passerines (Trost 1972). Body size varies geographically; the population breeding on Hudson Bay Mountain, BC is relatively large (on average, females are 34 g and males 35 g; Camfield et al 2010). There are 21 subspecies in North America, and their distributions range in elevation from sea level to 4000 m (Beason 1995). They prefer open areas with low lying and sparse vegetation; throughout their range, larks occupy diverse habitats such as shortgrass prairie, deserts, brushy flats, agricultural fields and alpine tundra (Beason 1995).

Their diet consists primarily of seeds in the winter, but adults are largely insectivorous during the breeding season (Beason 1995). This is especially prominent in high altitude and high latitude environments where individuals demonstrate high feeding rates associated with arthropod fallout (Beason 1995, Edwards and Banko 1976).

Horned Larks are socially monogamous and territorial, with breeding pairs uniformly dispersed within habitats (Beason 1995). Eggs are laid one per day until clutch completion, which is typically 2-5 eggs (Beason 1995). Incubation begins when the penultimate egg is laid and is performed solely by the female. Incubation typically lasts 12 days, followed by a 9 day nestling period in which both parents tend to their young (Camfield and Martin 2009, Beason 1995). The alpine population I studied exhibits high survival of both adults and juveniles and has strong natal philopatry.

## **STUDY AREA**

I studied a population of Horned Larks on Hudson Bay Mountain near Smithers, British Columbia, Canada (52°N, 127°W). This population breeds on a 4-km<sup>2</sup> area of alpine tundra, ranging from 1500-1850 m above sea level (Figure 1.1). Birds breeding on this site must cope with fluctuating daily temperatures, dropping near or below freezing every night and sometimes reaching over 40°C during the day (Camfield and Martin 2009). High winds, thick fog, and storms are common during the breeding season. The structurally simple tundra provides limited protection for nests (Martin and Wiebe 2004). Other bird species breeding on the tundra include Savannah Sparrows (*Passerculus sandwichensis*), American Pipits (*Anthus rubescens*), Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*Lagopus muta*). Nest predation was high throughout much of this study, largely due to Red Fox (*Vulpes vulpes*). Timing of snowmelt varies annually, and can occur late into the breeding season (snow persists through most of June). Camfield et al (2010) reported a breeding season of 38.5 days for Horned Larks, and a mean clutch initiation date of 31-May. However, annual variation in snowmelt leads to annual variation in clutch initiation dates (Table 1.1).

## **THESIS OVERVIEW**

Camfield and Martin (2009) described population-level patterns for Horned Lark incubation rhythms in relation to temperature on Hudson Bay Mountain, whereby parents invested more in their offspring at lower temperatures. The variation in these relationships, however, was large, particularly at low temperatures, which may indicate that adults do not always favour their eggs when it is cold. In Chapter 2, I examined variation in the relationship between incubation rhythms and ambient temperature among

four years representing different thermal regimes. I collected data in 2010 and 2011, while 2005 and 2006 data were provided by A.F. Camfield (Camfield 2008, Camfield and Martin 2009). Using linear mixed effects models, I compared time on the nest, mean on-bout duration, mean recess duration and recess frequency with ambient temperature during the early morning (06:00-08:00) across the 2005, 2006, 2010 and 2011 breeding seasons. At this time, females had spent over 7 h incubating in near freezing conditions, and so needed to leave their nest to forage; however, as temperatures were still  $< 5^{\circ}\text{C}$ , embryos were at a high risk of chilling below the physiological zero temperature during incubation recesses. Thus, the parent-offspring trade-off was heightened during this time period. In 2010, a year with cold overnight temperatures, birds spent more time off the nest as ambient temperature increased than in other years. I have demonstrated annual variation within a population in how incubation behaviour was influenced by ambient temperature. Additionally, when faced with greater energetic constraints, larks shifted investment in favour of themselves rather than their clutch.

During the collection of these incubation rhythm data, I found that daytime incubation recesses were, on average, approximately 11 min; however, I observed several instances throughout the study where females took recesses significantly longer than this, occasionally lasting several hours. These extended recesses appeared to coincide with bad weather and, as such, often left eggs exposed to severe ambient conditions for considerable periods. I wanted to determine how important these extended recesses were in the incubation strategy of alpine Horned Larks, what might be driving this behaviour and whether it was associated with any apparent ecological or fitness consequences. In Chapter 3, I examined the prevalence of extended incubation recesses (recesses lasting  $\geq 59$  min) in this population of Horned Larks. Extended recesses were generally rare, comprising  $< 1\%$  of the total number of recesses taken. However, extended recesses occurred in all years and were taken by multiple individuals across several days. Larks took more, and longer extended recesses in 2010 and 2011, the two coldest years of the study. Extended recesses tended to occur during bad weather events, seemingly reflecting the adults need to take care of themselves during energetically stressful situations. There were potential fitness consequences resulting from these extended recesses; incubation period appeared to be lengthened in two nests that took multiple, long breaks and hatch



rate (embryo viability) dropped from 94% in the first three years to 81% in 2011. I have shown that lark embryos can tolerate considerable cooling, but within limits.

Chapter 4 summarizes the conclusions of the two data chapters and places these results in a broader context. I also suggest gaps in existing knowledge and further research needed.

Table 1.1 – Vital rates of Horned Larks breeding on Hudson Bay Mountain across four years. Results are presented as mean  $\pm$  SE or proportions and sample sizes are in brackets. Julian dates are based on 1 = 1 January. All estimates are based on the number of nests within that year for which data were available for that particular parameter, and include first nests, renests and second broods.

Demographic	Year			
	2005	2006	2010	2011
Clutch initiation date	148 $\pm$ 0.89 (33)	152 $\pm$ 0.91 (43)	153 $\pm$ 0.33 (12)	154 $\pm$ 1.01 (15)
Clutch size	3.69 $\pm$ 0.10 (52)	3.61 $\pm$ 0.08 (80)	3.79 $\pm$ 0.10 (33)	3.83 $\pm$ 0.10 (35)
Prop eggs hatched <sup>a</sup>	0.93 $\pm$ 0.02 (42)	0.94 $\pm$ 0.02 (54)	0.92 $\pm$ 0.05 (22)	0.81 $\pm$ 0.05 (11)
Prop chicks fledged <sup>b</sup>	0.97 $\pm$ 0.02 (30)	0.96 $\pm$ 0.02 (37)	1.00 (8)	1.00 (7)
Prop nests fledged	0.54 (57)	0.46 (81)	0.24 (34)	0.18 (38)
Prop nests abandoned	0.05 (57)	0.04 (81)	0.03 (34)	0.13 (38)
Prop nests predated	0.40 (57)	0.51 (81)	0.74 (34)	0.68 (38)
Nest survival <sup>c</sup>	0.42 (56)	0.37 (81)	0.27 (36)	0.18 (37)

<sup>a</sup> Proportion of eggs hatched was calculated as number of nestlings/clutch size based on the number of nests that successfully hatched at least 1 egg.

<sup>b</sup> Proportion of chicks fledged was calculated as number of fledged chicks/number of hatched nestlings based on the number of nests that successfully fledged at least 1 chick.

<sup>c</sup> Nest survival is the probability that a nest fledged at least one nestling and was estimated following the method described in Mayfield (1975).

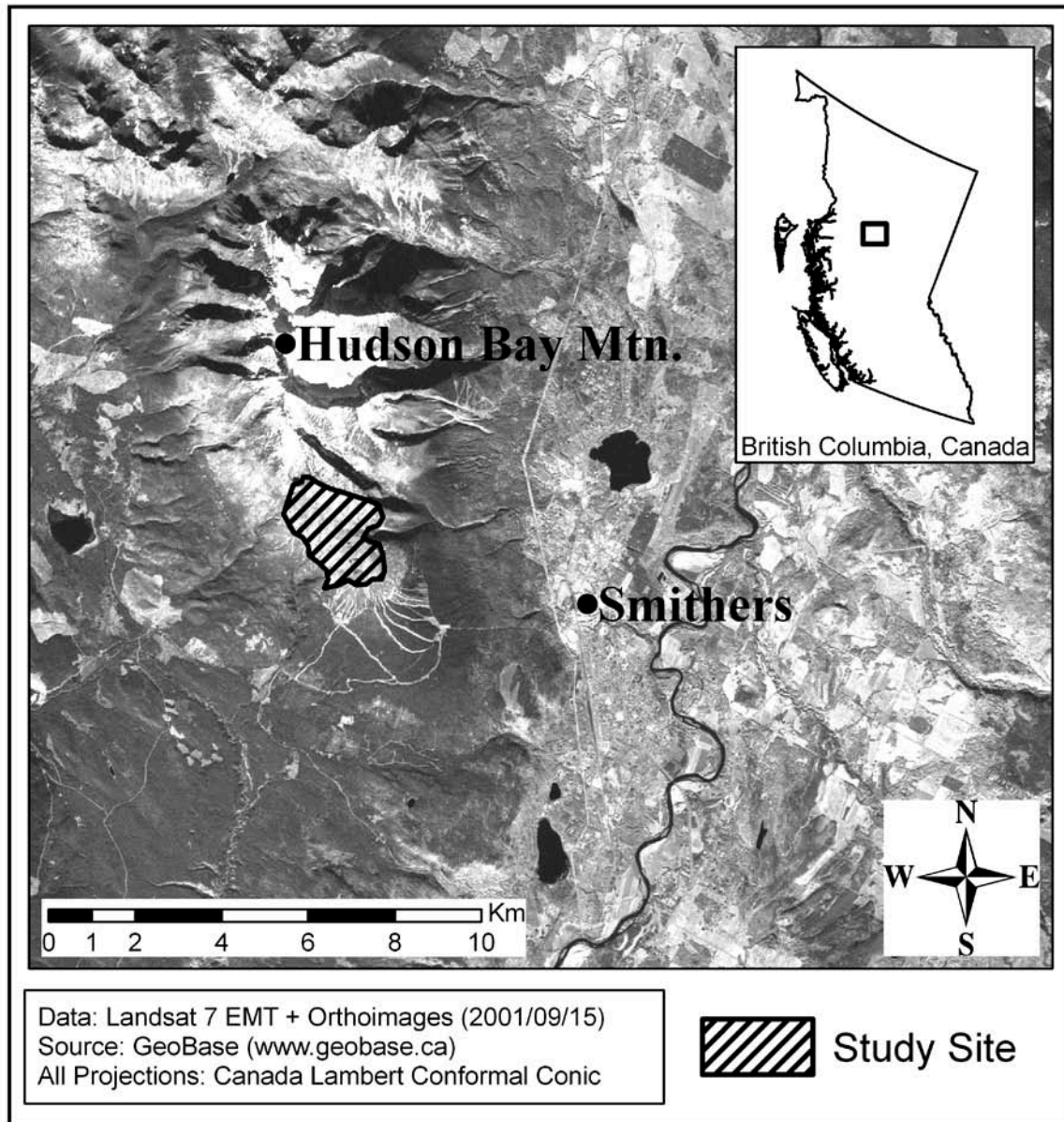


Figure 1.1 – Study area for Horned Larks located on Hudson Bay Mountain, Smithers, British Columbia, Canada (Map prepared by Matt Tomlinson, reprinted from Camfield 2008 with permission from A. Camfield and M. Tomlinson).

## CHAPTER 2: EFFECT OF THERMAL REGIME ON INCUBATION RHYTHMS OF AN ALPINE BREEDING SONGBIRD

### INTRODUCTION

Incubation is an energetically expensive phase of avian reproduction (Tatner and Bryant 1993, Williams 1996), during which incubating adults must expend energy to create a buffered thermal environment for their eggs while also meeting their own somatic requirements (White and Kinney 1974, Conway and Martin 2000a). In small-bodied species exhibiting single-sex intermittent incubation, this can lead to a trade-off for the parent between incubating to ensure embryo viability and foraging for self-maintenance (Williams 1996, Conway and Martin 2000a, b). This trade-off is intensified in cold environments such as alpine habitats because as ambient temperatures approach extreme highs or lows, both the rate of egg warming or cooling and the metabolic rate of the parent increase (Drent 1975, Haftorn 1988, Martin and Wiebe 2004). It is assumed that alpine songbirds need to maintain the same thermal environment for their eggs as birds in more moderate habitats, but must do so under more challenging conditions (Carey 2002, Creswell et al 2004). As a result, alpine birds must work harder to resolve this trade-off and ensure successful reproduction (Martin and Wiebe 2004).

Avian embryos require a particular range of temperatures in order to develop (Webb 1987, Haftorn 1988). When defining this range, thermal tolerance of Domestic Fowl (*Gallus gallus domesticus*) embryos is the standard model used: eggs must be maintained between the physiological zero temperature (PZT, generally considered 26°C) and the upper lethal temperature (ULT, generally considered 40.5°C) and optimal embryo development occurs at 36-38°C (Lundy 1969, Drent 1975). However, the universal application of these temperatures may not be appropriate as embryo thermal tolerance likely varies across species (Webb 1987, Jia et al 2010). Field studies of wild birds suggest that these assumed optimal conditions are rarely achieved in nature, where mean egg temperatures are usually 32-35°C irrespective of incubation strategy or body size (Williams 1996, Reid et al 2002). In temperate ecosystems, embryos must be maintained at temperatures that are typically higher than ambient conditions. Periodic cooling during

incubation can reduce embryonic growth efficiency and produce lower quality nestlings (Olson et al 2006, Ardia et al 2010). From the perspective of the embryo, adults should increase attentivity at lower temperatures to maximize survival of their clutch. However, the energetic requirements of incubating parents also change with ambient temperature. As homeotherms, birds have a thermoneutral zone (TNZ) delineated by an upper and lower critical temperature, and when ambient temperature falls outside this zone, metabolic rates increase (Webster et al 1993). The TNZ varies across species and may be narrower in incubating birds (Conway and Martin 2000a). In small birds, the energy requirements of an incubating adult can increase substantially below the lower critical temperature (Biebach 1984, Haftorn and Reinertsen 1985). Consequently, at low ambient temperatures, adults may need to reduce nest attentivity to compensate for their increased metabolic requirements. The conflicting needs of adults and embryos, and the fact that foraging and incubating are mutually exclusive, means that parents may need to adjust their behaviour in order to maximize fitness (Jones 1989), shifting investment either towards self-maintenance or egg survival (Drent 1975). These conflicts should be most evident in cold ambient conditions such as in alpine or arctic habitats (Carey 2002), where variation in attentivity is expected to have consequences for survival probability.

Given the potential, and conflicting, effects on both embryos and parents, ambient temperature should influence incubation behaviour. A relationship between incubation rhythms and temperature has been demonstrated in many species across a variety of habitats (Conway and Martin 2000a, Londono et al 2008, Camfield and Martin 2009, Kovarik et al 2009). Conway and Martin (2000a) proposed a nonlinear framework for how incubation rhythms of small-bodied intermittent incubators should change with ambient temperature. They suggested on-bout and recess duration should decrease (to minimum bout duration) as temperatures cool below the zone of thermal tolerance for embryos and adults, and similarly decrease as temperatures warm above this zone (up until a point where birds no longer leave the nest). Data from Orange-crowned Warblers (*Oreothlypis celata*) in Arizona supported their hypothesis (Conway and Martin 2000a). However, Camfield and Martin (2009) found that recess duration of Horned Larks (*Eremophila alpestris*) incubating on Hudson Bay Mountain near Smithers, BC was not

related to ambient temperature and that the relationship between temperature and on-bout duration was non-linear; on-bout duration decreased as temperatures warmed to 12-13°C, and then increased above that point. In their study of an alpine population of Meadow Pipits (*Anthus pratensis*) in the Czech Republic, Kovarik et al (2009) also found no relationship between recess duration and temperature, though on-bout duration followed a pattern similar to what Conway and Martin observed. These inconsistencies in the reported relationship between incubation rhythms and ambient temperature point to variability in the pattern across species, habitats and populations. The error bars in these relationships suggested that there might be variability within populations as well. A single framework for assessing the relationship between attentivity and temperature is likely inappropriate, as there are probably many factors relating to life history and environment that influence how incubating parents decide to spend their time.

A potential source of variation in this relationship is the thermal environment in which birds are incubating. The alpine breeding Horned Larks and Meadows Pipits would have experienced much colder, harsher and more variable conditions than the Orange-crowned Warblers in Arizona. These different environmental conditions could have accounted for the conflicting results, as how a bird responds to temperature may depend on the range of temperatures to which it is exposed. Furthermore, fluctuating thermal regimes in an environment could lead to within-population variability. Several studies show that incubation behaviour changes as adult energetic constraints are alleviated or heightened by experimental heating or cooling. In response to nest heating during incubation, both Pectoral Sandpipers (*Calidris melanotos*) and Tree Swallows (*Tachycineta bicolor*) increased nest attentiveness, while European Starlings (*Sturnus vulgaris*) increased fledgling success (Creswell et al 2004, Ardia et al 2009, Reid et al 2000). Tree Swallows also responded to experimental cooling; they reduced incubation time and as a result, egg temperatures were lower (Ardia et al 2010). Similarly, Zebra Finches (*Taeniopygia guttata*) had reduced egg temperatures when incubating under colder conditions (Nord et al 2010). Therefore, if a population is exposed to different thermal regimes or weather, particularly in an environment that regularly experiences a

wide range of temperatures, adults may manage their time on and off the nest differently as the temperature changes.

I examined the relationship between incubation attentivity and ambient temperature in a population of alpine breeding Horned Larks across four years with variable thermal regimes. Time of day is known to influence attentivity (Conway and Martin 2000a, Kovarik et al 2009), and nights were consistently near or below freezing for > 7 h, thus I focused on the early morning period (06:00-08:00), when the trade-off between adult and embryonic needs is likely heightened. In colder years (due to greater thermal stress overall), adults should face stronger energetic trade-offs between their clutch and their self-maintenance. If thermal regime does influence nest attentivity of incubating Horned Larks, I expected that from 06:00-08:00, the relationship between time on the nest (attentivity) and ambient temperature would differ among years where ambient temperature varied. Increased time off the nest appears to reflect adults favouring their own somatic needs (Voss et al 2006, Ardia et al 2009). Therefore, if adults favoured their self-maintenance in colder ambient conditions, I expected these different relationships could be reflected in a steeper slope (reduced attentivity as the risk of the embryo cooling decreases), a lower y-intercept (reduced attentivity overall) or a combination of the two, in colder years (Figure 2.1). Any of these relationships would increase time off the nest, indicating more time spent in self-maintenance. Conversely, if adults favoured their embryos under colder conditions, I predicted a shallower slope, a higher y-intercept or both in colder years. Adults are able to alter time on the nest through a combination of changes to on-bout duration, recess duration and/or recess frequency. Consequently, if incubating larks did display different attentivity-temperature relationships among years, I expected to also see among year variation in the relationships of one or more of these response variables with ambient temperature, as reflected in different slopes and/or y-intercepts.

## **METHODS**

### **Study species and study site**

Horned Larks (*Eremophila alpestris*) are small-bodied (25-40 g), ground-nesting passerines, exhibiting female-only intermittent incubation with no evidence for male incubation feeding (Beason 1995). Larks are widely distributed in North America, occupying open habitats with low, sparse vegetation, such as shortgrass prairie, deserts and alpine tundra (Beason 1995). I studied a population of Horned Larks on Hudson Bay Mountain near Smithers, British Columbia, Canada (52°N, 127°W) during the 2010 and 2011 breeding seasons. Two additional years of data (2005 and 2006) from a previous study on the same population at the same site were also available for analysis (Camfield 2008, Camfield and Martin 2009). The study site is approximately 4 km<sup>2</sup> with an elevation range of 1500-1850 m above sea level. Daily temperatures can fluctuate by 40°C and storms and below freezing temperatures can occur throughout the breeding season (Camfield and Martin 2009).

### **Data collection**

I searched for and monitored Horned Lark nests during the 2010 and 2011 breeding seasons (May through early August). I located nests by searching known lark territories or appropriate habitat, observing adults approaching or leaving their nest or by flushing incubating adults. Once found, I monitored nests every 3-5 days, more frequently near hatch and fledge dates, and recorded breeding demographics.

I used temperature data loggers (HOBO Pro Series, #H08-031-08, Onset Computer Co., Pocasset, MA, USA) to monitor incubation rhythms. The data loggers were placed within 2 m of the nest with the external temperature probe of the logger inserted into the nest cup. Simultaneous temperature recordings of ambient and nest temperatures (°C) were taken every 30 s, 24 h/day until the nest hatched or failed. I used temperature fluctuations in the nest to infer when the incubating female left and returned to her clutch. Behavioural observations were conducted at multiple nests over a range of temperatures to verify that temperature fluctuations recorded by the data loggers coincided with actual recesses and on-bouts (Camfield 2008, ECM unpublished data). As Horned Larks are



ground nesting songbirds, ambient temperature on the ground most closely approximates temperatures experienced at the nest; therefore, data loggers were placed in areas with similar aspect and protection from the wind as the nest. The probes did not touch the eggs, so I did not measure the actual egg/embryo temperatures. If nests were located after incubation was initiated, I calculated clutch initiation date by backdating from hatch. I used the following time intervals to calculate clutch initiation date: egg laying = 1 egg laid per day (thus, clutch size = duration of laying period), incubation = 12 days. I followed the protocol outlined in Camfield and Martin (2009), thus data collection was comparable in 2005 and 2006. All protocols were approved by the University of British Columbia Animal Care Committee (AUP numbers A07-0048 and A10-0128).

A weather station on the field site recorded daily temperature, precipitation, and wind speed throughout all breeding seasons.

### **Data analysis**

To classify years relative to one another in terms of thermal regime I used a method of cumulative daily temperature deviations following Myers and Pitelka (1979). For all four years, I had daily temperature readings for the duration of the breeding season (14-May to 22-July); I calculated a mean daily ambient temperature within each year as well as among years. The deviation from this daily mean within each year was then calculated by subtracting the mean for each day within that year from the among-year mean for that day. I then summed this deviation across the breeding season within each year to come up with a cumulative deviation from the “normal” temperature regime for these four years. This method allowed me to compare temperature regimes throughout the study to determine the extent to which breeding birds were exposed to variable annual conditions.

Following Camfield and Martin (2009), I used the program Rhythm (1.0; Cooper and Mills 2005) to select incubation recesses from temperature recordings in the nest. I considered an observation to be a recess if the temperature inside the nest dropped by more than 3°C for at least 3 min. I visually inspected the data using Raven Pro (1.3),

allowing me to confirm the recesses selected by Rhythm as well as manually select any recesses that Rhythm had not chosen but were also off-bouts (for example, a steep temperature drop lasting slightly less than 3 min). From these data, I calculated the initiation and duration of each recess and on-bout. The day was divided into 12, 2-h periods and for each period I calculated the total number of minutes the female was on the nest, the number of recesses and the mean duration of recesses and on-bouts. Recesses and on-bouts are not necessarily bound by the 2-h periods, and some observations were >120 min. If an activity (on-bout or recess) extended across multiple 2-h periods, I used the total time for the activity when calculating period means. This is particularly relevant for on-bouts in the 06:00-08:00 period because overnight incubation (which typically began between 20:00 and 23:00) sometimes continued into (and beyond) this time period, thus some mean values included overnight on-bouts.

In all years, some individuals took one or several “extended recesses”, long off-bouts lasting greater than 59 min (~1% of 2-h periods across the four years of study had mean recess duration  $\geq 59$  min). These extended recesses appeared to be in response to severe weather conditions (see Chapter 3) and added variance to the typical response to ambient temperature. Since I was interested in how individuals would normally respond to temperature, I excluded these data from this analysis, but consider the context of these long off-bouts in separate analyses (see Chapter 3).

To assess the relationship between attentivity and ambient temperature and how it varied across years, I used linear mixed effects models with a Restricted Maximum Likelihood (REML) method of parameter estimation. Mixed effects models allowed nest to be treated as a random effect, avoiding pseudoreplication as nests were sampled repeatedly over time (Pinheiro and Bates 2000). Although non-linear models may be the most appropriate way to view the relationship between incubation rhythms and temperature across a wide temperature gradient (Conway and Martin 2000a, Camfield and Martin 2009), I chose a linear model because the temperatures experienced between 06:00-08:00 were largely within the temperature range where Camfield and Martin (2009) observed a linear relationship (see Results). Visual inspection of the data also

suggested that a linear model was appropriate. For this analysis, I focused on the 06:00-08:00 period because it encompassed the most likely time period when a trade-off between self-care and care for offspring should occur or would be heightened. At this time ambient temperature was only slightly warmer than it was overnight (Figure 2.2a) and therefore the risk of eggs cooling was quite high; however, adults were likely energetically stressed after having just spent > 7 h in overnight incubation (Figure 2.2b).

Total time (min) on the nest from 06:00-08:00 was modeled as the response variable with ambient temperature at the nest as a fixed effect and nest as a random factor. Year was also a fixed factor and a temperature  $\times$  year interaction was included to determine if the relationship between time on the nest and temperature varied with year. These models also controlled for several other factors that can influence songbird incubation behaviour, including: clutch size, date, incubation day, percent vegetation cover at the nest, nest orientation, aspect of the nest location, and proportion of time spent in overnight incubation from 20:00 – 05:59 (included as fixed effects; Smith 1989, Wiebe and Martin 1998, Conway and Martin 2000b, Joyce et al. 2001, Wheelwright and Beagley 2005, Zimmerling and Ankney 2005, Kovarik et al 2009). Vegetation cover and overnight attentivity are proportion data and were therefore arcsine square root transformed (Zar 1999). Nest orientation and aspect were assigned to 1 of 4 categories based on their deviation from north (N, E, S or W).

To determine whether other components of incubation rhythms varied with ambient temperature, I examined relationships for mean on-bout duration, mean recess duration and recess frequency with ambient temperature, using the same fixed and random effects as above. On-bout and recess duration were log-transformed to achieve normality and modeled using the same framework as time on the nest. Recess frequency was modeled using a generalized linear mixed effects model with a Poisson distribution (Crawley 2007). Statistical analyses were performed using the package R (R Version 2.10.1; R Development Core Team 2009). Means are presented  $\pm$  SE.

## RESULTS

Incubation rhythms were recorded at 86 nests across the four years (2005: 16 nests, 2006: 38 nests, 2010: 16 nests, 2011: 16 nests). From 06:00-08:00, incubating females spent an average of  $89.71 \pm 0.66$  min of the total 120 min (75% of their time) on the nest. On average (including some overnight incubation), on-bouts were  $57.72 \pm 6.15$  min long. Females took  $4.13 \pm 0.09$  recesses, which lasted  $7.68 \pm 0.27$  min each. The proportion of time spent on the nest (attentivity) varied with time of day (Figure 2.2b). Despite variable overnight temperatures (means range from  $0.25 - 4.76^{\circ}\text{C}$ ), overnight attentivity was consistently high among years (ranging from 93 – 95%), while attentivity throughout the day varied across years (Figure 2.2b). Ambient temperatures experienced by the birds from 06:00-08:00 differed among years, 2010 was on average  $> 4^{\circ}\text{C}$  colder than 2005 and 2006 and  $> 2^{\circ}\text{C}$  colder than 2011 (Table 2.1). Additionally, the temperature ranges recorded at this time were narrower in 2010 ( $> 13^{\circ}\text{C}$ ) and 2011 ( $> 7^{\circ}\text{C}$ ) than 2005 ( $> 20^{\circ}\text{C}$ ) and 2006 ( $> 17^{\circ}\text{C}$ ; Table 2.1).

### Annual thermal regimes

The four years of this study each represented different thermal regimes. Cumulative temperature deviations from the daily average across the four years revealed that 2005 was a moderate year, 2006 from early June onward was much warmer than other three years, while 2010 and 2011 were generally much colder (Figure 2.3). Furthermore, the two colder years differed in what time of day was cold; 2010 was significantly colder overnight and in the early morning than the other three years while 2011 had comparable overnight temperatures to 2005 and 2006 but did not warm up during the day and had lower mid-day temperatures than 2010 (Figure 2.2a).

### Time on nest and ambient temperature

Time on the nest from 06:00-08:00 exhibited a negative linear relationship with ambient temperature; incubating Horned Larks decreased time on the nest as ambient temperature increased (Figure 2.4a). This relationship differed in one year of the study; 2010 had a significantly steeper slope than the other years (Table 2.2, Figure 2.4a). Time on the nest also varied with proportion of time spent incubating overnight (as expected

when measuring two periods close in time); birds spent more time on the nest from 06:00-08:00 when they spent more time incubating overnight (Table 2.2, Figure 2.5a), although, in general, time on the nest overnight did not vary among years (Figure 2.2b). The differing relationship in 2010 appeared to be driven by the colder temperatures in that year; however, 2010 was still significantly different when the data were re-analyzed excluding the lowest temperatures (-4.78 to -2.40°C, accounting for 2.6% of observations,  $n = 531$ ) not experienced in the other years (Contrast comparing 2010 vs. 2005, 2006 and 2011:  $t_{439} = -2.17$ ,  $P = 0.03$ ).

### **On-bout duration and ambient temperature**

Similar to time on the nest, mean on-bout duration decreased linearly with increasing ambient temperature; however, this relationship did not vary statistically across years (Table 2.2, Figure 2.4b). Mean on-bout duration also varied with Julian date, incubation day and proportion of time spent incubating overnight. On-bout duration decreased as Julian date and incubation day increased and on-bouts were longer when more time was spent in overnight incubation (Table 2.2, Figure 2.5b). On-bout duration also appeared to vary among aspects, with bout duration for nests on an East facing aspect differing from those on a North facing aspect (Table 2.2). However, this relationship may not be reliable as only one nest had an East facing aspect.

### **Recess duration and ambient temperature**

The relationship between mean recess duration and ambient temperature varied in one year of the study. Recess duration increased with increasing ambient temperature in 2010 but appeared to be unrelated to temperature in all other years (Table 2.2, Figure 2.4c). Recess duration also varied with time spent in overnight incubation, decreasing with increased time on the nest overnight (Table 2.2, Figure 2.5c). These relationships were still significant when the low, outlier points clustered on the bottom left portion of the figure (which represented mean recess durations of 0 min, where a bird did not leave the nest during that 06:00 – 08:00 observation) were excluded from analysis (Contrast comparing 2010 vs. 2005, 2006 and 2011:  $t_{424} = 2.42$ ,  $P = 0.02$ ). The steeper, positive, slope in 2010 did seem to be driven by the lower temperatures in that year, as 2010 was

no longer significantly different when re-analyzed without the coldest temperatures in 2010 (Contrast comparing 2010 vs. 2005, 2006 and 2011:  $t_{439} = -1.36$ ,  $P = 0.17$ ).

### **Recess frequency and ambient temperature**

Birds took more frequent recesses as ambient temperature increased and this relationship was consistent across years (Table 2.2, Figure 2.4d). Recess frequency also displayed a positive relationship with Julian date and incubation day and a negative relationship with proportion of time spent in overnight incubation (Table 2.2, Figure 2.5d).

## **DISCUSSION**

Horned Larks breeding on Hudson Bay Mountain are confronted with annual variation in their thermal environment. I have described annual variation within a population in the relationship between nest attentivity and temperature, which is seemingly related to the variable thermal regimes. Among years, the proportion of time spent on the nest overnight was consistent (mean = 94%), while attentivity varied throughout the day. In 2010, when overnight temperatures were much colder, females spent less time on the nest early in the morning as temperatures warmed than in other years. This appeared to be accomplished through shorter recesses at colder temperatures in 2010, while in other years recess duration was unrelated to temperature. Larks appeared to make behavioural decisions with respect to temperatures they experienced throughout the day. When faced with greater energetic demands, they shifted investment towards self-maintenance by more readily leaving the nest and foraging for longer bouts, even at the risk of chilling their clutch below the physiological zero temperature.

Conditions during overnight incubation can influence decisions made the following day. For example, in incubating Great Tits (*Parus major*), daily energy expenditure was inversely related to nighttime ambient temperature (Bryan and Bryant 1999). In my study, despite marked temperature differences across years, birds maintained high attentivity overnight. Low nightly temperatures should force incubating larks to increase metabolic heat production in order to maintain suitable egg temperatures

(Carey 2002). In 2010, which was roughly 4°C colder at night than other years, overnight incubation could have been more energetically costly. Zebra Finches more than doubled their metabolic rate when incubating overnight at 10°C versus 28°C (Nord et al. 2010). Heating nest boxes of incubating Great Tits by a mean of 3.4°C overnight saved the adult approximately 7 kJ of energy (6% of normal daily energy expenditure during incubation) per night (Bryan and Bryant 1999). Swain's (1991) measurements of metabolic rates and energy reserves of breeding Horned Larks captured in Wyoming suggested their energetic reserves should sustain a bird overnight unless the minimum temperature dropped below freezing. If overnight temperatures drive the decisions larks make early in the morning, it could explain why incubation rhythms in 2011 were comparable to those in 2005 and 2006 even though overall temperatures in 2011 were colder. In 2010, larks likely faced heightened energetic costs overnight that carried over into heightened costs during the day. Time spent in overnight incubation (which is likely influenced by night temperatures) was related to all four incubation variables during the 06:00-08:00 time period. Onset and cessation of overnight incubation did not appear to vary among years (Figure 2.2b), so birds were not reducing their overnight bout to compensate for increased energetic demands. Thus, from 06:00-08:00, when incubating birds typically ended their overnight session and commenced daytime incubation patterns, in 2010 females likely had a greater energy deficit than incubating females in the other years.

For single-sex, intermittent incubating birds in an extreme environment, adult and offspring needs may directly conflict (Carey 2002, Conway and Martin 2000a). Adults are unable to forage and incubate simultaneously and so must make decisions about how to divide their time, which may benefit their self-maintenance to the detriment of their offspring or vice versa. I observed a negative relationship between time on the nest and ambient temperature; as temperatures warmed up and the risk of the eggs cooling decreased, females spent less time incubating. Consistent with my predictions, female larks in 2010, the coldest year of the study, displayed a stronger response to temperature early in the morning than females in other years, indicative of a behavioural shift towards favouring self-maintenance over reproduction. The freezing point of chicken embryos is estimated as -2°C (Lundy 1969), and attentivity was generally very high at temperatures

near this point (experienced more frequently in 2010), suggesting that when the risk to the embryos was highest, females prioritized their eggs. However, at temperatures above 1 or 2°C, adults spent more time off the nest in 2010, exposing their eggs to suboptimal temperatures for longer than in other years, shifting investment more towards themselves. This was likely a compensatory response to the greater energy deficit accrued overnight in 2010.

Even though the “normal response” to temperature did not vary in 2011, larks seemed to be more challenged by the temperature regime in that year than in 2010. The extended recesses excluded from analyses in this chapter, which often coincided with bad weather events, were more common in colder years and were especially prevalent in 2011 (see Chapter 3). Extended recesses also tended to be longer in 2011. Embryos in 2011 were frequently exposed to near freezing conditions for extended periods of time, which may explain why the hatching rate of eggs dropped from 94% in the first three years, to 81% in 2011. Colder diurnal temperatures in 2011 appeared to pose a greater ecological challenge to the larks than the cold overnight conditions in 2010.

Incubating Horned Larks displayed a positive correlation between recess duration and ambient temperature early in the morning in 2010. This relationship seemed to be driven by shorter recesses at colder temperatures in 2010, and likely functioned to limit embryo exposure to conditions that could result in lethal chilling. Recess duration for Horned Larks at the same site in other years was unrelated to temperature, which was also the general response to temperature observed by Camfield and Martin (2009). Consequently, examining only general behavioural patterns may mask the finer scale responses of birds to more localized conditions.

Food limitation also impacts energetics and incubation behaviour (Conway and Martin 2000b, Martin 2002, Londono et al 2008). Incubating Wheatears (*Oenanthe oenanthe*), Pied Flycatchers (*Ficedula hypoleuca*) and Karoo Prinia (*Prinia maculosa*), all decreased recess duration in response to experimental food supplementation (Moreno 1989, Smith et al 1989, Chalfoun and Martin 2007). Similarly, Australian Reed Warblers



(*Acrocephalus australis*), Bewick's Wrens (*Thryomanes bewickii*) and House Wrens (*Troglodytes aedon*) increased attentivity when provided with supplemental food (Eikenaar et al 2003, Pearse et al 2004). It is feasible that the different relationships I observed in 2010 were caused by decreased food availability in that year. Horned Larks on Hudson Bay Mountain forage on both insects and plant material (Beason 1995) and, like other alpine birds, rely heavily on arthropod fallout on snow patches (Antor 1995). If there was less food available in 2010, birds may have had to spend more time off the nest foraging to obtain the same amount of food.

My findings suggest that in energetically stressful situations, incubating Horned Larks shifted investment towards self-maintenance rather than towards the needs of their clutch. When exposed to an environmental perturbation, breeding organisms sometimes enter into an "emergency life history stage", shifting investment away from reproduction and into survival (Wingfield 2003). The extended recesses I observed may be an example of such behaviour. For a long-lived species (individuals of this population live up to 7 years, unpublished data), with high survival rates (Camfield et al 2010) living in an unpredictable environment, it is likely a good strategy to invest in survival and future reproduction rather than risk prohibitively high energy loss in favour of a current reproductive attempt.

Even though larks in 2010 demonstrated a tendency to favour their self-maintenance over their eggs, they still maintained high attentivity, particularly at very low temperatures when embryos could freeze. Even during the warmest part of the day, the proportion of time spent incubating was greater than 50%. Full day nest attentivity ranged from 76% (2010 and 2011) to 80% in 2005. This is comparable to species in other systems; Conway and Martin (2000b) estimated 75% mean daily attentivity for 95 passerine species in North America. Horned Larks seem well suited to breeding in challenging alpine habitats, maintaining high levels of attentivity even under harsh conditions. However, the stronger response to temperature in the coldest year demonstrates that even a robust species has upper limits of tolerance.

Behavioural plasticity is just one of several ways that alpine breeding birds are able to cope in a challenging environment (Martin and Wiebe 2004). Multi-year studies allow us to observe a larger suite of behavioural responses in order to determine the limitations of an alpine species' ability to cope with environmental change.

Table 2.1 – Ambient temperatures (°C) experienced on Hudson Bay Mountain, BC during 06:00-08:00 across four years of study.

Means presented  $\pm$  SE.

<b>Year</b>	<b>Mean ambient temperature (°C)</b>	<b>Temperature range (°C)</b>
2005	4.82 $\pm$ 0.29	-1.52 – 18.83
2006	4.70 $\pm$ 0.22	-2.41 – 14.68
2010	0.25 $\pm$ 0.33	-4.78 – 8.34
2011	2.60 $\pm$ 0.25	-0.98 – 6.21

Table 2.2 – Results of general linear mixed effects models predicting total minutes on the nest, mean on-bout duration and mean recess duration and generalized linear mixed effects model for recess frequency of a population of Horned Larks incubating from 06:00-08:00 across four breeding seasons (2005, 2006, 2010, 2011) on Hudson Bay Mountain, British Columbia ( $n = 545$ ). On-bout and recess duration were log-transformed while vegetation cover and overnight incubation were arcsine square root transformed to meet assumptions of normality. Significant results are in bold, and marginally significant results are underlined. In the presence of a significant temperature  $\times$  year interaction, temperature and year main effects are not considered significant (even when  $P < 0.05$ ).

Parameter	Total minutes on nest			On-bout duration (min)			Recess duration (min)			Recess frequency <sup>1</sup>		
	Estimate	$t$	$P$	Estimate	$t$	$P$	Estimate	$t$	$P$	Estimate	$Z^1$	$P$
	$\pm$ SE			$\pm$ SE			$\pm$ SE			$\pm$ SE		
Intercept	67.25 $\pm$			6.02 $\pm$			3.13 $\pm$			0.17 $\pm$		
	19.89	3.38	<b>0.001</b>	1.21	4.99	<b>&lt;0.001</b>	0.84	3.72	<b>0.0002</b>	0.72	0.24	0.81
Temperature	-2.52 $\pm$			-0.12 $\pm$			0.08 $\pm$			0.06 $\pm$		
	0.54	-4.68	<b>&lt;0.001</b>	0.03	-3.76	<b>0.0002</b>	0.03	3.37	0.001	0.02	2.90	<b>0.004</b>
Clutch size	-0.69 $\pm$			0.03 $\pm$			-0.03 $\pm$			0.04 $\pm$		
	1.41	-0.49	0.63	0.08	0.36	0.72	0.06	-0.46	0.64	0.05	0.72	0.47
Julian date	-0.14 $\pm$			-0.02 $\pm$			0.001 $\pm$			0.09 $\pm$		
	0.11	-1.27	0.20	0.01	-3.04	<b>0.003</b>	0.004	0.32	0.75	0.004	2.40	<b>0.02</b>
Incubation	-0.29 $\pm$			-0.06 $\pm$			-0.01 $\pm$			0.04 $\pm$		
day	0.22	-1.31	0.19	0.01	-4.57	<b>&lt;0.001</b>	0.01	-1.37	0.17	0.01	5.04	<b>&lt;0.001</b>

Parameter	Total minutes on nest			On-bout duration (min)			Recess duration (min)			Recess frequency <sup>1</sup>		
	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>Z</i> <sup>1</sup>	<i>P</i>
	± SE			± SE			± SE			± SE		
Aspect E <sup>2</sup>	-10.89 ±			-2.27 ±			-1.01 ±			1.35 ±		
	17.24	-0.63	0.53	1.05	-2.16	0.03	0.76	-1.33	0.19	1.08	1.24	0.21
Aspect S <sup>2</sup>	-4.23 ±			-0.69 ±			0.11 ±			0.38 ±		
	8.53	-0.50	0.62	0.51	-1.35	0.18	0.33	0.32	0.75	0.27	1.41	0.16
Aspect W <sup>2</sup>	-3.06 ±			-0.28 ±			0.27 ±			0.05 ±		
	4.76	-0.64	0.52	0.29	-0.98	0.33	0.19	1.45	0.15	0.16	0.28	0.78
Orientation	2.74 ±			0.05 ±			-0.13 ±			-0.04 ±		
E <sup>2</sup>	2.37	1.16	0.25	0.14	0.35	0.73	0.09	-1.42	0.16	0.08	-0.50	0.62
Orientation	-6.44 ±			-0.53 ±			-0.03 ±			0.33 ±		
S <sup>2</sup>	5.55	-1.16	0.25	0.34	-1.57	0.12	0.23	-0.14	0.89	0.19	1.76	0.08
Orientation	12.40 ±			1.52 ±			0.82 ±			-1.06 ±		
W <sup>2</sup>	13.96	0.89	0.38	0.85	1.77	0.08	0.64	1.27	0.21	1.03	-1.03	0.30
Veg cover	1.12 ±			0.16 ±			0.05 ±			-0.05 ±		
	4.62	0.24	0.81	0.28	0.58	0.56	0.18	0.29	0.77	0.16	-0.32	0.75
Overnight	41.37 ±			1.05 ±			-1.06 ±			-0.70 ±		
	6.82	6.06	<b>&lt;0.001</b>	0.42	2.51	<b>0.01</b>	0.32	-3.28	<b>0.001</b>	0.27	-2.55	<b>0.01</b>

Parameter	Total minutes on nest			On-bout duration (min)			Recess duration (min)			Recess frequency <sup>1</sup>		
	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>Z</i> <sup>1</sup>	<i>P</i>
	± SE			± SE			± SE			± SE		
2005 <sup>2</sup>	-0.55 ±			-0.13 ±			0.07 ±			0.08 ±		
	3.92	-0.14	0.89	0.24	-0.55	0.58	0.16	0.40	0.69	0.14	0.54	0.59
2006 <sup>2</sup>	-2.00 ±			-0.14 ±			-0.05 ±			-0.001 ±		
	3.04	-0.67	0.51	0.18	-0.75	0.45	0.12	-0.43	0.67	0.11	-0.01	0.99
2011 <sup>2</sup>	-5.21 ±			-0.29 ±			0.19 ±			0.15 ±		
	3.72	-1.40	0.17	0.23	-1.28	0.20	0.16	1.21	0.23	0.14	1.10	0.27
Temp*2005 <sup>2</sup>	1.70 ±			0.04 ±			-0.10 ±			-0.01 ±		
	0.67	2.53	<b>0.01</b>	0.04	0.94	0.35	0.03	-3.07	<b>0.002</b>	0.03	-0.53	0.60
Temp*2006 <sup>2</sup>	1.54 ±			0.06 ±			-0.07 ±			-0.02 ±		
	0.59	2.61	<b>0.01</b>	0.04	1.55	0.12	0.03	-2.58	<b>0.01</b>	0.02	-0.78	0.44
Temp*2011 <sup>2</sup>	1.80 ±			0.09 ±			-0.08 ±			-0.04 ±		
	0.95	1.89	<u>0.06</u>	0.06	1.50	0.13	0.05	-1.69	<u>0.09</u>	0.04	-1.05	0.29

<sup>1</sup> Recess frequency are count data and were therefore assessed using a generalized linear mixed model allowing for a Poisson distribution. As a result, parameters were assessed using a Z-test rather than a *t*-test

<sup>2</sup> Aspect, orientation and year are categorical variables and were therefore assessed in relation to one of the categories. Aspect and orientation were assigned to categories based on their deviation from north (N, E, S, W). N was used as the reference group in the

analysis and thus does not appear in the table. For year, and consequently the temperature  $\times$  year interaction, 2010 was the reference group and therefore does not appear in the table.

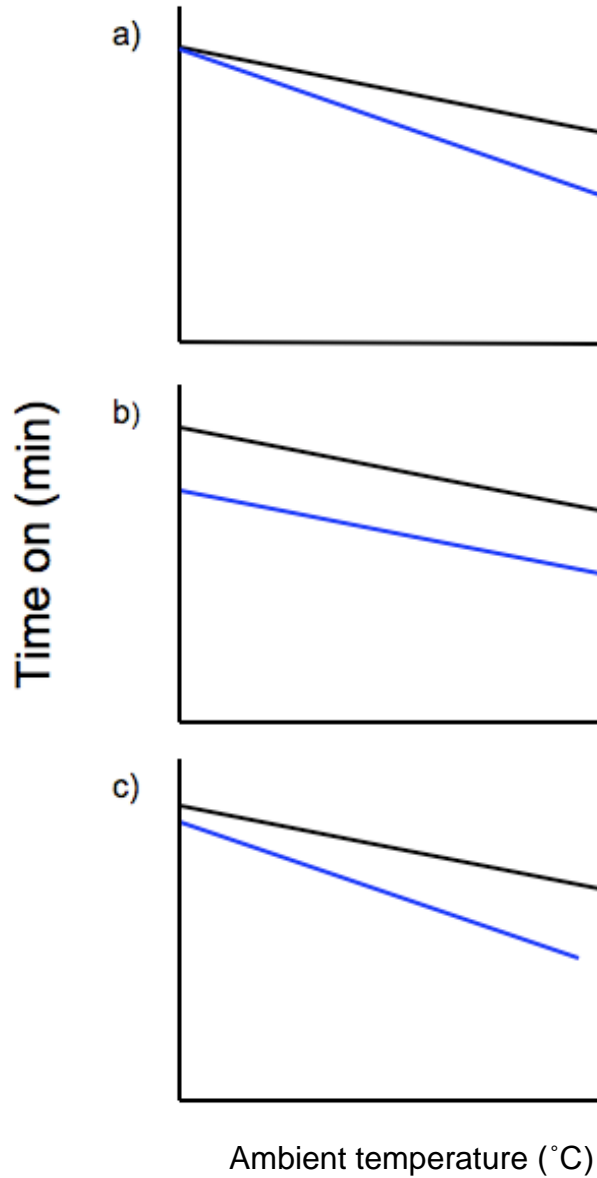


Figure 2.1 – Predictions of potential relationships between time on the nest (minutes) and ambient temperature ( $^{\circ}\text{C}$ ) in a cold year. Black lines represent the expected relationship in a typical year and blue lines represent potential relationships in a colder year. Panel a) shows a steeper slope in a cold year, whereby adults would increase time off the nest as the risk to the embryo decreases, b) shows a lower y-intercept in a cold year, whereby adults decrease time on the nest overall and c) depicts a combination of the previous two.



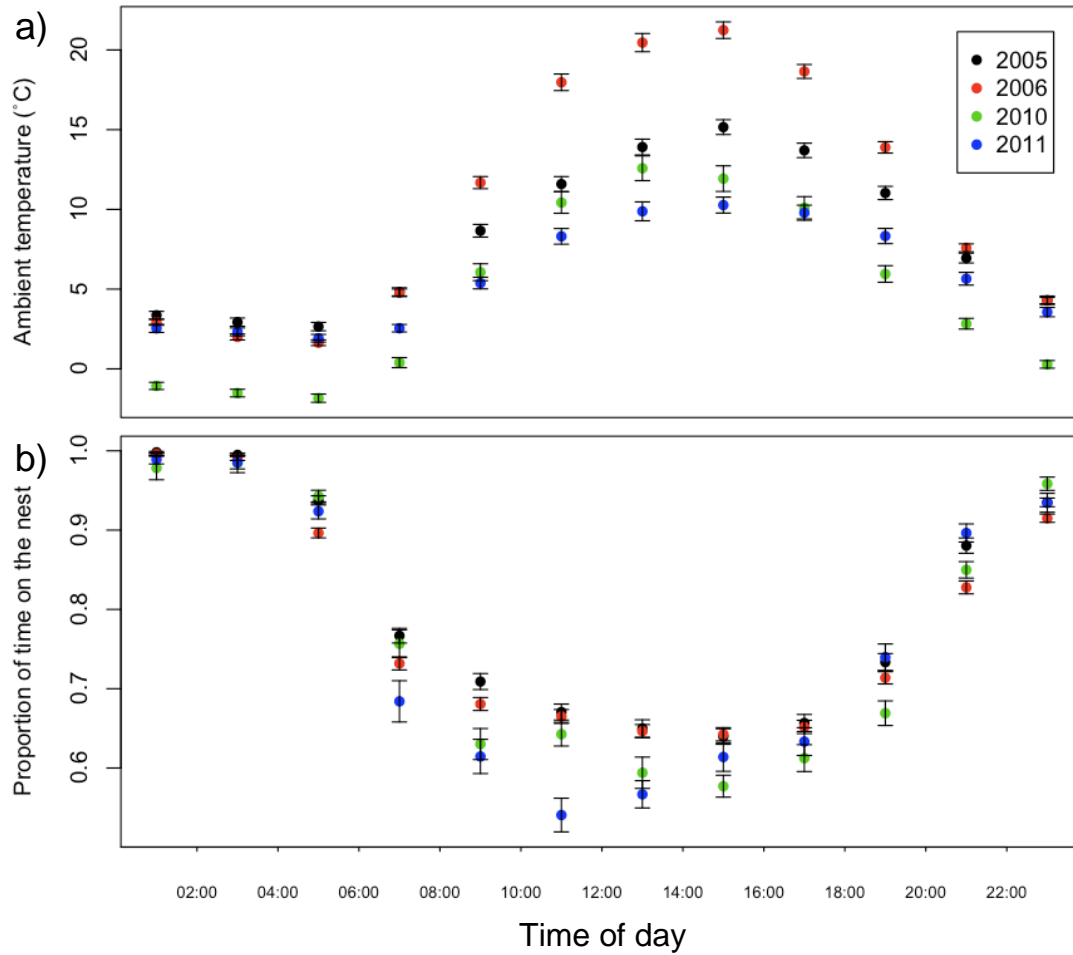


Figure 2.2 – Mean ( $\pm$  SE) a) ambient temperature ( $^{\circ}$ C) and b) attentivity (proportion of 2-h period spent on nest) in each 2-h time period across the four years of study. Time periods containing extended recesses were included in calculation of these period means to illustrate the full range of temperatures experienced as well as changes to daytime attentivity.

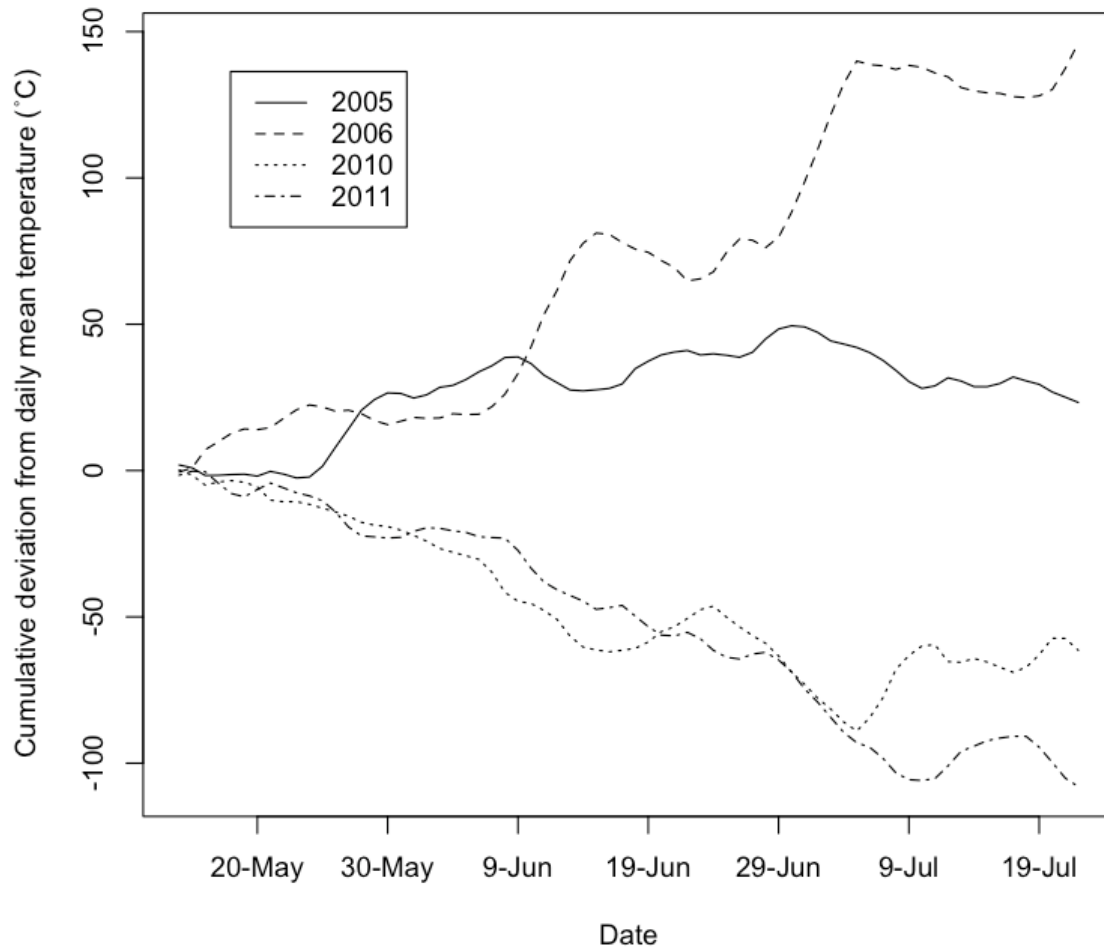


Figure 2.3 – Cumulative temperature deviations from the daily mean across the four years of study. A zero baseline indicates an average year, positive values indicate a relatively warmer year and negative values indicate a relatively colder year.

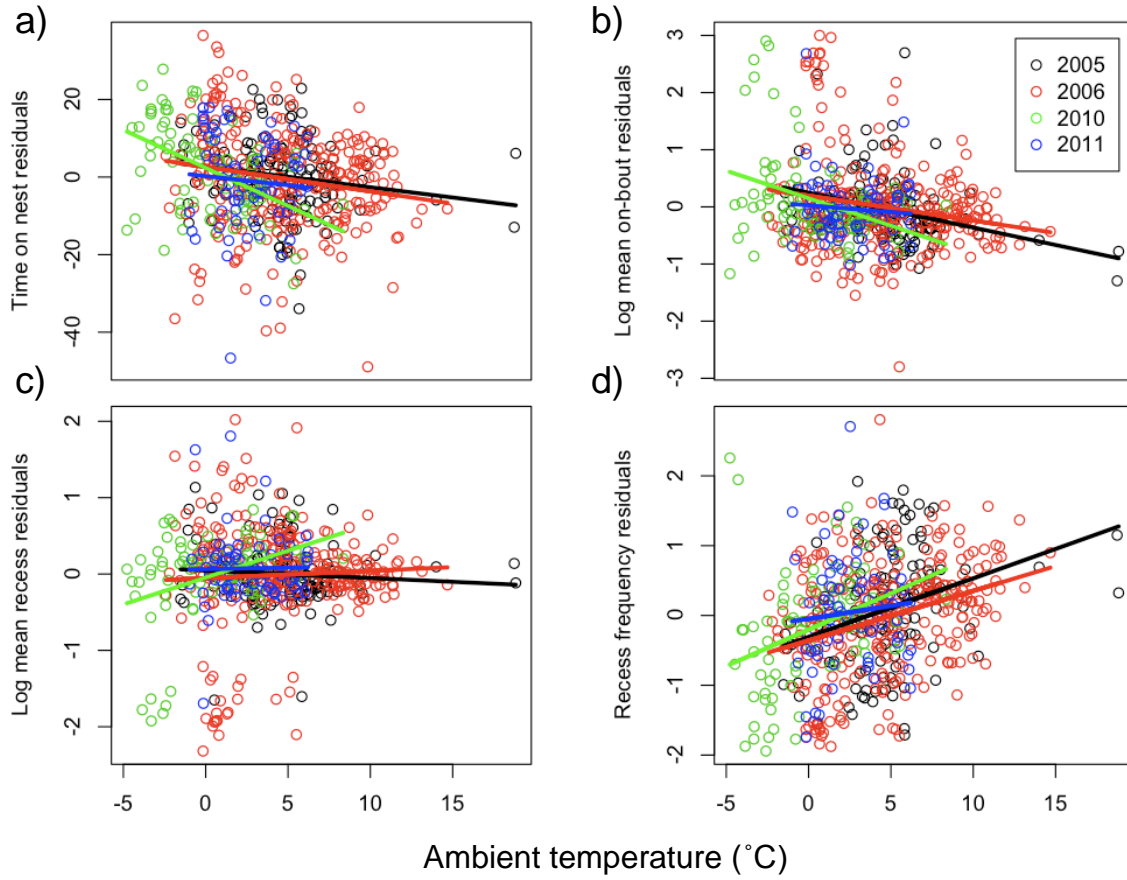


Figure 2.4 – Linear relationships between a) total time on the nest (min), b) mean on-bout duration (min), c) mean recess duration (min) and d) recess frequency, with ambient temperature during 06:00-08:00 across the four years of study. Statistical results associated with these relationships are presented in Table 2.2.

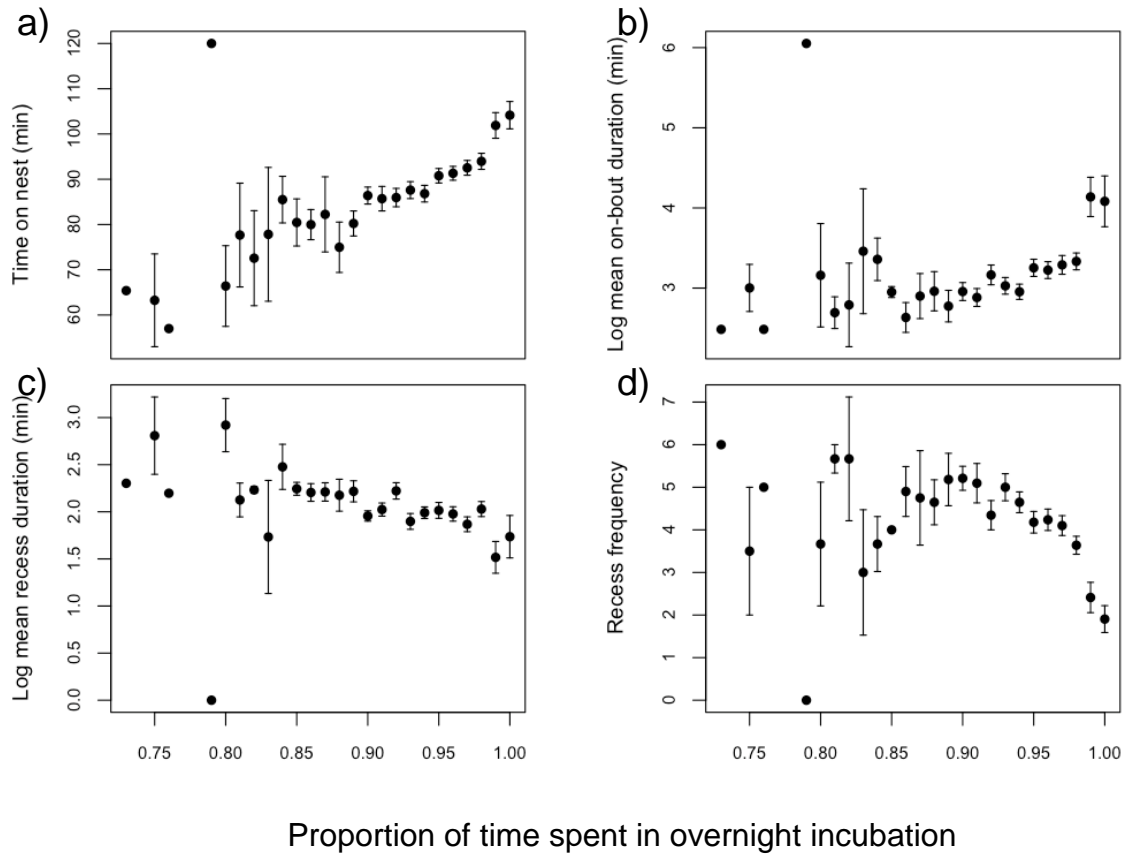


Figure 2.5 – Relationships during the 06:00-08:00 period of a) total time on the nest, b) mean on-bout duration, c) mean recess duration and d) recess frequency with proportion of time spent in overnight incubation (20:00-05:59) across the four years of study. Statistical results associated with these relationships are presented in Table 2.2.

## CHAPTER 3: PREVALENCE OF EXTENDED INCUBATION RECESSES IN AN ALPINE POPULATION OF HORNED LARKS

### INTRODUCTION

The alpine is a harsh environment characterized by a short growing season, daily temperature fluctuations of up to 40°C, as well as stochastic weather events, storms and sub-zero temperatures throughout the year (Martin 2001, Camfield 2008). The energetic costs of breeding are elevated in alpine habitats (Carey 2002). For birds, incubation may be particularly challenging because in cold ambient conditions, more energy must be invested to create a suitable thermal environment for embryos (Williams 1996, Creswell et al 2004). In small-bodied species with single-sex intermittent incubation, conflicting needs of the embryos and adults result in a trade-off, where the incubating parent must divide their time between incubation and foraging (Webb 1987, Conway and Martin 2000a). Parents can adjust investment, favouring either self-maintenance or egg survival, to maximize fitness (Drent 1975, Jones 1989). In a cold and capricious environment, a shift towards the adult could compromise embryo viability, whereas a shift towards the clutch could result in prohibitively high energy loss for the parent.

Incubation behaviour is probably restricted by the parent's energetic needs (Bryan and Bryant 1999, Creswell et al 2004, Ardia et al 2009, Nord et al 2010). Incubating adults may abandon their nest (temporarily or completely) when energetic constraints are high. Seabirds, particularly those that nest in cavities, often leave eggs unattended and exposed to ambient conditions for several hours or days at a time (Boersma and Wheelwright 1979, Blight et al 2010, Divoky and Harter 2010). This “egg neglect” occurs because incubating adults forage far from where they breed and may be unable to return to their nests due to poor food supply or harsh weather (Boersma and Wheelwright 1979, Blight et al 2010). Seabird embryos remain viable despite repeated occurrences of egg neglect (Boersma and Wheelwright 1979). Similar behaviours have also been documented in other avian species in response to energetic constraints. Blood Pheasants (*Ithaginis cruentus*) incubating at high elevation in China leave their nests every morning for over 6.5 h (because of low quality food), exposing eggs to temperatures below their

physiological requirements for development (Jia et al 2010). Alpine breeding Eurasian Dotterel (*Charadrius morinellus*) in Scotland sometimes neglect their clutches for > 2 h at a time, typically during bad weather (Holt 2002). When faced with long periods of bad weather while incubating, females of four passerine species in Norway as well as high elevation Dusky Flycatchers (*Empidonax oberholseri*) in California were observed deserting their nests for several hours, likely in response to energetic constraints imposed by the inclement weather (Haftorn 1988, Morton and Pereyra 1985). Long recesses may also compensate for long on-bouts. On-bout and recess duration in alpine Meadow Pipits (*Anthus pratensis*) were positively correlated with previous bout duration (Kovarík et al 2009) and brood neglect during chick rearing in Northern Gannets (*Morus bassanus*) was more common after long periods of attendance (Lewis et al 2004).

These extended recess behaviours reflect the incubating parent's need to direct energetic investment towards their self-maintenance rather than towards reproduction. In some cases, it could indicate entry into an “emergency life history stage”, where high stress from an unpredictable environmental event causes an animal to reduce effort or abandon reproduction (Wingfield et al 1998, Wingfield 2003). Protracted periods of bad weather (i.e. heavy precipitation and/or low temperatures) have caused this in breeding birds (Wingfield 2003). Hormonal responses mediate such events, and the tendency to enter an emergency life history stage often relates to the animal's value of current versus future reproduction (Bókonyi et al 2009); for example, a long-lived species with many future opportunities to breed will be more likely to engage in this behaviour. It has been suggested that neglect events are a typical behaviour used by passerines to cope with severe weather (Haftorn 1988) and may be essential to successful alpine breeding (Holt 2002). Determining frequency as well as triggers of neglect in a particular species or population may reveal what environmental conditions they find challenging.

Neglect behaviours have been documented in a number of high elevation bird species, but it is unknown to what extent they occur in other alpine species. While studying incubation rhythms of an alpine breeding population of Horned Larks (*Eremophila alpestris*), I observed some individuals taking extended incubation recesses.

In this study, I analyzed this behaviour to determine the prevalence of extended recesses in this system, what triggered females to take extended breaks from incubation, and whether this behaviour had detectable ecological and/or fitness consequences. I predicted that extended recesses were stress-related responses to harsh weather events, as observed in a few other passerines (Morton and Pereyra 1985, Haftorn 1988) and would be more common in colder years and would occur more frequently on particularly cold days, or during storms due to increased energy demands on incubating females. Alternatively, if extended recesses were compensating for a long on-bout, I expected recess duration would be correlated with previous on-bout duration, mean on-bout duration in the previous 2-h period, or both, because a longer on-bout should result in a longer recess. With respect to ecological/fitness consequences, periods of egg cooling have lengthened the incubation period in a variety of species, ranging from passerines to galliforms to seabirds (Boersma and Wheelwright 1979, Lyon and Montgomerie 1987, Holt 2002, Ardia et al 2010, Jia et al 2010). Reduced nest attentiveness decreased hatching success in an arctic passerine (Lyon and Montgomerie 1987). Thus, I expected that several long recesses by a single nest would extend the incubation period and could reduce embryo viability.

## **METHODS**

### **Study species and area**

I studied an alpine population of Horned Larks on Hudson Bay Mountain, British Columbia, Canada (52°N, 127°W) during the 2010 and 2011 breeding seasons (early May through July). The Horned Lark is a small (25-40 g) songbird exhibiting female-only, intermittent incubation, with no evidence for male incubation feeding (Beason 1995). The study population breeds within a 4-km<sup>2</sup> area of alpine tundra, covering an elevation range of 1500-1850 m above sea level. Harsh and variable conditions are common; temperatures at this site can vary by > 40°C in a single day, while below freezing temperatures and storms occur throughout the breeding season (Camfield and Martin 2009). I also used two additional years of data (2005 and 2006) from a previous study on this population in my analysis (Camfield 2008, Camfield and Martin 2009).

## **Data collection**

During the 2010 and 2011 breeding seasons, I located Horned Lark nests by systematically searching known lark territories or appropriate habitat, by observing adult larks during nest building or chick feeding and/or by flushing incubating females. I monitored each nest regularly (every 3 to 5 days and more frequently around expected hatch/fledge dates) until it fledged or failed and recorded information on vital rates.

In each year, I recorded incubation rhythms at some of the nests using temperature data loggers (HOBO Pro Series, #H08-031-08, Onset Computer Co., Pocasset, MA, USA). I placed the data loggers within 2 m of the nest and inserted the external temperature probe into the nest cup. The data logger took simultaneous temperature recordings of ambient and nest temperatures ( $^{\circ}\text{C}$ ) every 30 s, 24 h/day until the eggs hatched or the nest failed. Temperature changes in the nest indicated when the female left and returned to her clutch. Behavioural observations over a range of temperatures and nests confirmed that temperature fluctuations recorded by the data loggers coincided with actual recesses and on-bouts (Camfield 2008, ECM unpublished data). The temperature probes did not touch the eggs, so I did not measure actual egg/embryo temperatures. If nests were located after incubation was initiated, I calculated clutch initiation date by backdating from hatch date using the following time intervals: egg laying = 1 egg laid per day (thus, clutch size = duration of laying period), incubation = 12 days (Camfield and Martin 2009). I followed the protocol outlined in Camfield and Martin (2009), so data collection was similar in all four years of the study. All protocols were approved by the University of British Columbia Animal Care Committee (AUP numbers A07-0048 and A10-0128).

A weather station on the field site recorded daily temperature, precipitation, and wind speed throughout all breeding seasons.

## **Data analysis**

I used Rhythm (1.0; Cooper and Mills 2005) to select incubation recesses from nest temperature recordings; a recess was chosen when the nest temperature dropped by  $\geq 3^{\circ}\text{C}$  for at least 3 min. I then used Raven Pro (1.3) to visually examine the data and



manually choose any recesses that Rhythm had not selected but also appeared to be off-bouts (i.e., a steep drop in temperature lasting slightly less than 3 min). This method, which was also followed for 2005 and 2006 data (Camfield and Martin 2009), allowed me to determine the initiation and duration of each incubation recess. I defined an extended recess as a recess lasting  $\geq 59$  min, which was approximately 2 standard deviations greater than the mean daytime recess duration (mean recess duration = 10.92 min, SD = 23.92). I wanted to restrict my analysis to absences that would be ecologically significant to embryos, i.e. recesses that were likely to result in severe egg cooling. This required only the inclusion of events that were very far removed from typical behaviour, as typical passerine incubation strategies maintain egg temperatures within the assumed physiological requirements for embryonic development (Haftorn 1988). Two standard deviations may be a conservative approach; however, this seemed necessary as I have not measured egg cooling rates in this system and eggs in ground nests may cool relatively slowly (Zerba and Morton 1983), particularly in nests that are well lined, such as these lark nests (Møller 1991). I searched for any recess lasting  $\geq 59$  min, and recorded the year, nest, date, time of day, duration of recess, mean ambient temperature during the 2-h period in which the recess began, previous on-bout duration, mean on-bout duration from the previous 2-h period, mean ambient temperature and weather on the day it occurred. For each nest that experienced extended recesses, I noted the fate (success or failure) and the duration of the incubation period (if available).

For statistical analysis, I compared clutch size and hatching success among years using linear models (one-way ANOVA). I used an arcsine square root transformation on the proportion of eggs hatched prior to analysis (Zar 1999). I regressed extended recess duration against previous on-bout duration and mean on-bout duration from the previous 2-h period, using linear mixed effects models with nest as a random factor, to account for repeated measurements within nests (Pinheiro and Bates 2000). Analyses were performed in R version 2.10.1 (R Development Core Team 2009). Means are presented  $\pm$  SE.

## RESULTS

Incubation rhythms were monitored at 86 Horned Lark nests over four years (16 in 2005, 38 in 2006, 16 in 2010 and 16 in 2011). In each year, birds were exposed to a different temperature regime. Temperatures in 2005 were relatively moderate, daytime temperatures were warmer in 2006, while 2010 and 2011 were both relatively cold (Figure 3.1). Specifically, 2010 was generally colder overnight, while 2011 was colder during the day (see Chapter 2). Mean ( $\pm$  SD) daytime recess duration was  $10.92 \pm 23.92$  min ( $n = 4076$  2-h periods), however, I observed 70 instances in which females took recesses lasting 59 min or longer. These extended recesses represented  $< 1\%$  of the total number recesses taken; however, they occurred in all years and were taken by several different individuals and on multiple days.

Overall, extended recesses were rare among Horned Larks incubating on Hudson Bay Mountain. Extended recesses were most common in the two coldest years of the study (60% occurred in 2010 and 2011), and most prevalent in 2011. Both the proportion of 2-h periods in which mean recess duration was  $\geq 59$  min and the proportion of the total number of recesses taken in each year that were  $\geq 59$  min were highest in the coldest years (Figure 3.2). Extended recesses were also longer in cold years; the longest recess in 2005 was 76 min and in 2011, it was 387 min (Figure 3.3). Similarly, a greater proportion of nests took extended recesses on a greater proportion of days in the cold years (Figure 3.4). Daytime attentivity (the proportion of time spent incubating between 06:00-20:00) declined in cold years, from  $69 \pm 0.6\%$  in 2005 to  $64 \pm 1.2\%$  in 2011, a decrease of approximately 42 min per day (Table 3.1).

Long breaks from incubation occurred throughout the day, and over the course of the study at least one extended recess was initiated in each 2-h period (across all nests) with the exception of the 02:00-04:00 period (Figure 3.5). The distribution of the timing of extended recesses during the day varied among years. In 2005, four out of five extended recesses were taken in the afternoon/early evening. Those taken in 2006 occurred throughout the day but were most common in the late afternoon. In 2010 and

2011, extended recesses occurred throughout the day but several were taken early in the morning as well as later in the afternoon (Figure 3.5).

Duration of extended recesses ( $n = 70$ ) was not related to previous on-bout duration ( $t_{34} = 1.67$ ,  $P = 0.10$ ) or mean on-bout duration in the previous 2-h period ( $t_{34} = 0.93$ ,  $P = 0.36$ ). Rather, extended recesses tended to coincide with cold weather, particularly in 2010 and 2011. Across all years, they occurred on days with a mean daily ambient temperature ranging from  $-0.15$  to  $8.75$  °C. In 2005, 2010 and 2011, most of the extended recesses were taken on days in which the mean ambient temperature was in the coldest quartile (0-25% range of the data), whereas in 2006, most recesses occurred on more moderate days (25-75% range of the data; Figure 3.6). In 2010 and 2011, several long recesses occurred on a few storm days. In 2010, 18 of the 20 extended recesses taken occurred from 12-Jun to 14-Jun. These days had bad weather, with low daily temperatures (Figure 3.1) as well as rain, snow, hail and fog. Of the 15 nests that contained data loggers at this time, 8 (or 53%) took at least one extended recess. The 22 extended recesses taken in 2011 occurred over a greater number of days; however, again multiple recesses occurred on a few bad weather days. In 2011, 41% (9 of 22) of the extended recesses occurred on two days; six on 24-Jun, a cold day (Figure 3.1) with heavy rainfall and three on 1-Jul during a snowstorm. The three longest recesses recorded (one 387 min and two 304 min in duration) occurred on 24-Jun, and one nest took two recesses each over 4 h in duration. All five nests monitored on 24-Jun and the two nests monitored on 1-July each took at least one extended recess.

Horned Larks laid an average of  $3.70 \pm 0.05$  eggs per clutch ( $n = 200$  nests), which did not vary across years (ANOVA,  $F_{3,196} = 1.05$ ,  $P = 0.37$ ). However, the proportion of eggs in a clutch that hatched varied among years (ANOVA,  $F_{3,127} = 3.13$ ,  $P = 0.0279$ ), and was significantly lower in 2011 (Table 3.2) declining from 94% in the first three years to 81% in 2011 (Table 3.1). Two nests that each took multiple extended recesses also appeared to have a prolonged incubation period. In 2010, a single female took nine extended recesses, and incubated her clutch for at least 14 days, at which point the nest was predated though it had not yet hatched. Similarly, a single female in 2011

took four extended recesses, and hatched two of her three eggs after at least 14 days of incubating. Incubation periods for this population typically range from 12-13 days (Camfield and Martin 2009) and so the behaviour of these females appeared to extend their incubation period by 1-2 days.

## **DISCUSSION**

Small-bodied bird species exhibiting single-sex incubation must leave their nest to forage, and as a result, their embryos commonly experience periods of cooling. Long periods of cooling may be experienced if the parent takes extended incubation absences; this study identified the context of such events for a population of alpine breeding Horned Larks. The extended recesses I observed, which lasted from ~ 1 to 6.5 h, were more common in colder years and often coincided with bad-weather events. They seemed to reflect a shift in investment towards self-maintenance and were likely a function of energetic constraints on the incubating parent. Although generally rare, extended recesses occurred in all years and were taken by multiple individuals. During some storms extended recesses were utilized by all sampled individuals, and likely represent an important strategy for coping with such extreme events. More common and longer extended recesses may have imposed fitness costs to larks by lengthening the incubation period in some individuals and could have contributed to reduced hatching success in one year. Nevertheless, Horned Lark embryos appeared quite tolerant to considerable periods of cooling, although there seemed to be a limit to this tolerance. In general, colder thermal regimes posed a greater challenge for this population, and cold diurnal temperatures appeared more difficult than cold nocturnal temperatures.

Multiple factors could stimulate an incubating parent to take a long recess. A poor quality food source was the suggested cause for Blood Pheasants (Jia et al 2010) while for Eurasian Dotterel it was in response to storms and poor weather events (Holt 2002). Extended recesses could also be a means of compensating for a long on-bout, as bout duration is often positively correlated with previous bout duration (Kovarík et al 2009). In general, Horned Lark extended recesses were not associated with a prior long on-bout (although this could have been the cause for some of these events). Instead, as predicted,

these extended recesses appeared to be stress induced. In cold years, an incubating parent should face higher energetic costs, which could affect body condition. A number of observational and experimental studies have demonstrated support for this relationship. Experimental nest heating in Pectoral Sandpipers (*Calidris melanotos*) increased nest attendance and lowered rates of adult mass loss compared to control nests (Creswell et al 2004). Uniparental incubating male Eurasian Dotterels lost more mass than those assisted by females (i.e. when energetic constraints were lifted; Holt et al 2002). White-tailed Ptarmigan (*Lagopus leucura*) took more, longer recesses in a year when body condition was also lower (Wiebe and Martin 1997). Results from these studies corroborate the patterns in Horned Larks: I observed more and longer extended recesses in the two coldest years of my study, and these largely coincided with energetically stressful events such as cold weather and storms.

Individual quality may have also contributed to the tendency to take extended recesses, as not all birds were equally affected by cold conditions. On storm days, not all individuals took long recesses, even on days when multiple birds engaged in this behaviour. For example, on 1-July 2011, the female at one nest took two recesses of more than two hours at approximately 07:00 and 12:00, during the storm, whereas the female at a second nest spent > 11 h incubating overnight, and took her first recess (lasting 85 min) after 12:00. Individual quality influences investment in incubation, such that a higher-quality individual should have more energy to direct towards reproduction and thus should invest more in incubation (i.e. spend more time on the nest) than a lower-quality individual (Ardia and Clotfelter 2007). Female Zebra Finches (*Taeniopygia guttata*) fed high-protein pre-laying diets invested more early in incubation, lengthening on-bout duration between early and middle incubation compared to those fed low-protein diets which increased on-bout duration from mid to late incubation (Gorman and Nager 2003). Rhinoceros Auklets (*Cerorhinca monocerata*) engaged in egg neglect (reducing time on the nest) more often in a year when food availability was limited and adult body condition (an index of individual quality) was reduced (Blight et al 2010). Tree Swallows (*Tachycineta bicolor*) with an experimentally lowered body condition via feather clipping reduced the percentage of time on the nest by > 6% compared to control individuals

(Ardia and Clotfelter 2007). These studies demonstrate that a reduced body condition can lead to less time spent incubating. Body condition should vary among individuals within each year and may shape a bird's ability to cope with energetic stressors. In a cold year, there may be more low-quality individuals, which could account for the increase in extended recesses.

Periods of cooling commonly extend the incubation period (Olson et al 2006, Martin et al 2007). A population of wild Blood Pheasants (which took long recesses daily) incubated 10 days longer than a captive bred population (37 days versus 27-29 days; Jia et al 2010). Female Snow Buntings (*Plectrophenax nivalis*) widowed early in incubation, reduced time on the nest (due to the loss of male incubation feeding) and incubated for 13.4 days compared to 12 days for control individuals (Lyon and Montgomerie 1987). Experimental cooling of Tree Swallow nests moderately (but significantly) increased incubation period relative to controls (14.9 days compared to 14.1 days; Ardia et al 2010). Incubation periods of Eurasian Dotterel increased with declining nest attendance (Holt 2002). Extended recesses resulted in reduced overall nest attendance for Horned Larks and may have increased the incubation period for some individuals; however, this was difficult to quantify as nest predation was high in these two cold years and few nests survived to hatch.

Extended recesses could have substantial ecological implications for Horned Larks if they cause protracted incubation periods. An extended incubation period can increase energetic costs to the embryo (Vleck and Vleck 1987). For instance, periodically cooled Zebra Finch embryos had less yolk reserves and lower growth efficiency after 12 d of incubation than controls (Olson et al 2006). A longer development period would also require more energy from the parent. However, nest predation is likely the most critical ecological cost for this population. The probability of nest predation increases with a longer developmental period (Ricklefs 1969, Conway and Martin 2000b, Martin and Wiebe 2004, Tieleman et al 2004). In this system, > 50% of nests were predated (115 predated out of 210 nests in 4 years), and approximately 6% of nests were lost daily

(unpublished data). Every extra day spent incubating would therefore pose serious fitness costs in this environment.

The effect of extended recesses on lark reproductive success depends on how tolerant their embryos are to cooling before hatching success is affected. Domestic Fowl (*Gallus gallus domesticus*) are the typical model used for thermal tolerance of avian embryos. Their physiological zero temperature (PZT, the temperature below which development is suspended) is approximately 26°C (Lundy 1969), and is commonly applied to all avian species (Webb 1987, Haftorn 1988, Conway and Martin 2000a). However, cold tolerance of developing embryos and the consequent effects of cold exposure on hatching success are not well defined or understood, especially for passerines. Although I did not measure egg temperatures, it is a safe assumption that nests left exposed for several hours on this site cooled to temperatures well below 26°C. Extended recesses demonstrate that Horned Lark embryos in the alpine can tolerate long periods of substantial cooling, although the reduced hatch rate in 2011 could indicate an upper limit to this tolerance. Long incubation recesses do not appear to affect hatching success in seabirds, Eurasian Dotterel or Blood Pheasants (Boersma and Wheelwright 1979, Holt 2002, Jia et al 2010). However, hatch rate was lower for early widowed Snow Buntings, likely due to decreased incubation time (Lyon and Montgomerie 1987), and neglect may have reduced hatching success in an American Kestrel (*Falco sparverius*) nest (Sockman and Schwabl 1998). The lower hatch rate I observed in 2011 could have been caused by reduced nest attendance, increased cold exposure over all, or both. Clearly, avian embryos, across many orders, can tolerate periods of cooling; however, the degree of cold tolerance and the consequences may vary among species, especially when considering differences in body size and adaptation to cold environments.

Rare events can have a disproportionate influence on shaping the ecology, physiology and evolution of an organism (Gutschick and BassiriRad 2003). Extreme weather events, fire and resource pulses are just a few examples of events that are infrequent but elicit huge ecological responses from organisms (Gutschick and BassiriRad 2003, Katz et al 2005, Norris and Martin 2010). The extended recesses I

observed, although rare, may have had a disproportionately large ecological effect on some individuals. If they reduced reproductive success or enhanced adult survival, as appeared to be the case, their occurrence would have made a substantial difference in the success of the individual. Despite being rare (a less conservative definition, for example, mean recess duration + SD, 35 min would have still represented only ~1% of total recesses), their prevalence during storm events suggested that extended recesses represent an important component of the incubation strategy of alpine breeding birds.

The inherently unpredictable nature of alpine environments means that effectively coping with such challenges is vital for successful breeding, although there may be a threshold of environmental variability above which coping mechanisms are insufficient (Martin and Wiebe 2004). The flexibility to be able to shift investment towards oneself when conditions are poor is likely essential to successfully breeding in alpine habitats.



Table 3.1 – Annual estimates of proportion of total daytime (06:00-20:00) spent in incubation and proportion of total eggs in a clutch that successfully hatched, for Horned Larks on Hudson Bay Mountain. Proportion of daytime spent incubating was calculated for nests in which incubation rhythms were monitored. Hatch rate was calculated for all nests that survived to hatch, including nests for which incubation rhythms were not monitored.

Year	Proportion of daytime on nest		Proportion of eggs hatched	
	Mean $\pm$ SE ( <i>n</i> )	Range	Mean $\pm$ SE ( <i>n</i> )	Range
2005	0.69 $\pm$ 0.006 (16)	0.51 – 0.93	0.93 $\pm$ 0.02 (42)	0.50 – 1.0
2006	0.67 $\pm$ 0.005 (38)	0.28 – 0.92	0.94 $\pm$ 0.02 (54)	0.67 – 1.0
2010	0.65 $\pm$ 0.008 (16)	0.42 – 0.89	0.92 $\pm$ 0.03 (24)	0.50 – 1.0
2011	0.64 $\pm$ 0.012 (16)	0.24 – 0.90	0.81 $\pm$ 0.05 (11)	0.50 – 1.0

Table 3.2 – Parameter estimates from a linear model assessing variation in hatching success of Horned Lark nests on Hudson Bay Mountain among four breeding seasons ( $n = 131$ ). The overall significant ANOVA (see text) suggested means differed among years. The year 2011 is not shown in this table as it was the reference year;  $P$ -values compare each year with 2011. Significant  $P$ -values are indicated in bold.

Parameter	Estimate $\pm$ SE	$t$	$P$
Intercept	1.21 $\pm$ 0.08	15.93	<b>&lt;0.001</b>
2005	0.23 $\pm$ 0.09	2.67	<b>0.009</b>
2006	0.25 $\pm$ 0.08	3.04	<b>0.003</b>
2010	0.21 $\pm$ 0.09	2.32	<b>0.02</b>

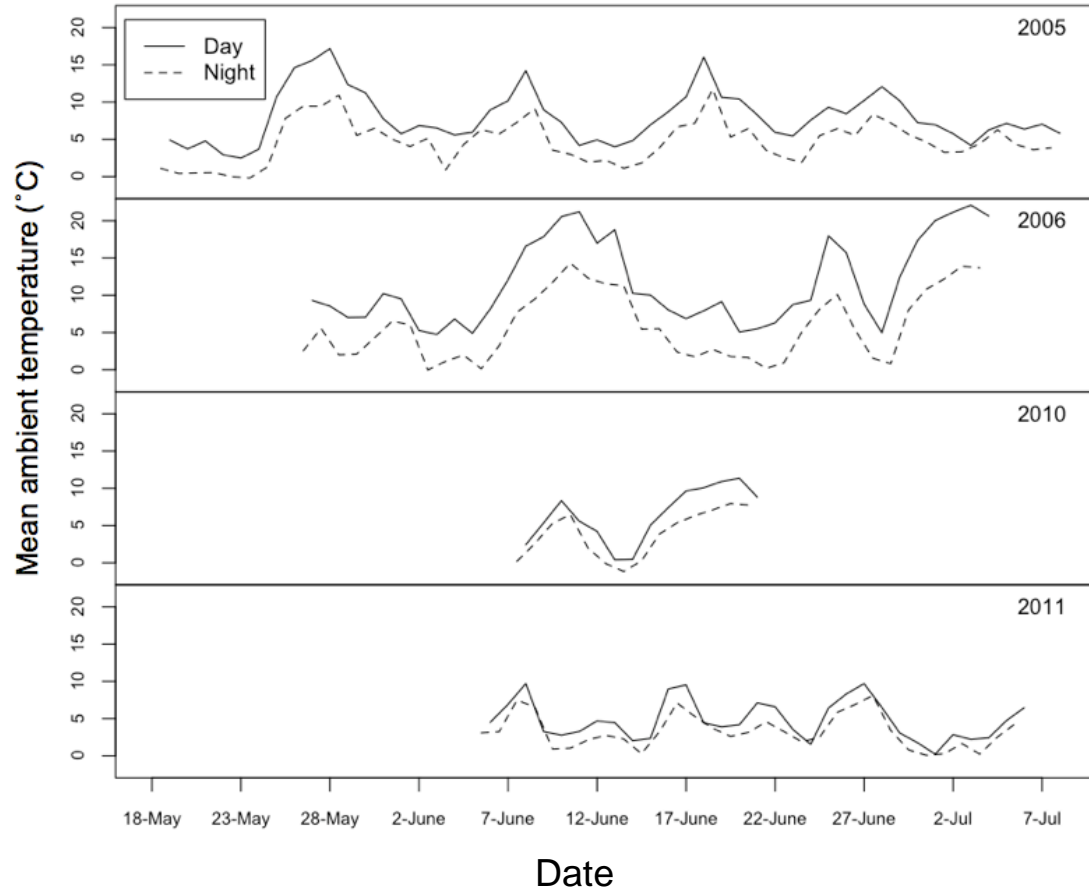


Figure 3.1 – Mean daily (06:00-19:59) and nightly (20:00-05:59) temperatures (°C) for the study area on Hudson Bay Mountain across four breeding seasons. Temperature data were collected from a weather station located on the field site. Dates for each year represent the portion of the season for which Horned Lark incubation rhythms were monitored.

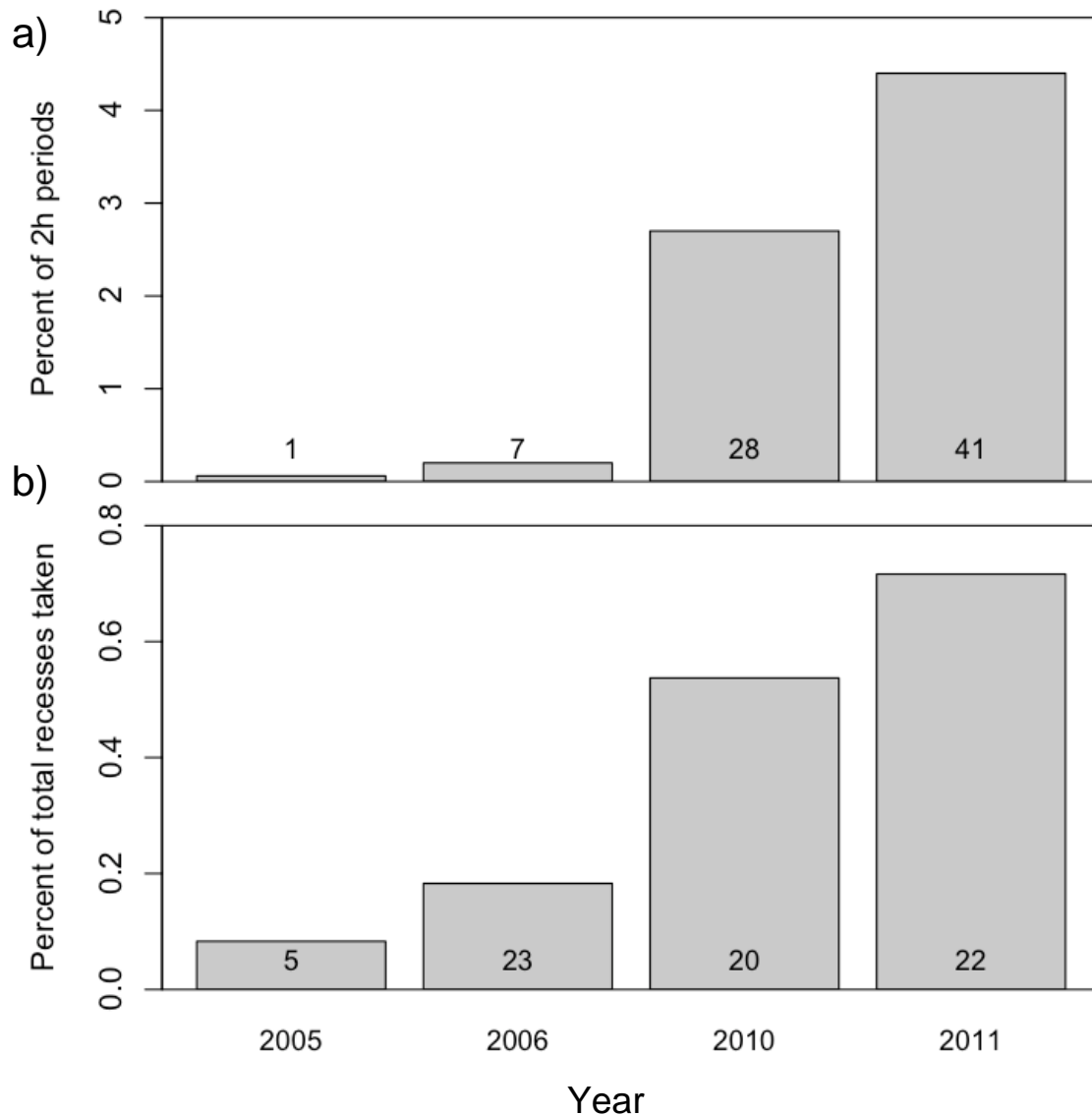


Figure 3.2 – Prevalence of extended recesses in the incubation behaviour of Horned Larks breeding on Hudson Bay Mountain, BC across four years. Panel a) depicts percentage of 2-h periods sampled within each year where the mean recess duration was  $\geq 59$  min and b) shows the percentage of the total recesses recorded each year that were  $\geq 59$  min in duration. Numbers on the bars represent a) the number of 2-h periods and b) the number of recesses that were  $\geq 59$  min, in each year. The total number of recesses taken varied among years: 5 (2005), 23 (2006), 20 (2010) and 22 (2011).

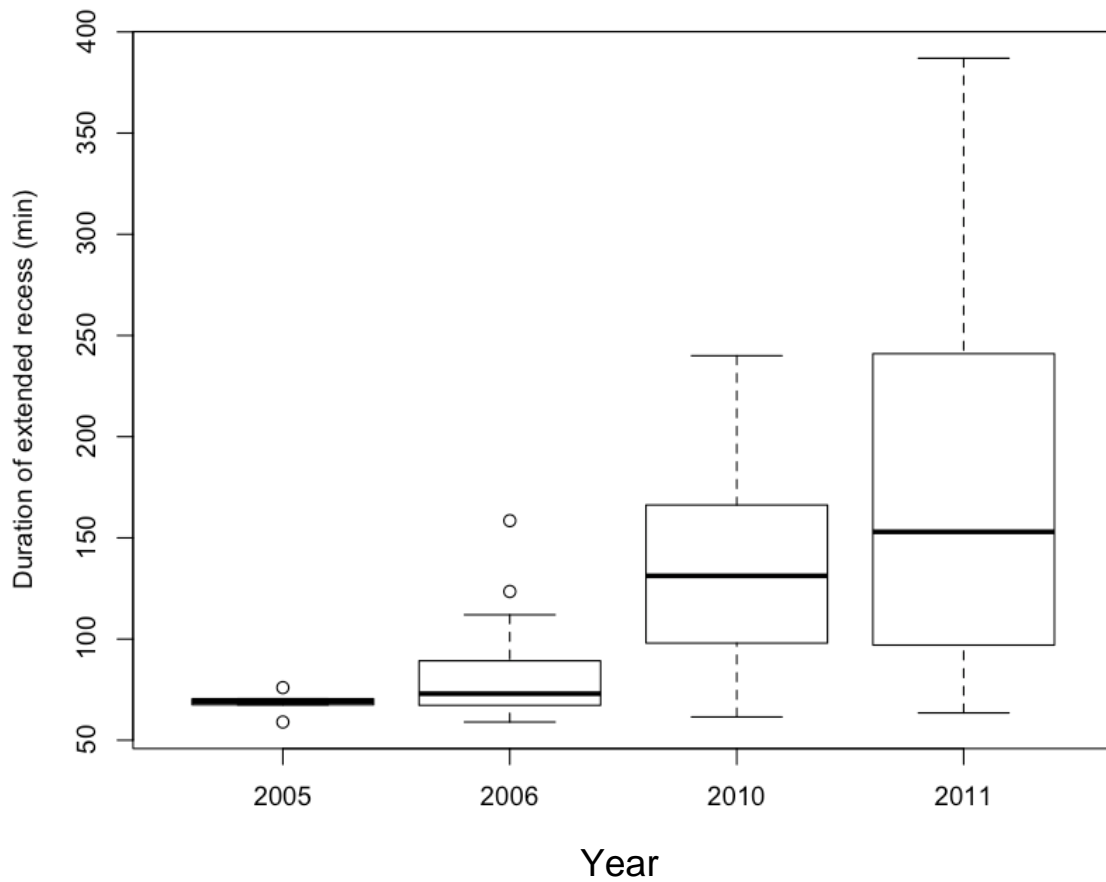


Figure 3.3 – Duration of extended recesses (min) taken by incubating Horned Larks on Hudson Bay Mountain among four breeding seasons. The mid-line of each box represents the median, while the box is delineated by the 25<sup>th</sup> and 75<sup>th</sup> percentiles (containing the middle 50% of the data). The whiskers (dashed vertical lines) represent either the minimum and maximum values or approximately 2 SDs, in which case outliers are represented as open circles.

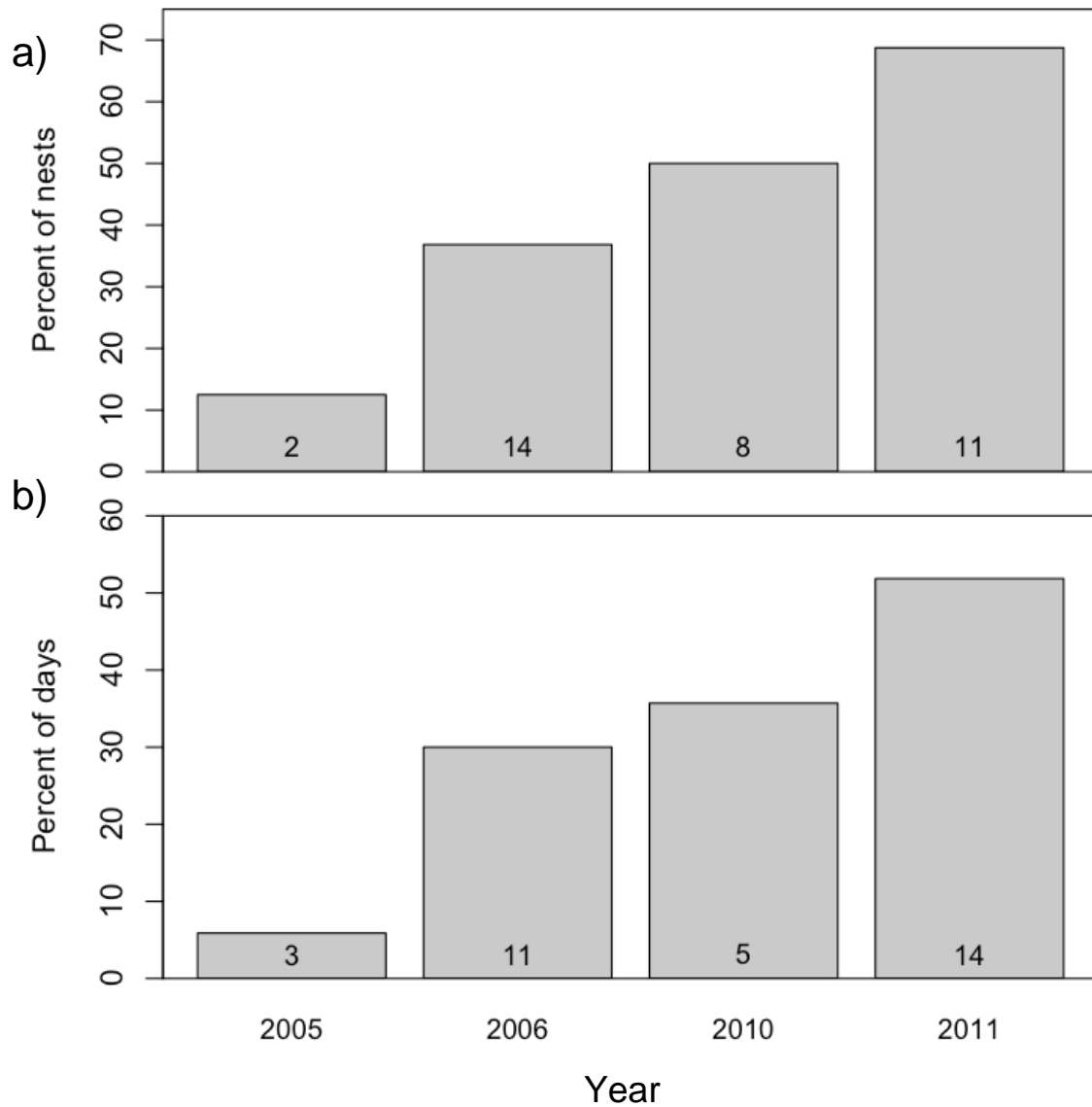


Figure 3.4 – Percentage of a) Horned Lark nests sampled in which the female took at least one extended recess and b) days sampled on which at least one extended recess occurred. Numbers on the bars represent a) the number of nests that took extended recesses and b) the number of different days on which extended recesses occurred, in each year.

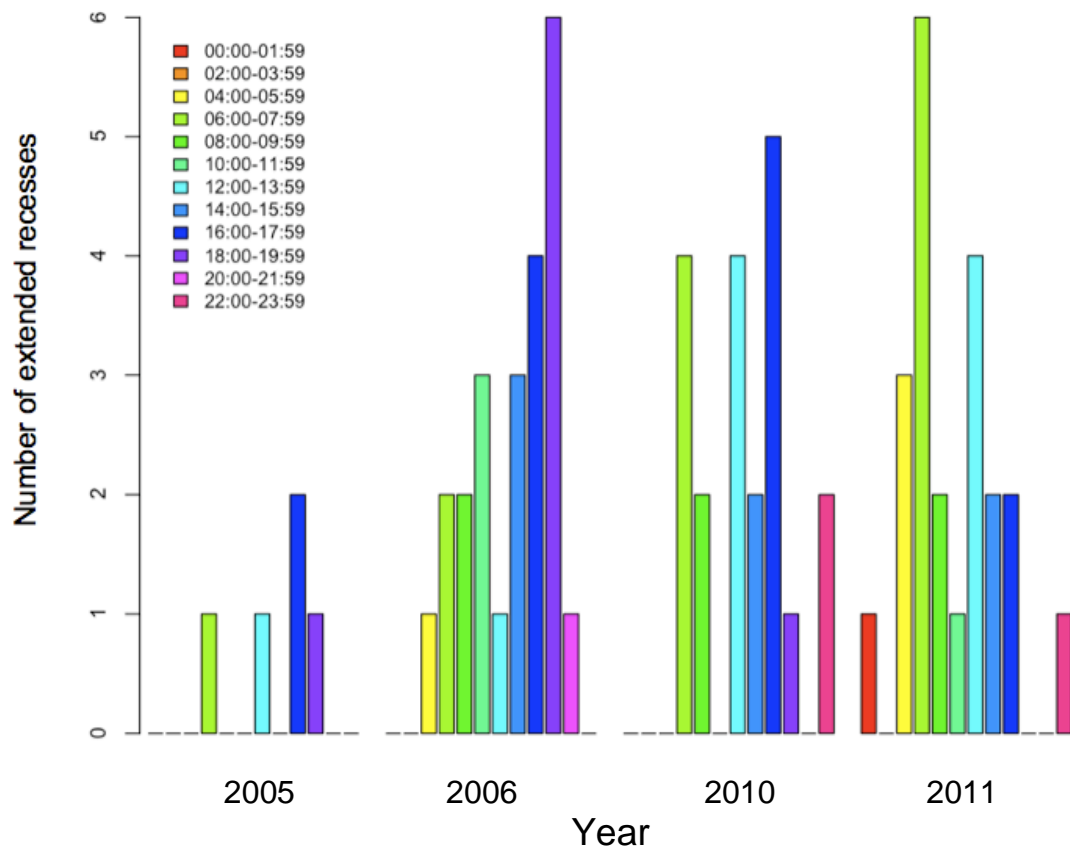


Figure 3.5 – Distribution of extended recesses initiated by incubating Horned Larks in each of twelve 2-h periods throughout the 24 h day. Each bar represents the number of extended recesses initiated within that 2-h period in that year.

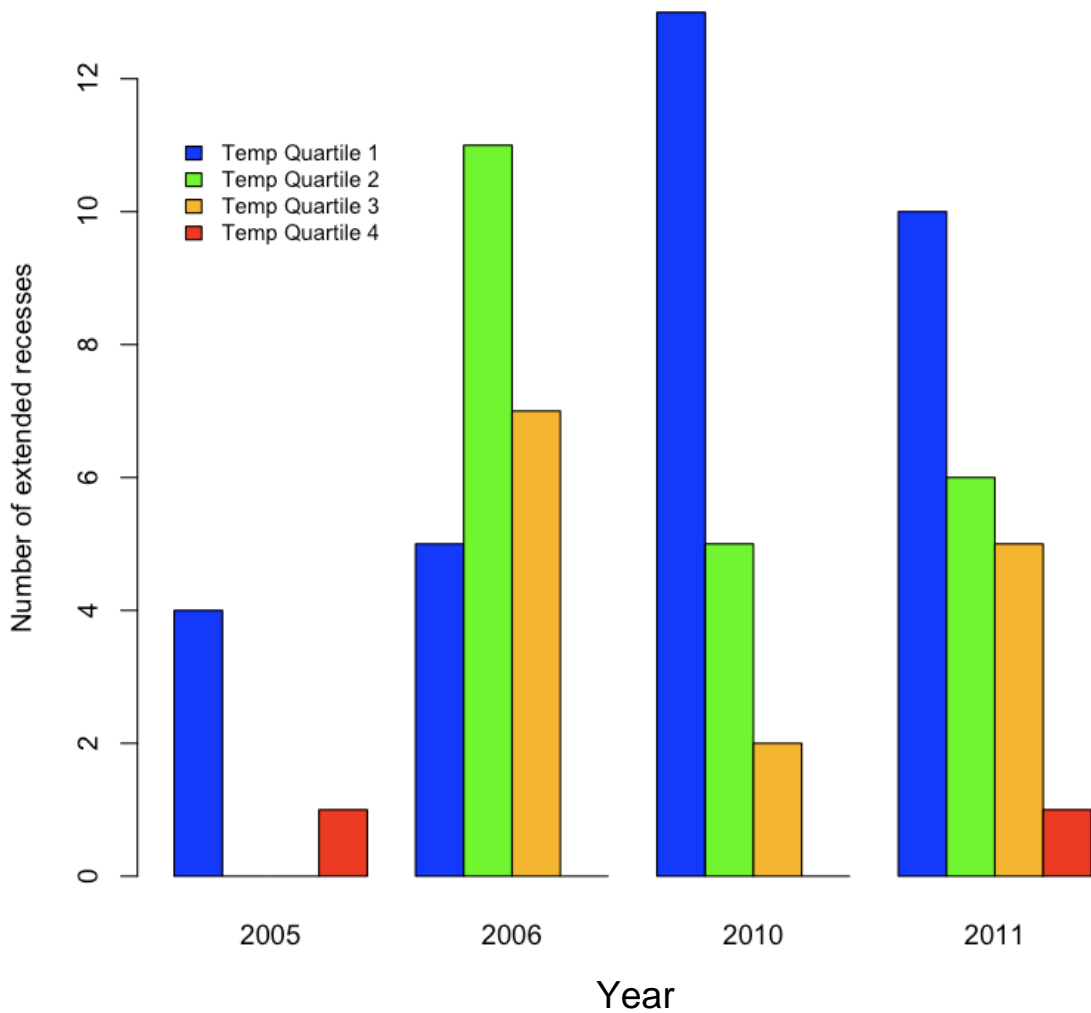


Figure 3.6 – Number of extended recesses distributed across mean daily ambient temperature quartiles, among years. Each bar represents the number of extended recesses taken in that year on a day in which mean temperature fell within that quartile. Quartiles represent different temperature ranges for each year and are delineated by 0, 25, 50, 75 and 100% values. These values are, respectively, 2005: 1.46°C, 4.05°C, 5.84°C, 8.32°C, and 14.35°C; 2006: -0.36°C, 4.83°C, 6.39°C, 9.93°C, and 18.75°C; 2010: -3.09°C, 2.45°C, 4.49°C, 7.42°C, and 17.98°C; 2011: -0.62°C, 2.25°C, 4.06°C, 6.46°C, and 12.83°C.



## CHAPTER 4 – GENERAL CONCLUSIONS AND IMPLICATIONS

### GENERAL CONCLUSIONS

Alpine birds possess a suite of behavioural, morphological or physiological adaptations in order to successfully breed (Martin and Wiebe 2004). For example, some high elevation songbirds display a dampened stress response, allowing them to breed through inclement weather (Bears et al 2003), and birds living at high altitude may build thicker, more insulated nests than those at low elevation (Potapov 2004). This study investigated behavioural mechanisms used by incubating Horned Larks in the alpine to understand how this species copes with the environmental variability characteristic of this habitat. Observations of larks life history characteristics and survival show that they are able to maintain high time and energy investments in their offspring and are well adapted to breeding in the alpine; however, individual decisions regarding management of the parent-offspring trade-off during incubation can vary with environmental conditions and energetic constraints.

Many studies report a relationship between incubation behaviour and ambient temperature, the nature of which varies among species and habitats (Conway and Martin 2000a, Camfield and Martin 2009, Kovarik et al 2009). I compared this relationship in alpine breeding larks among four thermally distinct years during a time of day when the parent-offspring conflict is expected to be strongest. In a year that was cold overnight, larks spent more time off the nest from 06:00-08:00 as ambient temperatures warmed, suggesting that a colder thermal regime may have caused parents to shift investment from reproduction towards self-maintenance (Chapter 2). Further evidence of this shift was presented and discussed in Chapter 3, where I described larks taking occasional extended incubation recesses ( $\geq 59$  min). These recesses were more common in cold years, often coincided with severe weather events, and may have reduced reproductive success. Cold diurnal temperatures posed a greater challenge for incubating larks than cold overnight temperatures, as extended recesses were more prevalent and hatching rate of eggs was reduced in a year with low daytime temperatures. By examining variability within

behavioural responses, we may gain a more complete understanding of how incubating adults reconcile parent-offspring trade-offs and what conditions they find challenging.

Focusing on specific times or abiotic conditions can reveal much about how and why birds vary their incubation rhythms. It is well established in the literature that many factors interplay to affect how a bird manages its time on the nest. In addition to ambient temperature, the time of day, stage of incubation, nest microhabitat and clutch size are just some of the many variables contributing to incubation time allocation decisions (Smith 1989, Wiebe and Martin 1998, Joyce et al. 2001, Wheelwright and Beagley 2005, Kovarik et al 2009, Camfield and Martin 2009). Describing a single species- or population-level pattern of how incubation behaviour is related to ambient temperature may not fully capture how that species or population manages the parent-offspring trade-off. In reality, we can expect this relationship to vary, particularly at extreme temperatures, based on some of the aforementioned variables. Examining only broad-scale patterns could mask key behavioural nuances, which may represent important strategies for successful breeding (e.g. extended recesses). I argue that to understand how a bird manages the trade-off between incubation and foraging, it may be more informative to look at finer scale responses during ecologically relevant times (as I have done in Chapter 2) than to quantify an overall behavioural pattern (such as Conway and Martin 2000a).

The thermal environment in which a bird incubates appears to shape behavioural responses to temperature. My study revealed is that it is not realistic to expect birds incubating in very different thermal environments to behave similarly, as I have shown that even within a population, variable annual thermal regimes can produce different behavioural patterns. Conway and Martin (2000a) described a nonlinear, theoretical relationship between incubation behaviour and ambient temperature for small-bodied species with intermittent incubation. They predicted on-bout and recess duration should increase as temperatures warm to the zone of thermal tolerance for embryos and adults, and decrease as temperatures warm beyond this zone (up until a point where birds no longer leave the nest). Their field data from Orange-crowned Warblers (*Oreothlypis*

*celata*) substantiated these predictions; however, studies of single-sex incubating songbirds in the alpine do not follow this pattern (Camfield and Martin 2009, Kovarik et al 2009). The thermal environment in which a species is incubating, and how well adapted that species is to their thermal environment, would certainly affect how they behave in relation to temperature. The Conway and Martin model, though generally accepted, may be very limited in its ability to inform expected relationships between incubation behaviour and temperature unless we incorporate more information on species across a wide range of environments, particularly extremes.

Although they are relatively rare, the extended recesses I have described are probably an essential component of Horned Lark incubation behaviour. Neglect behaviour is common in seabirds (Boersma and Wheelwright 1979, Blight et al 2010), and I have found descriptions among various other avian species, including: Ring-billed Gulls (*Larus delawarensis*), American Kestrel (*Falco sparverius*), Eurasian Dotterel (*Charadrius morinellus*), Red-necked Grebes (*Podiceps grisegena*), Blood Pheasants (*Ithaginis cruentus*), and Mountain Plovers (*Charadrius montanus*; Chardine and Morris 1983, Sockman and Schwabl 1998, Holt 2002, Nuechterlein and Buitron 2002, Jia et al 2010, Skrade and Dinsmore 2012). A number of triggers for egg neglect have been put forth, such as poor food quality, inclement weather and predation avoidance (Boersma and Wheelwright 1979, Holt 2002, Nuechterlein and Buitron 2002, Jia et al 2010) and it has been suggested long incubation recesses are an important behavioural strategy for coping with energetic stressors (Haftorn 1988, Holt 2002). In songbirds, neglect has been observed in a few species during severe weather (Morton and Pereyra 1985, Haftorn 1988) and nocturnal neglect occurs in some cavity-nesting species, although it is not clear what triggers such events (Wang and Beissinger 2009, Wang and Weathers 2009). A comprehensive discussion of this behaviour is lacking for passerines. My findings strengthen the idea that this is a stress related response to energetic constraints (Morton and Pereyra 1985, Haftorn 1988). The parent's decision to take care of itself during inclement weather would leave eggs exposed to low temperatures for a considerable length of time. Horned Lark embryos are clearly able to withstand substantial periods of cooling, although the extent of this tolerance is still unknown. Extended recesses may be

very important for maintaining high adult survival, which appears to be a critical strategy to successful breeding in the alpine (Sandercock et al 2005, Bears et al 2009).

## **IMPLICATIONS**

Alpine habitats appear to be particularly vulnerable to climate warming; some mountain areas are warming approximately twice as fast as the global average (Brunetti et al 2009, Chamberlain et al 2012). Horned Larks seem quite well adapted to current conditions; while lark populations across North America are declining, the Hudson Bay Mountain population is stable or slightly increasing (Camfield et al 2010, Sauer et al 2011). However, an increase in unpredictable events in an already harsh environment can create severe stress, which may push alpine birds beyond their limits of tolerance (Wingfield et al 2011). Larks appeared to favour themselves during such energetic stressors, which may have led to fitness consequences in the form of longer incubation periods and/or reduced hatching success. If these consequences persisted across many years, there could be serious demographic implications, even for a robust species like Horned Larks. Alpine areas may be important refuge habitat for generalist species as low elevation habitat is destroyed (Camfield 2008). If these areas become unsuccessful breeding habitats, alpine generalist songbirds may be left with little suitable habitat.

## **FUTURE RESEARCH**

To understand parent-offspring trade-offs during incubation, we require more studies looking at fine-scale responses during energetically stressful times. Broad, population-level patterns are very useful for understanding the general way in which birds behave and manage their time spent incubating. Additionally, by examining particular time periods or temperature ranges we gain further insight into specific mechanisms underlying the trade-off. Long-term studies are also important, as they capture a wider range of variation, increasing the likelihood of observing behaviours under energetically stressful conditions.

Experimental manipulations of energetic conditions are required to fully understand how Horned Larks manage their parent-offspring trade-off. Future studies on

this population examining the effects of experimental nest heating and cooling, experimental manipulation of body condition and experimentally supplemented diets on incubation behaviour would test some of the mechanisms I have proposed (e.g. Ardia and Clotfelter 2007, Ardia et al 2009, 2010). Through a series of experiments that heighten or alleviate various energetic constraints, we could more specifically determine what conditions incubating Horned Larks find challenging, as well as their limits to tolerance.

In general, our understanding of embryonic thermal tolerance is lacking, which hinders our understanding of the range of potential parent-offspring trade-offs during incubation. The Domestic Fowl (*Gallus gallus domesticus*) embryo, a large species with precocial young, remains the standard model for embryonic development in relation to temperature (Lundy 1969, Haftorn 1988, Conway and Martin 2000a), when it is likely inadequate, especially for small-bodied passerines with altricial development. Perhaps optimal physiological conditions are similar across species; however, these conditions are rarely met in nature (Williams 1996). Thus, understanding tolerance to suboptimal temperatures is more relevant. Species likely vary a great deal (Webb 1987), which limits the predictive power of our current model. We need further studies that combine observations of incubation behaviour and embryo temperatures, across a wide range of species and habitats, particularly extreme environments, to understand the extent to which embryos are thermally tolerant, and how this may shape (or be shaped by) parental behaviour.

## WORKS CITED

- Antor, R.J. 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *Journal of Avian Biology* **26**: 81-85.
- Ardia, D.R., and Clotfelter, E.D. 2007. Individual quality and age affect responses to an energetic constraint in a cavity-nesting bird. *Behavioral Ecology* **18**: 259-266.
- Ardia, D.R., Perez, J.H., Chad, E.K., Voss, M.A. and Clotfelter, E.D. 2009. Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *Journal of Animal Ecology* **78**: 4-13.
- Ardia, D.R., Perez, J.H., and Clotfelter, E.D. 2010. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proceedings of the Royal Society B* **277**: 1881-1888.
- Bears, H., Smith, J.N.M, and Wingfield, J.C. 2003. Adrenocortical sensitivity to stress in dark-eyed juncos (*Junco hyemalis oregonus*) breeding in low and high elevation habitat. *Ecoscience* **10**: 127-133.
- Bears, H., Martin, K., and White, G.C. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. *Journal of Animal Ecology* **78**: 365-375.
- Beason, R.C. 1995. Horned lark (*Eremophila alpestris*). In *The Birds of North America*, No. 195 in A. Poole, and F. Gill, editors. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sturnus vulgaris*). *Physiological Zoology* **57**: 26-31.
- Blight, L.K., Bertram, D.F., Williams, T.D. and Cowen, L. 2010. Interannual variation in egg neglect and incubation routine of rhinoceros auklets *Cerorhinca monocerata* during the 1998-1999 El Niño/La Niña events. *Marine Ornithology* **38**: 11-15.
- Boersma, P.D., and Wheelwright, N.T. 1979. Egg neglect in the procellariiformes: reproductive adaptations in the fork-tailed storm-petrel. *Condor* **81**: 157-165.
- Bókony, V., Lendvai, Á.Z., Liker, A., Angelier, F., Wingfield, J.C. and Chastel, O. 2009. Stress response and the value of reproduction: are birds prudent parents? *American Naturalist* **173**: 589-598.
- Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R., and Schöner, W. 2009. Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. *International Journal of Climatology* **29**: 2197-2225.

- Bryan, S.M., and Bryant, D.M. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proceedings of the Royal Society of London B* **266**: 157-162.
- Camfield, A.F. 2008. Life history tradeoffs, incubation behaviour and conservation of horned larks (*Eremophila alpestris*) [dissertation]. University of British Columbia, Vancouver, BC.
- Camfield, A.F. and Martin, K. 2009. The influence of ambient temperature on horned lark incubation behaviour in an alpine environment. *Behaviour* **146**: 1615-1633.
- Camfield, A.F., Pearson, S.F., and Martin, K. 2010. Life history variation between high and low elevation subspecies of horned larks *Eremophila* spp. *Journal of Avian Biology* **41**: 273-281.
- Carey, C. 2002. Incubation in extreme environments. Pages 238-253 in *Avian incubation: behaviour, environment and evolution* (D.C. Deeming, Ed.). Oxford University Press, UK.
- Chalfoun, A.D., and Martin, T.E. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Animal Behaviour* **73**: 579-585.
- Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A., and Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. *Ibis* **154**: 205-209.
- Chardine, J.W., and Morris, R.D. 1983. Nocturnal desertion patterns: influence on hatching synchrony in ring-billed gulls *Larus delawarensis*. *Ibis* **125**: 389-396.
- Conway, C.J., and Martin, T.E. 2000a. Effects of ambient temperature on avian incubation behavior. *Behavioural Ecology* **11**: 178-188.
- Conway, C.J., and Martin, T.E. 2000b. Evolution of passerine incubation behaviour: influence of food, temperature, and nest predation. *Evolution* **54**: 670-685.
- Cooper, C.B., and Mills, H. 2005. New software for quantifying incubation behavior from time-series recordings. *Journal of Field Ornithology* **76**: 352-256.
- Crawley, M.J. 2007. *The R book*. Wiley Publishing.
- Creswell, W., Holt, S., Whitfield, D.P., Mellanby, R.J., Norton, D. and Waldron, S. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology* **15**: 498-507.

- Divoky, G.J., and Harter, B.B. 2010. Supernormal delay in hatching, embryo cold tolerance and egg fostering in the black guillemot *Cephus grylle*. *Marine Ornithology* **38**: 7-10.
- Dobson, F.S. 1992. Body mass, structural size, and life-history patterns of the Columbian ground squirrel. *American Naturalist* **140**: 109-125.
- Drent, R.H. 1975. Incubation. Pages 333-420 in *Avian biology*. Vol. 5. (D.S. Farner and J.R.King, Eds.). Academic Press, New York.
- Edwards, J.S., and Banko, P.C. 1976. Arthropod fallout and nutrient transport: a quantitative study of Alaskan snowpatches. *Arctic and Alpine Research* **8**: 237-245.
- Eikenaar, C., Berg, M. L. and Komdeur, J. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. *Journal of Avian Biology* **34**: 419-427.
- Ghalambor, C.K., and Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**: 494-497.
- Gorman, H.E., and Nager, R.G. 2003. State-dependent incubation behaviour in the zebra finch. *Animal Behaviour* **65**: 745-754.
- Gutschick, V.P., and BassiriRad, H. 2003. Extreme events as shaping physiology, ecology and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist* **160**: 21-42.
- Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scandinavica* **19**: 97-110.
- Haftorn, S., and Reinertsen, R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* **102**: 470-478.
- Holt, S. 2002. Uniparental incubation in a cool climate: behavioural adaptations in the Eurasian Dotterel [dissertation]. University of Stirling, Stirling UK.
- Holt, S., Whitfield, D.P., Duncan, K., Rae, S., and Smith, R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation of constraint? *Journal of Avian Biology* **33**: 219-224.
- Jia, C.X., Sun, Y.H., and Swenson, J.E. 2010. Unusual incubation behavior and



- embryonic tolerance of hypothermia by the blood pheasant (*Ithaginis cruentus*). Auk **127**: 926-931.
- Jones, G. 1989. Optimizing time off the nest during incubation in female swallows (*Hirundo rustica*). Functional Ecology **3**: 303-309.
- Joyce, E.M., Sillett, T.S., and Holmes, R.T. 2001. An inexpensive method for quantifying incubation patterns of open-cup nesting birds, with data for black-throated blue warblers. Journal of Field Ornithology **72**: 369-379.
- Katz, R.W., Brush, G.S., and Parlange, M.B. 2005. Statistics of extremes: modeling ecological disturbances. Ecology **86**: 1124-1134.
- Kovarik, P., Pavel, V. and Chutny, B. 2009. Incubation behaviour of the meadow pipit (*Anthus pratensis*) in an alpine ecosystem of central Europe. Journal of Ornithology **150**: 549-556.
- Lewis, S., Hamer, K.C., Money, L., Griffiths, R., Wanless, S., and Sherratt, T.N. 2004. Brood neglect and contingent foraging behavior in a pelagic seabird. Behavioural Ecology and Sociobiology **56**: 81-88.
- Londono, G.A., Levey, D.J., Robinson, S.K. 2008. Effects of temperature and food on incubation behaviour of the northern mockingbird, *Mimus polyglottos*. Animal Behaviour **76**: 669-677.
- Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. Pages 143-176 in The fertility and hatchability of the hen's egg (T.C. Cartin, and B.M. Freeman, Eds.). Oliver and Boyd, Edinburgh.
- Lyon, B.E., and Montgomerie, R.D. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? Behavioral Ecology and Sociobiology **17**: 279-284.
- Martin, K. 2001. Wildlife in alpine and sub-alpine habitats. Pages 285-310 in Wildlife-habitat Relationships in Oregon and Washington (D.H. Johnson, and T.A. O'Neil, Eds.). Oregon State University Press.
- Martin, K., Stacey, P.B., and Braun, C.E. 2000. Recruitment, dispersal and demographic rescue in spatially-structured white-tailed ptarmigan populations. Condor **102**: 503-516.
- Martin, K., and Wiebe, K.L. 2004. Coping mechanisms of arctic and alpine breeding birds: extreme weather and limitations to reproductive resilience. Integrative Comparative Biology **44**: 177-185.

- Martin, M., Camfield, A.F., and Martin, K. 2009. Demography of an alpine population of savannah sparrows. *Journal of Field Ornithology* **80**: 253-264.
- Martin, T.E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London B* **269**: 309-316.
- Martin, T.E., Auer, S.K., Bassar, R.D., Niklison, A.M. and Lloyd, P. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* **61**: 2558-2569.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**: 456-466.
- Møller, A.P. 1991. The effect of feather nest lining on reproduction in the swallow *Hirundo rustica*. *Ornis Scandinavica* **22**: 396-400.
- Moreno, J. 1989. Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe* (L.). *Ardea* **77**: 107-115.
- Morton, M.L., and Pereyra, M.E. 1985. The regulation of egg temperatures and attentiveness patterns in the dusky flycatcher (*Empidonax oberholseri*). *Auk* **102**: 25-37.
- Myers, J.P., and Pitelka, F.A. 1979. Variations in summer temperature patterns near Barrow, Alaska: analysis and ecological interpretation. *Arctic and Alpine Research* **11**: 131-144.
- Nord, A., Sandell, M.I. and Nilsson, J.A. 2010. Female zebra finches compromise clutch temperature in energetically demanding incubation conditions. *Functional Ecology* **24**: 1031-1036.
- Nuechterlein, G.L., and Buitron, D. 2002. Egg neglect and prolonged incubation in the red-necked grebe. *Waterbirds* **25**: 485-491.
- Olson, C.R., Vleck, C.M., and Vleck, D. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* **79**: 927-936.
- Pearse, A.T., Cavitt, J.F., and Cully, J. F., Jr. 2004. Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson Bulletin* **116**: 23-30.
- Pinheiro, J., and Bates, D. 2000. *Mixed-effects models in S and S-Plus*. Springer, New York, NY.
- Potapov, R.L. 2004. Adaptation of birds to life in high mountains in Eurasia. *Acta*

- Zoologica Sinica **50**: 970-977.
- R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Reid, J.M., Monaghan, P. and Ruxton, G.D. 2000. Resource allocation between reproduction phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London B* **267**: 37-41.
- Reid, J.M., Ruxton, G.D., Monaghan, P., and Hilton, G.M. 2002. Energetic consequences of clutch temperature and clutch size for a uniparental intermittent incubator: the starling. *Auk* **119**: 54-61.
- Ricklefs, R.E. 1965. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**: 1-48.
- Sandercock, B.K., Martin, K., and Hannon, S.J. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* **86**: 2176-2186.
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, Jr., D. J. and Link, W.A., 2011. The North American Breeding Bird Survey, Results and Analysis 1966 - 2009. Version 3.23.2011 USGS Patuxent Wildlife Research Center, Laurel, MD.
- Skrade, P.D.B., and Dinsmore, S.J. 2012. Incubation patterns of a shorebird with rapid multiple clutches, the mountain plover (*Charadrius montanus*). *Canadian Journal of Zoology* **90**: 257-266.
- Smith, H.G. 1989. Larger clutches take longer to incubate. *Ornis Scandinavica* **20**: 156-158.
- Smith, H. G., Kallander, H., Hultman, J., and Sanzen, B. 1989. Female nutritional state affects the rate of male incubation feeding in the pied flycatcher *Ficedula hypoleuca*. *Behavioural Ecology and Sociobiology* **24**: 417-420.
- Sockman, K.W., and Schwabl, H. 1998. Hypothermic tolerance in an embryonic American kestrel (*Falco sparverius*). *Canadian Journal of Zoology* **76**: 1399-1402.
- Swain, S.D. 1991. Metabolism and energy reserves of brood-rearing horned larks (*Eremophila alpestris*). *Comparative Biochemistry and Physiology* **99**: 69-73.
- Tatner, P., and Bryant, D.M. 1993. Interspecific variation in daily energy expenditure during avian incubation. *Journal Zoology of London* **231**: 215-232.

- Tieleman, B.I., Williams, J.B., and Ricklefs, R.E. 2004. Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds. *Functional Ecology* **18**: 571-577.
- Trost, C. H. 1972. Adaptations of horned larks (*Eremophila alpestris*) to hot environments. *Auk* **89**: 506-527.
- Vleck, C.M., and Vleck, D. 1987. Metabolism and energetics of avian embryos. *Journal of Experimental Zoology Supplement* **1**: 111-125.
- Voss, M.A., Hainsworth, F.R. and Ellis-Felege, S.N. 2006. Use of a new model to quantify compromises between embryo development and parental self-maintenance in three species of intermittently incubating passerines. *Journal of Thermal Biology* **31**: 453-460.
- Wang, J.M., and Beissinger, S.R. 2009. Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Animal Behaviour* **78**: 601-613.
- Wang, J.M., and Weathers, W.W. 2009. Egg laying, egg temperature, attentiveness, and incubation in western bluebird. *Wilson Journal of Ornithology* **121**: 512-520.
- Webb, D.R. 1987. Thermal tolerance of avian embryos: a review. *Condor* **89**: 874-989.
- Webster, A.J.F., Tuddenham, A., Saville, C.A. and Scott, G.B. 1993. Thermal stress on chickens in transit. *British Poultry Science* **34**: 267-277.
- Wheelwright, N.T., and Beagley, J.C. 2005. Proficient incubation by inexperienced savannah sparrows *Passerculus sandwichensis*. *Ibis* **147**: 67-76.
- White, F.N., and Kinney, J.L. 1974. Avian incubation: interactions among behavior, environment, nest and eggs result in regulation of egg temperature. *Science* **186**: 107-115.
- Wiebe, K.L., and Martin, K. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. *Wildlife Biology* **3**: 219-227.
- Wiebe, K.L., and Martin, K. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour*. **56**: 1137-1144.
- Williams, J.B. 1996. Energetics of avian incubation. Pages 375-415 *in* Avian energetics and nutritional ecology (C. Carey, Ed.). Chapman and Hall, London, United Kingdom.

- Wilson, S., and Martin, K. 2010. Variable reproductive effort for two ptarmigan species in response to spring weather in a northern alpine ecosystem. *Journal of Avian Biology* **41**: 319-326.
- Wilson, S., and Martin, K. 2011. Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. *Population Ecology* **53**: 459-471.
- Wingfield, J.C. 2003. Control of behavioural strategies for capricious environments. *Animal Behaviour* **66**: 807-816.
- Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S., Ramenofsky, M., and Richardson, R.D. 1998. Ecological bases of hormone-behavior interactions: the “emergency life history stage”. *American Zoologist* **38**: 191–206.
- Wingfield, J.C., Kelley, J.P., and Angelier, F. 2011. What are extreme environments and how do organisms cope with them? *Current Zoology* **57**: 363–374.
- Zar, J. H. 1999. *Biostatistical analysis*, 3rd ed. Prentice Hall, Upper Saddle River, NJ.
- Zerba, E., and Morton, M.L. 1983. Dynamics of incubation in mountain white-crowned sparrows. *Condor* **85**: 1-11.
- Zimmerling, J.R., and Ankney, C.D. 2005. Variation in incubation patterns of red-winged blackbirds nesting at lagoons and ponds in eastern Ontario. *Wilson Bulletin* **117**: 280-290.