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RESEARCH ARTICLE

Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success

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ABSTRACT

We examined the impact of daily and severe multiday weather events on nest survival of Horned Larks (*Eremophila alpestris*) and Savannah Sparrows (*Passerculus sandwichensis*) breeding sympatrically in alpine habitat. The two species' thermal regimes varied. The breeding season of Horned Larks was ~2°C colder and had more precipitation and more storms than that of Savannah Sparrows, which initiated laying 2 wk later. The breeding season of Savannah Sparrows was, on average, 27% shorter than that of Horned Larks. Overall daily nest survival (DNS) was similar for the two species, but Savannah Sparrows had more failure due to abandonment (33% of nests) than Horned Larks (10%). Using Program MARK and Akaike's Information Criterion model selection to evaluate effects of daily and cumulative temperature and precipitation on DNS, we found no direct effect of daily temperature on nest survival, but nest survival declined in colder years for both species. For Horned Larks, the top nest survival models included a decline in DNS with increasing nest age and number of storm events, and a temperature × storm interaction. Daily nest mortality (DNM) increased by 8–9× over background failure levels during cold storms (average = 5°C), but there was little change in DNM during warmer storms (8°C). For Savannah Sparrows, the top nest survival models included a negative influence of cumulative precipitation. The top model's predicted DNM was ~4.6× higher after ≥2 days of precipitation than following days without rain. Both species coped well with the range of daily temperatures and single days of precipitation typical of alpine habitats, but the earlier-breeding Horned Larks were more susceptible to storm events, whereas extended precipitation events most strongly affected Savannah Sparrow nest survival. The ability of these songbirds to persist in alpine habitats may depend partly on the proportion of "cold" and "warm" storm events in future alpine climates.

Keywords: alpine, daily nest survival, extreme weather events, Horned Lark, precipitation, Savannah Sparrow, storms, temperature–precipitation interactions

Efectos del clima severo en la reproducción de aves canoras simpátricas en un ambiente alpino: las interacciones de extremos climáticos influyen en el éxito de anidación

RESUMEN

Examinamos el impacto de eventos climáticos severos de uno o varios días en la supervivencia de los nidos de dos especies (*Eremophila alpestris* y *Passerculus sandwichensis*) que se reproducen simpátricamente en un hábitat alpino. Los regímenes térmicos variaron entre especies, siendo la temporada reproductiva de *E. alpestris* aproximadamente 2°C más fría y con mayor precipitación y tormentas que la de *P. sandwichensis*, que inició la puesta de huevos dos semanas después. La temporada reproductiva de *P. sandwichensis* fue 27% más corta en promedio que la de *E. alpestris*. La supervivencia diaria de los nidos (SDN) fue similar, pero en *P. sandwichensis* hubo mayor fracaso por abandono de los nidos (33%) en comparación con *E. alpestris* (10%). Usando el programa MARK y selección de modelos por AIC para evaluar los efectos de la temperatura diaria y acumulada y de la precipitación en la SDN, no encontramos un efecto directo de la temperatura diaria en la supervivencia de los nidos, pero la supervivencia de los nidos fue menor en años fríos para ambas especies. Para *E. alpestris* los mejores modelos de supervivencia incluyeron una disminución en la SDN con mayor edad de los nidos, número de tormentas y la interacción entre temperatura y tormentas. La mortalidad diaria de los nidos (MDN) se incrementó entre 8 y 9 veces en comparación con los niveles base durante las tormentas frías (promedio de 5°C), pero hubo poco cambio en la MDN durante tormentas más cálidas

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(8°C). Para *P. sandwichensis* los mejores modelos de supervivencia de los nidos incluyeron una influencia negativa de la precipitación acumulada. El mejor modelo predijo que la MDN era aproximadamente 4.6 veces mayor luego de 2 o más días de precipitación que en los días siguientes sin lluvia. Mientras que ambas especies se ajustaron bien al rango de temperaturas diarias y los días únicos de precipitación típicos de los hábitats alpinos, *E. alpestris* fue más susceptible a tormentas debido a que inicia su reproducción más temprano, mientras que lo periodos extendidos de lluvia impactaron más fuertemente la supervivencia de los nidos de *P. sandwichensis*. La habilidad de estas aves canoras para persistir en los hábitats alpinos podría depender en parte de la proporción de tormentas "cálidas" y "frías" en el clima alpino del futuro.

Palabras clave: Alpino, *Eremophila alpestris,* eventos de clima extremo, *Passerculus sandwichensis*, precipitación, supervivencia diaria de nidos, tormentas, interacción entre precipitación y temperatura

INTRODUCTION

Ambient environmental conditions are considered to strongly influence avian breeding success because eggs and nestlings require a consistent warm environment (about 36–40°C) for normal development (Ardia et al. 2010). In temperate biomes, parent birds must make up a thermal deficit or excess of 10–40°C or more from ambient conditions by heating and cooling their offspring over a period of several weeks while meeting their own somatic requirements (Conway and Martin 2000a, 2000b, Camfield and Martin 2009). Although cold or inhospitable weather is considered to be an energetic challenge with potential fitness costs (Hendricks and Norment 1991, Martin and Wiebe 2004, 2006, Smith et al. 2010), the difference in the ecological costs to birds breeding in normal vs. extreme weather conditions has received little study until recently (Skagen and Yackel Adams 2012, Pipoly et al. 2013, Conrey et al. 2016). In general, we have little direct knowledge as to which elements of ambient weather constitute "extreme conditions" for bird species within or across habitats, which has hampered our ability to refine predictions about the impacts of climate change. We explore this topic for 2 sympatric songbirds breeding in an alpine environment.

Global average temperatures are increasing, with significant rates of increase in the past half century (Hurrell and Trenberth 2010, IPCC 2013). Many habitats are expected to experience changes in average temperature and precipitation regimes, but in the Pacific Northwest of North America and elsewhere, the frequency and severity of extreme weather events are increasing in the form of snow, rain, or wind storms (Diaz and Bradley 1997, Easterling et al. 2000). An increase in the frequency of extreme weather is predicted to pose strong challenges for wildlife, particularly if they occur during the most physiologically demanding periods of the year, such as during breeding or migration (Katz and Brown 1992, Martin and Wiebe 2004, Moreno and Møller 2011). Episodes of extreme environmental conditions, especially if their duration is prolonged, may also exceed the energetic reserves of breeding birds, resulting in the birds shifting to an emergency life-history stage in which they alter their physiology and behavior to maximize their chance of survival, usually resulting in their reproductive failure (Wingfield 2003, Moreno et al. 2015). Extreme weather may also affect species indirectly by influencing other ecological factors such as food availability, energetic demands of predators, or the availability of alternative prey (Smith and Wilson 2010, Fisher et al. 2015, Sherry et al. 2015). In order to predict the resilience of birds to climate change, we need to know the conditions that pose the strongest challenge for breeding birds, and the degree to which species vary in their tolerance of these conditions (e.g., Wilson and Martin 2010, Conrey et al. 2016).

The frequency and amplitude of environmental stochasticity increase with elevation, thus increasing the energetic and ecological challenges for birds living in high mountains (Martin 2001, Jentsch et al. 2007, Bears et al. 2009). Although the timing of snowmelt is a constraint on when ground-nesting species can initiate breeding, suitable nesting conditions may vary among species (Smith and Andersen 1985, Martin et al. 2009, Wilson and Martin 2010). The frequency and duration of storm events that often occur at high elevations early in the breeding season can pose strong energetic challenges to breeding efforts, including complete nest failure (Bears et al. 2003, MacDonald et al. 2013). In such conditions, birds may experience trade-offs related to the timing of nest initiation. Initiating breeding early in the season maximizes the time available for fledgling development as well as for second or replacement clutches. However, nesting earlier may involve increased nest failure, resulting from more inclement weather or from higher predation risk due to easier detection by, or greater energetic needs of, predators (Byrkjedal 1980, Martin and Wiebe 2004, Smith and Wilson 2010). Breeding later in the season may incur lower risks related to inclement weather, but then the time to produce a second brood or a replacement clutch is restricted (Barba et al. 1995, Wilson and Martin 2008, Martin 2014). Strong annual variability in the severity of conditions, as occurs regularly in alpine environments, may result in birds developing plastic responses to extreme or delayed conditions (i.e. tracking spring weather and adjusting their breeding phenology). If they are unable to track conditions, they will likely suffer lower productivity

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in cold or inclement years (Møller et al. 2008, Fletcher et al. 2013). Various species may manage this trade-off differently, depending on their ability to cope with extreme conditions and the relative fitness costs of producing fewer or less well-developed young. Ultimately, the consequences of wildlife responses to extreme meteorological events will depend on ecological and life-history traits of species (Sandercock et al. 2005, Wilson and Martin 2010).

To examine how different species manage environmental constraints imposed by alpine environments, we studied the impact of average and extreme weather conditions on the nest survival of 2 sympatric ground-nesting songbirds on Hudson Bay Mountain (HBM), near Smithers, British Columbia, Canada (52°N, 127°W). Horned Larks (*Eremophila alpestris*) and Savannah Sparrows (*Passerculus sandwichensis*) are wide-ranging, open-country species that are elevation generalists, breeding from sea level to >4,000 m elevation (Beason 1995, Wheelwright and Rising 2008, Martin et al. 2009, Camfield et al. 2010). In an earlier study, we found that Horned Larks and Savannah Sparrows breeding on HBM partitioned their nesting niches temporally and spatially, with Horned Larks initiating breeding in more exposed nest sites and ~2 wk earlier than Savannah Sparrows, whereas Savannah Sparrows nested in taller vegetation with significantly more concealment (MacDonald et al. 2016). Both species appear to be well adapted to breeding in alpine habitats, and both have adopted a slower life-history strategy (with reduced reproductive rates compensated by higher annual survival) compared to their low-elevation conspecifics (Martin et al. 2009, Camfield et al. 2010, MacDonald et al. 2013, 2014).

Here, we evaluate which components of ambient weather conditions (daily temperature, precipitation) and more extreme weather (prolonged or intense rain events, snow storms) influence nesting success during the incubation and nestling stages for each species, given that daily nest mortality (DNM) varied seasonally (incubation, nestling stages) and for each species (MacDonald et al. 2016). First, we examined whether nest failure rates of the 2 species varied among years in relation to average seasonal temperature. Given that Horned Larks took more extended recesses in colder years, especially in association with storm events (MacDonald et al. 2013), we predicted that nest failure rates would be higher in colder years. Next, we examined responses to both individual weather elements and their interaction effects to determine whether impacts of weather were consistent between the 2 sympatric-breeding songbirds. Horned Larks have earlier breeding dates and more exposed nests than Savannah Sparrows, and we predicted that Horned Larks would experience (1) higher rates of nest failure and (2) relatively more failure due to abandonment than to depredation, in comparison to Savannah Sparrows. Finally, we reviewed songbird responses to weather variability across a range of open habitats to examine what types of normal and extreme weather events are most influential on reproductive success in high-elevation (alpine) vs. low-elevation open habitats (Arctic tundra, grassland, shrub steppe).

METHODS

Study Species and Site

We studied Horned Larks and Savannah Sparrows at HBM during 2003–2007 and 2010–2011 as part of a long-term study on the life history and demography of songbirds breeding in northern alpine regions in western North America (Camfield et al. 2010, MacDonald et al. 2014). The study site was a 4 km^2 area of subalpine meadows (about 1,500–1,650 m above sea level [a.s.l.]) and alpine tundra above (about 1,650–2,000 m a.s.l.). The alpine and upper subalpine zone is a simple habitat with little vertical vegetative structure. The timing of snowmelt varies annually, with patches of snow persisting through most of June, and the overall length of the growing season is considerably reduced in comparison to low-elevation habitats used by these species (Camfield et al. 2010, MacDonald et al. 2014). Daily breeding-season temperatures fluctuate widely at the site, dropping near or below freezing on most nights and sometimes exceeding 40°C at ground level during the day (Camfield and Martin 2009, MacDonald et al. 2013, 2014). Strong winds and storms involving snow or rain occur throughout the nesting period, with more frequent and extreme events earlier in the breeding season (Figure 1).

Data Collection

During the breeding season (May–July), we located nests of Horned Larks (1,650–1,875 m) and Savannah Sparrows (1,523–1,811 m) by systematically searching known territories and appropriate habitat, by observing adults during nest building or chick feeding, and by flushing incubating or brooding females. We searched for both species in 2003–2007 and for Horned Larks only in 2010 and 2011. We monitored nests every 3–5 days (and more frequently near expected hatch or fledge dates) until the nest fledged or failed. Failed nests were classified as depredated (empty nest cup with all contents removed prior to estimated fledge date) or abandoned (dead nestlings or cold eggs on ≥2 consecutive visits). For nests found after incubation was initiated, date of first egg was back-calculated from hatch, following Camfield et al. (2010) for Horned Larks and Martin et al. (2009) for Savannah Sparrows. For both species, we used information on the dates on which all nests were known to be active to estimate the length of the breeding period for each year. There were cases in most years where a single nest remained active for several days after nesting had stopped

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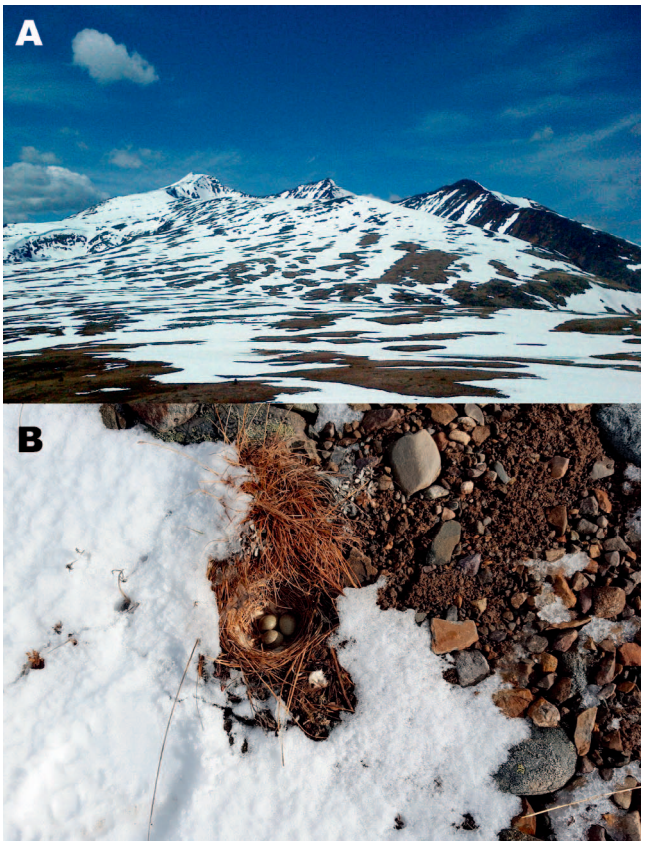


FIGURE 1. Horned Larks start breeding when there is still extensive snow cover on Hudson Bay Mountain Study area, British Columbia. **(A)** May and early June (photo credit: K. Martin). **(B)** Horned Lark nest with eggs after extensive snow storm on 30 May 2016 (photo credit: Devin de Zwaan).

for all other breeding pairs; therefore, as a more reflective measure for the population, we used the inner 90% of active nest dates as an index of breeding-period length. For all nests, we collected data on nest-site characteristics after fledge or failure (for detailed field methods, see MacDonald et al. 2016).

Weather Data

Weather data for this analysis were obtained from 2 sources: (1) a HOBO weather station located at the study site (HOBO Micro Station Logger H21-002; Onset Data Loggers, Bourne, Massachusetts, USA; 1,695 m) and (2) a weather station at Smithers Airport (522 m), located ~8 km from the study area. The HOBO station was installed in 2005 and recorded measurements of total daily precipitation and daily means for temperature, wind speed, and wind direction. The Smithers Airport data were used to predict weather data at HBM for 2003 and 2004 and for some periods in 2005–2007 and 2010–2011 when the HOBO field weather station did not operate. For temperature, these predictions were based on a regression of daily weather from HBM and Smithers Airport using all days for which temperature data were available for both stations. Daily temperature at Smithers Airport and HBM were closely correlated ($r = 0.88$), and for missing days at HBM we used the regression equation to predict daily temperature: $\text{Temp}_{\text{HBM}} = 1.204^{*}\text{Temp}_{\text{SA}} - 9.589$, where Temp_{HBM} and Temp_{SA} are the respective daily temperatures for HBM and Smithers Airport. The amount of daily precipitation was more variable between the 2 sites, but they were consistent in whether any precipitation had occurred (81% of days when data were available at both locations). Therefore, we based our analyses on whether or not >1 mm of precipitation occurred as a categorical variable. We also identified days when >10 mm of precipitation occurred in a 24 hr period using HBM data if available and Smithers Airport data if not. We refer to these days as "storm events" (for definitions, see Table 1).

Nest Survival

For both species, we examined whether daily nest survival (DNS) from day t to $t+1$ was influenced by (1) mean daily temperature on day t, (2) single days of precipitation >1 mm on day t, (3) cumulative days of precipitation in which at least day t and $t-1$ had >1 mm of precipitation, (4) storm events in which >10 mm of precipitation occurred on day t, and (5) the interaction of mean daily temperature with storm and precipitation events (Table 1). Our earlier analyses found that Horned Lark DNS was influenced by year, season (time since onset of the breeding season), and nest age (days since first egg laid) but not by nest-site characteristics, whereas Savannah Sparrow DNS was influenced by nest concealment (amount of lateral cover at the nest), year, and nest age (MacDonald et al. 2016). Therefore, we included these variables in our models to control for their influence on DNS while testing for weather effects.

DNS was analyzed using the nest survival module in Program MARK 6.0 (White and Burnham 1999, Dinsmore et al. 2002). Variables for daily temperature, occurrence of daily precipitation, cumulative precipitation, storm events, and interaction effects were added to the base model with the temporal and nest-site variables as described above (identified in MacDonald et al. 2016). Model selection and the effect size and confidence intervals (CIs) for parameter estimates were used to identify which weather variables were influential. Models were ranked using Akaike's Information Criterion for small sample size (AIC_c), and the ΔAIC_c values and Akaike weights (w_i) were used to infer support for each of the candidate models (Burnham and Anderson 2002). Because some of our models contained polynomial terms or interactions, we report coefficients from the top model rather than averaging across the candidate set. However, when the top model did not have clear support based on w_i, we discuss the

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TABLE 1. Description of covariates included in nest survival models testing the influence of weather and storm events on nest success of alpine-breeding Horned Larks and Savannah Sparrows on Hudson Bay Mountain, British Columbia, Canada (2003–2011).

Covariate	Description
Temperature	Mean daily temperature (°C)
Precipitation	>1 mm precipitation in 24 hr (binary)
Cumulative precipitation	≥2 consecutive days of precipitation
Storm events	>10 mm precipitation in 24 hr
Year	2003–2011
Time of season	Day of breeding season
Nest age	Nest age in days since first egg laid
Nest-site cover	Percent lateral cover around nest (see MacDonald et al. 2016)

variation in the coefficients across the suite of models within 2 AIC_c units of the top model. It is possible that some of the previously detected effects of temporal or nest-site variables (MacDonald et al. 2016) were actually related to weather. To test this, we ran additional models that included the top weather variables but with one of the temporal or nest-site variables removed and then compared model support. There was no support for any of these models that had one of the top temporal or nest-site terms removed, which indicates that the effects of temporal, nest-site, and weather variables were independent for each species.

We also estimated average annual DNS, using the model with year alone in an analysis of random effects (Cooch and White 2013). With this approach, the individual year estimates are assumed to originate from a random process governed by a common mean and temporal variance. This common mean represents average nest success, with the standard error representing annual variance in nest success (i.e. process variance). These annual estimates were then used in a linear regression to test how average DNS was influenced by the average daily temperature over the breeding season. This second analysis tests whether colder years have a negative influence on overall nesting success across the entire season. Results are presented ± SE.

RESULTS

Weather

For each species, we estimated the average temperature and precipitation experienced during the respective nesting period. During the Horned Lark breeding season, daily mean temperatures on the study area averaged 6.83°C across all years, ranging from a low of 4.73°C in 2011 to a high of 8.48°C in 2004 (Table 2). On average, in each year there were 24.3 days with precipitation >1 mm, 11.6 cases with ≥2 consecutive days of precipitation >1 mm, and 2.3 storm events during the Horned Lark breeding season. Across years, daily temperatures during the Savannah Sparrow breeding period averaged 8.99°C and ranged from a low of 7.13°C in 2007 to a high of 10.22°C in 2004 (Table 2). Annually, there was an average of 18.8 days of precipitation >1 mm, 10 cases with ≥2 consecutive days of precipitation >1 mm, and 1.5 storm events. We do not make direct interspecies comparisons because we lack completely overlapping datasets of years for each species.

Effects of Annual Mean Temperature on Daily Nest Survival

Average DNS was lower in colder years for both species (Figure 2). Linear model coefficients predicting annual DNS from annual temperature were $\hat{\beta}_{annual.temp} = 0.009 \pm 0.004$ (95% CI: 0.002–0.016) for Horned Larks and $\hat{\beta}_{annual.temp} = 0.016 \pm 0.007$ (95% CI: 0.008–0.023) for Savannah Sparrows. Savannah Sparrows had a stronger increase in annual DNS with temperature compared to

TABLE 2. Annual breeding-season weather conditions for Horned Larks (HOLA; 2003–2007, 2010–2011) and Savannah Sparrows (SAVS; 2003–2004, 2006–2007) on Hudson Bay Mountain, British Columbia, Canada. Estimates were restricted to the range of observed nesting dates for each species. Using the inner 90% percentile of the nesting period for each species, Savannah Sparrows initiate breeding 10 days later and finish 4 days earlier than Horned Larks.

	Temperature (°C)		Precipitation days		Cumulative precipitation days		Storm events		Period of nest activity (days)	
Year	HOLA	SAVS	HOLA	SAVS	HOLA	SAVS	HOLA	SAVS	HOLA	SAVS
2003	7.06	9.03	23	20	10	10	2	2	52.8	41.0
2004	8.48	10.22	25	20	14	13	3	2	56.8	37.4
2005	6.61	–	28	–	15	–	2	–	56.7	–
2006	8.37	9.60	18	13	8	5	2	0	53.1	39.6
2007	6.59	7.13	23	22	11	12	2	2	45.3	33.7
2010	5.36	–	25	–	9	–	0	–	46.3	–
2011	4.73	–	28	–	14	–	5	–	41.0	–
Overall	6.83	8.99	24.29	18.75	11.57	10.0	2.28	1.5	50.3	37.9

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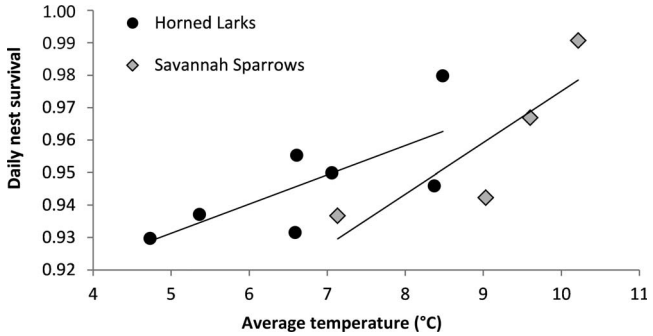


FIGURE 2. Annual estimates of daily nest survival (DNS) of Horned Larks (2003–2007, 2010–2011) and Savannah Sparrows (2003–2004, 2006–2007) on Hudson Bay Mountain, British Columbia, Canada, in relation to annual average daily temperatures (°C). Linear regression lines show the relationship of annual mean temperature and annual DNS for each species.

Horned Larks, but with CIs on the slope estimates that broadly overlapped.

Effects of Weather on Daily Nest Survival

Horned Lark. Nest survival analyses for Horned Larks were based on 280 nests across 7 yr (2003–2007, 2010–2011), with an effective sample size of 2,687 exposure days. The mean period of nest activity for Horned Larks across all years was 50.3 days, with a minimum of 41.0 days in 2011 and a maximum of 56.8 days in 2004 (Table 2). Nearly 90% of nest failure for Horned Larks was due to nest predation, with just over 10% due to abandonment (Figure 3). Using a variance component analysis with year, we estimated average DNS to be 0.954 ± 0.009, corresponding to an average nest success of 0.322 ± 0.075 for a 24-day nest cycle (mean = 24.4 days, $n = 27$ nests). The basal model for our analysis of weather effects included year effects, a linear increase in DNS over the course of the breeding season, and a decline in DNS as nest age increased (MacDonald et al. 2016). The top model with weather variables contained 67% of the model weight and included an interaction of storms and temperature (Table 3). The second-best model with only storms had 23% of model weight. Coefficients for the top model were $\hat{\beta}_{storm} = -3.17 \pm 0.90$, $\hat{\beta}_{temp} = -0.01 \pm 0.02$, and $\hat{\beta}_{storm*temp} = 0.37 \pm 0.23$; the positive interaction with temperature indicates that DNM was 9.0× and 8.2× higher during cold storm events compared to background levels (days with normal weather) for the incubation and nestling stages, respectively (Figure 4A). Horned Lark DNS was not influenced by temperature alone nor by single or cumulative days of >1 mm precipitation, as either additive or interaction effects (Table 3).

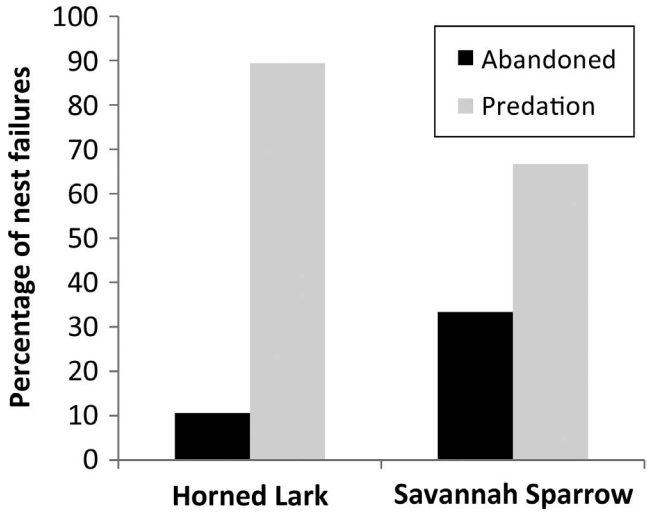


FIGURE 3. Percentage of nest failures attributed to either abandonment or predation in two sympatric alpine songbird species on Hudson Bay Mountain, British Columbia, Canada (2003–2007, 2010–2011).

TABLE 3. Model selection results for effects of weather on daily nest survival (DNS) of Horned Larks on Hudson Bay Mountain, British Columbia, Canada (2003–2007, 2010–2011). All models included an effect of year, time of season, and nest age based on previous analyses (MacDonald et al. 2016). Models tested the influence of weather on DNS from day t to $t + 1$.

Model (year + time + age) +	ΔAIC	w_i	K
+ storms*temp	0.00	0.671	12
+ storms	2.11	0.233	10
+ storms + temp	4.10	0.086	11
year + time + age	10.62	0.003	9
+ c.precip	12.47	0.001	10
+ precip	12.62	0.001	10
+ temp	12.64	0.001	10
+ c.precip + temp	14.48	0.000	11
+ precip + temp	14.63	0.000	11
+ c.precip*temp	14.79	0.000	12
+ precip*temp	16.63	0.000	12
intercept	26.04	0.000	1

Notes: ΔAIC = change in Akaike's Information Criterion, w_i = Akaike weights, K = number of model parameters, year = calendar year, time = linear seasonal effect, age = age of the nest, temp = mean temperature on day t, precip = >1 mm precipitation on day t, cumulative (c.) precip = >1 mm precipitation on at least day t and $t - 1$, and storms = >10 mm precipitation on day t.

Savannah Sparrow. Nest survival analyses for Savannah Sparrows were based on 87 nests over 4 yr (2003–2004, 2006–2007), with an effective sample size of 880 exposure days. Savannah Sparrows started nesting, on average, 10 days later and ended 4 days earlier than Horned Larks; their nest activity period averaged 37.9 days, with a minimum of 33.7 days in 2007 and a maximum of 41.0 days in 2003. In contrast to our predictions, abandonment was a greater source of nest failure for Savannah Sparrows than for Horned Larks, with 33% of nests being abandoned

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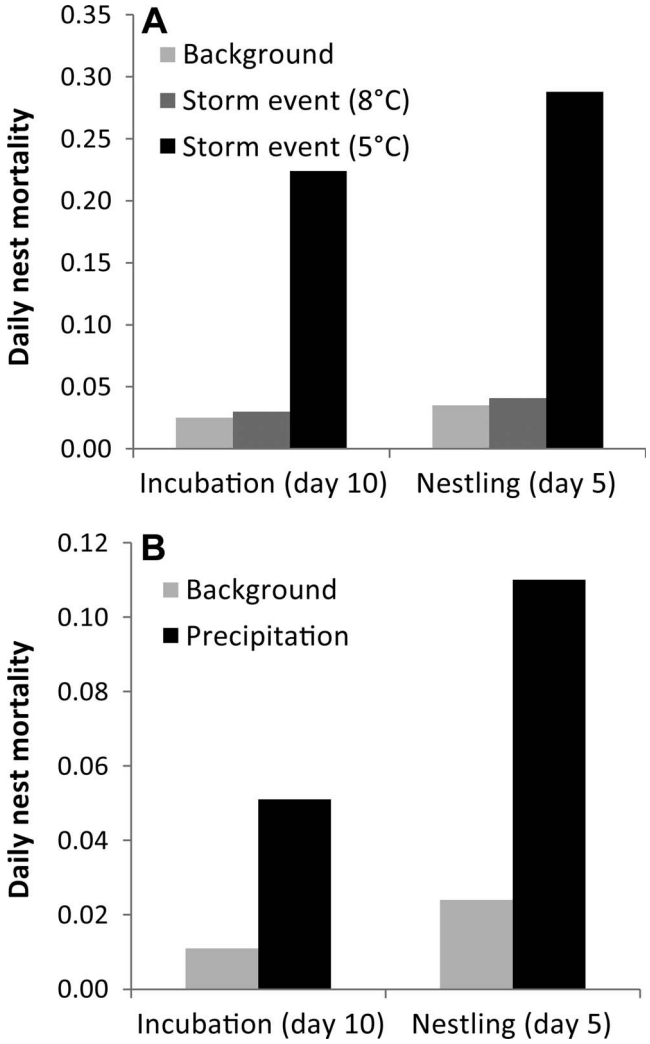


FIGURE 4. Daily nest mortality (DNM) during incubation and nestling stages in relation to (**A**) background conditions and warm (8°C) and cold (5°C) storms for Horned Larks (2003–2007, 2010–2011) and (**B**) background conditions and precipitation for Savannah Sparrows (2003–2004, 2006–2007) on Hudson Bay Mountain, British Columbia, Canada. DNM for Horned Larks was 8.2–9.0× higher during colder storm events (5°C) compared to background levels, and DNM was 4.6× higher for Savannah Sparrows after ≥2 consecutive days of precipitation (>1 mm/24 hr).

and 67% failing as a result of nest predators (Figure 3). Average DNS for Savannah Sparrows was 0.961 ± 0.014, with an expected nest success of 0.356 ± 0.137 based on a 26-day nest cycle (mean = 26.3 days, $n = 16$ nests). The basal model without weather effects included differences in DNS among years, a positive effect of the amount of lateral cover at the nest, and an interaction between nest age and nesting stage whereby DNS increased from laying through to the end of incubation, declined abruptly at hatching, and then increased again through the nestling period (MacDonald et al. 2016).

TABLE 4. Model selection results for effects of weather on daily nest survival (DNS) of Savannah Sparrows on Hudson Bay Mountain, British Columbia, Canada (2003–2004, 2006–2007). All models included an effect of year, lateral cover at the nest ("lateral"), and an interaction between nest age and stage ("age.int"; see text for details) based on earlier analyses (MacDonald et al. 2016). Models tested the influence of weather on DNS from day t to $t + 1$.

Model (year + lateral + age.int)	ΔAIC	w_i	K
+ c.precip*temp	0.00	0.240	10
+ storms	0.51	0.186	9
+ c.precip	0.86	0.156	9
+ c.precip*temp	0.95	0.149	11
+ storms+temp	1.66	0.104	10
year + lateral + age.int	3.04	0.052	8
+ precip*temp	3.90	0.034	11
+ temp	4.15	0.030	9
+ precip	4.44	0.026	9
+ precip + temp	4.71	0.022	10
intercept	28.69	0.000	1

Notes: ΔAIC = change in Akaike's Information Criterion, w_i = Akaike weights, K = number of model parameters, year = calendar year, time = linear seasonal effect, age = age of the nest, temp = mean temperature on day t, precip = >1 mm precipitation on day t, cumulative (c.) precip = >1 mm precipitation on at least day t and $t - 1$, storms = >10 mm precipitation on day t.

The smaller sample size of nests and fewer storms experienced by Savannah Sparrows led to convergence issues in the estimation of storm × temperature interactions. Therefore, we were only able to consider storms as an additive effect. The top model with weather effects included a negative influence of cumulative days of precipitation ($\hat{\beta}_{\text{c.precip}} = -1.60 \pm 0.58$; Figure 4B and Table 4) and a negative influence of temperature ($\hat{\beta}_{\text{temp}} = -0.08 \pm 0.046$). On average, temperatures were 5.91 ± 0.39°C during cumulative precipitation days and 10.09 ± 0.37°C on days with no precipitation. Predictions from the top model indicate that DNM was ~4.6× higher following ≥2 days of precipitation than following days without precipitation (Figure 4B). Savannah Sparrows were also negatively influenced by storm events ($\hat{\beta}_{\text{storm}} = -2.58 \pm 0.86$), similarly to Horned Larks (Table 4). A model with an interaction between cumulative days of precipitation >1 mm and temperature suggested higher DNS when temperatures were warmer ($\hat{\beta}_{\text{c.precip*temp}} = 0.31 \pm 0.28$), but with a wide standard error and CIs that broadly overlapped zero. Single days of precipitation >1 mm did not influence Savannah Sparrow DNS, nor was there evidence for an interaction effect with temperature.

We compared responses for birds breeding in a range of open habitats and found generally that there were minimal responses to daily temperatures and precipitation in high-elevation and high-latitude birds, but birds responded

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positively to temperatures and negatively to high precipitation in lower-elevation open habitats (Table 5). Most species in all systems exhibited negative responses to acute precipitation, but responses to acute temperature events varied, with more muted responses in high-elevation and high-latitude environments. Moreover, the type and extent of responses varied across stages of the nesting cycle, altering the overall impact of extreme events (e.g., Pérez et al. 2016).

DISCUSSION

Weather events influenced both Horned Larks and Savannah Sparrows breeding on HBM, but the 2 species had different responses to extreme precipitation events. Since Horned Larks initiated breeding ~2 wk earlier than Savannah Sparrows and chose more exposed nest sites, they were typically exposed to more storms and extreme weather events. For Horned Larks, an interaction between temperature and precipitation resulted in much higher nesting failure during cold storms than during storms at warmer temperatures. Savannah Sparrows, which nested later and in denser vegetation, experienced higher direct failure due to weather than Horned Larks, with most of their weather-related failure due to extended periods of precipitation. Although daily temperature alone had limited influence on nesting success, both species experienced lower DNS in colder years. Overall, Savannah Sparrows had lower tolerance of more extreme weather than Horned Larks, but they had similar nesting success, in part because their delayed nesting season coincided with more benign weather conditions.

In high-elevation and high-latitude habitats, birds are generally able to deal with high environmental variability (Martin and Wiebe 2004, Smith and Wilson 2010). However, within an ecosystem, sympatric species may vary in their tolerance. For example, in alpine habitats of the southwestern Yukon, Canada, clutch initiation and clutch size of Rock Ptarmigan (*Lagopus muta*; slow life-history strategy) were more strongly affected in years with delayed snowmelt and cold annual temperatures than those of the sympatric, congeneric White-tailed Ptarmigan (*L. leucura*; fast lifestyle) (Wilson and Martin 2010). In a second example, 2 Arctic passerines, Lapland Longspur (*Calcarius lapponicus*) and White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), showed a negative correlation in nestling growth and arthropod biomass (food availability) in a cold and wet year compared to a year with more moderate conditions, but each species varied in its ability to cope physiologically with these stressful conditions (Krause et al. 2016, Pérez et al. 2016).

The 2 sympatric alpine songbirds in our study experienced different thermal regimes for breeding despite sharing a common environment. As expected, both species were able to cope with typical alpine weather and generally showed few negative responses to single weather variables or single-day weather events. However, both species experienced fitness costs due to extended bouts of extreme weather, events that are increasing in frequency and severity in their habitats (IPCC 2013). By delaying breeding for 2 wk later than Horned Larks, Savannah Sparrows benefited from warmer and more benign breeding-season conditions and also experienced fewer extreme weather events (storms and days with heavy precipitation) during their nesting period. However, by delaying their breeding phenology, Savannah Sparrows incurred the ecological cost of a 27% shorter breeding season, on average (range: 22–34%), compared to Horned Larks (Table 2).

Because of the compressed growing season, birds in alpine habitats have a ~57% shorter breeding season than the same species at low elevation (Bears et al. 2009, Camfield et al. 2010, Martin 2014). Nesting early is beneficial because it may allow for multiple broods within a season (Smith and Andersen 1985) and more time for juveniles to develop before onset of fall migration; however, ground-nesting birds in alpine habitat are limited in their ability to nest early by the presence of snow. Across their range, Horned Larks breed in areas of minimal vegetation (Beason 1995), and in alpine habitat they often initiate clutches in the first snow-free patches exposed. Horned Larks may initiate breeding before Savannah Sparrows simply as a result of their preference for exposed habitat, given that the nest sites preferred by Savannah Sparrows become available only later in the season. Alternatively, Horned Larks are about twice the mass of Savannah Sparrows (~34 g [Camfield et al. 2010] vs. 18.2 ± 0.5 g [K. Martin personal observation], respectively), and therefore Savannah Sparrows may need to delay egg laying until warmer periods in order to meet the thermal requirements of self-maintenance and incubation in colder climates. In 2007, the coldest year, Savannah Sparrow eggs froze in the earliest-initiated nests, whereas Horned Larks incubated clutches throughout this period with no evidence of freezing (K. Martin personal observation). The larger size of Horned Larks may also confer greater physiological tolerance to the storms that occur more frequently at the beginning of the season.

Contrary to our predictions for failure type by species, rates of nest abandonment in our study—most likely due to harsh environmental conditions—were lower for the earlier-nesting Horned Larks, averaging only 10.6%, compared to 33.3% for Savannah Sparrows. Although this pattern was the opposite of our predictions, the higher abandonment rate for Savannah Sparrows compared to Horned Larks is consistent with the former's greater susceptibility to precipitation.

In temperate environments, studies at low elevations generally show a positive effect of temperature and average

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TABLE 5. Summary of qualitative effects of daily (acute) and annual weather on reproduction following nest initiation in high- and low-elevation open-country passerines.

Species	Location	Latitude, elevation (m a.s.l.)	Year(s) of study	Habitat type	Weather type	Weather variable, timing	Response variable	Qualitative effect	Comment	Reference
Horned Lark (*Eremophila alpestris*)	Hudson Bay Mountain, British Columbia, Canada	54°N ~1,500–1,900	2003–2007, 2010, 2011	Alpine tundra	Acute	Storm event (precipitation and cold), May–July	Nest survival	−	Temperature × precipitation interaction	Present study
Savannah Sparrow (*Passerculus sandwichensis*)		~1,500–1,650			Acute	Precipitation on ≥2 consecutive days, May–July		−		
Horned Lark and Savannah Sparrow		~1,500–1,900			Annual	Temperature, May–July		−	Declined in cold years for both species, esp. SAVS	
American Pipit (*Anthus rubescens*)	Beartooth Mountains, Wyoming, USA	44°N 3,200	1987	Alpine	Acute	Snowstorm, July	Nesting success	−	79% nestling mortality	Hendricks and Norment 1991
		2,900		Subalpine				−	7% nestling mortality; nestlings > 11 day survived (age of endothermy)	
Red-faced Warbler (*Cardellina rubrifrons*)	Arizona, USA	32°N 2,300–2,700	2008	High-elevation riparian	Acute	Snowstorm, May	Nest abandonment	−	68% of nests abandoned	Decker and Conway 2009
Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*)	Alaska, USA	68°N	2013–2014	Arctic tundra	Annual	Mean maximum temperature, June–July	Nestling growth rate	No effect	Lower arthropod biomass. Shrub-nests reduce heat loss?	Pérez et al. 2016
Lapland Longspur (*Calcarius lapponicus*)								+		
Gambel's White-crowned Sparrow						Precipitation, June–July	Nestling growth rate	−		
Lapland Longspur								−		
Lapland Longspur	Churchill, Manitoba, Canada	58°N ~10	1965	Tundra	Acute	Storm (cold, wind, rain), July 8–9	Nesting success	−	87% of 62 nests destroyed; 95% of 57 nests lost nestlings from exposure; nests with eggs were unaffected	Jehl and Hussell 1966

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TABLE 5. Continued.

Species	Location	Latitude, elevation (m a.s.l.)	Year(s) of study	Habitat type	Weather type	Weather variable, timing	Response variable	Qualitative effect	Comment	Reference
Smith's Longspur (*C. pictus*)										
Savannah Sparrow										
Horned Lark										
Northern Wheatear (*Oenanthe oenanthe*)	Central Sweden	59°N ~30	1994–2012	Agricultural (cavity-nesting)	Acute	Rainfall (days >10 mm), single and multiple days	Fledging success	−	Second half of nestling period; parental nest visitation rate declined	Öberg et al. 2015
							Recruitment success	−	Rain first half of nestling period	
Loggerhead Shrike (*Lanius ludovicianus*)	Alberta, Canada	50°N ~600–800	1992–1993	Dry mixed grass prairie	Annual	Temperature Precipitation, May–July	Nest survival, partial brood loss	+ −	Higher daily nest survival during warmer temperatures, lower precipitation	Collister and Wilson 2007
Vesper Sparrow (*Pooecetes gramineus*)	North Dakota, USA	46°N ~800	1987–1989	Grassland	Annual	Drought, May–June	Clutch size	No effect		George et al. 1992
							Percent hatch	−	Nest abandonment	
							Young fledged	−		
							Nesting success	−	Incubation; combination of heat stress and declining food availability?	
Horned Lark	Colorado, USA	40°N ~1,500	1997–2012	Shortgrass steppe	Acute	Hot day, dry day >10 mm rain	Nest survival	−	Nest survival decreased during drought, high temperatures, and rainstorms	Skagen and Yackel Adams 2012, Conrey et al. 2016
McCown's Longspur (*Thynchophanes mccownii*)										
Chestnut-collared Longspur (*C. ornatus*)						Hot days, dry periods	Clutch size	−		
Lark Bunting (*C. melanocorys*)					Annual	Warmer, dryer years	Clutch size	−		
Western Meadowlark (*Sturnella neglecta*)							Nest survival	−		
							Productivity	−		
Mountain Plover (*Charadrius montanus*)	Colorado, USA	39°N ~1,500	2001–2006	Grassland	Acute	Heavy rain, prolonged drought, May–June	Nest survival	−		Dreitz et al. 2012

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TABLE 5. Continued.

Species	Location	Latitude, elevation (m a.s.l.)	Year(s) of study	Habitat type	Weather type	Weather variable, timing	Response variable	Qualitative effect	Comment	Reference
Song Sparrow (*Melospiza melodia*)	California, USA	38°N <50	1980–2000	Coastal scrub	Annual	Wetter, cooler temperatures	Nest survival, number of fledglings, length of breeding season	+	Reproductive success increased with rain, peaked at above average rainfall	Chase et al. 2005
Rufous-crowned Sparrow (*Aimophila ruficeps*)	California, USA	32°N <50–80	1997–1999	Semiarid coastal scrub	Annual	Rain, summer	Fledging rate	+	Rainfall causes variation in fecundity via effects on food availability and nest predation	Morrison and Bolger 2002
Wrentit (*Chamaea fasciata*) Spotted Towhee (*Pipilo maculatus*) California Towhee (*P. crissalis*) Rufous-crowned Sparrow	California, USA	32°N <50–80	2001–2002	Semiarid coastal scrub	Annual	Dry year, April–June (2002 lowest rainfall in 150 yr)	Mean reproductive output	−	Low arthropod abundance (food availability) in dry year	Bolger et al. 2005

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precipitation on avian breeding success, but often a negative effect of above-average rainfall (Morrison and Bolger 2002, Chase et al. 2005, Collister and Wilson 2007, Pérez et al. 2016) and sometimes of below-average temperatures (Table 5). Thus, extreme precipitation events frequently lower nesting success in both high-elevation (e.g., Hendricks and Norment 1991, Decker and Conway 2009, present study) and low-elevation environments (Fisher et al. 2015, Conrey et al. 2016). Open-country birds breeding in warmer environments at lower elevations and latitudes are also susceptible to hot weather over short periods and drought conditions over longer periods (George et al. 1992, Bolger et al. 2005).

Meteorological conditions can have complex effects on breeding success because the effects of overall weather and of extreme conditions can differ across different stages of reproduction. A study on the effects of extreme weather on the reproductive success of House Sparrows (*Passer domesticus*) found that hatching success increased with the number of extremely hot days, fledging success did not vary with weather conditions, and the frequency of extremely hot days reduced body mass and tarsus length of fledglings; but overall, the development of mass and tarsus were positively related to average daily temperatures (Pipoly et al. 2013). In alpine and high-latitude habitats, birds cope quite well with extreme weather events of short duration but may suffer reduced reproductive success when subjected to prolonged inclement weather, especially during the nestling phase.

Interactions among Weather Variables: Warm and Cold Storms

Weather variables are often included in wildlife breeding-success studies as background variables, with limited study on the explicit impacts of weather on breeding success. Usually weather variables are considered in isolation, using temperature or precipitation as a proxy variable or to examine interactions between ecological (food, predation risk) and weather variables. We found that Horned Larks and Savannah Sparrows were not affected by typical alpine weather but observed a novel, though intuitive, interaction effect for Horned Larks, in that the impact of "warm storm" events (~8°C) were minimal whereas "cold storm" events increased DNM by 8–9× during the incubation and nestling periods. We found a similar but less influential response for Savannah Sparrows for days with heavy precipitation and temperature.

These findings have a strong potential to inform and predict the impacts of climate change on alpine species if we can determine the interactions between temperature and storm events. If warmer conditions prevail during the breeding season, the impacts of storm and precipitation events may be mitigated because these species' coping responses should be sufficient. If colder temperatures during storms are anticipated, then songbirds will be strongly challenged by increasing bouts of extreme weather. In the latter case, Horned Larks would benefit from adopting the strategy used by Savannah Sparrows and delaying the onset of their breeding season to achieve more tolerable conditions. Given the slower life-history strategy adopted by some alpine generalist birds, reducing their breeding-season length may not have a large fitness impact, given that population growth is more strongly determined by the survival of adults and independent fledglings than by nesting success (Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010). Although high-elevation species may be generally more tolerant of extreme variability in temperature compared to low-elevation species, our data indicate that increasing frequency of storms with climate change could pose problems for birds breeding at all elevations. Measuring multiple environmental conditions during species-specific breeding seasons may be useful in determining whether interaction effects between weather variables would be effective predictors of climate-change impacts on temperate songbirds.

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Author contributions: K.M. and S.W. conceived the experimental design and methods. E.C.M., A.F.C., and M.M. collected data. S.W. analyzed the data. K.M. and S.W. wrote the paper. S.A.T. contributed substantial materials.

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