LRH: *de Zwaan et al.*

RH: Alpine weather effects on nestling growth

Timing and intensity of weather events shape nestling development strategies in three alpine breeding songbirds

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Abstract

Across taxa, offspring size traits are linked to survival and life-time fitness. Inclement weather can be a major constraint on offspring growth and parental care. Despite the adaptive benefits of larger offspring, we have a limited understanding of the relative effects of severe weather events across developmental stages or different coping strategies among species. We investigated the influence of inclement weather on offspring size traits within populations of three alpine breeding songbirds in British Columbia: 1) horned lark (*Eremophila alpestris*), 2) dark-eyed junco (*Junco hyemalis*), and 3) savannah sparrow (*Passerculus sandwichensis*). Using a sliding window approach, we identified the most influential temporal periods and weather variables from pre-clutch initiation to 7-days post-hatch. We identified two critical periods that best predicted offspring size: 1) near clutch initiation, and 2) the nestling stage. Horned larks were resilient to colder average temperatures as nestlings but were vulnerable to extreme cold events and multi-day storms. The smaller-sized dark-eyed junco and savannah sparrow were less resilient to temperature but more robust to storms. Colder average temperatures during the nestling stage were associated with smaller wings and tarsi but not mass for juncos, while sparrow nestling size declined with colder conditions during clutch initiation. We hypothesize that junco nestlings may respond to suboptimal temperatures by allocating resources to mass gain, while savannah sparrows may minimize exposure by nesting nearly 3 weeks later. Finally, we assessed support for maternal affects acting through mass at hatch and the glucocorticoid hormone corticosterone (CORT). Notably for larks, colder temperatures during clutch initiation were associated with suppressed nestling feather CORT and subsequently larger size, highlighting a potentially adaptive CORT-mediated maternal effect. By identifying vulnerable developmental periods, we gain insight into the eco-evolutionary processes shaping offspring growth in alpine species, with implications for reproductive success in an increasingly unpredictable climate.

Fundamental to ecology and evolution is understanding the sources of variation in offspring development, as offspring size is often positively associated with survival and life-time fitness across taxa (Ronget et al. 2017, Marshall et al. 2018). Inclement weather and temperature regimes can strongly influence offspring development in homeothermic vertebrates (Gillooly et al. 2002, Nord and Giroud 2020), and thus the developmental period represents a prime target for selection to maximize fitness of both offspring and their parents (Rollinson & Rowe 2015, Vindenes and Langangen 2015). Altricial songbird development occurs across several well-defined stages: ovum development (internal), egg incubation (external), and the nestling stage. While distinct, these stages are not compartmentalized, as conditions that affect development in one stage can influence subsequent stages (Monaghan 2008, O'Connor et al. 2014). In addition, songbird offspring are dependent on parental care, such that the development of offspring size traits reflects both parental and offspring responses to prevailing conditions (Auer and Martin 2017). Inclement weather can stimulate adaptive coping mechanisms in both parents and offspring, reallocating limited resources and promoting or constraining development (Williams 2012, Wingfield et al. 2017).

Nestlings grow rapidly over a compressed period, such that even short disruptions in growth can negatively influence size at fledge and post-fledging survival (McCarty and Winkler 1999, Naef-Daenzer and Keller 1999, Cox et al. 2014). Inclement weather can constrain size trait growth by imposing thermoregulatory challenges that force investment in mass and thermogenesis at the expense of linear size traits (i.e., wing, tarsus; Arendt 1997, Ricklefs et al. 1994). For example, tree swallow (*Tachycineta bicolor*) nestlings from experimentally heated nests differentially increase wing growth without observable differences in other size traits (Dawson et al. 2005). More commonly, associations between weather and nestling growth are linked to food resources, either by altering resource availability or by affecting the ability of parents to deliver food (Stodola et al. 2010, Tuero et al. 2018, Pipoly et al. 2020). Being highly dependent on parental care, altricial offspring have a limited capacity to respond to inclement weather and therefore the effectiveness of coping mechanisms depends largely on parental investment (Auer and Martin 2017, de Zwaan et al. 2019).

During reproduction, females must partition resources between parental care and self-maintenance (i.e., survival; van Noordwijk and de Jong 1986). Resource-challenged females may reduce investment in incubation or provisioning nestlings in favour of self-preservation activities like foraging; increasing nest exposure to inclement weather (Williams 2012). Reduced nest attentiveness during incubation can lead to cooled embryos (Coe et al. 2015) and subsequently constrained nestling growth (Nord and Nilsson 2011, Ospina et al. 2018). In addition, inclement weather experienced by the female prior to clutch initiation may influence offspring development through 'maternal effects' (Wolf and Wade 2009). Stressful environments can induce high plasma levels of glucocorticoids (such as corticosterone) in females which, in turn, flow passively into the developing egg yolk and can reduce nestling growth (Love et al. 2005, Saino et al. 2005). Alternatively, there is evidence that females may anticipate challenging conditions, laying larger eggs with more nutrients to increase nestling size at hatch (Mousseau and Fox 1998), or regulating the deposit of androgens to increase growth rate and glucocorticoids to improve reactivity to stressors (Love and Williams 2008, Weber et al. 2018). Anticipatory effects may therefore be important in harsh, unpredictable environments by producing larger, more robust offspring (Crino and Breuner 2015).

In nature, there are a broad range of weather events and severities experienced across developmental stages that could impact offspring size traits. Our understanding of their relative effects is limited because temperature and precipitation are often highly correlated with time of season, making it difficult to separate the influence of specific variables in field studies (Harriman et al. 2017, Pärt et al. 2017). In stochastic habitats like the alpine however, unpredictable weather events fluctuate greatly within and among seasons (Martin et al. 2017). Therefore, the timing of clutch initiation dictates the environmental constraints and parental care limitations experienced at different stages of development, promoting significant variation in exposure among clutches even within the same general period (e.g., early season). Additionally, while species may differ in their adaptive histories, reflecting evolved life-history strategies with separate optima under prevailing conditions (Chevin and Hoffmann 2017), the strength of inference increases when evaluating patterns of within-population variation among species living in a common habitat. Doing so allows us to assess whether associations between offspring size traits and inclement weather are simply proximate responses to environmental constraints or reflect adaptive coping mechanisms that differ among similar species.

We investigated the influence of inclement weather on offspring size trait variation within populations of three ground-nesting songbirds breeding in two alpine habitats: 1) horned lark (*Eremophila alpestris*), 2) dark-eyed junco (*Junco hyemalis*), and 3) savannah sparrow (*Passerculus sandwichensis*). Horned lark and savannah sparrow were breeding in sympatry. Specifically, we assessed the: i) relative effect of temperature and precipitation variables on nestling size traits, ii) importance of severity (i.e., extreme weather events), and iii) relative influence of the timing of inclement weather across developmental stages (ova development, incubation, nestling stage). In addition, if weather during ova development had an effect, we assessed: iv) support for potential physiological mechanisms underlying maternal effects, including nestling size at hatch and corticosterone. We predicted that all species would respond most strongly to severe weather events like storms and extreme cold (Wingfield et al. 2017). We also expected the strongest effects to occur during the late incubation and early nestling stage when females must balance time on the nest with self-feeding and provisioning nestlings (Williams 2012). Finally, we investigated: iv) differences in relative weather effects and timing among species. Given that horned lark (34.1 ± 0.2 g; mean ± SE) are larger than dark-eyed junco (18.0 ± 0.1 g) and savannah sparrow (18.2 ± 0.5 g) in our alpine study populations, we predicted offspring size trait development for larks would be more robust to challenging weather conditions.

Methods

Focal species

We studied high elevation populations of horned lark, savannah sparrow, and Oregon dark-eyed junco (*J. h. oreganus*) in British Columbia, Canada. Horned larks (HOLA) are open-country songbirds that breed in sparsely vegetated habitats such as short-grass prairies, desert, and tundra from 0 to over 4000 m above sea level (a.s.l.; Beason 2020). Savannah sparrow (SAVS) are also open-country specialists that inhabit cultivated fields, meadows, and alpine tundra > 2000 m a.s.l. in British Columbia (Ryder 2015), but, unlike horned lark, associate with taller grasses and shrubs (e.g., *Salix* sp; MacDonald et al. 2016). Dark-eyed junco (DEJU) breed in open-forest and shrub-dominated habitats from 0–3775 m a.s.l. (Nolan et al. 2020).

For these species, alpine populations lay an average of 4 eggs per nest (range: HOLA and DEJU = 2–5; SAVS = 2–6) and predominantly raise one complete brood per season, with evidence for occasional double brooding (Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010). Larks and juncos begin initiating clutches by mid-May, while savannah sparrows initiate later, from early- to mid-June. Average incubation periods last 10–14 days for horned lark (average = 12.0), 9–15 days (average = 12.5) for savannah sparrow, and 11–14 days for dark-eyed junco, while the nestling period ranges from 7–13 days (average = 9.4), 9–15 days, and 9–12 days, respectively (de Zwaan et al. 2019, Nolan et al. 2020, Wheelwright and Rising 2020). Regardless of elevation, females of each species lay one egg a day and usually begin incubation on the penultimate egg (Beason 2020, Nolan et al. 2020, Wheelwright and Rising 2020). Incubation is entirely the responsibility of the female without mate feeding, and both parents provision nestlings (Ketterson et al. 1992, Goullaud et al. 2018, Wheelwright and Rising 2020).

Study sites

(i) Hudson Bay Mountain

We studied savannah sparrows from 2003 to 2004 and horned larks from 2015 to 2018 in approximately 3 km^2 of subalpine and alpine habitat on Hudson Bay Mountain (HBM) near Smithers, British Columbia, Canada (54.8°N, 127.3°W). Savannah sparrows occurred primarily between 1500 and 1800 m above sea level (a.s.l.) in both alpine tundra and open sub-alpine habitat consisting of scattered krummolz subalpine fir (*Abies lasiocarpa*) and willow shrubs (*Salix* sp.) interspersed with alpine meadows. Horned larks nested entirely above treeline from 1650 to 2000 m a.s.l. This site is characterized by high winds and fluctuating temperatures (Camfield and Martin 2009). Snowmelt varies considerably but often extends into mid-June, resulting in compressed breeding seasons (Camfield et al. 2010). Over the study periods (2003–

2004 and 2015–2018), day-time temperatures (0400–2200 hrs) averaged 3.0°C (range: 1.4°C to 5.5°C) for the first half of the breeding season (May 1 to June 15) and 8.9°C (6.6°C to 10.7°C) for the second half (June 16 to July 31). Total precipitation over the full breeding season averaged 129 mm with a low of 73 mm in 2018 and a high of 178 mm in 2017.

(ii) Mount Mackenzie

From 2013 to 2015, we studied Oregon dark-eyed juncos between 1900 and 2200 m a.s.l. on Mount Mackenzie near Revelstoke, B.C. Canada (51.0°N, 118.2°W). This habitat is considered predominantly subalpine, including stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir with patches of transitional alpine meadows and tundra. Snowmelt occurred from June to early July, slightly later than on HBM. Average day-time temperature was 1.7°C (range: 0.6°C to 3.1°C) from May to mid-June and 8.3°C (range: 7.8°C to 9.0°C) from mid-June through July. Compared to HBM, total precipitation over the breeding season was nearly double, averaging 252 mm with a low of 225 mm in 2015 and a high of 294 mm in 2013.

Field methods

For all species, nests were located by systematic territory searches and behavioural observation. Nests were monitored every 2–3 days except for near hatch and fledge when we switched to daily nest visits. At 7-days post-hatch (day 0 = hatch date), we measured wing length (± 0.5 mm), tarsus length (± 0.02 mm), and mass (± 0.01 g). For savannah sparrows, only tarsus length and mass were measured. Junco nestlings were measured every 2 days starting at hatch; however, we limited our consideration to measurements at 7-days to allow for comparisons among species. Infrequently, nestlings were measured at 6- or 8-days post-hatch, and thus we also recorded age of measurement to control for this variation. Each nestling was banded with one U.S. Geological Survey (USGS) numbered aluminum band and 2–3 plastic colour bands for subsequent identification.

To address potential maternal effects stemming from weather conditions near clutch initiation, we used mass at day 0 or 1 as an indicator of hatch size for juncos (2013–2015) and feather corticosterone (CORT) from 0 to 5-days post-hatch for horned lark (2015–2016). Feather corticosterone is a minimally invasive measurement of the stress response. It allows one to approximate CORT accumulation over time as it deposits along the feather during growth, which is particularly useful when all feathers grow over the same period (e.g., nestling feather growth; Jenni-Eiermann et al. 2015, Romero and Fairhurst 2016). We removed ~ 5 feathers from the dorsal tract of two lark nestlings per nest. Feather CORT was extracted using a methanol-based technique (Bortolotti et al. 2008; Appendix S1).

Weather data

(i) Hudson Bay Mountain

Precipitation and temperature variables were recorded using two HOBO weather stations (Onset Computer Co., Pocaset, MA, USA): 1) a U30-NRC station for 2015 and 2016, and 2) an RX3000 satellite station for 2018. Both stations were located at 1,695 m a.s.l. and within 1.2 km of all nests. Temperature sensors were positioned approximately 3 m above ground. Raw weather data were recorded every 4 min and then averaged hourly.

Weather data were missing for 2003, 2004, and parts of 2017. To estimate precipitation for these periods, we used values from the Smithers Regional Airport ~ 8 km from our site (station ID = 1077498l; elevation = 522 m). Precipitation amount was poorly correlated between stations, but station 10774981 correctly identified days on HBM with or without precipitation (≥ 1 mm) 81% of the time, and storm events (≥ 10 mm) 90% of the time (Martin et al. 2017). Therefore, we classified each day as a precipitation day or storm event using a binomial 0 or 1. For temperature, we interpolated hourly estimates of air surface temperature from the 8 nearest grid points in the National Centers for Environmental Prediction (NCEP) R-1 dataset using the R package “RNCEP” (Kemp et al. 2012). Comparisons of the interpolated estimates with existing measurements from the study site were highly correlated ($r_p = 0.91$), validating this method. A non-zero intercept for the association between interpolated and measured temperature indicated an elevational effect, so we subtracted the value of the intercept (1.78°C) from all interpolated estimates to align with the true temperature measurements.

(ii) Mount Mackenzie

For 2013 and 2014, we used hourly temperature data from a weather station owned by the local ski resort (Revelstoke Mountain) situated at 1950 m a.s.l. within our study site. Temperature data were missing for 2015, so we retrieved hourly recordings from a nearby station located at 1850 m a.s.l. on neighbouring Mount Revelstoke (~ 8.5 km from Mount Mackenzie), part of the Provincial Snow Survey Network (station ID: 2A06P; B.C. Ministry of Environment and Climate Change Strategy 2019). Values from the two sites were highly correlated in 2013 and 2014 ($r_p = 0.98$) but differed by an intercept, so we used the following equation for conversion:

$$\text{Mount MacKenzie} = -3.53 + 1.12\ (\text{station 2A06P})$$

We also extracted precipitation values from station 2A06P as precipitation data were not available from the ski resort weather station at our site. We compared station 2A06P values to those from the Revelstoke airport (WMO station ID: 1176745), located ~ 3.5 km from our study site but at 445 m in elevation. While total precipitation correlated poorly, recorded precipitation and storm events matched for 90% of days during the breeding season. Since station 2A06P is at approximately the same elevation as our study site and displays high concordance with weather patterns within the proximate region, we conclude that its precipitation data accurately represents conditions experienced at our study site

Due to the use of multiple weather stations, we restricted the weather variables we considered to five for which we had a high degree of confidence and that were comparable among study sites: (1) average daily temperature, (2) daily hours ≤ 10°C, (3) daily hours ≤ 5°C, (4) precipitation days (≥ 1 mm/day), and (5) storm events (≥ 10 mm/day). Daily hours below the 10°C and 5°C threshold reflect cumulative temperature challenges for developing eggs and young. In larks, 10°C is an ecologically relevant threshold, below which females increase incubation efforts (MacDonald et al. 2014) and, during the nestling stage, can prolong offspring development (de Zwaan et al. 2019). However, species or individuals may vary in their ability to respond to moderate challenges, so we also considered hours ≤ 5°C to address more extreme conditions that may have pronounced effects on early-life development (Pérez et al. 2016). Daily average temperatures were calculated as the average of each day between dawn and dusk (0400–2200 hrs) to reflect the period when nest contents were most likely to be exposed to ambient temperatures, as night-time incubation attentivity is > 90% (Camfield and Martin 2009). Hours below 5 and 10°C were the sum of hours below each threshold within the same exposure period.

Statistical analysis

To assess the influence of weather on offspring development and identify the most critical time periods across early-life stages (pre-laying, incubation, nestling stage), we used a two-step process. First, for each candidate weather variable, we used a sliding window approach to identify the time period where each variable showed the strongest relationship with nestling size. Then, for each size trait (wing length, tarsus length, mass), we fit a global General Additive Mixed-effects Model (GAMMs) which included all selected weather variables. Penalized regression splines allowed us to examine non-linear associations between weather variables and size traits within a modeling framework that reduced weather variables to linear effects or dropped them entirely from the model where added complexity did not contribute to overall fit. All weather variables were standardized to allow comparisons among traits and species. All analyses were conducted in R 3.6.3 (R Core Team 2020).

Sliding window analysis

Sliding window approaches systematically test associations between weather metrics and biological variables of interest across all possible time windows within a specified period, and then rank each subsequent model with Akaike Information Criterion (AIC; van de Pol et al. 2016). With nestling size traits as the response variables, we built models that assessed all windows within a 30-day period prior to nestling measurement at 7-days post-hatch for each nest. This time period encompasses the incubation and nestling stage, as well as, an average of 8–10 days prior to clutch initiation for each species. For many songbirds, ova development takes approximately 3–5 days when nutrients and hormones are transferred from female to offspring (Williams 2012). Therefore, 8–10 days prior to clutch initiation should be sufficient to capture the ova development period across species. We constrained the tested time windows to a minimum of 3 days and a maximum of the full 30 days. The minimum window was chosen to avoid spurious correlations with single weather events and to allow for weather patterns prolonged enough to stimulate physiological and behavioural responses in the female and nestlings.

All possible time windows were ranked using AIC relative to the null model. The null models included age of measurement, brood size, and clutch initiation date as fixed effects, and nest ID as a random effect to account for non-independence among nestlings of the same nest. The top time windows were chosen based on the lowest AIC if it was a significantly better fit than the null (ΔAIC < –2). If more than one window occurred within 2 AIC of the top window, the one with the strongest β-coefficient was chosen. If drastically different time windows occurred within the top models (e.g., 30–20 and 7–0 days), then both windows were selected for that weather variable. Due to the large number of comparisons inherent to sliding window approaches, we additionally ran each model on 100 randomized datasets to determine the likelihood of selecting the same top models by chance (Type 1 error; van de Pol et al. 2016). Only weather variables where the observed results were different from the randomized analyses ($P < 0.10$) were selected as candidate variables. The sliding window analysis was conducted using R package “climwin” (Bailey and van de Pol 2015).

Model structure and selection

For each size trait, we used all selected candidate weather variables to build a global GAMM using the ‘mgcv’ package (Wood 2011). Age at measurement, brood size, and clutch initiation date were included as covariates in each model, with nest ID as a random effect. For each weather variable, we fit thin-plate regression splines with a maximum of 3 possible knots to test for potential non-linear associations. Models were fit using Restricted Maximum Likelihood (REML) and incorporating penalties for both smoothing factors and the null space. Based on the fit to the data, this process determines whether a variable should be a smoothed term (2 or 3 knots), a linear term, or be removed from the model (Wood 2003). Variables were removed from the model if their estimated degrees of freedom (edf) were less than 0.5, retained as a linear term between 0.5 and 1.5, and retained as a smoothed term if greater than 1.5. If all weather variables were linear, a linear mixed-effects model was fit to the selected model structure using ‘lme4’ (Bates et al. 2015). We evaluated collinearity among linear terms using the Variance Inflation Factor (VIF) and retained weather variables with a VIF < 3. Standardized β-coefficients were extracted as effect sizes and associations were considered significant if the 95% confidence interval did not include zero.

Path analysis

Environmental conditions prior-to and during clutch initiation may influence offspring size traits through several different mechanisms under the definition of maternal effects. Path analysis can assess the relative strength of individual effects by separating the partial regression coefficients for each individual pathway within a causal network (Shipley 2009). Piecewise path analysis integrates multiple, independently fit models, allowing one to address associations among longitudinal data in a way that is robust to relatively small sample sizes (Lefchek 2016).

Using the horned lark and dark-eyed junco data, respectively, we fit piecewise path models to test two of these mechanisms: 1) corticosterone deposition, and 2) size at hatch. In both cases, we fit two sequential sub-models. For horned larks, the first sub-model tested the influence of temperature during clutch initiation on nestling feather corticosterone (0–5 days post-hatch). We then fit individual sub-models describing the subsequent effect of feather CORT on each size trait (wing length, tarsus length, and mass). Using the same model structure, we fit mass at hatch as the intermediate variable for dark-eyed juncos in place of feather CORT. Since hatch measurements were at either 0- or 1-day post-hatch, we used the residuals from a mass by measurement age regression as our metric of mass at hatch to correct for a daily increase in nestling mass. To represent alternative mechanisms, we also included a direct pathway for both models to describe the relative effect of early temperature conditions on offspring size traits independent of the effect through feather CORT or mass at hatch. The exact temperature variable and specific time windows tested were chosen based on the sliding window and modelling approaches described previously. In all sub-models, we included measurement age, brood size, clutch initiation date, and temperature during the nestling period as covariates and nest ID as a random effect. For the full hypothesized path structures, see Appendix S1: Figure S1. We used

D-separation tests to identify the most parsimonious path models (Shipley 2013) and a Markov chain Monte Carlo (MCMC) approach to evaluate sample size adequacy. See Appendix S1 for full evaluation details and results.

Results

We measured 361 horned lark, 120 dark-eyed junco, and 96 savannah sparrow nestlings from a combined 170 nests. At 7-days post-hatch, horned lark nestlings were considerably larger and heavier than dark-eyed junco and savannah sparrow (Table 1). First nests for horned lark and dark-eyed junco were initiated at approximately the same time (mid-May) and had a breeding season length of about 50 days (first to last clutch initiation; Table 1). Savannah sparrows began breeding nearly 3 weeks later than larks, resulting in a breeding season that was 56% shorter (Table 1). During the 30-day period prior to nestling measurement, horned larks experienced the coldest temperatures but fewer storms and precipitation days, while dark-eyed junco and savannah sparrow experienced comparable weather conditions (Table 1).

Sliding window results

Across species, the sliding window analysis identified two general time periods where weather influenced offspring development: 1) from several days before clutch initiation to early incubation (approximately 30–15 days prior to nestling measurement at 7-days post-hatch), and 2) the nestling stage (7–0 days). The type of weather variable operating within these time windows and extent of its influence differed among species and size traits (Fig. 1; Appendix S1: Table S1). When both average daily temperature and hours ≤ 10°C were selected, these occurred within the same time window and were strongly correlated ($r_p > 0.90$). Thus, we hereafter report only daily temperature as an indicator of average or mild temperature effects, as well as, hours ≤ 5°C to reflect periods of extreme cold.

Response to weather conditions

1. Horned Lark

Following model selection, average temperature near clutch initiation (23–14 days prior to measurement) and extreme cold during the nestling stage (7–0 days) were the most influential temperature predictors for the development of size traits in lark nestlings. Greater clutch initiation temperatures were associated with reduced wing length (β = –2.6) and mass (β = –1.2), but not tarsus length (Figure 2A, Figure 3A). Greater periods of extreme cold during the nestling stage were linked to smaller nestlings across all size traits (Figure 2A, Figure 3B). In addition, lark nestlings responded most strongly to storm events during the late incubation and nestling period. A greater frequency of storms 12–2 days and 20–2 days prior to measurement was associated with reduced wing and tarsus length, respectively. However, there was no evidence that storm frequency influenced mass (Figure 2B). Importantly, only multiple storm events during this time period influenced size trait development, as there was no observable response to a single storm, indicating a possible response threshold (Figure 2B; Figure 4A).

2. Dark-eyed junco

Colder temperatures during the nestling stage (7–0 days prior to measurement) were also associated with reduced wing and tarsus length for juncos. However, in contrast to larks, average temperatures rather than periods of extreme cold were associated with this reduced growth (Figure 2A). While wing length (β = 1.9) and tarsus length (β = 0.6) were greater with increasing average temperatures (Figure 3B), mass at 7-days post-hatch was unrelated (Figure 2A). Dark-eyed junco nestlings were also smaller in size when exposed to multiple storm events during the nestling stage (5–0 days). Nestling mass was smaller on average when multiple storms occurred during this period (β = –1.3), but there was no effect following a single storm (β = –0.7; Figure 2B; Figure 4B). In contrast to larks, storms did not influence either wing or tarsus length (Figure 2B).

3. Savannah sparrow

Savannah sparrow nestling development responded most strongly to average temperature prior to clutch initiation (30–23 days prior to measurement), with greater average temperature associated with longer tarsi (β = 0.7; Figure 2A; Figure 3A). There was no association between nestling size trait development and storms. Instead, a greater frequency of precipitation days prior to clutch initiation and during early incubation (30–12 days) was strongly associated with greater nestling mass (β = 1.8; Figure 2B). During this period, precipitation days and average daily temperature were highly correlated ($r_p = 0.72$) and in the absence of precipitation, greater temperature was positively associated with mass (β = 0.9, 95% confidence interval = 0.2 – 1.2). Therefore, while precipitation was the better predictor, it was not possible to separate the influence of precipitation and temperature on nestling mass development for savannah sparrows during this period. See Appendix S1: Table S2 for full model outputs.

Path analysis for larks and juncos

Following model selection, the horned lark path model included only the indirect influence of early development temperatures on nestling size traits through feather CORT. For dark-eyed junco, direct and indirect pathways through mass at hatch were supported (Appendix S1: Table S3). The fixed and random effect structure of each model explained a moderate to large proportion of the observed size trait variation among nestlings (Figure 5).

For horned larks, average daily temperature prior-to and during clutch initiation (23–14 days prior to measurement) was positively associated with nestling feather corticosterone measured at 5-days post-hatch (Figure 5A). In turn, increased feather CORT was negatively associated with wing length and mass, but not tarsus length (Figure 5A). Temperature during the nestling period had no effect on feather CORT, indicating that the nestling glucocorticoid response is not related to cold extremes during the early nestling stage (Figure 5A).

For dark-eyed junco, average daily temperature around the clutch initiation period (30–19 days) had no apparent influence on mass at hatch (Figure 5B). However, cold early temperatures were associated with longer wing and tarsus through an alternative, unmeasured mechanism (Figure 5B). As expected, mass at hatch predicted larger size traits at 7-days post-hatch (Figure 5B).

Discussion

We identified two general periods where offspring size traits were most influenced by inclement weather during: 1) clutch initiation, and 2) the nestling stage. We demonstrate greater resilience to cold extremes in horned lark, but also greater susceptibility to precipitation events than dark-eyed junco and savannah sparrow. We further highlight the potential for maternal effects stemming from cold temperatures during the clutch initiation period. These effects were positive or potentially anticipatory in larks and juncos, but detrimental for savannah sparrows.

Temperature effects during the nestling stage

While colder temperatures during the nestling stage were associated with smaller offspring size traits in horned larks, this effect was only expressed during periods of extreme cold (hours ≤ 5 °C), indicating resilience to alpine weather conditions. In contrast, dark-eyed junco nestlings were smaller in response to colder average temperatures (i.e., more moderate temperature challenges). Cold temperatures are a well-known stressor that can constrain nestling size growth (Dawson et al. 2005, Pérez et al. 2016, Andreasson et al. 2018), with variation among species and populations potentially reflecting differences in nestling resource allocation or parental investment (Eeva et al. 2002, Mainwaring and Hartley 2016, Auer and Martin 2017). Nestling horned lark at 7-days post-hatch were nearly 66% heavier than dark-eyed junco, and therefore may be better able to conserve heat and develop endothermy at an earlier age (Dunn 1975). Interestingly, junco mass was not associated with ambient temperature, potentially indicating resource allocation to mass and thermoregulatory capacity at the expense of size traits (Arendt 1997). While experiments are required to verify differential growth in response to inclement weather, prioritizing mass over size highlights a potential physiological coping mechanism at the nestling level that may differ among species.

In contrast, there was no association between temperature during the nestling stage and offspring size traits in savannah sparrows. This is surprising given their smaller size and previously documented higher nest mortality during periods of suboptimal weather (Martin et al. 2017). However, the earliest savannah sparrow nests were initiated nearly 3 weeks later than both horned lark (sympatric breeder) and dark-eyed junco such that the minimum average temperature experienced during any nesting attempt was significantly higher for savannah sparrows (Table 1). In fact, Martin et al (2017) proposed late breeding as a potential strategy for savannah sparrow to avoid cold storms and reduce the probability of nest failure. Warmer temperatures associated with later breeding likely also benefit offspring development.

Storm thresholds and precipitation effects

While there was no observable influence of a single storm, multiple storms during the nestling stage constrained offspring growth in both horned lark and dark-eyed junco. This aligns with the concept of multiple or cumulative stressors where individuals may be resilient to suboptimal conditions up to a specific threshold (allostasis; Wingfield et al. 1998). The effect sizes of multiple storms were larger for horned lark and affected more size traits. Dark-eyed juncos may be more robust to storm events, although this result should be treated with caution as the number of horned lark nestlings experiencing multiple storms was relatively small and likely does not capture the full range of variability. If representative, however, this difference could reflect variation in nest microsite characteristics. Junco nests have greater average nest cover (60–90%; Walsberg et al. 2005, Sperry et al. 2008) and are often placed under shrubs or sub-alpine trees, while horned lark nests are extremely exposed (22.3 ± 1.2% cover) and placed well away from taller vegetation (MacDonald et al. 2016, de Zwaan and Martin 2018). A more protected nest environment may partially buffer offspring from precipitation and reduce parental energy requirements.

For savannah sparrows, storm events did not influence offspring mass or size traits, despite cold storms being particularly detrimental to their nest success (Martin et al. 2017). Again, this could reflect differences in timing of breeding which, although it does not reduce the number of storms birds experience, would limit exposure to ‘cold storm’ events; a combined stressor which is likely more energetically taxing (Martin et al. 2017, Wingfield et al. 2017). Instead, warm precipitation prior to and during incubation was positively associated with nestling mass in savannah sparrows. Precipitation during the nestling stage can be detrimental to offspring growth (Morganti et al. 2017); however, warm, wet conditions also promote insect abundance (Tuero et al. 2018) which can increase nestling growth if precipitation occurs prior to hatch (Pipoly et al.

2020). Therefore, our results likely reflect a positive influence of temperature and precipitation on food availability during peak nestling growth.

Maternal effects

Anticipatory maternal effects have the potential to prepare offspring for uncertain developmental environments (Marshall and Uller 2007). Investment in egg size has been suggested as a potential anticipatory maternal effect in response to a suboptimal maternal environment across taxa (Rollinson & Rowe 2015, Kvalnes et al. 2018). Dark-eyed junco did not appear to alter offspring mass at hatch in response to temperatures near clutch initiation. Substantial variation in mass at hatch was observed among nests, independent of weather. This may reflect differences among females in their ability to invest in egg size or maintain temperature consistency during incubation (Kim and Monaghan 2006, Krist 2011). Importantly, clutch initiation temperatures influenced offspring size after controlling for mass at hatch, providing support for alternative mechanisms that we were unable to address.

Hormone-based mechanisms have the potential to influence nestling growth independent of hatch size (Moore et al. 2019). For horned larks, colder temperatures near clutch initiation were associated with reduced feather CORT in nestlings and, subsequently, larger offspring size traits. This is consistent with evidence that high corticosterone levels can constrain nestling growth (Wingfield and Sapolsky 2003). Similarly, a challenging maternal environment can elevate plasma CORT levels in females which subsequently diffuses into the egg yolk (Love and Williams 2008). Greater corticosterone in the yolk has been associated with lower baseline CORT levels and improved CORT regulation in nestlings (Tilgar et al. 2016, Weber et al. 2018). CORT down-regulation could also explain why extreme cold during the nestling stage did not influence feather CORT (Wada et al. 2009). We therefore provide preliminary support for a CORT-mediated maternal effect of inclement weather on offspring size trait development. However, we cannot rule out that corticosterone levels may reflect associated changes in other hormones, such as androgens. Research addressing alternative physiological indices and further validating feather CORT dynamics in nestlings is required (Harris et al. 2016).

Finally, while we lacked the data to address potential maternal effects in savannah sparrows, it is worth noting that they were the only species where colder temperatures during clutch initiation were associated with smaller nestlings. This indicates that a suboptimal maternal environment may have negative consequences on offspring growth, whether it be through physiological maternal effects or reduced parental care (Moore et al. 2019). This and previous results for the negative effects of inclement weather on incubation success (Martin et al. 2017) provide support for the concept that savannah sparrows may employ a late breeding reproductive strategy because they are less resilient to colder temperatures.

Conclusion

Extreme weather events are expected to be increasingly frequent, particularly in already stochastic habitats like the alpine and arctic (IPCC 2018). Identifying critical stages where alpine songbird reproduction is most vulnerable to inclement weather is fundamental to predicting future reproductive success under a changing climate. Horned larks were resilient to colder average temperatures but were vulnerable to prolonged periods of extreme cold and multi-day storms. The smaller dark-eyed junco and savannah sparrow appeared less resilient to temperature challenges but were robust to storm events, keeping in mind that storms may be associated with cold or warmer temperatures (Martin et al. 2017). Junco nestlings may cope with extreme alpine temperatures by allocating resources to mass gain at the expense of size traits like wing length. Savannah sparrows may evade environmental constraints by nesting later in the season when conditions are more benign. Overall, we provide evidence for variation in stage-specific vulnerabilities to inclement weather and the potential for different adaptive coping strategies among alpine species. Future research comparing our focal species to an intermediate-sized alpine breeding songbird (e.g., American pipit *Anthus rubescens*; 21 g) or comparing intra-specific populations across environmental gradients would further advance our understanding of early-life resilience to stochastic environments.

Authors' Contributions

DRD, KM, and AD conceived the ideas; DRD, JLG, and KM collected the data; DRD analysed the data and led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

Data and code will be uploaded to the Figshare data repository when manuscript is published and are currently available upon request.

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Conflict of Interest

The authors declare no conflict of interest.

Ethics Statement

All procedures and protocols for this study were approved by the University of British Columbia's Animal Care Committee (A03-0095, A13-0073, and A15-0027) and are in accordance with the Canadian Council on Animal Care's national guidelines. All data were also collected under a Scientific Permit for Capture and Banding of Migratory Birds from Environment and Climate Change Canada (10365 BO, 10365 DS, and 10761 J).

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Tables

Table 1. Average nestling size traits (± standard error) at 7-days post-hatch, clutch initiation date, and weather conditions (± standard deviation) experienced over the 30-day window of each individual nesting attempt across species. Sample size depicts number of nestlings and nests in brackets. For clutch level traits and weather, values in brackets represent the range. First egg is the average clutch initiation date for the entire breeding season, including first nests and re-nests, and the range is the earliest and latest initiated nest across years to depict breeding season length. Temperature hours indicate the average number of hours per day (see Methods for further details).

Variables	Horned lark	Dark-eyed junco	Savannah sparrow
	n = 361 (110)	*n* = 120 (35)	*n* = 96 (26)
Nestling size traits			
Wing length (mm)	39.1 ± 0.4	29.2 ± 0.5	
Tarsus length (mm)	19.6 ± 0.1	18.6 ± 0.1	18.7 ± 0.2
Mass (g)	20.6 ± 0.2	12.4 ± 0.2	13.8 ± 0.2
Clutch level traits			
First egg (Julian day)*	162 ± 13 (138–189)	175 ± 13 (142–194)	170 ± 8.5 159 – 188
Weather			
Avg temp (°C)	6.7 ± 2.4 (3.2–10.9)	7.9 ± 2.0 (3.1–10.2)	7.7 ± 1.1 (5.1–9.3)
Hrs ≤ 10°C	13.8 ± 3.0 (8.0–17.8)	11.0 ± 1.8 (9.5–16.2)	12.9 ± 2.3 (10.5–17.6)
Hrs ≤ 5°C	7.4 ± 3.7 (2.2–13.7)	6.5 ± 2.7 (3.3–12.7)	5.1 ± 1.9 (2.0–9.5)
Storm events	1.1 ± 0.8 (0–3)	2.0 ± 1.3 (0–5)	1.8 ± 0.8 (1–3)
Precipitation days	8.3 ± 2.8 (4–15)	12.5 ± 3.8 (4–19)	13.2 ± 1.2 (10–15)

* Julian date: May 1 = 121.

Figures

Figure 1. Sliding window results for horned lark (dark blue), dark-eyed junco (light blue), and savannah sparrow (orange). Only traits that passed the randomization test and time windows that had a better fit than the null (≤ -2AIC) are included. A darker colour intensity indicates a greater number of selected time windows overlap, while light intensity has less support. Each cell represents 1 day.

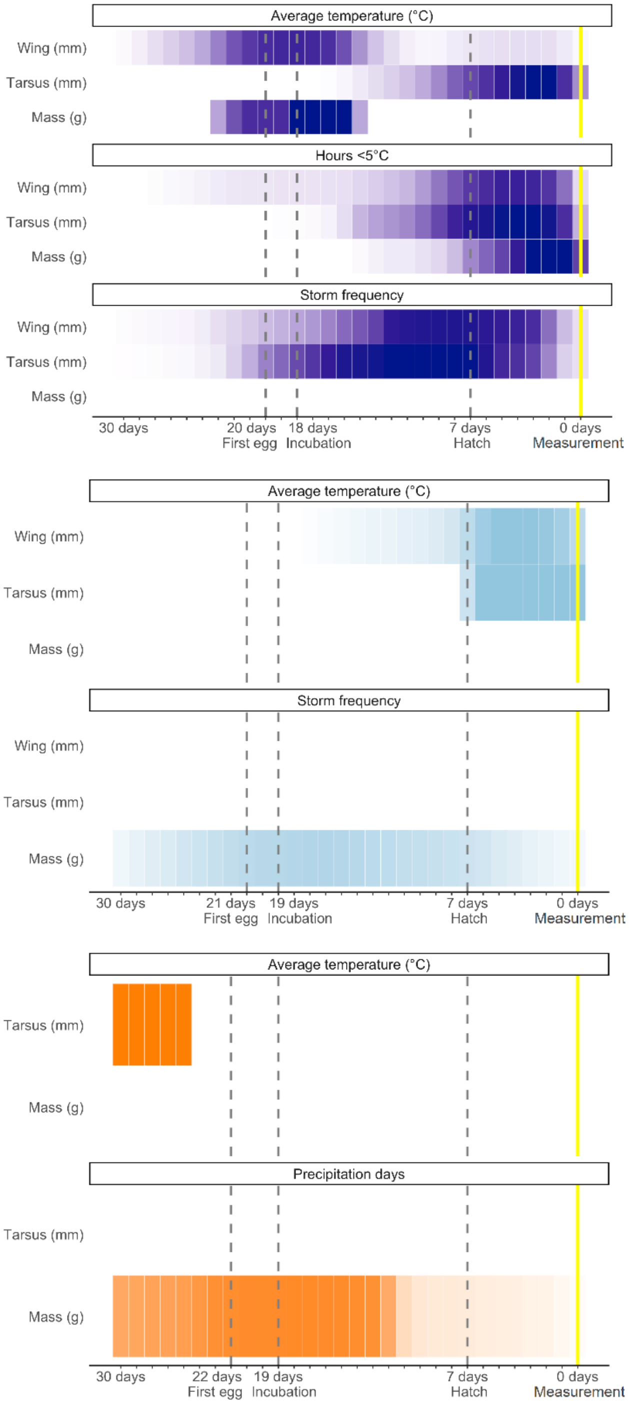

Figure 2. Standardized model effect sizes for (A) temperature and (B) precipitation weather variables. The approximate windows in brackets (clutch initiation, incubation, and nestling stage) are generalizations to facilitate comparisons among species and size traits. Error bars depict 95% confidence intervals and an effect is considered significant if the error bars do not overlap zero (grey dashed line). ‘Storms (1)’ is the effect of one storm over the time window relative to zero storms and ‘Storms (2)’ is the effect of two storms.

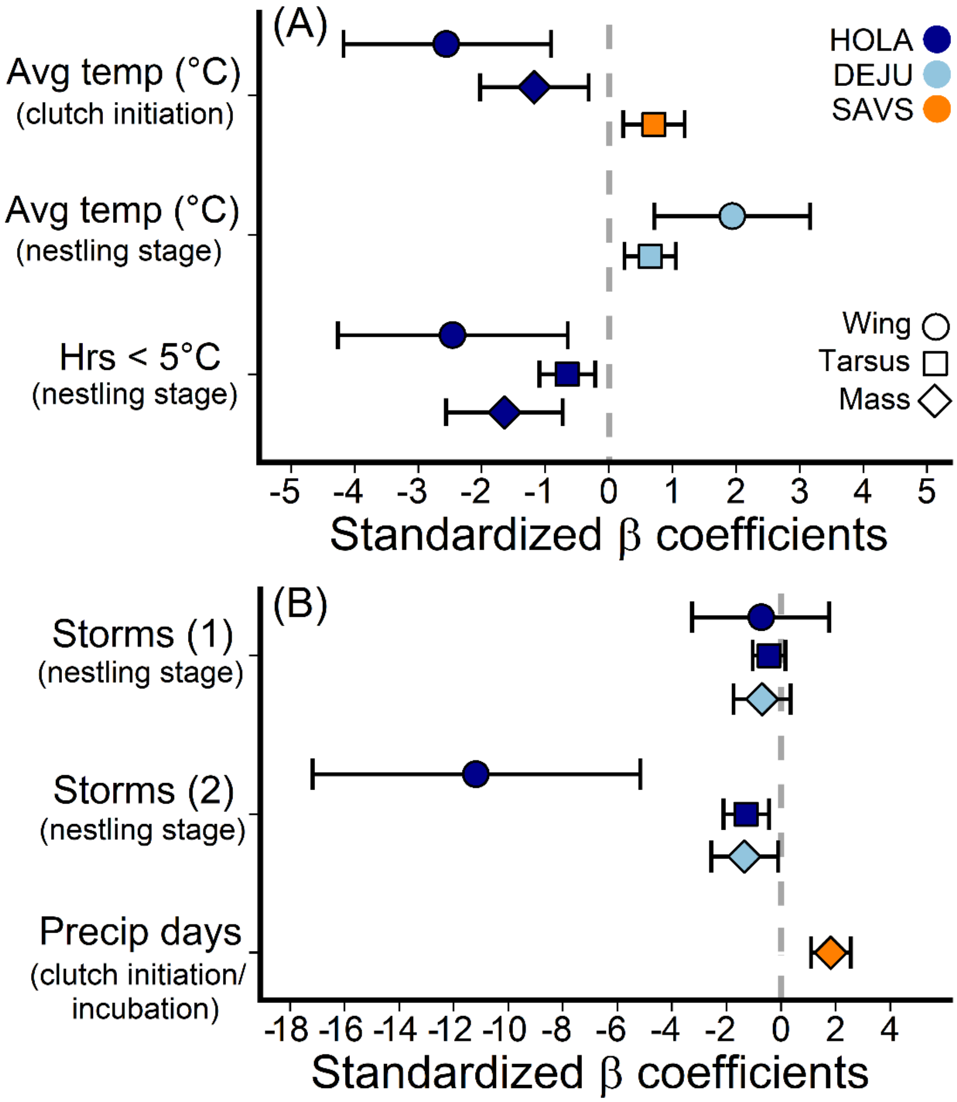

Figure 3. Temperature association for horned lark (HOLA), dark-eyed junco (DEJU), and savannah sparrow (SAVS) during the (A) clutch initiation period (HOLA = 23–14 days prior to measurement date; SAVS = 30–25) and (B) nestling stage (7–0). Lines represent the predicted trends from the linear mixed effects models, controlling for variation within nests, and the shaded areas are 95% confidence intervals of the partial residuals. Importantly, in panel B positive temperature values are colder for HOLA (turquoise) and warmer for DEJU (blue) because of the nature of the temperature variable (hours ≤ 5°C and average daily temperature, respectively). All axes represent relative differences where zero indicates the mean value. Size traits were standardized to facilitate comparison such that 1 unit = 1 standard deviation change.

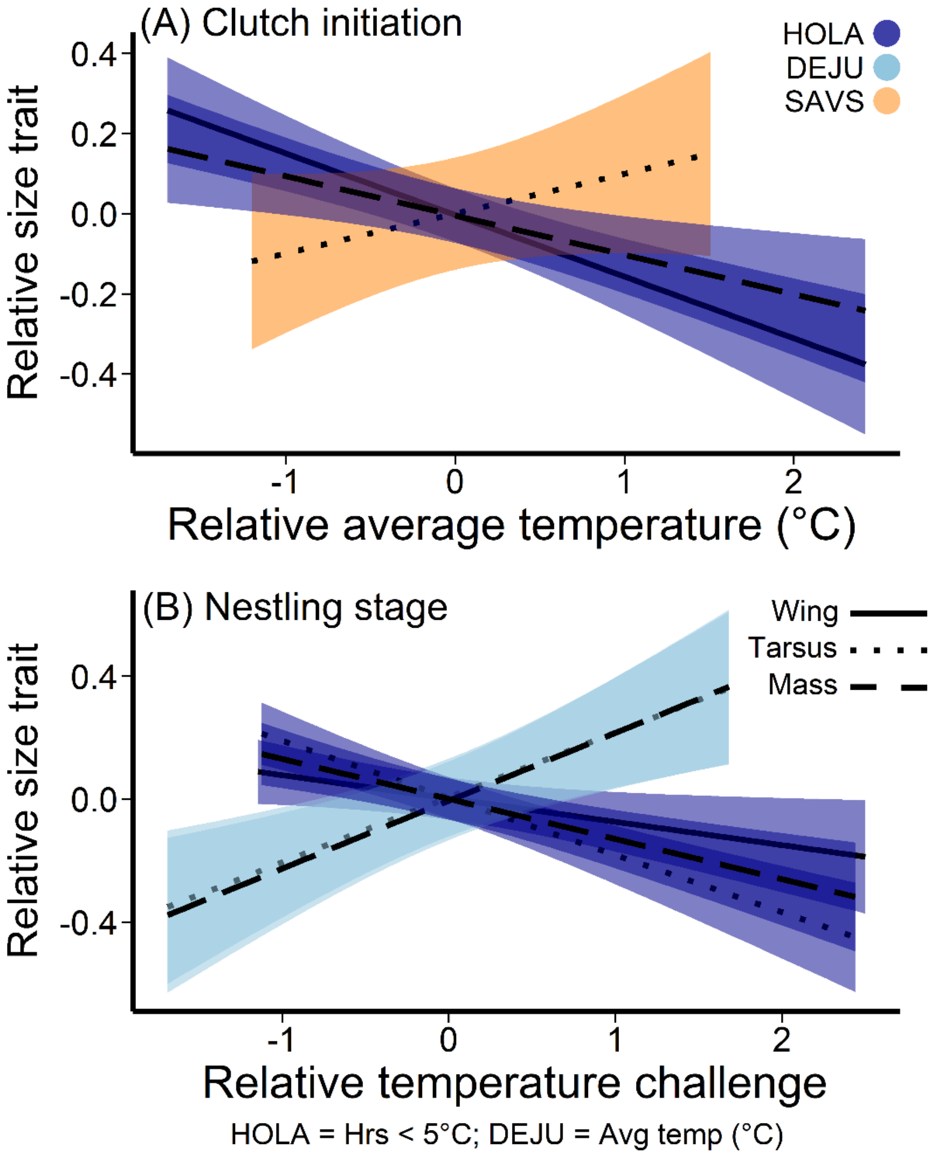

Figure 4. Influence of storm events during the nestling stage on (A) horned lark (HOLA) wing and tarsus length, and (B) dark-eyed junco (DEJU) mass. Points represent the raw data points and an asterisk indicates a significant difference from zero storms. The scaled trait length was standardized such that each unit is one standard deviation change from the mean at zero.

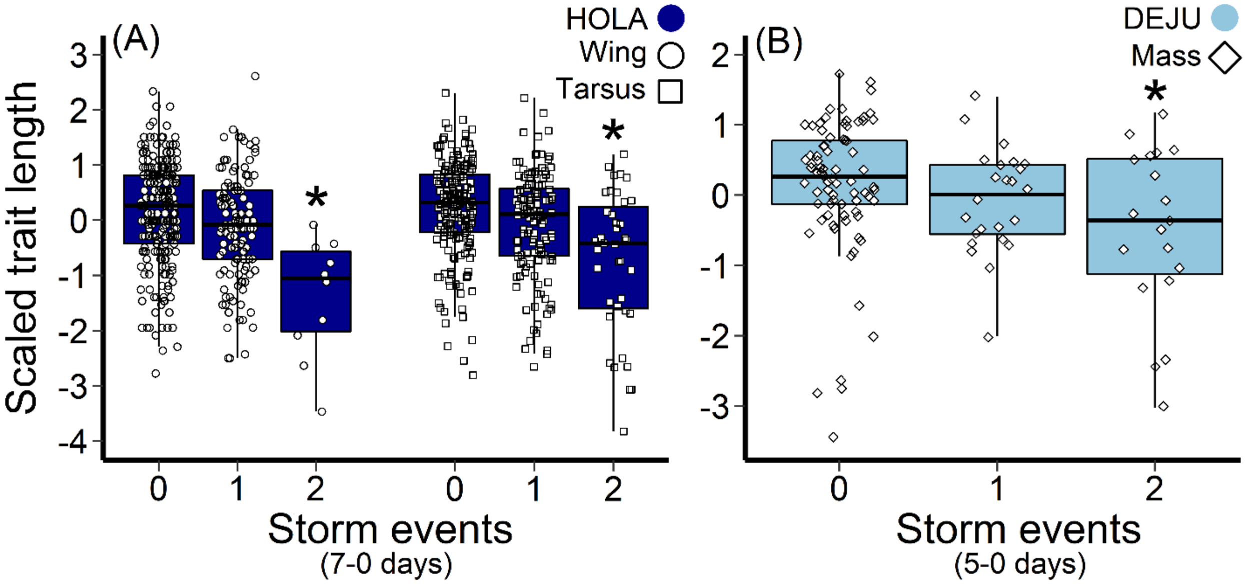

Figure 5. Final path models for (A) horned lark and (B) dark-eyed junco. Solid lines are positive associations while dashed lines are negative. Black arrows are significant while thin, grey arrows are not. R^2 for each variable includes the marginal and conditional R^2 in brackets, or the variance explained by just the fixed effects versus variance explained by the fixed and random effects combined. Values within the circles between the different size traits represent correlations among size traits but do not contribute to the R^2 values.