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E–Natural History Note

Experimental Amelioration of Harsh Weather Speeds Growth and Development in a Tropical Montane Songbird

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abstract: Organisms living at high elevations generally grow and develop more slowly than those at lower elevations. Slow montane ontogeny is thought to be an evolved adaptation to harsh environments that improves juvenile quality via physiological trade-offs. However, slower montane ontogeny may also reflect proximate influences of harsh weather on parental care and offspring development. We experimentally heated and protected nests from rain to ameliorate harsh montane weather conditions for mountain blackeyes (*Chlorocharis emiliae*), a montane songbird living at approximately 3,200 m asl in Malaysian Borneo. This experiment was designed to test whether cold and wet montane conditions contribute to parental care and postnatal growth and development rates at high elevations. We found that parents increased provisioning and reduced time spent warming offspring, which grew faster and departed the nest earlier compared with offspring from unmanipulated nests. Earlier departure reduces time-dependent predation risk, benefitting parents and offspring. These plastic responses highlight the importance of proximate weather contributions to broad patterns of montane ontogeny and parental care.

Keywords: life history, mountain blackeye (*Chlorocharis emiliae*), nestling period, ontogeny, developmental plasticity.

Introduction

Understanding the causes of life-history variation is a primary goal of life-history theory (Pianka 1970; Roff 1992), yet elevational patterns remain poorly understood. One such pattern is that many taxa exhibit slower intra- and interspecific growth and development at higher elevations compared with lower elevations (Bronson 1979; Mathies and Andrews 1995; Badyaev and Ghalambor 2001; Morrison and Hero 2003; Hodkinson 2005; Boyle et al. 2016). Slower ontogeny is often thought to coevolve with increased survival in later life stages (McCay 1933; Arendt 1997; Metcalfe and Monaghan 2003; Lee et al. 2012), yet many studies have failed to find higher adult survival at high elevations (Blanckenhorn 1997; Tatar et al. 1997; Badyaev and Ghalambor 2001; Morrison et al. 2004; Boyle et al. 2016; Caruso and Rissler 2019; Scholer et al. 2019). The lack of increased survival with slower growth and development challenges traditional evolutionary explanations and invokes a possible role of phenotypic plasticity in elevational patterns of ontogeny (Stearns 1989).

Understanding the extent to which slow growth and development may reflect plastic responses to harsh environmental conditions is critical because the implications for fitness strongly differ from those resulting from evolved physiological trade-offs (Martin et al. 2007). For example, slow growth can yield fitness benefits when growth reflects evolved physiological trade-offs with traits (e.g., enhanced immune function) that improve offspring quality (Arendt 1997; Arendt et al. 2001; Metcalfe and Monaghan 2003). Alternatively, plastically reduced growth and development rates imposed by poor environmental conditions can have fitness consequences by producing offspring with inferior phenotypes (Desai and Hales 1997; Lindström 1999; Metcalfe and Monaghan 2001; Lee et al. 2013). Here, we explore the possibility that harsh weather conditions typical of high elevations underlie plastic responses that contribute to broad patterns of slow growth and development.

Songbirds (order: Passeriformes) typify elevational development patterns because they generally exhibit slower growth and development at higher elevations (Badyaev 1997; Badyaev and Ghalambor 2001; Bears et al. 2009; Lu et al. 2010; Hille and Cooper 2015; Boyle et al. 2016). Moreover, high-elevation environments exhibit colder ambient

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temperatures and often increased rainfall compared with lower elevations (Barry 1992; Kitayama 1992; Nagy and Grabherr 2009). Harsh weather can negatively impact avian growth and development rates (Erikstad and Spidso 1982; Murphy 1985; Konarzewski and Taylor 1989; de Zwaan et al. 2019), and these effects may contribute to the pattern of slower growth and development at high elevations. However, studies have generally focused on the adaptive significance of slower growth and development among montane species (e.g., Badyaev and Ghalambor 2001; Hille and Cooper 2015), while, to our knowledge, experimental tests of the effects of harsh weather in high-elevation populations do not exist.

Birds have evolved extensive parental care, which can help offset the negative effects of harsh abiotic conditions (Clutton-Brock 1991). Brooding (warming) and food provisioning are two critical aspects of parental care during the nestling (postnatal) stage of altricial birds that contribute to growth and development rates. Time spent brooding young can increase when temperatures are colder (Johnson and Best 1982; Rosa and Murphy 1994; Wiebe and Elchuk 2003), and montane birds may increase brooding rates to offset colder temperatures at high elevations. However, brooding may constrain the time that parents have to feed their dependent young (Johnson and Best 1982; Radford et al. 2001; Yoon et al. 2016; Mitchell et al. 2017), which may cause slower growth and development (Ricklefs 1976; Martin 1987). Thus, a possible mechanism by which the harsh weather of high elevations might cause plastic reductions in the growth and development rates of montane songbirds is through a need to increase brooding (warming), which reduces offspring provisioning.

We experimentally tested the hypothesis that parental brooding and provisioning patterns are influenced by harsh montane weather, which contributes to slower postnatal growth and development rates, by ameliorating nest microclimates of a tropical montane songbird species in Malaysian Borneo. We heated and protected nests from rain to test predictions that ameliorated climate conditions (1) reduced parental brooding rates, (2) increased offspring provisioning rates, and (3) yielded faster nestling growth and development rates. Alternatively, if slower montane ontogeny primarily reflects evolved physiological mechanisms, we expect little change in growth and development rates when nests are experimentally protected from montane weather during brooding, regardless of parental responses.

Material and Methods

Study Site and Species

We studied mountain blackeyes (*Chlorocharis emiliae*) from 2013 to 2017 in the forest surrounding the Laban Rata station on Mount Kinabalu, Malaysian Borneo (~3,200 m asl; 06°03′N, 116°34′E). Mountain blackeyes are small (mean ± SE: 16.22 ± 0.04 g; $n = 576$ adults) songbirds in the white-eye family (family: Zosteropidae; order: Passeriformes) and are endemic to the tallest mountain peaks in Borneo (Gawin et al. 2014). Mountain blackeyes build small, cup-shaped nests, generally in the upper layers of the stunted montane canopy. Nest predation on this species and at this site is relatively low (A. E. Mitchell and T. E. Martin, unpublished data), and as a result, their nests do not appear to be as inconspicuous as many other species on Mount Kinabalu. The mean elevation for nests that we studied was 3,281 ± 5 m, and the mean nest height was 3.8 ± 0.1 m. Mountain blackeyes lay only one egg per nesting attempt, which is not uncommon for a tropical bird nesting above 3,000 m asl (Boyce et al. 2015). Both males and females brood and feed the single nestling.

Mount Kinabalu is a granitic mountain formation, and it is the tallest mountain on the island of Borneo at 4,095 m asl (Sheldon et al. 2015). The area surrounding the Laban Rata station on Mount Kinabalu is characterized as either upper montane tropical cloud forest or tropical subalpine forest, depending on the author and classification scheme used (Kitayama 1992, 1995). The climate at the site is very wet, with annual rainfall averaging approximately 3,000 mm per year (Aiba and Kitayama 1999).

Nest Monitoring

We located nests using parental behavior cues and systematically searching trees and shrubs. We monitored nests every 24 or 48 h, following Martin and Geupel (1993), to determine precise hatching and fledging dates. We used hatching and fledging dates to determine the length of the nestling period, a proxy for postnatal development, which we defined as the total number of days the chick was in the nest. We filmed nests across the duration of the nestling period to quantify parental brooding and offspring provisioning rates. Cameras were placed >5 m from nests and started recording within 1 h of sunrise, and end times varied as a result of different battery capacities. Videos that were used to evaluate parental behavior ranged from 3 to 8 h (mean ± SE: 6.0 ± 0.1 h). Experimental nests were video recorded for 41 total days for a total of 246 h, whereas unmanipulated nests were video recorded for 67 days for a total of 398 h. Nestlings were weighed and measured at roughly the same time every other day to estimate mass, wing chord, and tarsus growth (Martin 2015).

Experimental Heating and Covering

Experimental nests were selected opportunistically among nests found before hatching. All experimental nests received a treatment of both supplemental heat and rain protection simultaneously, and this treatment was applied before eggs hatched and the onset of measurements during the nestling period. To heat the nests, we attached a small plastic heating strip (Kapton Heaters, model KHLVA-105) to the bottom of mountain blackeye nests using green metal wire. A rectangle of aluminum foil was placed below the heating strip to force heat up into the nest. To reduce conspicuousness, we then placed a strip of camouflage tape over the bottom of the aluminum foil so that only the camouflage tape was visible to the parent birds (see fig. 1). The heater was attached to the nest before the start of the nestling period and connected to a 12-V dry cell automotive battery on the first day of the nestling stage. We changed the batteries every 2 or 3 days to maintain a continuous heat supply. All experimental nests were also protected from rain using a piece of plywood (approximately 30 cm × 40 cm) wired to vegetation 40 cm directly above each nest (see fig. 1). We were able to successfully heat and cover nine nests for the duration of the nestling period (range: 13–16 days), and these were compared with 38 unmanipulated nests in which the entire duration of the nestling period could be observed. No nests were abandoned in response to the experimental treatment, but one nest was lost to predation.

We compared experimental nests with unmanipulated nests rather than with a true control to provide a conservative comparison of our treatment. A true control would have required manipulations at nests, which can increase brooding and reduce provisioning rates as a result of increased perceptions of predation risk (LaManna and Martin 2016). Our hypothesis predicted decreased brooding and increased provisioning rates with experimental amelioration of weather. A true control would have accounted for possible parental responses due to manipulations, but it may have also magnified differences between experimental and control groups because of such opposing responses to risk. Therefore, we chose to use unmanipulated nests for comparisons.

Mountain blackeye parents continuously removed thermistor wires inserted into nests, preventing precise measurements of mean temperature increases due to the experiment. However, an experiment using the same equipment with the addition of a thermostat that cut power supply during parental on bouts raised egg temperatures by 1.32°C (Ton and Martin 2017). Thus, because of our constant heat supply, our experiment likely exceeded the 1.32°C increase reported by Ton and Martin (2017).

Weather Data

Weather variables were included as covariates in our models to account for the impacts they may have on behavior and ontogenetic traits. We recorded ambient temperature, rainfall, and wind speed using a centrally located weather station without canopy cover at our field site (see Aiba and Kitayama 2002). Ambient temperature was measured using a Vaisala HMP35C temperature and humidity probe (Vaisala, Helsinki, Finland) placed 1.5 m off the ground, which took measurements every 10 s. Rainfall

Figure 1: *Left*, Photograph of mountain blackeye nest with experimental heating strip covered with camouflage duct tape. This photograph is of a finished and detached nest and does not show the rain cover that was simultaneously affixed above the nest. *Right*, Photograph of mountain blackeye nest with experimental rain cover protecting the nest contents. Note that this photograph was taken before the heating strip was attached, but both heat and cover treatments were administered simultaneously for all experimental nests.

was measured with a TE525MM tipping-bucket rain gauge (Texas Electronics, Dallas, TX) with a sensitivity of 0.1 mm per tip. Wind speed was measured with an R.M. Young 03001 wind sentry (R.M. Young, Traverse City, MI) every 10 s. All readings were recorded by a CR10 data logger (Campbell Scientific, Logan, UT). Using these data, we calculated mean temperature (°C), total rainfall (mm), and mean wind speed (m/s) per 24-h period. We analyzed parental behavior traits relative to weather covariates by using the means of the calendar days that the nests were filmed. Length of the nestling period relative to weather variables was analyzed by taking means of all weather variables for all days that the nests were active.

Statistical Analyses

We analyzed all data using the program R (ver. 3.5.1; R Development Core Team 2018). For analyses of parental behavior, we truncated the nestling period to days 1–7 because pin break, the point at which young are expected to effectively thermoregulate (see Cheng and Martin 2012), occurs on day 6 or 7 for mountain blackeyes. To normalize across different video-monitoring lengths, brooding rate was quantified as the proportion of each video that either parent spent sitting on the nest multiplied by 100 to yield a percentage, and feeding rate was the number of feeding trips per hour. We report total brooding and feeding rates because mountain blackeyes are monomorphic, preventing sex-specific analyses.

We tested two separate linear mixed effects models using the package lme4 (Bates et al. 2015) to determine the effects of the climate amelioration treatment on both brooding and nestling feeding rates (response variables). Experimental treatment was included as a fixed factor, and daily mean ambient temperature, rainfall, and wind speed values were included as continuous covariates. For the brooding model, feeding rate was also included as a covariate to test for a relationship between the two parental behaviors (brooding and feeding). Unique nest identification was included as a random effect in both models to account for repeated measures from multiple videos per nest. We compared candidate models with all combinations of weather covariates using Akaike information criterion corrected for small sample sizes (AICc) and selected the model with the lowest AICc value (Burnham and Anderson 2004). Once final models were selected, we tested interactions between experimental treatment and any remaining weather covariates. We used the r.squaredGLMM package in MuMIn (Barton 2019) to generate effect sizes following Nakagawa and Schielzeth (2013).

We ran a linear model to examine differences in length of nestling period between experimental and unmanipulated nests. Initially, we included ambient temperature, rainfall, and wind speed as covariates, but they were insignificant (see "Results") and were dropped. We used nonlinear mixed models to fit logistic growth curves and determine the growth rate constant (K), which corrects for repeated measures within nests and tests for differences between treatment and unmanipulated groups, following Sofaer et al. (2013). All data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.6m905qfwr; Mitchell et al. 2020).

Results

Feeding Rates

Our feeding model tested the effects of our experimental treatment on parental provisioning while including age and three weather variables as covariates (see below). Our final model showed that, compared with unmanipulated nests, parents from experimental nests increased the rate of food delivery to nestlings while accounting for rain and nestling age (table A1; fig. 2*A*). The fixed effects of our feeding model explained 39% of the total variance in parental feeding rates (marginal R^2), and when random effects were included, the model explained 70% of the total variance (conditional R^2).

At both experimental and unmanipulated nests, mountain blackeye parents increased nestling feeding rates as nestlings aged (table A1; fig. 2*A*). Parents fed nestlings less often with increasing rain (table A1; fig. 3*A*) across experimental and unmanipulated nests. The interaction between rain and experimental treatment was not significant ($P = .241$) and was dropped from the final model. Neither ambient temperature nor wind speed explained variation in nestling feeding rates (temperature: $P = .423$; fig. 3*B*; wind speed: $P = .630$; fig. 3*C*), and both were excluded from the final model based on AICc model selection.

Brooding Time

Our brooding model tested the effects of experimental treatment on brooding time with nestling age, feeding rate, and three weather variables included as covariates (see below). Our final model showed that parents from experimental nests brooded less than parents from control nests while accounting for wind speed, nestling age, and feeding rate (table A2; fig. 2*B*). The fixed effects of our brooding model explained 47% of the total variation in brooding behavior (marginal R^2), and when random effects were included, the model explained 52% of the total variance (conditional R^2).

At both experimental and unmanipulated nests, mountain blackeye parents decreased nestling brooding as nestlings aged (table A2; fig. 2*B*). Brooding by parents in both

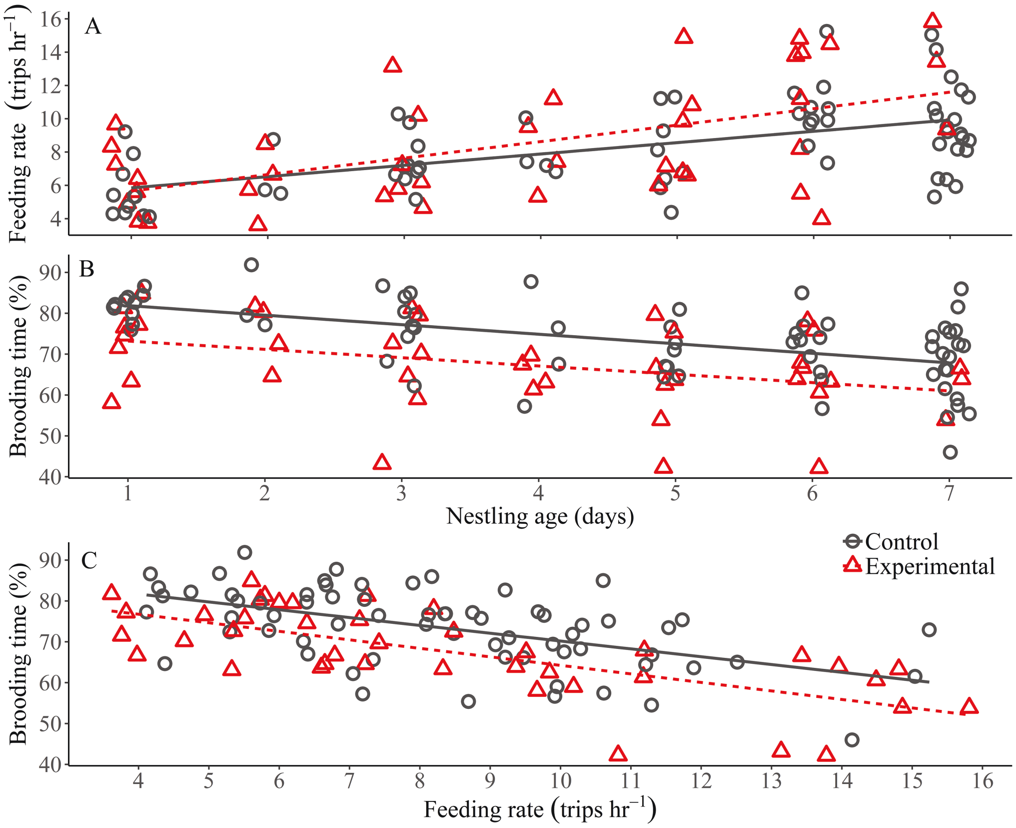

Figure 2: Effects of heat and rain cover treatment on parental behavior traits. *A*, Feeding rate is the number of times an adult bird visited the nest with food divided by the duration of the video. *B*, Brooding time is the percentage of the total video duration that parents spent warming the young. The nestling period is truncated at day 7 owing to the expected achievement of homeothermy around this time. *C*, Brooding time plotted against feeding rate shows the trade-off between these two parental duties. Lines are regression lines from general linear models.

experimental and unmanipulated nests increased with wind speed while accounting for nestling age and feeding rate (table A2; fig. 3*F*). The interaction between wind speed and experimental treatment was not significant ($P = .170$) and was dropped from the final model. Mean ambient temperature and rainfall did not explain variation in brooding behavior (temperature: $P = .534$; fig. 3*E*; rain: $P = .295$; fig. 3*D*) and were also excluded from the final model based on AICc model selection. In the final model, brooding time was strongly and negatively associated with feeding rate while accounting for nestling age and wind speed (table A2; fig. 2*C*).

Nestling Growth and Development Rates

Nestlings in experimentally heated and covered nests fledged earlier than those in unmanipulated nests ($\beta = -0.63$, $P = .031$, adjusted $R^2 = 0.08$; fig. 4*A*). Unmanipulated nestlings fledged in 14.63 ± 0.13 (mean ± SE) days compared with 14.0 ± 0.24 days for experimental nestlings. Nestling period was not explained by temperature, rainfall, or wind speed ($P = .783$, $P = .882$, and $P = .787$, respectively), and these were dropped from the final model. The shortened nestling periods in nests with experimentally ameliorated weather conditions reflected faster nestling growth rate for mass ($P = .012$; fig. 4*B*) and wing chord ($P = .032$; fig. 4*C*) but not for tarsus length ($P = .499$; fig. 4*D*).

Discussion

Tests of the relative importance of plastic responses to weather conditions at high elevations are critical for understanding the causes of the broad elevational pattern of slower growth. With increasing elevation, mountains become progressively colder (5°–10°C per 1,000 m asl) and often have higher or less predictable rainfall, at least in the montane zone (Barry 1992; Kitayama 1992). Results from our experiment demonstrate that harsh montane weather contributes to slower postnatal growth and development in mountain blackeyes, a tropical songbird living in high-

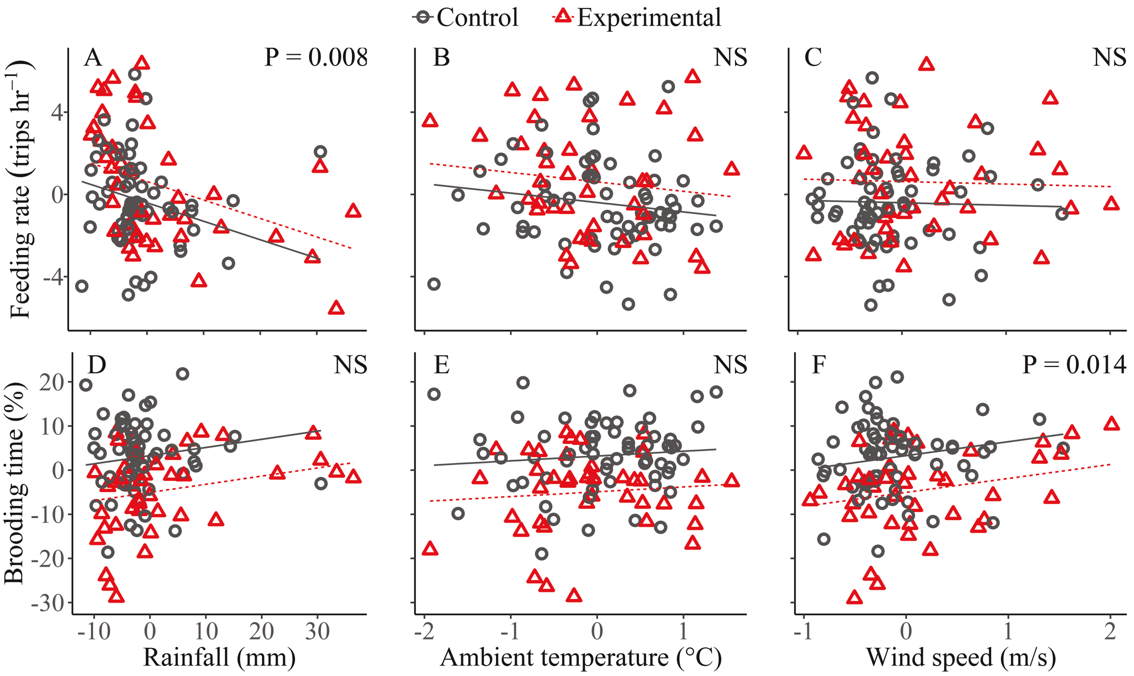

Figure 3: Partial correlation plots showing relationships between residuals of offspring feeding (*A*–*C*) and parental brooding (*D*–*F*) and residuals of three weather covariates: rainfall, ambient temperature, and wind speed. Each plot is corrected for the effects of the other two weather covariates and age of the nestlings.

elevation habitats. Nestlings from nests that were simultaneously warmed and protected from rain fledged earlier (fig. 4*A*) and gained mass and grew their wings faster (fig. 4*B*, 4*C*). Thus, montane weather clearly can be an important proximate influence on elevational patterns of ontogeny.

The effects of weather on growth and development at high elevations can be mediated by parental care. For altricial songbird parents, food provisioning and brooding are two of the most time-consuming parental duties (Kendeigh 1952; Clutton-Brock 1991; Starck and Ricklefs 1998), and our study shows that these behaviors are clearly sensitive to weather. Wind can increase heat loss of young through convective cooling, but mountain blackeye parents increased brooding with increasing wind speed (table A2; fig. 3*F*). Variation in ambient temperature did not predict brooding time in our study (fig. 3*E*), likely as a result of relatively low daily variance at our site (Kitayama 1992, 1995; Aiba and Kitayama 1999). However, higher brooding rates associated with colder weather have been observed in locations with more variable ambient temperatures (Johnson and Best 1982; Rosa and Murphy 1994; Wiebe and Elchuk 2003). The decrease in brooding time when we warmed and covered nests (fig. 2*B*) indicates that cold temperatures and rainfall at high elevations are important influences on parental behavior patterns that affect offspring growth and development.

The need to increase brooding time when conditions are colder and wetter may be important for growth and development through effects on offspring provisioning. Our results demonstrated a trade-off between parental brooding and offspring provisioning (fig. 2*C*) and showed that this trade-off shifted toward more offspring provisioning (fig. 2*A*) when brooding demands were reduced (fig. 2*B*) by experimentally ameliorated weather conditions. This increased feeding rate due to reduced brooding time was associated with faster growth of nestling mass and wings (fig. 4*B*, 4*C*). Of course, faster growth and development in our experimental nests may also be caused by reduced allocation of resources for thermoregulation (i.e., shivering) leading to increased allocation for tissue growth (Cheng and Martin 2012; Węgrzyn 2013). Selection may also favor allocation for wing growth to improve predator evasion and effective locomotion after fledging (Martin et al. 2018). Hence, faster mass gain and wing growth among nestlings in our experiment (fig. 4*B*, 4*C*) potentially reflect such resource allocation when harsh weather conditions are ameliorated.

Negative impacts of harsh weather conditions on avian growth have been demonstrated experimentally in two previous studies, both of which took place at lower elevations (Dawson et al. 2005; Rodríguez and Barba 2016). Interestingly,

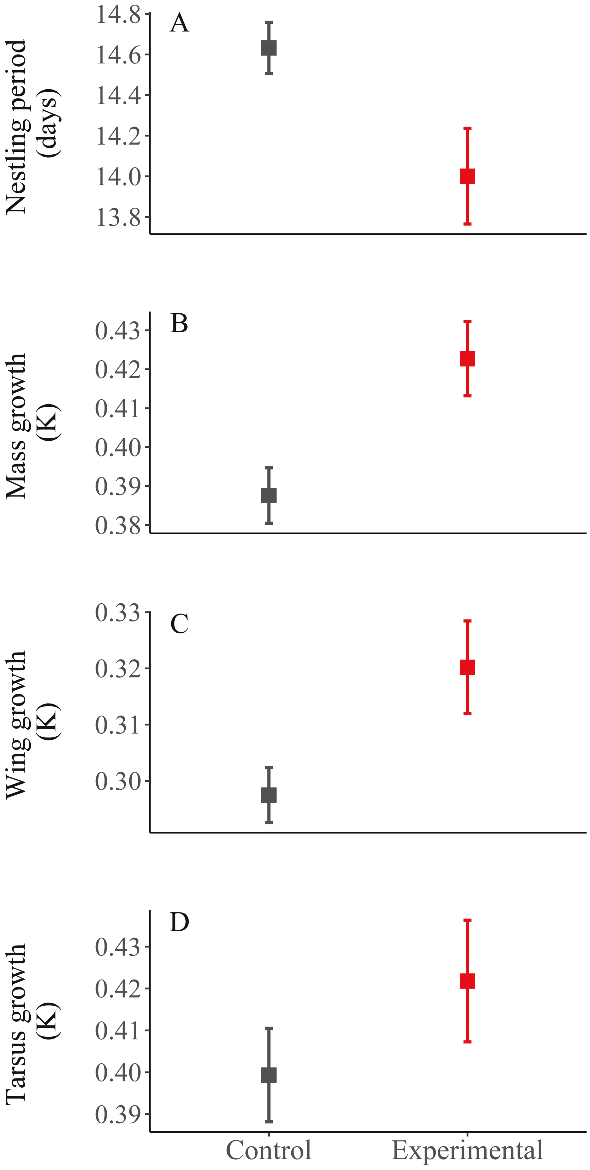

Figure 4: Effects of experimental treatment on growth and development rates. *A*, Difference in mean duration of nestling period in days between experimental and unmanipulated nests. *B–D*, Effects of experimental heat/cover treatment on growth rate constant (*K*) for nestling mass (*B*), wing chord (*C*), and tarsus (*D*). Squares represent the growth rate constant (*K*) of treatment versus unmanipulated nests using nonlinear mixed models (Sofaer et al. 2013). Error bars show standard errors of the mean.

Dawson et al. (2005) found that warmer nest temperatures increased growth rates of wing feathers despite no difference in parental feeding rates. Similarly, Rodriguez and Barba (2016) reduced nestling growth rates with experimental cooling despite no change in brooding constancy, but they did not examine feeding rates. Given the trade-off between brooding and feeding (fig. 2*C*) and the potential importance of each behavior to offspring growth and development, both behaviors should be studied together when considering the effects of weather on ontogeny.

The life-history consequences of behavioral plasticity across elevations remain important to understand. Our results clearly demonstrate that harsh weather contributes to slow growth at high elevations, and previous studies show that slower growth can create fitness costs when caused by extrinsic sources (Desai and Hales 1997; Lindström 1999; Metcalfe and Monaghan 2001; Martin et al. 2007; Lee et al. 2013). Moreover, nest predation is a time-dependent source of mortality such that longer nestling periods increase risk of predation for offspring (Martin 2015). Yet there may also be adaptive benefits to slower growth at high elevations due to intrinsic physiological trade-offs (e.g., Badyaev and Ghalambor 2001). Slower growth resulting from plastic responses to harsh weather can yield very different fitness consequences than slower growth resulting from evolved physiological trade-offs that benefit offspring. While we tested the impact of extrinsic factors on growth and development, our experiment was unable to assess the extent to which slow growth and development reflect intrinsic factors. Further experimental tests are needed to shed light on the relative importance of extrinsic versus intrinsic (i.e., proximate vs. adaptive) sources of slow montane growth and development. Ultimately, the role of plastic responses by parents and offspring to harsh weather conditions should be more carefully considered in future elevational life-history studies.

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Statement of Authorship

A.E.M. and T.E.M. conceived the ideas; A.E.M., J.B., and A.A. conducted the fieldwork; K.K. operated the weather station; A.E.M. and T.E.M. analyzed the data; A.E.M. wrote the initial draft of the manuscript; and A.E.M., J.B., A.A., K.K., and T.E.M. all contributed to editing the manuscript.

APPENDIX

Table A1: Model output from linear mixed effects model showing the effects of experimental heat and cover treatment, nestling age, and rainfall on offspring feeding rates

Predictor variable	β	SE	df	P
Experiment	1.53	.72	38.58	.039
Age	.90	.09	78.85	<.001
Rain	−.05	.02	74.08	.014

Table A2: Model output from linear mixed effects model showing the effects of experimental heat and cover treatment, offspring feeding rate, nestling age, and wind speed on parental brooding time

Predictor variable	β	SE	df	P
Experiment	−7.28	1.76	23.54	<.001
Feeding	−1.54	.31	76.09	<.001
Age	−1.02	.42	100.66	.017
Wind speed	3.24	1.20	102.85	.008

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