2021

EFFECTS OF WEATHER, PARENTAL BEHAVIORAL PLASTICITY, AND LIFE HISTORY TRAITS ON OFFSPRING GROWTH, DEVELOPMENT, AND ENERGY EXPENDITURE IN SONGBIRDS

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Recommended Citation

Mitchell, Adam Elliot, "EFFECTS OF WEATHER, PARENTAL BEHAVIORAL PLASTICITY, AND LIFE HISTORY TRAITS ON OFFSPRING GROWTH, DEVELOPMENT, AND ENERGY EXPENDITURE IN SONGBIRDS" (2021). *Graduate Student Theses, Dissertations, & Professional Papers*. 11740.
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EFFECTS OF WEATHER, PARENTAL BEHAVIORAL PLASTICITY, AND LIFE HISTORY TRAITS ON OFFSPRING GROWTH, DEVELOPMENT, AND ENERGY EXPENDITURE IN SONGBIRDS

By

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Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Fish and Wildlife Biology

The University of Montana
Missoula, MT

April 2021

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Effects of weather, parental behavioral plasticity, and life history traits on offspring growth, development, and energy expenditure in songbirds

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ABSTRACT

Weather creates energetic and survival challenges for organisms that can influence demography. Harsh weather often causes increased energy expenditure in adults, but how weather affects other life stages is less well understood. Juveniles are especially vulnerable because they must use energy to survive weather effects and maintain growth and development while having poorly developed thermoregulatory capabilities. Juveniles that spend energy overcoming harsh weather can have delayed growth and maturation, which can negatively affect competitive abilities, survival, and lifetime fitness. Understanding weather effects on offspring is particularly challenging in altricial species because parents have evolved strategies to ameliorate such effects. However, the degree to which parents ameliorate harmful effects of weather on offspring varies within and across species due to environmental and evolutionary constraints. Our ability to predict accurate ecological ramifications of climate change are currently limited by a paucity of studies of weather effects on developing offspring, and how parents are able and willing to mitigate these effects. This dissertation aims to fill such gaps in knowledge using empirical data within and across species of songbirds on 3 continents.

In chapter 1, I tested whether slower growth and development of organisms living at high elevations is caused by harsh weather. At a study site at ca. 3200 m asl in Malaysian Borneo, I found that Mountain Blackeye (*Chlorocharis emiliae*) parents in experimentally heated and covered nests warmed their young less and provisioned more often. This behavioral plasticity resulted in faster mass gain and wing growth, and earlier fledging of young. Thus, slower growth and development of montane organisms partially reflects proximate responses to harsh weather.

In chapter 2, I used samples from 664 nestlings across 54 species on 3 continents to test for proximate and evolutionary sources of offspring daily energy expenditure (DEE). Within species, heavier rain, colder T_a, and fewer siblings were each correlated with higher nestling DEE, highlighting the importance of weather and huddling with siblings on offspring energy use. Across species, DEE was positively correlated with adult and juvenile mortality, illustrating the evolved component of DEE that can be shaped by selection from age-specific mortality.

In chapter 3, I simulated rain above nests of 5 species of songbirds in Malaysian Borneo to test the direct effects of rain on offspring DEE and parental behavior, and how these responses varied across nest type. Parents in enclosed nests did not change their behavior in response to rain, while parents in open nests brooded their young more, leading to no difference in nestling DEE in either nest type. These results suggest that parents using exposed nest types can ameliorate costs of short-term rain on young through behavioral plasticity. These results also suggest that parents using open nests may need to modify their behavior in locations where rain is predicted to increase from climate change.

ACKNOWLEDGEMENTS

This dissertation is far beyond what I could have produced alone. First and foremost, I would like to thank my advisor, Tom, whose curiosity and enthusiasm for understanding the nuances of natural history and ecology helped catalyze my own interest in those topics. I believe one of the distinctions of a great scientist is to holistically understand what we know in order to pinpoint what we still do not know, something that Tom has clearly mastered, and instills upon his students. Tom has challenged me and broadened my scientific thinking in immeasurable ways, and I trust I am a far better scientist because of him. I am sincerely thankful for the support, guidance, opportunities, and experiences he has provided for me.

I would like to thank Bret Tobalske, Creagh Breuner, Jedediah Brodie, and Erick Greene on my dissertation committee for patience and constructive feedback in many aspects of my scientific development. Special thanks to Chad Bishop and other WBIO and DBS faculty and staff for logistical and other support throughout this degree. I have particular gratitude for Jeanne Franz, Jill Burke, Janean Clark, Wendy Maltonic, Johanna Anderson, Robin Hamilton, Vanetta Burton, Tina Anderson, and Deb Simmons.

I am appreciative of funding from the Wesley M. Dixon Graduate Fellowship, Bertha Morton Scholarship, Les Pengelly Scholarship, and the UM WBIO department. I would also like to thank to the Carl and Camilla Rietman Foundation for generously awarding myself and many others funding for advanced education.

I appreciate training and mentorship I received from Blair Wolf at the University of New Mexico, and Kristen Oliver for diligently processing samples in the lab. Far too many field technicians and bird lab employees contributed to data collection and processing to list here, but I am sincerely thankful for all of them. I hope that working on these projects was fulfilling and creates as many opportunities for them as it has for me.

I spent more than a decade of my life studying the nesting birds of Kinabalu Park in Sabah, Malaysia, that would become the product of this dissertation. While I fell in love with the birds first, I believe it was the people and culture of the Dusun communities surrounding Kundasang, Kiau, Bundu Tuhan, Ranau, and other small villages that maintained the richness of my experiences throughout the last decade. In particular, I am grateful for friendships with Anthonio Anthony, Lerry Gumbayong, Enroe bin Saudi, Rayner Langgim, Bonifatrino Jurunin, Robby Sapinggi, Annuar Jain, and Alim Biun. They enthusiastically shared so much local knowledge that undoubtably enriched and influenced my perspectives on life as well as the research I was conducting. I always considered it a privilege to study in their native land, and I cannot thank them enough for sharing their land, homes, culture, and friendships with me. I would also like to thank Mr. Lawrence Soon and the Laban Rata guesthouse staff for incredible hospitality and friendship while living at this remote field site. Mr. Sani Gourdin and others at Universiti Malaysia Sabah provided laboratory space and equipment, without which few of the results in chapters 2 and 3 could have been obtained.

Throughout my time in the Martin lab and associated international field work, I have been surrounded by a cohesive group of lab mates that have become some of my most valued friends, mentors, and co-adventurers. In particular, conversations with Andy Boyce have added clarity to my sometimes disorganized mind, both personally and scientifically. Many of my scientific achievements can be traced back to his support in one way or another. James Mouton, Riccardo Ton, and William Blake have also been amazing friends, mentors, and outdoor recreation comrades who have helped balance my life perfectly throughout this degree. Juan Oteyza, Joe LaManna, Karolina Fierro-Calderón, and Mark Mainwaring have been valuable lab

mates and friends during my time at UM as well. Maggie Blake, Connor Armstad, Julia Brandauer, and Ahvi Potticary helped with data, lab, and field logistics an almost infinite number of times, and have turned out to be wonderful and supportive friends. I am also appreciative of the next cohort of lab members that selflessly assisted with field work and practice talks, contributed to general camaraderie, and also provided me opportunities to be a mentor. Thank you to Tim Forrester, Sarah Straughan, Elise Zarri, and Holly Jackson.

A terrific group of current or former Missoula friends that have not yet been listed have also become an important circle of support for me, including Jessie Golding, Caroline and Will Deacy, Anne Shaefer, Mandy Slate, and Ellen Pero. Jordan Boersma and Cameron Rutt have been amazing friends, supporters, and scientific peers, and I value field and social experiences shared with both of them immensely. Thanks to other friends, including Josh, Luke, Chris, Katie, Leah, Scott, J.D., and many more for the support you may or may not have known you gave me.

I would like to thank various scientific mentors at different stages of my education that I attribute my love of science to. Thank you to Norm Devereux and Val Frolov for challenging me at CHS, Mike LeMaster, Bryan Dutton, Irja Galvan, Mark Van Steeter, and John Minahan for engaging me at WOU and teaching me foundational concepts that are relevant to the research presented in this dissertation. Thanks also to various field crew leaders, including Tracey Johnson, Annika Samuelsen, Ania Majewska, and Justyn Stahl for teaching me field skills that helped me collect data throughout my dissertation work. I am thankful for the opportunities these skills have provided for me.

I would like to sincerely thank my parents, Peggy and Tom, for the unlimited support they have always given me. I grew up hearing that there were few limits to what I could achieve, and this encouraged me to ignore persistent doubts and fears throughout this degree. Thank you both for your unconditional love and support, and for the unique phenotype I inherited and learned from you that makes me so curious about the natural world. Thanks also to my siblings, Eric and Cherie, for being patient, understanding, and encouraging. Knowing that you always believed in me helped me persevere. I look up to both of you in many ways and am proud to be your brother.

Sara, in addition to important scientific mentorship, the love, support, and patience you have shown me has balanced out a sometimes stressful and intense period of my life. You have enriched my life with joy, humor, and companionship, and I am truly thankful for the enormous role you played throughout the completion of this degree. Ellie, though you could not care less, you have seen me through more than you know. Thank you for every kiss and joyful wag. I also thank Gregg, Lisa, Walt, and Taylor Williams, and Han-A Park for their support throughout.

Reading about fascinating breeding biology patterns written almost a century ago by pioneering ornithologists were an early and consistent source of inspiration to me. Among them, Alexander Skutch, David Lack, Reginald Moreau, Philip Ashmole, Charles Kendeigh, Margaret Morse Nice, and others created the foundation to the field of study that I pursue. I am amazed when I think how fortunate those early scientists were to be able to pursue their research, sometimes through world wars, pandemics, and systemic oppression. I am humbled to have been given similar opportunities, admittedly through much more favorable conditions. I recognize not everyone is so fortunate, and I am grateful for the circumstances in my life outside of my control that have allowed me to pursue the highest levels of education available.

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Introduction

Weather, such as air temperature, rain or drought, and wind, creates energetic and survival challenges for organisms that can influence fitness and population demography (MacArthur 1972; Grant & Boag 1980; Owen-Smith 1990; Coulson *et al.* 2001; Brown *et al.* 2004; Moreno & Pape Møller 2011). Adults must devote a portion of their energy budgets to cope with environmental conditions (Scholander *et al.* 1950; Boyle *et al.* 2020), but weather can also influence other life stages. Juveniles are particularly vulnerable because they must survive weather effects while maintaining growth and development (Seltmann *et al.* 2009; Boersma & Rebstock 2014; Ropert-Coudert *et al.* 2015; de Zwaan *et al.* 2019; Sauve 2021), all while having poorly developed thermoregulatory capabilities (Dunn 1980; Arendt 1997; Starck & Ricklefs 1998; Price & Dzialowski 2018). Currently, the physiological effects of weather on juvenile life stages are poorly studied, which limits our understanding of how climate change may influence organisms and their populations (Sauve 2021).

Rising global temperatures (Pachauri & Mayer 2014) have caused dramatic impacts on organisms and their populations (Walther *et al.* 2002; Parmesan 2006; Sekercioglu *et al.* 2008). Though less well studied, rainfall patterns are also expected to shift in many regions (Allan & Soden 2008; Trenberth 2011; Westra *et al.* 2013; Ummenhofer & Meehl 2017). Rain often positively influences populations through indirect effects on lower trophic levels (Grant & Boag 1980; Owen-Smith 1990; Sillett *et al.* 2000; Russell *et al.* 2002), but wetting from rain can also have negative direct effects through energetic costs associated with increased heat loss of individuals (Lustick & Adams 1977; Stalmaster & Gessaman 1984; Webb & King 1984; Wilson *et al.* 2004; Voigt *et al.* 2011). In endothermic offspring, energy spent on thermoregulation from weather (Hull 1965; Weathers 1992; Dykstra & Karasov 1993) may not be available for growth and development, causing critical delays in juvenile life stages (de Zwaan *et al.* 2019). Delayed development from extrinsic sources can have immediate fitness costs through increased predation (Remeš & Martin 2002; de Zwaan *et al.* 2019), and long-term costs including lower competitive ability, survival, and lifetime fitness (Desai & Hales 1997; Lindström 1999; Metcalfe & Monaghan 2001; Lee *et al.* 2012). Due to clear ramifications for animal populations, understanding the effects of weather on offspring energy expenditure should be an important objective in ecology, yet surprisingly little is currently known.

Understanding the effects of weather on offspring energy expenditure is particularly challenging because parental care has evolved in many taxa to ameliorate such effects (Clutton-Brock 1991). However, life history theory posits that natural selection should not always favor increased parental care (Williams 1966; Trivers 1974; Hirshfield & Tinkle 1975; Clutton-Brock 1991; Roff 1992). For example, longer-lived species were less willing to provide parental care when exposed to a nest predator than shorter-lived species, illustrating effects of evolved life histories on parental care strategies (Ghalambor & Martin 2001; Oteyza *et al.* 2020). Similarly, species should be expected to vary in the degree to which parents protect developing young during weather challenges, and such variation should influence energetic costs of weather in offspring. Studies exploring variation in parental care and offspring responses to weather may elucidate how species with different life histories and parental care strategies will be impacted by climate change.

Nest construction is another parental care strategy that can help ameliorate the effects of weather on offspring (Collias & Collias 1984; Hansell 2005). Protection from predation is most often considered the primary function of nests (Nice 1957; Jeanne 1975; Rand & Dugan 1983; Skutch 1985; Orizaola *et al.* 2003), yet nest advantages during inclement weather have been recently highlighted (Heenan *et al.* 2015; Martin *et al.* 2017; Deeming & Campion Eloise 2018; Matysioková & Remeš 2018; Biddle *et al.* 2019). Nest designs vary within and among taxa, and in birds, open cup-shaped nests and enclosed, roofed nests are the two most common types (Collias & Collias 1984). If enclosed nests provide more weather protection than open nests, parental care during harsh weather may be relaxed in species using enclosed nests. Understanding the degree to which parental behavior and nest type interact to ameliorate weather effects on offspring will require comparative studies across species, but no such studies currently exist.

Throughout the chapters of this dissertation, I explore the above gaps in knowledge, and address important questions in ecology. To accomplish this goal, I present empirical data collected on songbirds from 4 disparate field sites: ca. 2350 m asl in the Coconino National Forest, Arizona, USA (34°32’N, 110°97’W), sea level in Koeberg Nature Reserve, Cape Town, South Africa (33°41’S, 18°27’E), and two separate sites in Kinabalu Park, Sabah, Malaysia (6°08’N, 116°56’E), ca. 1500 m asl at the park headquarters, ca. 3200 m asl at the Laban Rata station. In chapter 1, I conducted a heating experiment to test whether the slow growth found in high elevation organisms reflects harsh montane weather conditions. In chapter 2, I tested the proximate (within species) influences of air temperature, rainfall, and brood size, and the evolutionary (among species) influences of growth rate, adult and juvenile mortality on nestling energy expenditure. I used field metabolic rate data from 664 individual nestlings from 54 species across 3 continents to answer specific questions in chapter 2. In chapter 3, I used a rain simulation experiment to test the direct effects of rain on nestling energy expenditure, and whether parents in open nests must alter their behavior to ameliorate the effects of rain more than parents using enclosed nests.

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Chapter 1: 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 slower than those at lower elevations. Slow montane ontogeny is thought to be an evolved adaptation to harsh environments that improve juvenile quality via physiological tradeoffs. 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 ca. 3200 m asl in Malaysian Borneo. This experiment was designed to test if cold and wet montane conditions contribute to parental care and post-natal 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 to 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.

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 to 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 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 temperatures and often increased rainfall compared to 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 & Ghalambor, 2001; Hille & 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 (post-natal) stage of altricial birds that contribute to growth and development rates. Time spent brooding young can increase when temperatures are colder (Johnson & Best, 1982; Rosa & Murphy, 1994; Wiebe & 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 harsh weather of high elevations might cause plastic reductions in growth and development rates of montane songbirds is through a need to increase brooding (warming) that reduces offspring provisioning.

We experimentally tested the hypothesis that parental brooding and provisioning patterns are influenced by harsh montane weather which contributes to slower post-natal 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 when nests are experimentally protected from montane weather brooding regardless of parental responses.

METHODS

Study site and species—We studied Mountain Blackeyes (*Chlorocharis emiliae*) from 2013-2017 in the forest surrounding the Laban Rata station on Mt. Kinabalu, Malaysian Borneo (ca. 3200 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 resultingly, their nests do not appear to be as inconspicuous as many other species on Mt. Kinabalu. Mean elevation for nests that we studied was 3281 ± 5 m, and 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 3000 m asl (Boyce et al. 2015). Both males and females brood and feed the single nestling.

Mt. Kinabalu is a granitic mountain formation, and is the tallest mountain on the island of Borneo at 4095 m asl (Sheldon et al. 2015). The area surrounding the Laban Rata station on Mt. 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 ca. 3000 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 24-48 hours following Martin and Geupel (1993) to determine precise hatching and fledging dates. We used hatching and fledging dates to determine nestling period length, a proxy for post-natal 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 one hour of sunrise, and end times varied due to different battery capacities. Videos used to evaluate parental behavior ranged from 3-8 hours (mean ± SE = 6.0 ± 0.1 hours). Experimental nests were videoed 41 total days for a total of 246 hours, whereas unmanipulated nests were videoed for 67 days for a total of 398 hours. 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 figure 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 batteries every 2-3 days to maintain a continuous heat supply. All experimental nests were also protected from rain using a piece of plywood (approx 30 x 40 cm) wired to vegetation 40 cm directly above each nest (see figure 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 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 due to 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 may also have 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, due to 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 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 Inc., Helsinki, Finland) placed 1.5 m off the ground, which took measurements every 10 seconds. Rainfall was measured with a TE525MM tipping bucket rain gauge (Texas Electronics Inc., Dallas, TX, USA) with a sensitivity of 0.1 mm per tip. Wind speed was measured with an R.M. Young 03001 Wind Sentry (R.M. Young, MI, USA) every 10 seconds. All readings were recorded by a CR 10 data logger (Campbell Scientific Inc., Logan, UT, USA). Using these data, we calculated mean temperature (°C), total rainfall (mm), and mean wind speed (m/s) per 24-hour period. We analyzed parental behavior traits relative to weather covariates by using the means of the calendar days that the nests were filmed.

Nestling period length 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 program R version 3.5.1 (R 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 6-7 for Mountain Blackeyes. To normalize across different video monitoring lengths, brooding rate was quantified as the proportion of each video 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 nestling period length between experimental and unmanipulated nests. Initially, we included ambient temperature, rainfall, and wind speed as covariates, but they were insignificant (see results) and so were dropped. We used non-linear mixed models to fit logistic growth curves and determine the growth rate constant (*K*) following Sofaer et al. (2013), which corrects for repeated measures within nests and tests for differences between treatment and unmanipulated groups.

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 to unmanipulated nests, parents from experimental nests increased the rate of food delivery to nestlings while accounting for rain and nestling age (table A1, figure 2A). The fixed effects of our feeding rate model explained 39 percent of the total variance in parental feeding rates (marginal R^2) and including random effects the model explained 70 percent 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, figure 2A). Parents fed nestlings less often with increasing rain (table A1, figure 3A) across experimental and unmanipulated nests. The interaction between rain and experimental treatment was not significant ($P = 0.241$) and was dropped from the final model. Neither ambient temperature nor wind speed explained variation in nestling feeding rates (temperature: *P* = 0.423, figure 3B; wind speed: 0.630, figure 3C) 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, figure 2B). The fixed effects of our brooding model explained 47 percent of the total variation in brooding behavior (marginal R^2) and including random effects the model explained 52 percent of the total variance (conditional R^2).

At both experimental and unmanipulated nests, Mountain Blackeye parents decreased nestling brooding as nestlings aged (table A2, figure 2B). Brooding by parents in both experimental and unmanipulated nests increased with wind speed while accounting for nestling age and feeding rate (table A2, figure 3F). The interaction between wind speed and experimental treatment was not significant (*P* = 0.170) and was dropped from the final model. Mean ambient temperature and rainfall did not explain variation in brooding behavior (temperature: *P* = 0.534, figure 3E; rain: *P* = 0.295, figure 3D) 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, figure 2C).

Nestling growth and development rates—Nestlings in experimentally heated and covered nests fledged earlier than in unmanipulated nests (*B* = -0.63, *P* = 0.031, adjusted R^2 = 0.08; figure 4A).

Unmanipulated nestlings fledged in 14.63 ± 0.13 (mean ± SE) days compared to 14.0 ± 0.24 days for experimental nestlings. Nestling period was not explained by temperature, rainfall, or wind speed (*P* = 0.783, 0.882, and 0.787, 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* = 0.012; figure 4B) and wing chord (*P* = 0.032; figure 4C), but not tarsus length (*P* = 0.499; figure 4D).

DISCUSSION

Tests of the relative importance of plastic responses to weather conditions at high elevations is critical for understanding the causes of the broad elevational pattern of slower growth. With increasing elevation, mountains become progressively colder (5-10°C per 1000 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 post-natal growth and development in Mountain Blackeyes, a tropical songbird living in high elevation habitats. Nestlings from nests that were simultaneously warmed and protected from rain fledged earlier (figure 4A) and gained mass and grew their wings faster (figure 4B, 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, figure 3F). Variation in ambient temperature did not predict brooding time in our study (figure 3E), likely due to 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 & Best, 1982; Rosa & Murphy, 1994; Wiebe & Elchuk, 2003). The decrease in brooding time when we warmed and covered nests (figure 2B) 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 tradeoff between parental brooding and offspring provisioning (figure 2C) and showed that this tradeoff shifted towards more offspring provisioning (figure 2A) when brooding demands were reduced (figure 2B) by experimentally ameliorated weather conditions. This increased feeding rate due to reduced brooding time was associated with faster growth of nestling mass and wings (figure 4B, 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) to increased allocation for tissue growth (Cheng and Martin 2012; Wegrzyn 2013). Selection may also favor allocation towards 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 (figure 4B, 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, 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 (figure 2C) 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 tradeoffs (e.g., Badyaev and Ghalambor 2001). Slower growth resulting from plastic responses to harsh weather can yield very different fitness consequences than 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 reflects intrinsic factors. Further experimental tests are needed to shed light on the relative importance of extrinsic versus intrinsic (i.e., proximate versus 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.

ACKNOWLEDGEMENTS

Bret W. Tobalske, Cameron L. Rutt, and two anonymous reviewers provided insightful comments on the manuscript. We thank former and current members of the Martin lab group for invaluable feedback and support throughout all steps of the study. Special thanks to Rayner Langgim for field assistance, Connor Armstad, Ahva Potticary, Margaret Riordan, and Julia Brandauer for field and data coordination and assistance. We also appreciate the video bird lab for watching and tabulating many hours of videos. Mr. Lawrence Soon and the management/staff at Laban Rata guesthouse were particularly generous and provided logistical and social support. We appreciate collaborative assistance from Dr. Rimi Repin with Sabah Parks and many staff members at Kinabalu Park. AEM is grateful to Dr. Sara Williams for academic and moral support. This work in general was supported by the National Science Foundation (DEB-1241041, DEB-1651283, IOS-1656120). AEM was supported by the WBIO department at the University of Montana, a Wesley M. Dixon graduate fellowship, the Carl and Camilla Rietman Scholarship, and a Bertha Morton Scholarship. This work was conducted under auspices of University of Montana IACUC #059-10TMMCWRU. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflicts of interest.

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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 so 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 yet, but both heat and cover treatments were administered simultaneously for all experimental nests.

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

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; ambient temperature, rainfall, and wind speed. Each plot is corrected for the effects of the other two weather covariates and age of the nestlings.

Figure 4. Effects of experimental treatment on growth and development rates. Red squares represent experimentally heated and covered nests and black squares represent unmanipulated nests. A) shows the difference in mean nestling period duration in days between treatment and

unmanipulated nests. Plots B-D show the effects of experimental heat/cover treatment on growth rate constant *K* for nestling mass (B), wing chord (C), and tarsus (D). Points represent growth rate constant *K* of treatment versus unmanipulated nests using non-linear mixed models (Sofaer et al. 2013). Error bars are standard errors of the mean.

FIGURES

Figure 1

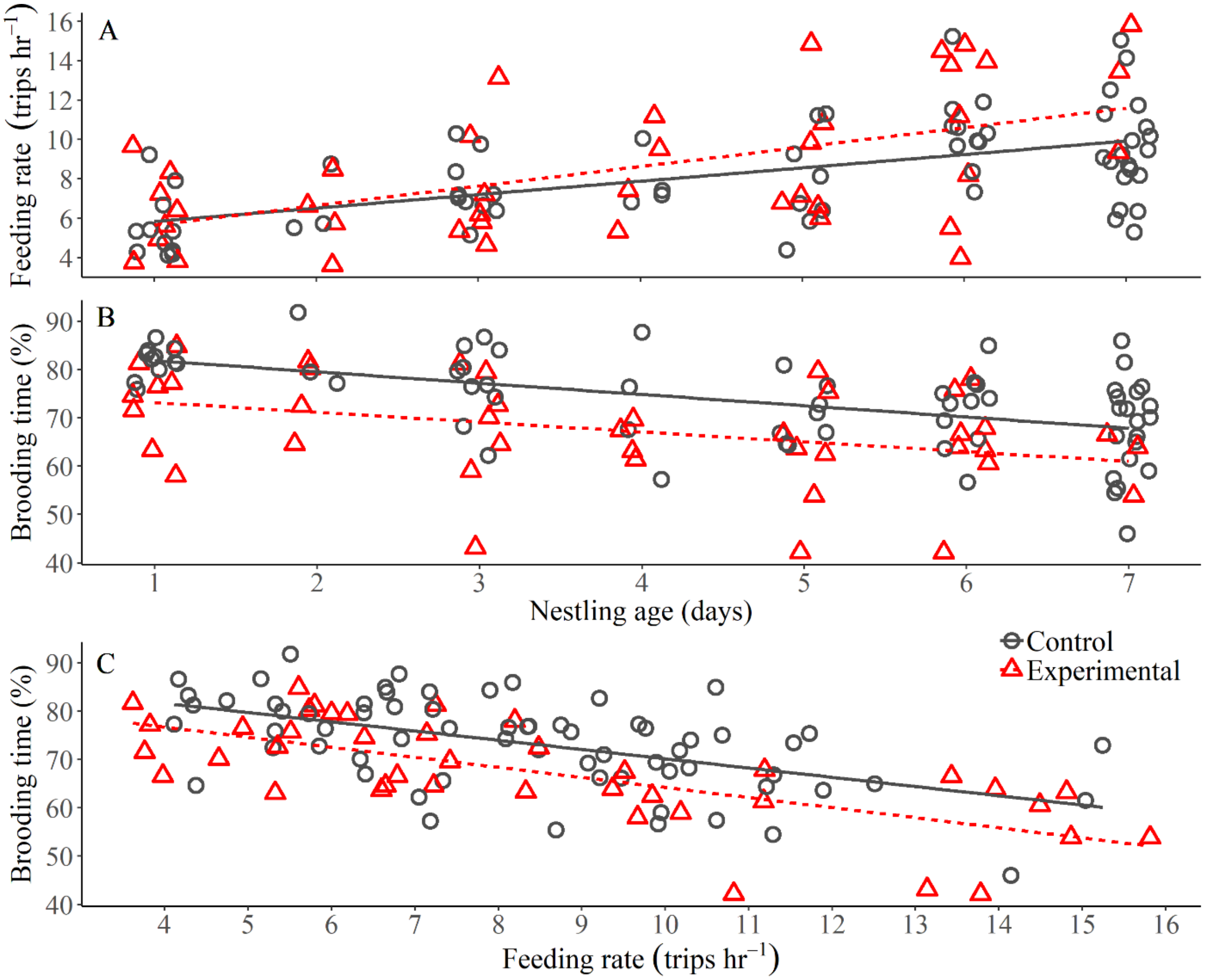
A
B
C
Feeding rate (trips hr^{-1})
16
14
12
10
8
6
4
Brooding time (%)
90
80
70
60
50
40
1
2
3
4
5
6
7
Nestling age (days)
Control
Experimental
4
5
6
7
8
9
10
11
12
13
14
15
16
Feeding rate (trips hr^{-1})

Figure 2

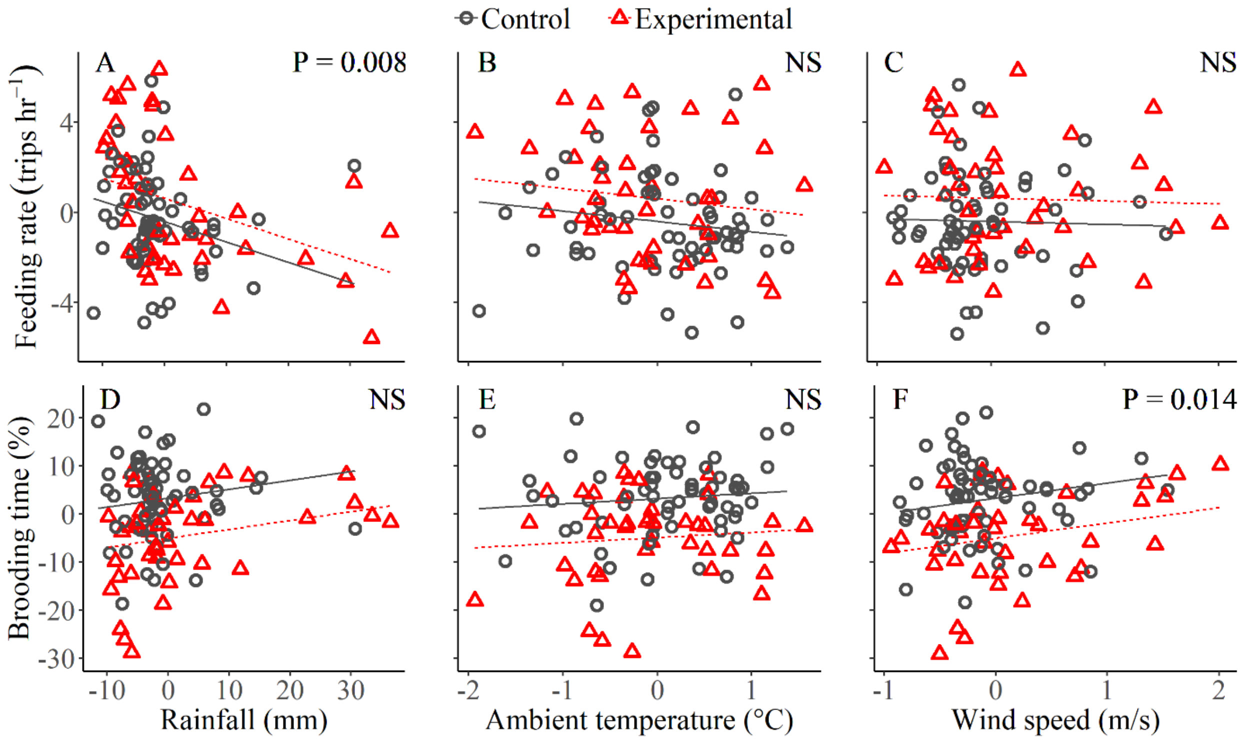
Control
Experimental
A
P = 0.008
B
NS
C
NS
D
NS
E
NS
F
P = 0.014
Feeding rate (trips hr^{-1})
Brooding time (%)
4
0
-4
20
10
0
-10
-20
-30
-10
0
10
20
30
Rainfall (mm)
-2
-1
0
1
Ambient temperature (°C)
-1
0
1
2
Wind speed (m/s)

Figure 3

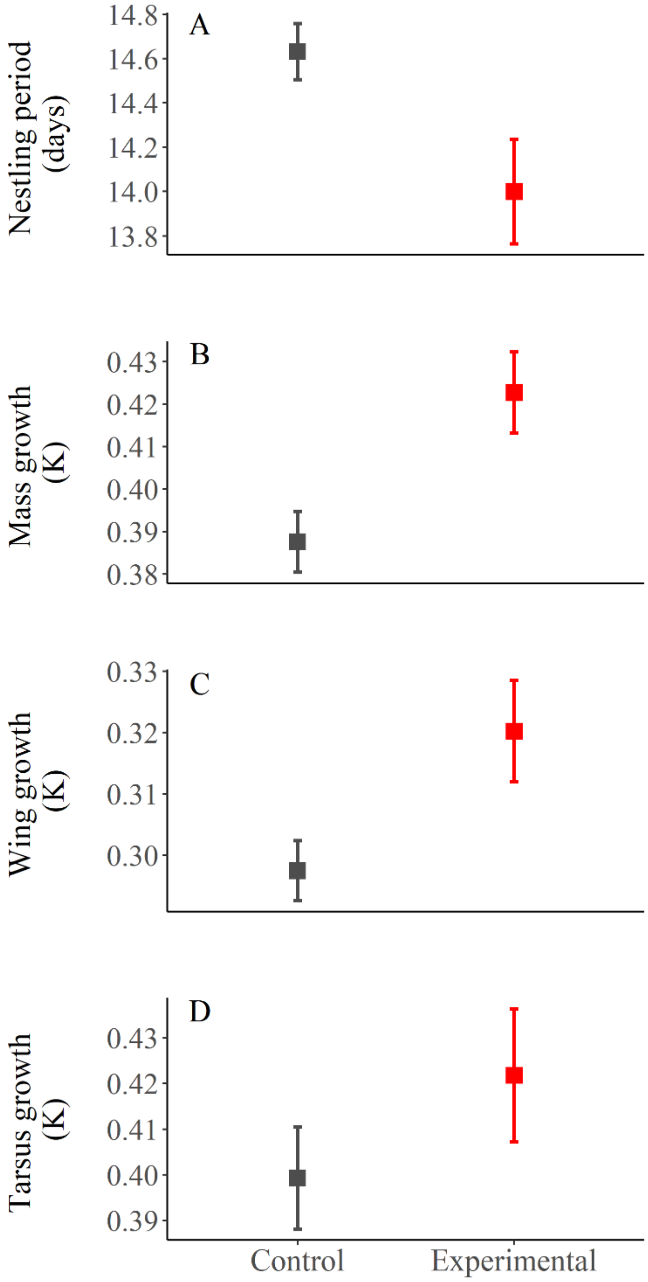
A
Nestling period (days)
14.8
14.6
14.4
14.2
14.0
13.8
B
Mass growth (K)
0.43
0.42
0.41
0.40
0.39
0.38
C
Wing growth (K)
0.33
0.32
0.31
0.30
D
Tarsus growth (K)
0.43
0.42
0.41
0.40
0.39
Control
Experimental

Figure 4

APPENDIX

Table A1: Top model output of a linear mixed-effects model showing the effects of experimental heat and cover treatment, nestling age, and rain on offspring feeding rates.

Predictor variables	β	*SE*	*df*	*P*
Experiment	1.53	0.72	38.58	0.039
Age	0.90	0.09	78.85	< 0.001
Rain	-0.05	0.02	74.08	0.014

Table A1: Top model output of a linear mixed-effects model showing the effects of experimental heat and cover treatment, feeding rate, nestling age, and wind speed on parental brooding time.

Predictor variables	β	*SE*	*df*	*P*
Experiment	-7.28	1.76	23.54	<0.001
Feeding	-1.54	0.31	76.09	<0.001
Age	-1.02	0.42	100.66	0.017
Wind speed	3.24	1.20	102.85	0.008

Chapter 2: Proximate and evolutionary sources of offspring energy expenditure in songbirds

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ABSTRACT

Understanding variation in offspring energy expenditure is important because it is critical for ontogeny. Weather may exert proximate effects on offspring energy expenditure but can be masked by parental care and sibling huddling. Across species, offspring energy expenditure variation may reflect evolved responses to growth or mortality. Climate change might alter offspring thermoregulatory costs, yet limited intra- and interspecific studies inhibit a general understanding of climate effects. We tested proximate and evolutionary causes of nestling daily energy expenditure (DEE) variation across 54 songbird species. Offspring DEE increased with rainfall and colder air temperatures suggesting parents do not always offset energetic costs of weather on young. DEE also increased with fewer siblings indicating huddling benefits. Across species, DEE increased with nestling and adult mortality, but not growth rate, emphasizing the evolutionary effects of mortality. Thus, proximate and evolutionary factors influenced offspring DEE across diverse species with differing life histories and climates.

INTRODUCTION

Understanding why rates of energy expenditure in developing offspring vary within and among species is important because of the consequences for growth and development (Case 1978; Olson 1992; West *et al.* 2001; McNab 2002). Energy expenditure may vary from proximate influences within species and evolved strategies among species. Proximate sources of variation in energy expenditure can reduce offspring quality and fitness (Desai & Hales 1997; Lindström 1999; Metcalfe & Monaghan 2001), while energy expenditure can also evolve among species in response to natural selection (Nagy 1987; Tieleman & Williams 2000; Anderson & Jetz 2005; Pontzer *et al.* 2014). Yet, the extent to which offspring energy expenditure varies within and among species and the causes of this variation are poorly studied.

Weather conditions may have important proximate ramifications for energy expenditure (Brown *et al.* 2004; Speakman 2005), which are particularly important for understanding climate change effects. Offspring energy expenditure may be greater in colder air temperatures due to increased energy demands of thermoregulation (Scholander *et al.* 1950; West 1965; Broggi *et al.* 2004). Similarly, rainfall may increase offspring energy expenditure due to increased conductance and heat loss from wetting (Lustick & Adams 1977; Webb & King 1984). However, the number of offspring per litter or brood can have contrasting effects on how young spend energy: more offspring can reduce thermoregulatory costs due to huddling (Royama 1966; Mertens 1969; Kunz & Hood 2000; Mckechnie & Lovegrove 2001; Gilbert *et al.* 2010), but may also increase individual energy expenditure costs through sibling competition (Godfray & Parker 1992; Hudson & Trillmich 2008). Due to these contrasts, the energetic consequences of brood size variation remain unclear, especially when combined with variable weather conditions experienced in the wild. Finally, parents in many taxa can ameliorate energy costs of weather conditions by warming or shielding young during cold and wet weather (Johnson & Best 1982; Wittenberger 1982; Barnett & Dickson 1989; Beintema & Visser 1989; Smith *et al.* 2018). Tests of the influence of weather and brood size on energy expenditure of offspring have primarily been conducted in laboratories, whereas field tests of altricial young being cared for by parents will provide a more ecologically relevant understanding of the causes of offspring energy expenditure variation. Yet, energy expenditure remains largely unstudied in wild offspring.

Among species, interspecific variation in energy expenditure may occur due to evolved differences. High offspring predation rates favor accelerated growth among species which may be supported by higher nestling energy expenditure (Case 1978; Arendt 1997; West *et al.* 2001; Remeš & Martin 2002; Ton & Martin 2016, 2020). In addition, species with low adult mortality are expected to reduce reproductive effort to conserve resources for future breeding attempts (Williams 1966; Hirshfield & Tinkle 1975; Ghalambor & Martin 2001; Martin 2002). Reduced reproductive effort may be manifested as reduced parental care, which could raise offspring thermoregulatory costs. As a result, species with lower adult mortality may have higher offspring energy expenditure. Alternatively, selection may favor reduced energy expenditure in species with lower adult mortality to minimize cellular damage caused by metabolism (Ricklefs & Wikelski 2002; Barja 2004; Hulbert *et al.* 2007). Yet, relationships between energy expenditure and both adult and juvenile mortality rates have not been tested among free-living offspring.

We estimated nestling daily energy expenditure (DEE) using the doubly-labeled water method for 54 species of wild, free-living songbirds (order: Passeriformes) across three continents. We tested the proximate response of nestling songbird DEE relative to three environmental factors: brood size, air temperature, and rainfall, as well as the evolutionary response to adult and nestling mortality and growth rates.

METHODS

Study areas and species

We sampled 664 nestling songbirds from 54 species at three locations (see Martin *et al.* 2015a for more details of study sites): ca. 2350 m asl in the Coconino National Forest, Arizona, USA (34°32’N, 110°97’W), sea-level in Koeberg Nature Reserve, Cape Town, South Africa (33°41’S, 18°27’E), and ca. 1450-1950 m asl in Kinabalu Park, Sabah, Malaysia (6°08’N, 116°56’E). We studied 18 species in Arizona, 12 species in South Africa, and 24 species in Malaysia (Table S1). We sampled Arizona birds from May to July 2016-2017, South African birds from August to October 2016, and Malaysian birds from February to June, 2016-2019. Nests were located using systematic and parental behavior techniques following Martin and Guepel (1993).

Metabolic measurements

We estimated daily energy expenditure (DEE) of nestling birds using the two-sample doubly-labeled water method following Speakman (1997). We administered a 2:1 mixture of ^2H_2O (99 atm%) and $H_2{}^{18}O$ (98 atm%) at a dose of 2.0 – 2.5 ml/kg of doubly-labeled water. Our samples were administered within one day of pin break, the day the 8th primary feather breaks from the sheath, to standardize for level of development across species. To administer the doubly-labeled water, we removed nestlings from their nests and weighed with Gempro 250 digital scale (MyWeigh, Phoenix, AZ, USA), accurate to 0.01 g. We then drew a mass-specific dose (see Table S2) of doubly-labeled water from a sealed vile using a lab-calibrated Hamilton syringe (Model numbers: 80501, 80601, 80701; Hamilton Company, Reno, NV, USA). The labeled water was injected intramuscularly into the pectoralis muscle. Leakage of label at the injection site was rare, but was noted in the field and results were screened by this variable to remove inaccurate values. No more than two nestlings were injected per nest.

After injection, nestlings were immediately returned to their nests so parents could resume normal activities while the labeled water equilibrated into the body water pool. The equilibration time was estimated based on body mass and ranged from 45 to 96 minutes following the equation in figure 13.1A from Speakman (1997, Table S2). After the estimated mass-specific equilibration time had lapsed, we returned to the nest and collected a 30-60 μl blood sample from the brachial vein using Fisherbrand non-heparinized microcapillary tubes. We then returned the nestling to the nest. We returned to the nest within ± 1 hour of 24 (94% of samples) or 48 hours after the initial blood sample and immediately weighed nestlings and took a second blood sample from the opposite wing as the first sample. We then returned the nestlings to the nest.

We sealed blood samples in microcapillary tubes using Critocaps (Leica Microsystems, Wetzlar, Germany) on each end and they were then held in a cooler with ice until the end of the day. Each afternoon, blood samples were spun at 12000 rpm for 3 minutes to separate plasma from red blood cells using a Combo V24 centrifuge (LW Scientific, Lawrenceville, GA, USA). We then transferred plasma into 100 μl microcapillary tubes and flame-sealed each end with a handheld butane torch (Nagy 1983). Flame-sealed samples were kept in a refrigerator until the end of each field season. At the end of each season, we micro-distilled all plasma samples to obtain pure water following Nagy (1983) and stored samples for subsequent isotope analyses.

We estimated background ^{2}H and ^{18}O levels at each site by taking blood samples of nestlings not injected with labeled water across the duration of each field season. This approach accounts for known seasonal variation in environmental isotope enrichments (Tatner 1990). We stored and distilled background samples the same as our enriched blood samples, and they were analyzed on the same equipment, but on separate runs to minimize variability due to instrument memory effects. We predicted background values for each isotope per site by modeling isotopic enrichments in parts per million (ppm) by Julian day. This relationship was quadratic in Arizona and Malaysia, and linear in South Africa (see Fig. S1).

We analyzed isotope concentrations using a Picarro L1102-I or a LGR DLT-100 liquid water isotope analyzer (Picarro Inc., Santa Clara, CA, USA) in the Center for Stable Isotopes at the University of New Mexico. Data were normalized to the IAEA water standard VSMOW. We estimated CO_2 production using the equation by Nagy (1980, 1983). CO_2 production was then converted to DEE using conversion factors based on daylength at each site during the breeding season and its influence on metabolizing primarily lipids during nighttime fasting versus a mixed diet during daytime activity. This yielded conversion factors of 26.3 J/ml CO_2 for Arizona, and 26.7 J/ml CO_2 for South Africa and Malaysia, based on Table 3 in Nagy (1983).

T_a and rainfall

To quantify the effects of the physical environment on nestling energetics, we measured air temperature and rainfall using a centrally located weather station at each site. In Malaysia and Arizona, we used an Onset data logging rain gauge with a tipping bucket and air temperature logger (Onset Computer Corporation, Bourne, MA, USA). Weather variables in South Africa were provided by Eskom Holdings from a meteorological station at the field site. We calculated both mean and minimum air temperature. Mean temperature was the mean air temperature (°C) recorded at the respective weather stations over the 24-hour measurement period and minimum temperature was the lowest air temperature recorded during the 24-hour period. Rainfall is reported as the total rainfall (mm) during the sampling interval. Our weather station in Malaysia was at 1600 m asl, and the field site spanned an elevational gradient of ca. 400 m asl. Therefore, to account for the linear decrease in temperature with increasing elevation, we used a predicted temperature value at this site based on the elevation of each nest and the lapse rate of 0.55°C*100 m^{-1} (Kitayama 1992).

Growth and age-specific mortality rates

We obtained growth rate constant K (Ricklefs 1968; Remeš & Martin 2002) for 13 Arizona species and 19 Malaysian species from Martin (2015), and 10 South African species from Martin et al. (2015b). We obtained daily nest predation estimates during the nestling period for the same species as above from Martin (2015). Daily nest predation was modelled using the logistic exposure method (Shaffer 2004). We obtained adult mortality estimates for the same South Africa and Arizona species from Martin et al. (2015a), and the same Malaysian species from Martin et al. (2017). Adult mortality was estimated using standard-effort netting plus re-sighting field methodology, which provides more accurate estimates than standard-effort netting alone (Martin *et al.* 2017).

Statistical analyses

We analyzed all data using program R ver. 3.5.1 (R Core Team 2018). To capture intraspecific variation in DEE among covariates, we retained all values that were ± 3*IQR for each species following Tukey's boxplot rule for far outliers (Tukey 1977). We assumed that far outliers reflected methodological errors and removed them from subsequent analyses. To test the effects of weather and brood size (number of young per nest) on DEE, we fit a linear mixed-effects model using package lme4 (Bates *et al.* 2015). We included species and nest identification as random effects to account for cross-species variation and repeated measures within nests, respectively. We modeled $\log_{10}$-transformed DEE as the dependent variable, and $\log_{10}$-transformed nestling body mass, temperature, rainfall, number of brood mates, and site as fixed effects. We plotted residuals of DEE against mass after correcting for species as a random effect to verify that we fully corrected for species effects in our mixed-effects model (Fig. S2). The average nestling body mass from the first and second sampling period was used in all intraspecific analyses. We also tested for site by mass interactions. We tested both T_{mean} and T_{min}, but only included T_{min} in the final model due to multicollinearity and a lower AIC value. We square root transformed rainfall to reduce zero-inflated values. We report conditional R^2 for mixed-effects models, which includes variance explained by both fixed and random effects, using the r.squaredGLMM function in the MuMIn package in R (Barton 2019), following Nakagawa & Schielzeth (2013).

For interspecific analyses, we calculated mean DEE values for each species to use as the dependent variable. We corrected DEE values for temperature, rainfall, and brood size effects based on our intraspecific results using package lsmeans (Lenth 2016). We further restricted mean DEE estimates to the most common brood size observed across all years for each species based on massive sample sizes (TEM unpubl. data). If the most common brood size for a given species accounted for less than half of all nests observed during the nestling period, we used the two most common brood sizes. This approach ensured that we captured most naturally occurring brood sizes while avoiding inflated DEE values expected from the smallest brood sizes for each species, or low DEE values due to excessively large brood sizes (Weathers & Sullivan 1991).

We used phylogenetic generalized least squares (PGLS) regression to account for phylogenetic structure among species (Felsenstein 1985). We obtained phylogenetic trees from www.birdtree.org (Jetz *et al.* 2012) with the Hackett backbone (Hackett *et al.* 2008), and constructed a majority-rules consensus tree from 1000 trees using program Mesquite (Maddison & Maddison 2009, Fig. S3). We used the gls function within program nlme (Pinheiro *et al.* 2018) to test the effects of $\log_{10}$ nestling body mass, adult mortality, nest predation, and growth rate while accounting for phylogenetic relationships using program ape (Paradis & Schliep 2018). The gls function does not provide an estimate for variance explained, so we used program caper to generate pseudo-R^2 values. We report allometric scaling exponents from PGLS analyses, but with all covariates except for nestling body mass removed from the model. We initially tested the effects of DEE on nestling growth without mortality covariates, and then tested for growth while accounting for adult mortality and nest predation. For each species, we used mean nestling mass values taken during pin break, the age in which we administered the doubly-labeled water. We $\log_{10}$ transformed both DEE and mass to normalize residuals.

RESULTS

Intraspecific analyses

Our mixed model explained 95% of the variation in nestling DEE. Body mass explained the majority of nestling DEE within species (Table 1), but slopes differed between sites (site by mass interaction: $P < 0.001$). While accounting for the other covariates in the model and the mass by site interaction, nestling DEE decreased with more nestlings in the nest (β ± SE; -0.017 ± 0.004, $P < 0.001$, Table 1, Fig. 1A) and warmer minimum air temperature (-0.003 ± 0.002, $P = 0.028$, Table 1, Fig. 1B), but increased with rainfall (0.005 ± 0.002, $P = 0.035$, Table 1, Fig. 1C).

Interspecific analyses

After controlling for phylogeny, body mass alone explained substantial variation in nestling DEE, with an allometric scaling exponent of 0.634 ± 0.042 ($R^2 = 0.81$, Table 2A, Fig. 2). Growth rate was not significantly correlated with nestling DEE when only accounting for body mass ($R^2 = 0.75$, $P = 0.784$, Table 2B, Fig. 3A). In our full model with mass, growth rate, nest predation, and adult survival, nestling DEE was not significantly correlated to growth rate ($R^2 = 0.85$, $P = 0.164$, Table 2C, Fig. 3B), but increased with both nest predation probability (2.631 ± 0.497, $P < 0.001$, Table 2C, Fig. 3C) and adult mortality probability (0.438 ± 0.117, $P = 0.001$, Table 2C, Fig. 3D).

DISCUSSION

Understanding the importance of environmental factors and evolved life history strategies on rates of energy expenditure is a critical goal of physiological ecology. The impact of environmental conditions on offspring energetics are particularly important because they can affect energy available for growth and development at a proximate level. Reductions in energy for growth may prolong juvenile stages and increase time-dependent mortality, while also reducing offspring quality with carry-over effects that reduce fitness in adult life stages (Desai & Hales 1997; Metcalfe & Monaghan 2001; Remeš & Martin 2002; Madsen & Shine 2008;

Monaghan 2008; Ardia *et al.* 2010; Nord & Giroud 2020). Our DEE measurements in >650 nestling songbirds across 54 species represents a large and unique effort to quantify proximate and evolutionary determinants of offspring energy expenditure relative to important weather variables and brood size.

Proximate effects

Climate change has caused shifts in average and extreme temperatures and rainfall (Pachauri & Mayer 2014; Ummenhofer & Meehl 2017), with physiological ramifications for populations and communities (Walther *et al.* 2002; Parmesan 2006; Sekercioglu *et al.* 2012). These shifting weather patterns make it important to understand the influence of weather on offspring energy expenditure, yet a consensus for weather effects is lacking. Offspring energy expenditure was found to increase with colder air temperatures within some (Weathers & Sullivan 1991; Dykstra & Karasov 1993), but not all (Williams & Nagy 1985) studies of altricial bird species, possibly reflecting an offset of costs by parental care (Johnson & Best 1982; Mitchell *et al.* 2020). However, our large dataset with many diverse species clearly demonstrates that nestling DEE generally increases with colder air temperatures (Table 1, Fig. 1B), despite parental care.

Rainfall may similarly influence energy expenditure (Voigt *et al.* 2011; Zelová *et al.* 2011; Boyle *et al.* 2020). Wetting increases conductance, heat loss, and thermoregulatory costs in laboratory studies (Lustick & Adams 1977; Webb & King 1984; McArthur & Ousey 1994; Voigt *et al.* 2011). Nevertheless, parents might ameliorate such costs through brooding or shielding young in nests (Johnson & Best 1982; Wittenberger 1982; Beintema & Visser 1989). Our results, however, demonstrate that nestling energy expenditure increased with more rainfall

(Table 1, Fig. 1C). To our knowledge, this is the first study to document the energetic consequences of rainfall in free-living offspring. This result emphasizes that parents are either unable or unwilling to entirely offset the energetic costs of weather on nestlings despite parents exhibiting substantial plasticity in response to weather (Best 1977; Johnson & Best 1982; Wittenberger 1982; Smith *et al.* 2018). Thus, rainfall may be detrimental due to offspring thermoregulatory demands competing for energy with key developmental processes in regions predicted to experience increases in rainfall (Pachauri & Mayer 2014).

The potential to ameliorate weather impacts is demonstrated by brood size effects. Thermal benefits of huddling have been observed in many taxa under laboratory conditions (Royama 1966; Mertens 1969; Kunz & Hood 2000; Gilbert *et al.* 2010), but the benefits of huddling in the wild under varying weather conditions are poorly studied, especially among offspring. Our expansive study of free-living nestlings confirms that they conserve energy when they have more siblings with which to huddle under natural weather conditions (Table 1, Fig. 1A). This result demonstrates that energy costs of increased activity observed with greater sibling competition (e.g., Kilner 2001; Rodríguez-Gironés *et al.* 2001) are outweighed by the energy savings of huddling in the wild. Thus, weather and brood size have clear proximate effects on offspring energy expenditure, which can have important consequences for offspring growth, survival, and fitness (Desai & Hales 1997; Lindström 1999; Metcalfe & Monaghan 2001).

Evolutionary effects

Rates of energy expenditure are also expected to evolve in response to natural selection (Nagy *et al.* 1999; Anderson & Jetz 2005). Yet, few comparative studies of offspring DEE exist. High levels of nest predation are expected to favor higher offspring energy use to fuel faster juvenile development (Case 1978; Arendt 1997; Ton & Martin 2016). Our results illustrate that species with higher nest predation rates had higher offspring DEE (Table 2C, Fig. 3C), but growth rate did not explain offspring DEE, either separately or while accounting for nest predation (Table 2B, C, Fig. 3A, B). Hence, the link between nest predation and offspring DEE is apparently not due to faster growth among high predation species. The fact that growth rate is correlated with nestling resting metabolic rate (RMR; Ton & Martin 2016) but not DEE suggests that the proximate influences of environmental conditions are more important than the evolved influence of growth on energy expenditure among free-living offspring. Similarly, the positive correlation between nest predation and DEE but not RMR (Ton & Martin 2020) remains puzzling, and further emphasizes a decoupling between resting and active metabolic rates (Koteja 1991; Ricklefs *et al.* 1996). One possible explanation from life history theory is that high nest predation might favor lower reproductive effort in parents to reduce energy spent on offspring with low survival probability (Gadgil & Bossert 1970; Schaffer 1974; Charlesworth 1980). Thus, parents in species with high nest predation might provide less care, and cause plastic increases in offspring DEE (e.g., Table 1, Fig. 1).

The pace of life hypothesis posits that metabolism underlies life history tradeoffs, and predicts that species with low adult mortality should have slower metabolic rates (Ricklefs & Wikelski 2002; Speakman *et al.* 2002; Wiersma *et al.* 2007; Scholer *et al.* 2019; Boyce *et al.* 2020; but see Glazier 2015; Speakman 2005). However, metabolic rates may differ between life stages (Glazier 2005; Pettersen *et al.* 2016), highlighting the importance of studying the link between adult mortality and metabolism across all life stages. Furthermore, previous studies testing the relationship between adult mortality and offspring metabolic rates have previously been limited to RMR in endotherms (Ton & Martin 2020), but selection should act more strongly on active rather than basal metabolism (Speakman 2005). Among the 42 songbird species we studied, those with higher adult mortality probability had higher nestling DEE (Table 2C, Fig. 3D), supporting the pace of life hypothesis. Thus, long-lived songbirds appear to have evolved reduced energy expenditure during the juvenile stage, possibly in response to deleterious effects of metabolic byproducts (Hulbert *et al.* 2007).

Conclusions

The energy that dependent offspring spend on daily activities clearly reflects plastic responses to environmental conditions and evolved responses from natural selection. Our analyses show that huddling with siblings provides important energy savings within songbird nests (Table 1, Fig. 1A). Weather also has important proximate effects on nestling energy expenditure, with nestlings spending more energy during colder days and rainier days (Table 1, Fig. 2B, C). Our results demonstrate that parents are either unable or unwilling to entirely offset these costs through behavioral modifications. Across species, selection in response to age-specific mortality appears to influence the evolution of nestling energy expenditure. Species with higher nest predation rates have higher energy expenditure (Table 2C, Fig. 3C), but according to our dataset, this is not due to more energy spent on faster growth (Table 2B, C, Fig. 3A, B). Similarly, species with higher mortality during the adult stage also have higher energy expenditure as nestlings, supporting the pace of life hypothesis (Table 2C, Fig. 3D). Together, these results illustrate the proximate and evolutionary influences of weather and life history traits on offspring energy expenditure within and across a large number of wild bird species.

ACKNOWLEDGEMENTS

We thank Jedediah Brodie, Jackson Birrell, and the Martin Lab for their insightful comments on this manuscript. We are especially appreciative of countless field technicians who found and monitored nests for this study. We thank K. Oliver for extensive work processing laboratory samples for analyses. Support for this work came from the National Science Foundation (DEB-1241041, DEB-1651283, IOS-1656120, IOS-1656273) and National Geographic Society (9875-16). We appreciate Sabah Parks and the Sabah Biodiversity Council for authorization and collaboration on this project in Malaysia, and Western Cape Nature Conservation Board in South Africa. AEM was supported by the WBIO department at the University of Montana, a Wesley M. Dixon graduate fellowship, the Carl and Camilla Rietman Scholarship, and a Bertha Morton Scholarship. This work was conducted under auspices of University of Montana IACUC #059-10TMMCWRU. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflicts of interest.

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TABLES

Table 1. Model output from a linear mixed effects model testing the proximate effects of nestling body mass (g), minimum air temperature (°C), rainfall (mm), brood size (# nestlings), site, and mass by site interactions on nestling daily energy expenditure (DEE; kJ day^{-1}). DEE and mass were $\log_{10}$-transformed to normalize residuals. Rainfall was square root transformed to reduce zero-inflation. The model also included random effects for species and individual nestling identification to account for repeated measures within nests. Arizona is the reference site in the model.

Predictors	β	SE	df	t-value	*P*
$\log_{10}$ mass	0.629	0.050	81.4	12.515	<0.001
Brood size	-0.017	0.004	447.1	-4.042	<0.001
Min air temp	-0.003	0.002	429.1	-2.211	0.028
Sqrt rainfall	0.005	0.002	412.4	2.111	0.035
Site: South Africa	-0.231	0.095	94.7	-2.445	0.016
Site: Malaysia	-0.142	0.070	80.6	-2.034	0.045
$\log_{10}$ mass*site:South Africa	0.334	0.085	95.6	3.936	0.000
$\log_{10}$ mass*site:Malaysia	0.051	0.058	80.6	0.878	0.382

Conditional R^2 = 0.95.

Table 2. Model outputs from phylogenetic generalized least squares (PGLS) regression showing the relationship between nestling daily energy expenditure (DEE; kJ day $^{-1}$), and A) mass (g) alone, B) mass and growth rate (*k*), and C) mass, adult mortality, nest predation, and growth rate using the 42 species with known estimates for these parameters. DEE and mass were $\log_{10}$-transformed in both models to normalize residuals.

Predictors	β	SE	t-value	*P*
A: N = 54 spp, λ = -0.13, R^2 = 0.81.				
$\log_{10}$ mass	0.634	0.042	14.9	< 0.001
B: N = 42 spp, λ = -0.18, R^2 = 0.75.				
$\log_{10}$ mass	0.654	0.059	11.2	< 0.001
Growth rate	0.066	0.240	0.3	0.784
C: N = 42 spp, λ = 0.29, R^2 = 0.85.				
$\log_{10}$ mass	0.740	0.051	14.5	< 0.001
Nest predation	2.631	0.497	5.3	< 0.001
Adult mortality	0.438	0.117	3.7	0.001
Growth rate	-0.323	0.227	-1.4	0.164

Figure 1. Regression lines and 95% confidence intervals from the residuals of nestling daily energy expenditure (DEE) in kJ day $^{-1}$ plotted against A) brood size (# nestlings), B) minimum air temperature (°C) and C) rainfall (mm). Each plot is corrected for the effects of $\log_{10}$-transformed mass, site, the interaction between mass and site, and the other two covariates. Corrections come from a linear mixed model including a random effect for species.

Figure 2. Allometric relationship of daily energy expenditure (DEE) in kJ day $^{-1}$ for 54 species of songbird nestlings across 3 field sites: Arizona, South Africa, and Malaysia. DEE and body mass (g) were both $\log_{10}$-transformed to normalize residuals. Four-letter species codes, common names, and Latin names are listed in Table S1.

Figure 3. Partial correlation plots showing residual nestling daily energy expenditure (DEE) in kJ day $^{-1}$ using the subset of species in which growth rate, nest predation, and adult mortality estimates were available. DEE is plotted against A) nestling growth rate correcting for mass only, B) nestling growth correcting for mass, nest predation, and adult mortality probability, C) nest predation rate correcting for mass, growth rate, and adult mortality rate, and D) adult mortality probability correcting for mass, growth rate, and nest predation. DEE and mass were $\log_{10}$-transformed to meet model assumptions.

Figure 4. Significant correlations between tested covariates and nestling daily energy expenditure. The direction of correlations is indicated by +/- signs above each arrow.

FIGURES

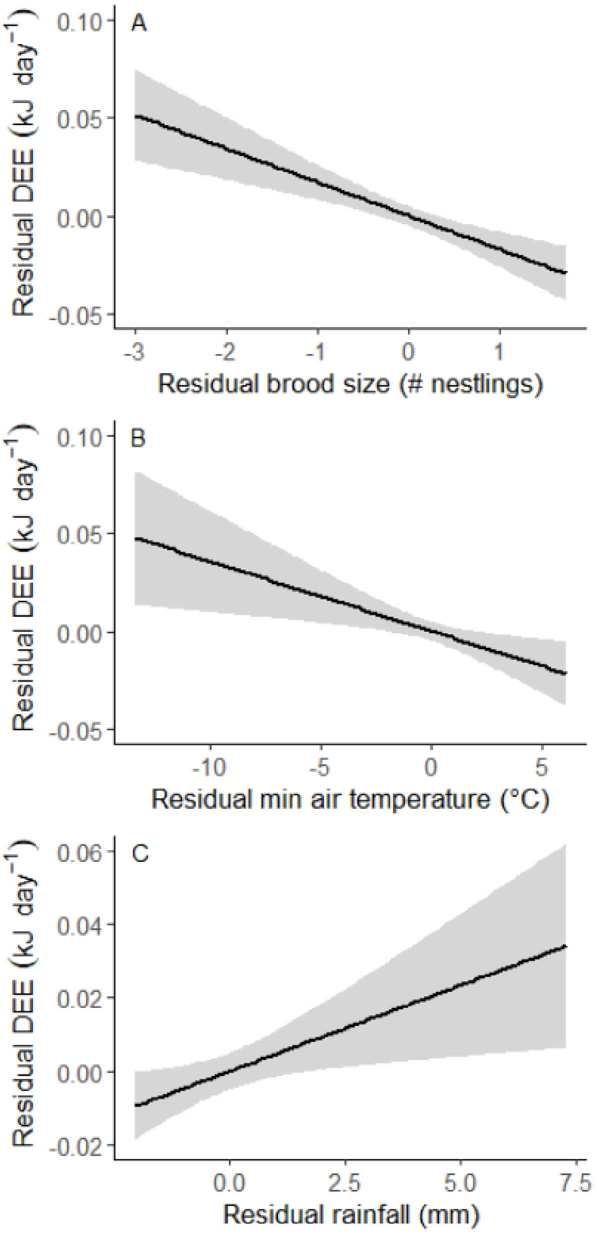

Figure 1.

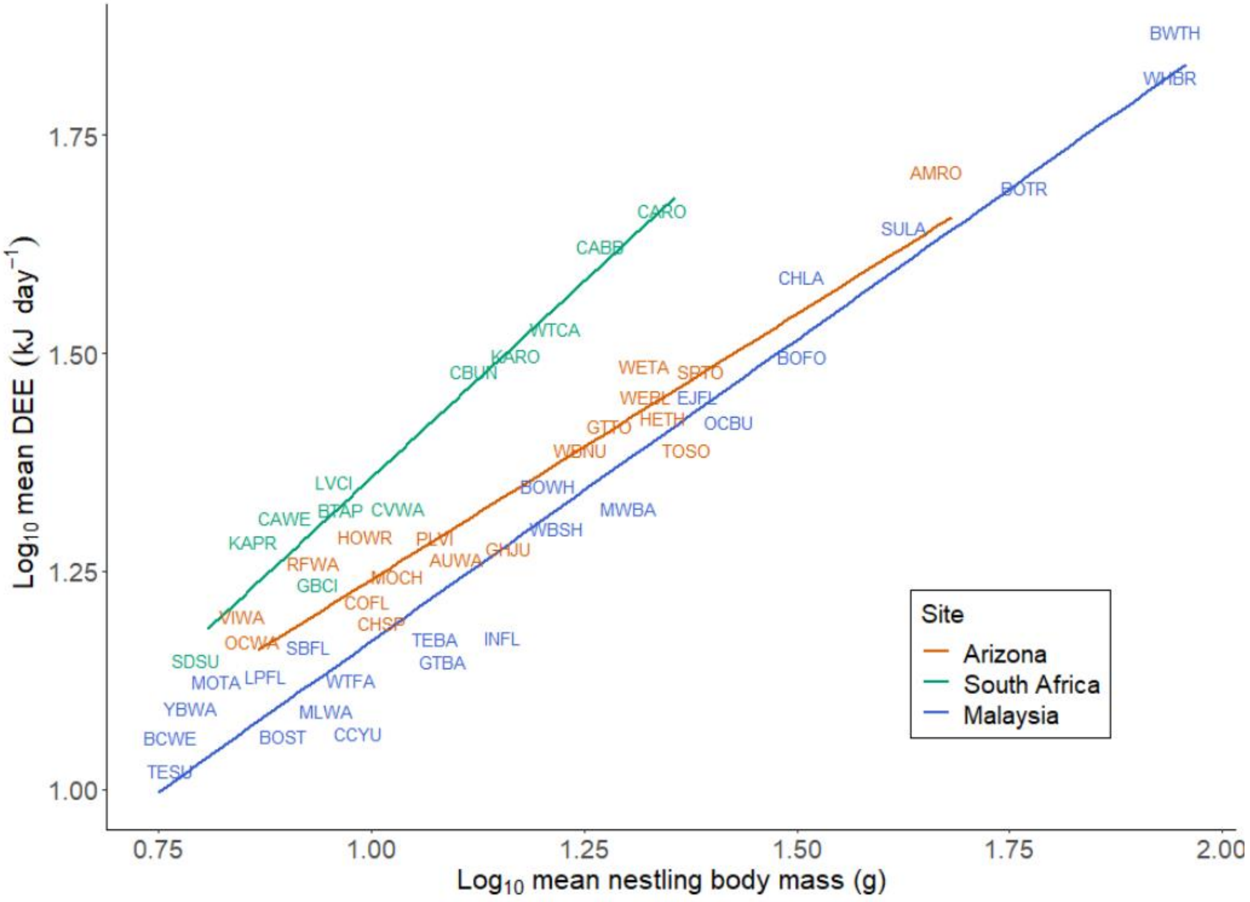
BWTH
WHBR
1.75
AMRO
BOTR
CARO
SULA
CABB
CHLA
WTCA
1.50
KARO
WETA
SPTO
BOFO
CBUN
WEBL
EJFL
GTTO
HETH
OCBU
WBNU
TOSO
LVCI
BOWH
BTAP
CVWA
MWBA
CAWE
HOWR
PLVI
WBSH
KAPR
GHJU
RFWA
AUWA
1.25
MOCH
GBCI
COFL
VIWA
CHSP
OCWA
SBFL
TEBA
INFL
SDSU
GTBA
MOTA
LPFL
WTFA
YBWA
MLWA
BCWE
BOST
CCYU
TESU
1.00
Log$_{10}$ mean DEE (kJ day^{-1})
0.75
1.00
1.25
1.50
1.75
2.00
Log$_{10}$ mean nestling body mass (g)
Site
Arizona
South Africa
Malaysia

Figure 2.

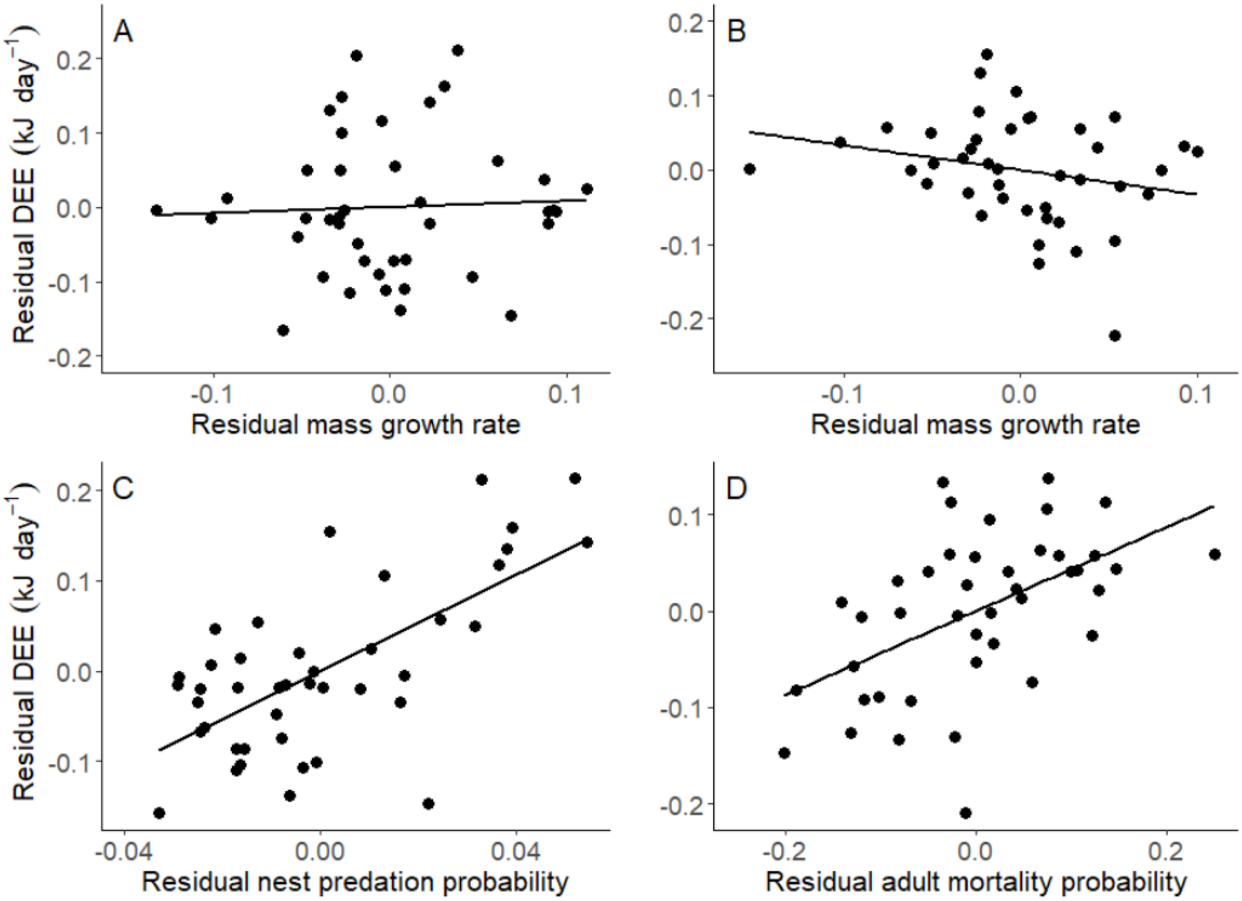
A
B
C
D
Residual DEE (kJ day^{-1})
Residual mass growth rate
Residual nest predation probability
Residual adult mortality probability
0.2
0.1
0.0
-0.1
-0.2
-0.04
0.00
0.04

Figure 3.

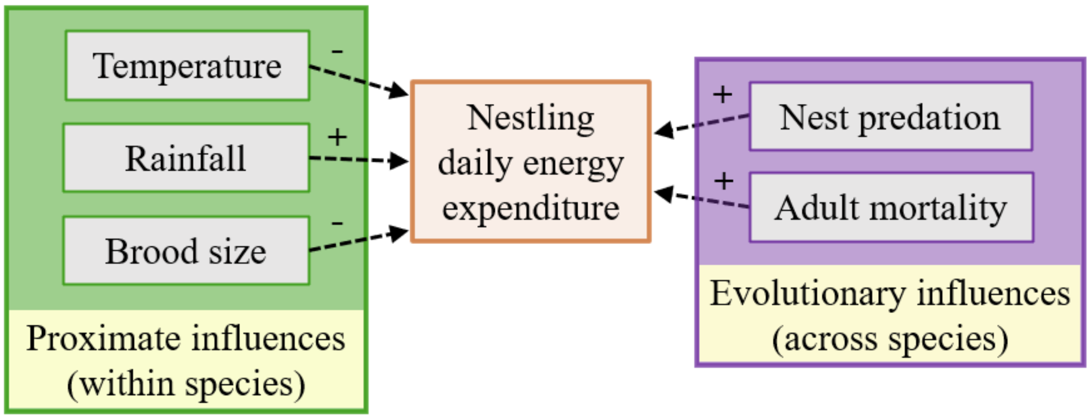
Temperature
-
Rainfall
+
Brood size
-
Proximate influences (within species)
Nestling daily energy expenditure
+
Nest predation
+
Adult mortality
Evolutionary influences (across species)

Figure 4.

SUPPLEMENTAL MATERIALS:

Table S1: Study species with four-letter codes, common names, and Latin names.

Spp code	Species	*Latin name*
Arizona		
AMRO*	American Robin	*Turdus migratorius*
AUWA*	Audibon's Warbler	*Setophaga coronata*
CHSP	Chipping Sparrow	*Spizella passerina*
COFL*	Cordilleran Flycatcher	*Empidonax occidentalis*
GHJU*	Grey-headed Junco	*Junco hyemalis*
GTTO*	Green-tailed Towhee	*Pipilo chlorurus*
HETH*	Hermit Thrush	*Catharus guttatus*
HOWR*	House Wren	*Troglodytes aedon*
MOCH*	Mountain Chickadee	*Poecile gambeli*
OCWA*	Orange-crowned Warbler	*Leiothlypis celata*
PLVI	Plumbeous Vireo	*Vireo plumbeus*
RFWA*	Red-faced Warbler	*Cardellina rubrifrons*
SPTO	Spotted Towhee	*Pipilo maculatus*
TOSO	Townsend's Solitaire	*Myadestes townsendi*
VIWA	Virginia's Warbler	*Leiothlypis virginiae*
WBNU*	White-breasted Nuthatch	*Sitta carolinensis*
WEBL*	Western Bluebird	*Sialia mexicana*
WETA*	Western Tanager	*Piranga ludoviciana*
South Africa		
BTAP*	Bar-throated Apalis	*Apalis thoracica*
CABB*	Cape Bulbul	*Pycnonotus capensis*
CARO*	Cape Robin-chat	*Cossypha caffra*
CAWE*	Cape White-eye	*Zosterops virens*
CBUN*	Cape Bunting	*Emberiza capensis*
CVWA*	Chestnut-vented Warbler	*Curruca subcoerulea*
GBCI*	Grey-backed Cisticola	*Cisticola subruficapilla*
KAPR*	Karoo Prinia	*Prinia maculosa*
KARO*	Karoo Scrub-robin	*Cercotrichas coryphoeus*
SDSU*	Southern Double-collared Sunbird	*Cinnyris chalybeus*
LVCI*	Levaillant's Cisticola	*Cisticola tinniens*
WTCA*	White-throated Canary	*Crithagra albogularis*
Malaysia		
BCWE*	Black-capped White-eye	*Zosterops atricapilla*
BOFO*	Bornean Forktail	*Enicurus leschenaulti*

BOST*	Bornean Stubtail	*Urosphena whiteheadi*
BOTR	Bornean Treepie	*Dendrocitta cinerascens*
BOWH*	Bornean Whistler	*Pachycephala hypoxantha*
BWTH*	Bornean Whistling-thrush	*Myophonus borneensis*
CCYU*	Chestnut-crested Yuhina	*Yuhina everetti*
CHLA*	Chestnut-hooded Laughingthrush	*Pterorhinus treacheri*
EJFL*	Eyebrowed-jungle Flycatcher	*Vauriella gularis*
GTBA*	Grey-throated Babbler	*Stachyris nigriceps*
INFL*	Indigo Flycatcher	*Eumyias indigo*
LPFL	Little Pied Flycatcher	*Ficedula westermanni*
MLWA*	Mountain Leaf-warbler	*Phylloscopus trivirgatus*
MOTA*	Mountain Tailorbird	*Phyllergates cucullatus*
MWBA*	Mountain Wren-babbler	*Gypsophila crassa*
OCBU*	Ochraceous Bulbul	*Alophoixus ochraceus*
SBFL*	Snowy-browed Flycatcher	*Ficedula hyperythra*
SULA	Sunda Laughingthrush	*Garrulax palliatus*
TEBA*	Temminck's Babbler	*Pellorneum pyrrogenys*
TESU*	Temminck's Sunbird	*Aethopyga temminckii*
WBSH*	White-browed Shortwing	*Brachypteryx montana*
WHBR	Whitehead's Broadbill	*Calyptomena whiteheadi*
WTFA*	White-throated Fantail	*Rhipidura albicollis*
YBWA*	Yellow-breasted Warbler	*Phylloscopus montis*

*Species with known adult mortality, nest predation, and growth rate estimates used for comparative analyses.

Table S2: Mass-specific injection volumes and equilibration times.

Mass (g)	Time (min)	Injection volume (μl)
5-15	45	20
16-25	54	40
26-35	69	60
36-45	78	90
46-55	84	110
56-65	89	140
66-75	93	160
76-85	96	190

Figure S1. Plots showing background isotope enrichment levels in parts-per-million (ppm) for ^{2}H (deuterium) and ^{18}O in A, B) Arizona, C, D) South Africa, and E, F) Malaysia. Background isotope data were distilled from blood samples taken from un-labeled nestlings at each study site over the duration of each field season. We modeled background isotope levels by Julian date to account for known seasonal changes in environmental isotope levels.

Figure S2. Residual plot from a mixed model using nestling DEE (kJ day $^{-1}$) as the dependent variable and nestling mass (g) as a fixed effect and species as a random effect. Nestling DEE and mass are both $\log_{10}$-transformed to meet assumptions of linearity. Four-letter species codes are listed in table S1.

Figure S3. Majority-rules consensus tree of all 54 species across the three different study sites. Arizona species are depicted in orange, South African species are green, and Malaysian species are blue. Branch lengths are drawn proportional to divergence time.

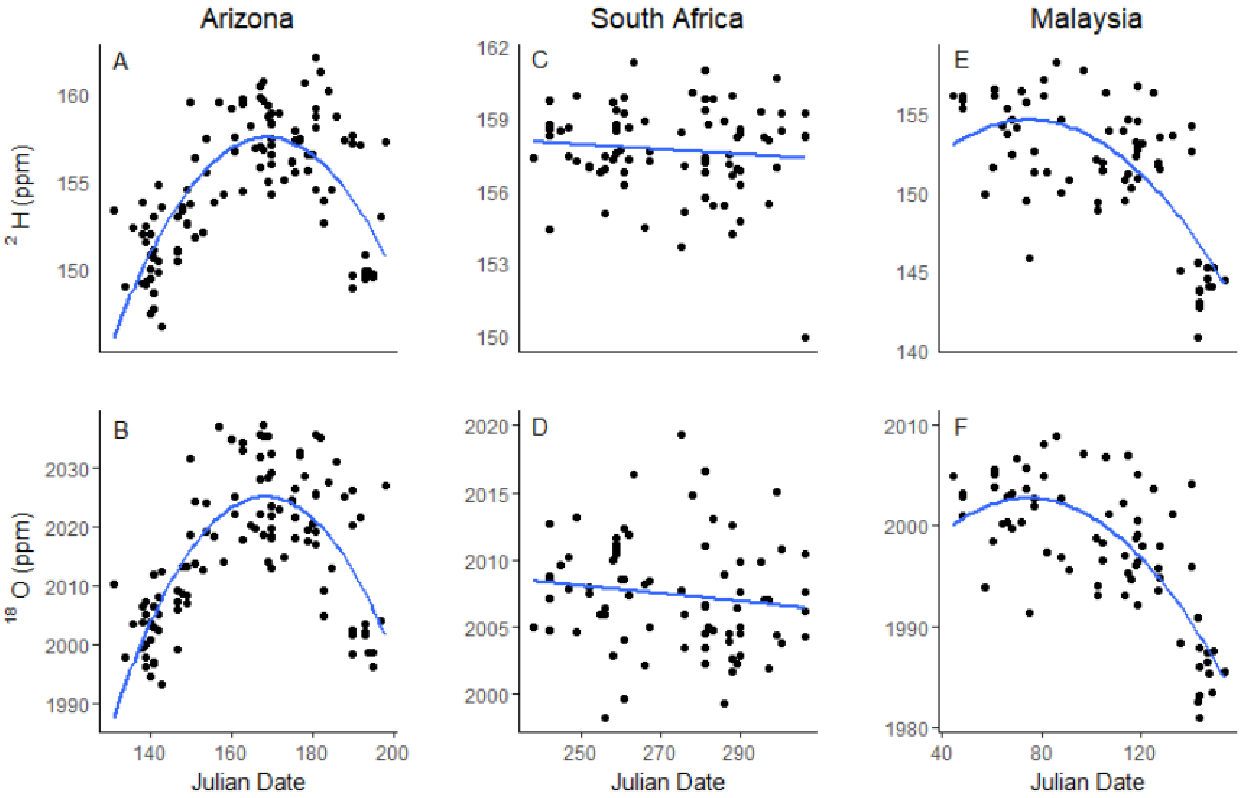
Arizona
South Africa
Malaysia
A
C
E
B
D
F
^{2}H (ppm)
^{18}O (ppm)
160
155
150
162
159
156
153
150
155
150
145
140
2030
2020
2010
2000
1990
2020
2015
2010
2005
2000
2010
2000
1990
1980
140
160
180
200
250
270
290
40
80
120
Julian Date
Julian Date
Julian Date

Figure S1.

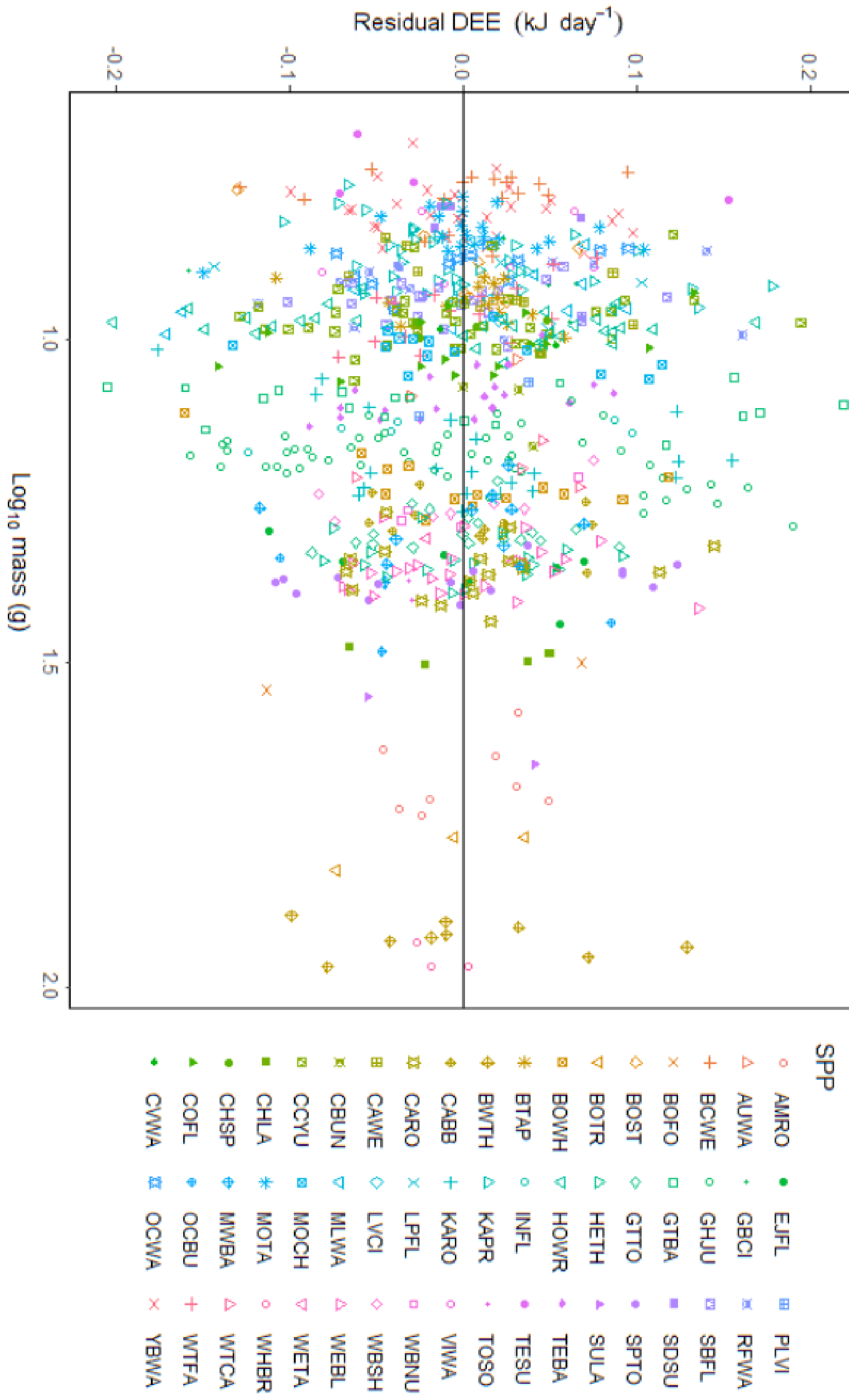
Residual DEE (kJ day^{-1})
-0.2
-0.1
0.0
0.1
0.2
Log$_{10}$ mass (g)
1.0
1.5
2.0
SPP
AMRO
AUWA
BCWE
BOFO
BOST
BOTR
BOWH
BTAP
BWTH
CABB
CARO
CAWE
CBUN
CCYU
CHLA
CHSP
COFL
CWWA
EJFL
GBCI
GHJU
GTBA
GTTO
HETH
HOWR
INFL
KAPR
KARO
LPFL
LVCI
MLWA
MOCH
MOTA
MWBA
OCBU
OCWA
PLVI
RFWA
SBFL
SDSU
SPTO
SULA
TEBA
TESU
TOSO
VIWA
WBNU
WBSH
WEBL
WETA
WHBR
WTCA
WTFA
YBWA

Figure S2.

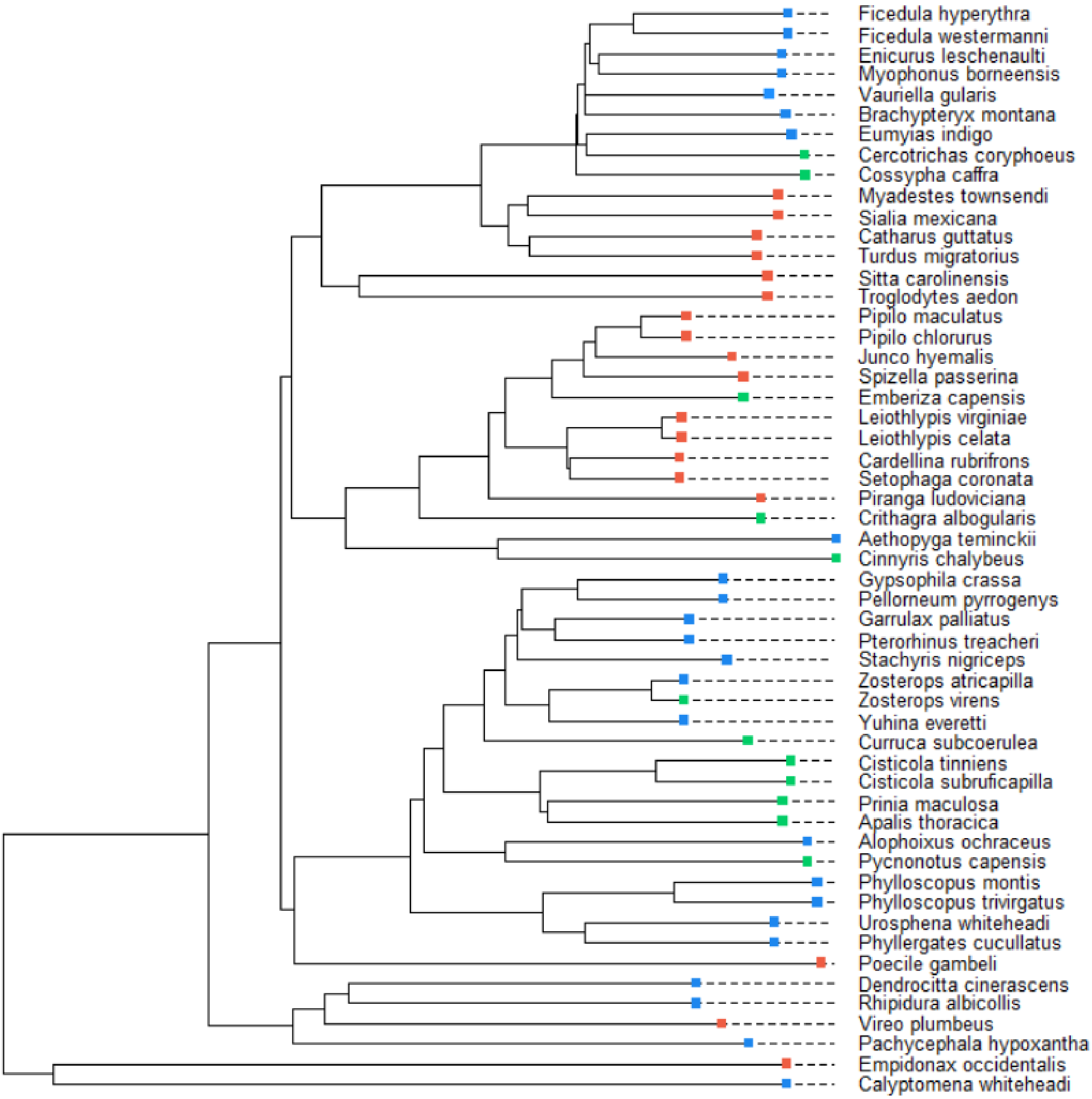
Ficedula hyperythra
Ficedula westermanni
Enicurus leschenaulti
Myophonus borneensis
Vauriella gularis
Brachypteryx montana
Eumyias indigo
Cercotrichas coryphoeus
Cossypha caffra
Myadestes townsendi
Sialia mexicana
Catharus guttatus
Turdus migratorius
Sitta carolinensis
Troglodytes aedon
Pipilo maculatus
Pipilo chlorurus
Junco hyemalis
Spizella passerina
Emberiza capensis
Leiothlypis virginiae
Leiothlypis celata
Cardellina rubrifrons
Setophaga coronata
Piranga ludoviciana
Crithagra albogularis
Aethopyga teminckii
Cinnyris chalybeus
Gypsophila crassa
Pellorneum pyrrogenys
Garrulax palliatus
Pterorhinus treacheri
Stachyris nigriceps
Zosterops atricapilla
Zosterops virens
Yuhina everetti
Curruca subcoerulea
Cisticola tinniens
Cisticola subruficapilla
Prinia maculosa
Apalis thoracica
Alophoixus ochraceus
Pycnonotus capensis
Phylloscopus montis
Phylloscopus trivirgatus
Urosphena whiteheadi
Phyllergates cucullatus
Poecile gambeli
Dendrocitta cinerascens
Rhipidura albicollis
Vireo plumbeus
Pachycephala hypoxantha
Empidonax occidentalis
Calyptomena whiteheadi

Figure S3.

Chapter 3: Songbird parents modify their behavior in open, but not enclosed nests to mitigate energetic effects of rain on nestlings

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ABSTRACT

Understanding the ecological effects of rainfall will be critical for predicting how species might respond to climate change, given expected shifts in frequency and magnitude of rain events. Rainfall creates challenges for breeding animals through physiological costs of heat loss on developing young, but parents in altricial species can potentially ameliorate such costs through shifts in behavior. In addition, many animal taxa build nests to raise young, and nest structure may influence the impact of rain on offspring and parents. Studies of the effects of rain on offspring and parents have generally been correlational which do not separate direct physiological effects of rain from indirect effects of other ecological factors that shift with rain (e.g., food, predation). We added experimental rain above nests of five songbird species using two common nest types, cup-shaped and enclosed, and measured parental brooding and food provisioning behaviors, and offspring energy expenditure. Experimental rain caused parents in open, but not enclosed nests to increase their brooding time, and resulted in no effect of rain on energy expenditure of nestlings. Offspring provisioning rate also did not change with experimental rain. These results illustrate an important influence of nest type on parental activity during rainfall. Our results also suggest that substantial shifts in parental behavior should be expected in open-nesting songbird species in regions that are expected to experience heavier rainfall in the future.

INTRODUCTION

Rainfall can create challenges for animals across life stages that affect demography (Grant and Boag 1980; Dickman et al. 1999; Dennis and Otten 2000; Coulson et al. 2001). Rain may be particularly challenging for developing offspring due to demands of growth and development and constraints rain may place on parents, yet direct effects of rainfall on offspring are surprisingly poorly studied. Most studies of the effects of rainfall on breeding organisms are correlational, which do not separate the indirect effects of rainfall on food availability (Grant and Boag 1980; Wingfield 1984; Wolda 1988; Owen-Smith 1990; Grant and Grant 1993; Russell et al. 2002; Lukas and Clutton-Brock 2017) and offspring predation (Martin 2007) from direct energetic costs of wetting (Lustick and Adams 1977; Webb and King 1984). Yet, experimental studies that manipulate rain can directly test rainfall effects on life stages that influence demography. Growing evidence that climate change may cause more frequent and severe precipitation events in the future (Allan and Soden 2008; Trenberth 2011; Westra et al. 2013; Pachauri and Mayer 2014; Ummenhofer and Meehl 2017) emphasizes our need to test the direct effects of rain on developing young.

Rainfall can have demographic ramifications through effects on offspring energetics. When endothermic offspring are wet from rain, they may spend additional energy on thermoregulation (e.g., Lustick and Adams 1977; Webb and King 1984). Energy spent on thermoregulation may not be available for growth and development (Brewster et al. 2013), which can delay independence and increase time-dependent mortality (Ricklefs 1979; Remeš and Martin 2002). Indeed, rainfall was associated with increased offspring energy expenditure across many species of songbirds (Mitchell et al. 2021). However, the effects of rain on offspring energy expenditure may have reflected cloud cover, temperature, or food availability rather than direct effects of rain (Mitchell et al. 2021). Experimental manipulations of rainfall provides the strongest test of the direct effects of rainfall on offspring energetics (Sauve 2021).

Parental care has evolved in altricial species, in part to reduce negative abiotic effects on offspring (Clutton-Brock 1991). For example, some songbird species attend their nests more during rain to reduce costs to young (Johnson and Best 1982; Heagy and Best 1983). However, nest construction is another parental care strategy that may offer rain protection (Collias and Collias 1984; Hansell 2005; Martin et al. 2017*a*), but rain protection is not generally considered a primary function of nests. Rather, protection from predation has been the most widely accepted hypothesis for the evolution of more complex, roofed nest structures in many taxa (Nice 1957; Jeanne 1975; Rand and Dugan 1983; Oniki 1985; Skutch 1985; Smith 1995; Orizaola et al. 2003; Hall et al. 2015). Yet, enclosed nests with roofs compared to open, cup-shaped nests (Fig. 1) may provide more thermal benefits than protection from nest predation (Martin et al. 2017*a*; Matysioková and Remeš 2018). Indeed, contents of wet nests lost more heat than dry nests in laboratory trials (Deeming and Campion Eloise 2018; Biddle et al. 2019), but such studies overlook parental behavior which can offset effects of rain on young. Whether parents spend more time protecting young in open, cup-shaped than enclosed nests to offset deleterious effects of rain remains untested.

Most songbirds (order: Passeriformes) build one of two types of nests: open, cup-shaped and enclosed, roofed nests (Collias and Collias 1984). We experimentally simulated rain above the nests of five songbird species in Malaysian Borneo to test whether rain increases offspring energy expenditure or if parents ameliorate such costs, and if these effects differed between nest types. Two of our five study species build open nests and three build enclosed nests, providing a replicated test of rainfall effects across nest types.

METHODS

Study areas and species

We studied the five species of nesting birds in Kinabalu Park, Sabah, Malaysia (6°08’N, 116°56’E) during the primary breeding season (February-June) from 2009 to 2019. Unmanipulated nests used as controls (see below) were studied from 2009 to 2017 and experiments were conducted between 2017 and 2019. We chose two species that build open cup-shaped nests and three species that build enclosed, domed nests. White-throated Fantail (*Rhipidura albicollis*) and Bornean Whistler (*Pachycephala hypoxantha*) represented the two open-cup nesting species, and Snowy-browed Flycatcher (*Ficedula hyperythra*), Grey-throated Babbler (*Stachyris nigriceps*), and White-browed Shortwing (*Brachypteryx montana*) represented enclosed nesting species (see Fig. 1). Nests were searched for and monitored following Martin and Guepel (1993). We conducted rain experiments during the nestling period, on the day after pin feathers broke from their sheaths to standardize developmental stage across species.

Experimental design

We created an artificial rain device using a custom-cut segment of bamboo and a bottle of filtered water as the rain source (Fig. 2). The bamboo was used to hold and camouflage the water bottle. We used a segment of bamboo appx. 11 cm in diameter by 1 m long. The segment of bamboo had a node in the middle which was partially hollowed out to hold the inverted water bottle in the center of the bamboo (Fig. 2). We attached the bamboo segment 1 m directly above the nest by tying it to existing vegetation. For the water source, we used a new 1.5 L bottle of filtered water for each experiment placed inside the bamboo segment. To create simulated rainfall, we unscrewed the cap of the water bottle and poked three holes in the cap in a triangular pattern with a 23-gauge needle. We then placed three new 23-gauge syringe needles in these holes in the cap and screwed the cap back on. These created the spigots from which the simulated rain drained. After the bottle was inverted and placed in the bamboo holder, a single air vent was poked through the bottom of the water bottle (now at the top) to release pressure and allow consistent water flow. The air vent hole was poked with the same 23-gauge needle as used for the holes in the cap. A small piece of fiberglass mesh window screen was placed over the bottom opening of the bamboo and held in place with a rubber band. This broke the stream of water coming from the three syringe tips into finer droplets to better simulate normal rainfall. Finally, vegetation was attached to the outside of the bamboo section with rubber bands to camouflage the apparatus to avoid disturbing the parents as much as possible. Before leaving the nest, we visually confirmed that the rain apparatus was fully covering the nest area. In controlled trials, the water bottles emptied in approximately 4 hrs.

Experiments took approximately 20 minutes to set up. We allowed parents to feed and brood young without disturbance following nighttime fasting for 1 to 3 hours after sunrise before setting up experiments. This approach also allowed us to standardize for natural variation in behavioral patterns since all videos were started within two hours of each other. This also allowed us to minimize effects of natural rainfall as much as possible since only 7.1 percent of rain at the field site fell between 6:00 am and 12:00 pm, by which time our experiments had been completed. Due to limited samples sizes per species, we used a combination of true experimental controls and unmanipulated nests (pseudo-controls) in our experiment. For true controls, the bamboo apparatus was placed above nests exactly like experimental rain treatments, but an empty water bottle was placed in the bamboo segment. True controls and pseudo-controls did not significantly differ and so we combined them to use as controls for statistical tests.

Doubly-labeled water

We estimated daily energy expenditure (DEE) of nestlings using the doubly-labeled water technique (Speakman 1997). We injected no more than two nestlings from each nest on pin break, the day before the rain experiment was performed. We injected a mass-specific dose of DLW using a 50 µl Hamilton syringe. The dose was injected into the breast muscle, and then we waited 45-55 minute for the water to equilibrate with the body water before taking the initial blood sample. At the end of the shower experiment the following day, and exactly 24 hours after the initial blood sample, a second blood sample was taken. All blood samples were capped with Critocaps (Leica Microsystems, Wetzlar, Germany) and stored in a cooler with ice until the end of the day when they were processed for longer-term storage. This included spinning the samples for three minutes at 12000 rpm using a Combo V24 centrifuge LW Scientific, Lawrenceville, GA, USA), transferring the plasma into separate 100 µl capillary tubes, flame-sealing both ends with a handheld butane torch, and refrigerating following Nagy (1983). Flame-sealed samples were stored until the end of each field season and then microdistilled following Nagy (1983). Microdistilled samples were then transported to the University of New Mexico and analyzed using a Picarro L1102-I liquid water isotope analyzer (Picarro Inc., Santa Clara, CA, USA). All data were normalized to IAEA water standard VSMOW. We estimated CO_2 production following equations provided by Nagy (1980, 1983) and converted CO_2 production to DEE using a conversion factor of 26.7 J ml^{-1} CO_2 following Nagy (1983; Table 3). Sample sizes per treatment group and species are listed in Table 1.

Parental behavior

To quantify parental behavior, we filmed nests using Sony HD video cameras or Sony Hi-8 handheld camcorders placed five or more m from each nest. Videos were watched at the University of Montana bird video laboratory, where parental brooding and feeding rates were tabulated as hours spent warming young (brooding) and number of trips to the nest with food (feeding) respectively. Parental behaviors were then divided by the number of hours of video to obtain hourly brooding and feeding rates per video. We only used videos that were >3 hrs, and the average video length was 5.02 ± 0.03 hrs (mean ± SE). Sample sizes per treatment group and species are listed in Table 1.

Statistical analyses

We modeled nestling DEE and parental behaviors (brooding and feeding) using linear mixed-effects models in the package lme4 (Bates et al. 2015). For nestling DEE (kJ d^{-1}), we included body mass (g), experimental treatment, nest type (open or enclosed), brood size (nestlings per nest), nestling age (days), and the interaction between experiment and nest type as fixed effects. Nest identity was included as a random intercept term to account for repeated measures because multiple video days were used for some nests. Species was also included as a random intercept term. Nestling DEE and mass were both $\log_{10}$-transformed to normally distribute residuals. We modeled parent brooding behavior (percent of each video parents spent warming young) with experimental treatment, nest type, brood size, nestling age, and the interaction between experiment and nest type as fixed effects. Nest identity and species were included as random intercept terms. Brood rate was square-root transformed due to zero-inflation. Feeding rate was modeled (number of trips to the nest with food per hour) using the same fixed and random effects as the brooding model (above). We report conditional R^2 values, which included variance explained for fixed and random effects, for all models following Nakagawa and Schielzeth (2013). All analyses were conducted using program R, version 3.5.1 (R Core Team 2018).

RESULTS

Log_{10} nestling DEE was positively and significantly correlated with $\log_{10}$ body mass (Table 2). After accounting for the effects of body mass, nestlings that received experimental rain did not spend more energy than control nests (Table 2, Fig. 3). After accounting for the effects of mass, higher nestling DEE in open versus enclosed nests was marginally significant (Table 2). Nestlings had significantly higher DEE when they were older or had fewer siblings (Table 2). Our mixed model explained 79% of the variation in nestling DEE.

Parents that received simulated rain spent more time brooding nestlings in open nests, but not in enclosed nests (Table 3, Figs. 4, 5). After accounting for the interaction of experiment and nest type, parents brooded more in nests with fewer and younger nestlings (Table 3). Our mixed model explained 82% of the variation in parental brooding time.

The rate that parents brought food to nestlings did not differ between experimental rain and control treatments or between nest types (Table 4, Fig. 6). The interaction between experimental rain and nest type was marginally significant (Table 4), but investigation of the interaction plot did not add any useful interpretation to our model (Fig. 7), so the interaction was dropped. Parents visited nests with food more often when broods had more, and older nestlings (Table 4).

DISCUSSION

Climate change studies primarily focus on temperature effects, but rainfall is also predicted to shift, becoming more frequent and variable over time (Allan and Soden 2008; Trenberth 2011; Westra et al. 2013; Pachauri and Mayer 2014). Correlational studies have demonstrated positive indirect effects of rainfall on demography through changes to higher and lower trophic levels, such as food availability (Grant and Boag 1980; Owen-Smith 1990; Rotenberry and Wiens 1991; Russell et al. 2002) and predation (Martin 2007). However, rainfall may also negatively affect populations through direct effects on dependent offspring. For example, wet European rabbit (*Oryctolagus cuniculus*) pups had higher resting metabolic rates (RMR) in colder temperatures than dry pups (Seltmann et al. 2009), which may utilize critical energy needed for growth (Brewster et al. 2013). Rainfall can also be a major source of mortality in poorly developed penguin chicks (Boersma and Rebstock 2014; Ropert-Coudert et al. 2015). Similarly, nestling Horned Larks (*Eremophila alpestris*) took longer to fledge when rain was accompanied by cold temperatures, which decreased their fledging success (de Zwaan et al. 2019). While we did not investigate the effects of our experiment on total development time, we found that simulated rainfall did not significantly affect energy expenditure in the nestling songbirds we studied (Table 2, Fig. 3). Energy spent on extrinsic factors during growth can have long-term consequences (Lindström 1999; Metcalfe and Monaghan 2001), yet our results show that songbirds may not always suffer costs associated with short term increases in precipitation.

The reason nestling energy expenditure did not increase with simulated rain is explained by the interaction between nest type and experimental treatment on brooding time: parents in open nests increased their brooding behavior in response to simulated rainfall while parents that constructed enclosed nests did not (Table 3, Figs. 4-5). The interaction between nest type and experimental treatment highlights two important results: 1) plasticity in parental behavior may at least partially shield offspring from deleterious direct effects of rainfall, and 2) rain protection from enclosed nests relax brooding constraints on parents more than cup-shaped nests. Parental care has evolved in many taxa to protect offspring from biotic and abiotic environmental uncertainty (Clutton-Brock 1991). Our study provides a novel example of how parental behavioral plasticity can interact with animal architecture to reduce costs associated with climate change.

Animal nests are primarily thought to be a location to safely contain eggs and offspring (Collias and Collias 1984; Hansell 2005). However, the specific function of different nest types is a long-standing debate. In birds, the evolution of enclosed versus open nest types has been most often assumed to be due to reduced nest predation rates for enclosed nests (Skutch 1949, 1985; Nice 1957; Oniki 1985; Hall et al. 2015). Recently, indirect evidence suggested that enclosed nests may be favored more by thermal benefits than nest predation (Martin et al. 2017*a*). Wet skin surfaces lose heat faster than dry (Lustick and Adams 1977; Webb and King 1984), therefore enclosed nests should also provide thermal benefits due to rain protection (Martin et al. 2017*a*). Indeed, wet nests cooled faster in laboratory trials (Deeming and Campion Eloise 2018; Biddle et al. 2019). Accelerated heat loss in parents and offspring can increase energetic costs of thermoregulation (Scholander et al. 1950; Weathers 1992) and may favor strategies that mitigate such costs. Our results provide direct evidence that enclosed nests offer thermal benefits since parents using enclosed nests did not alter their behavior during rain, whereas parents in open nests brooded their young more (Table 3; Figs 4-7). Accordingly, the observation that more bird species build enclosed nests in wet tropical latitudes than birds breeding in drier temperate regions (Collias and Collias 1984; Martin et al. 2017*a*) may be partially explained by rain protection benefits. However, extremely hot and dry environments can also favor enclosed nests to protect against solar radiation (Duursma et al. 2018). Thus, enclosed nests may be favored in both very wet and very dry habitats, while open nests may be favored in more moderate climates.

Rainfall can influence offspring provisioning in multiple ways regardless of nest type. In altricial species, parents must provision their dependent offspring to fuel growth and development (Clutton-Brock 1991; Starck and Ricklefs 1998). On one hand, rain can increase primary productivity (Fenner 1998), which can have positive influences on offspring provisioning through increases in food availability and improved parent body condition (Grant and Boag 1980; Dunbar et al. 2002; English et al. 2014; McNew et al. 2019). On the other hand, rain can increase thermoregulation and flight costs in adults (Stalmaster and Gessaman 1984; Wilson et al. 2004; Voigt et al. 2011; Ortega-Jimenez et al. 2016), making foraging for young more costly. Wetting from rain can also require parental warming to reduce the risk of hypothermia in offspring, thereby reducing time available for parents to provision young (Radford et al. 2001). Indeed, songbird parents often face time constraints from two competing duties during brood rearing: brooding and feeding young (Johnson and Best 1982; Yoon et al. 2016; Mitchell et al. 2017). Our finding that provisioning rates did not change with simulated rain suggests the non-brooding parent may be able to increase food delivery rates to compensate for brooding demands on the other parent, at least when rain is relatively short-term. Our study species all exhibit bi-parental care, but studies among species with uniparental care would test whether the single parent was forced to reduce provisioning rates in response to rain, yet such studies have not been conducted.

Our experiment simulated heavy rainfall for only 4 hrs, and therefore our inference is limited to short-duration rain events. However, even short-term rain can have substantial energetic consequences for adults (Stalmaster and Gessaman 1984; Wilson et al. 2004; Voigt et al. 2011; Ortega-Jimenez et al. 2016). While rain spanning multiple days is less common, the cumulative energetic costs of these long events may eventually constrain parental ability to mitigate them. Still, the degree to which parents are willing to mitigate rain effects may be expected to vary among species with different life histories. For example, long-lived species may not increase parental care as much as short-lived species during rainy periods due to lifetime fitness benefits of self-maintenance over parental care (Williams 1966; Hirshfield and Tinkle 1975; Clutton-Brock 1991; Roff 1992; Ghalambor and Martin 2001; Martin 2015; Martin et al. 2015). We studied five species of relatively long-lived tropical birds (Martin et al. 2017*b*), but future studies of shorter-lived species would test whether they are more willing to increase parental care to protect young from rain as predicted by life history theory.

In conclusion, our experimental manipulation of rain did not increase offspring energy expenditure of songbirds in either open or enclosed nest types. The lack of increased energy expenditure in offspring with experimental rain was associated with increased levels of brooding young in open nests, and protective roofs rather than parental warming in enclosed nests. Thus, our experiment provides direct evidence that enclosed nests can relax parental care requirements, adding more support to the hypothesis that enclosed nests may have evolved to reduce negative effects of harsh abiotic conditions. Furthermore, our results suggest that parental behavioral plasticity may compensate for rainfall in cup-nesting birds in regions predicted to receive increased rainfall in the future.

ACKNOWLEDGEMENTS

We thank the Martin lab for helpful comments on the manuscript. We also thank K. Oliver for processing isotope samples. We are grateful for Sabah Parks and the Sabah Biodiversity Council for providing collaborative support in Malaysia. Financial support came from the National Science Foundation (DEB-1241041, DEB-1651283, IOS-1656120, IOS-1656273), and National Geographic Society (9875-16). AEM was supported by the WBIO department at the University of Montana, a Wesley M. Dixon graduate fellowship, a Bertha Morton Scholarship, and the Carl and Camilla Rietman Scholarship. This work was conducted under auspices of University of Montana IACUC #059-10TMMCWRU. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflicts of interest.

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TABLES

Table 1. Sample sizes showing A) the number of nestlings (nests) sampled for nestling daily energy expenditure (DEE), and B) days (nests) filmed for parental behavior (brooding and feeding rate). Controls are a combination of true experimental controls and pseudo-controls, which were unmanipulated nests that received no treatment or sham control (see methods).

A. # of nestlings (nests) sampled for DEE

SPP	Control	Experimental rain
WTFA	14(8)	10(5)
BOWH	10(7)	2(2)
SBFL	16(12)	8(4)
GTBA	12(9)	10(7)
WBSH	7(6)	6(4)

B. # of videos (nests) filmed for parental behavior

SPP	Control	Experimental rain
WTFA	54(46)	5(5)
BOWH	61(55)	6(5)
SBFL	74(66)	5(4)
GTBA	69(56)	12(9)
WBSH	65(55)	6(5)

Table 2. Linear mixed-effects model of nestling daily energy expenditure (DEE, kJ d^{-1}) with experimental treatment, nest type, nestling mass, brood size, and nestling age as fixed effects. Species and nest identity were included as random intercept terms due to account for species variation and repeated measures within nests, respectively. Experiment by nest type interaction was initially included in the model but was non-significant (*P* = 0.429) and therefore dropped from the model. Nestling DEE and body mass were both Log_{10} transformed to meet model assumptions. Experimental controls and enclosed nests were the reference levels for experiment and nest type factors, respectively.

Variable	β	SE	df	t-value	*P*
Experiment (rain)	0.00	0.02	45.3	-0.06	0.955
Nest type (open)	0.06	0.02	2.3	2.89	0.086
Log_{10} mass	0.57	0.08	2.7	7.34	0.007
Brood size	-0.07	0.02	53.6	-4.26	<0.001
Nestling age	0.02	0.01	30.6	2.32	0.027

LMM: Log_{10} DEE ~ Experiment + Nest type + Log_{10} mass + Brood size + Nestling age + (1|SPP/Nest id)
Conditional R^2 (includes random effects) = 0.79

Table 3. Linear mixed-effects model showing the percent of time a parent bird brooded its nestlings with experimental treatment, nest type, brood size, and nestling age included as fixed effects. We also included an experiment by nest type interaction in the model to test for experimental effects by nest type. Species and nest identity were included as random intercept terms to account for species variability and repeated measures within nests, respectively. Brooding rate was square-root transformed to improve model fit due to zero-inflation. Experimental control and enclosed nests were the reference levels for experiment and nest type factors, respectively.

Variable	β	SE	df	t-value	*P*
Experiment (rain)	-0.42	0.30	287.8	-1.38	0.168
Nest type (open)	2.04	1.26	5.0	1.62	0.167
Brood size	-1.22	0.14	294.2	-8.80	<0.001
Nestling age	-0.30	0.09	287.8	-3.49	<0.001
Experiment (rain) * Nest type (open)	3.36	0.50	313.9	6.71	<0.001

LMM: sqrt(Brood percent) ~ Experiment*Nest type + Brood size + Nestling age + (1|SPP/Nest id)
Conditional R^2 (includes random effects) = 0.79

Table 4. Linear mixed-effects model of the rate in which parents brought food to provision young (trips hr^{-1}) with experimental treatment, nest type, brood size, and nestling age included as fixed effects. Species and nest identity were included as random intercept terms to account for species variability and repeated measures within nests, respectively. We initially tested for an interaction between experiment and nest type but dropped the interaction term from the final model due to marginal non-significance (*P* = 0.074) and to parsimoniously interpret parameter estimates. Experimental controls and enclosed nests were the reference levels for the experiment and nest type factors, respectively.

Variable	β	SE	df	t-value	*P*
Experiment (rain)	0.55	0.68	352.1	0.81	0.419
Nest type (open)	3.15	4.50	5.0	0.70	0.514
Brood size	3.85	0.41	314.2	9.50	<0.001
Nestling age	0.57	0.19	124.6	3.03	0.003

LMM: Feed rate ~ Experiment + Nest type + Brood size + Age + (1|SPP/Nest id)
Conditional R^2 (includes random effects) = 0.92

Figure 1. Photographs of our five study species and their respective nest types.

Figure 2. Photographs of experimental rain shower device constructed from a dried bamboo segment illustrating A) shower device set up without camouflage and B) shower device set up over White-browed Shortwing (*Brachypteryx montana*) nest with natural vegetation attached for camouflage.

Figure 3. Grouped boxplots showing the effect of experimental rain treatment on nestling daily energy expenditure (DEE) in kJ * d^{-1}. Nestling DEE was $\log_{10}$ transformed to meet model assumptions.

Figure 4. Grouped boxplots showing the effect of experimental rain treatment on brooding time. All brood sizes were used and point sizes scale with brood size.

Figure 5. Interaction plot showing that the effect of experimental rain treatment on brooding rate depends on the nest type.

Figure 6. Grouped boxplots showing the effect of experimental treatment vs control nests on offspring provisioning rate (feeding rate). All brood sizes were used and point sizes are scaled to brood size.

Figure 7. Plot showing the interaction between experimental rain treatment and nest type on feeding rate.

FIGURES

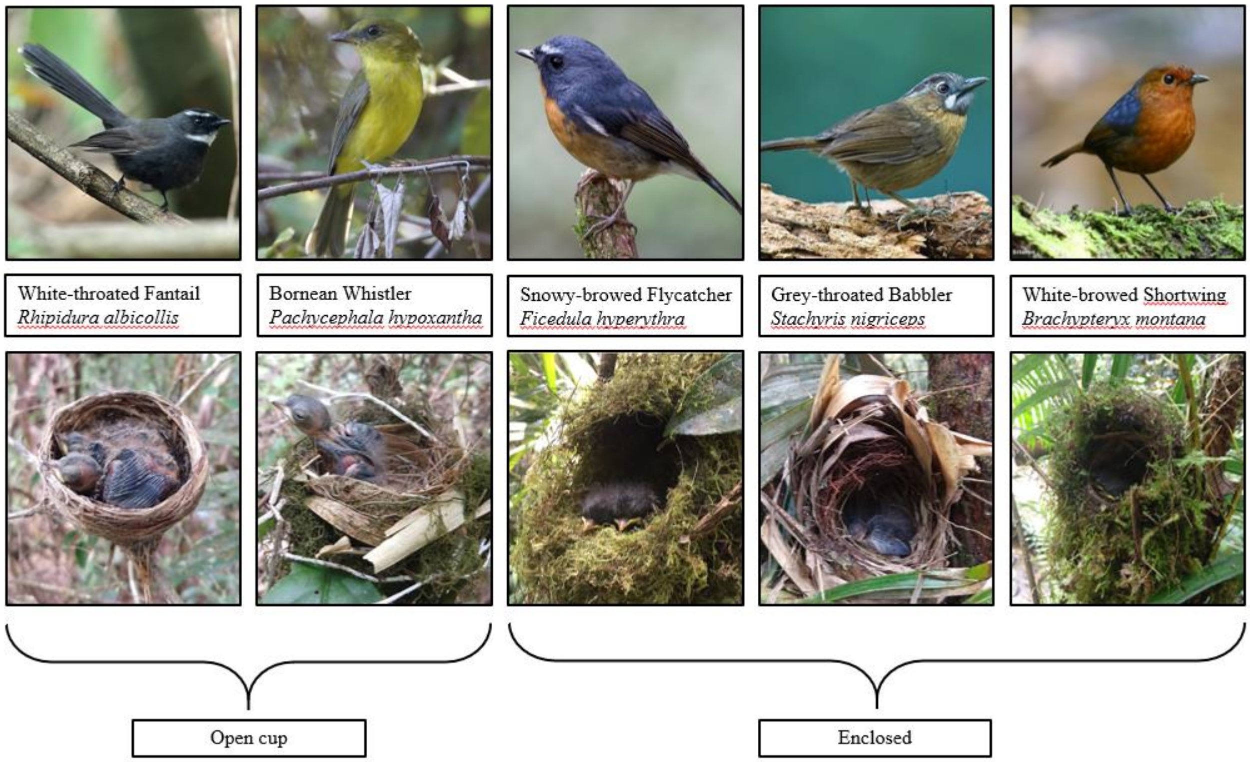


Figure 1.

Figure 2.

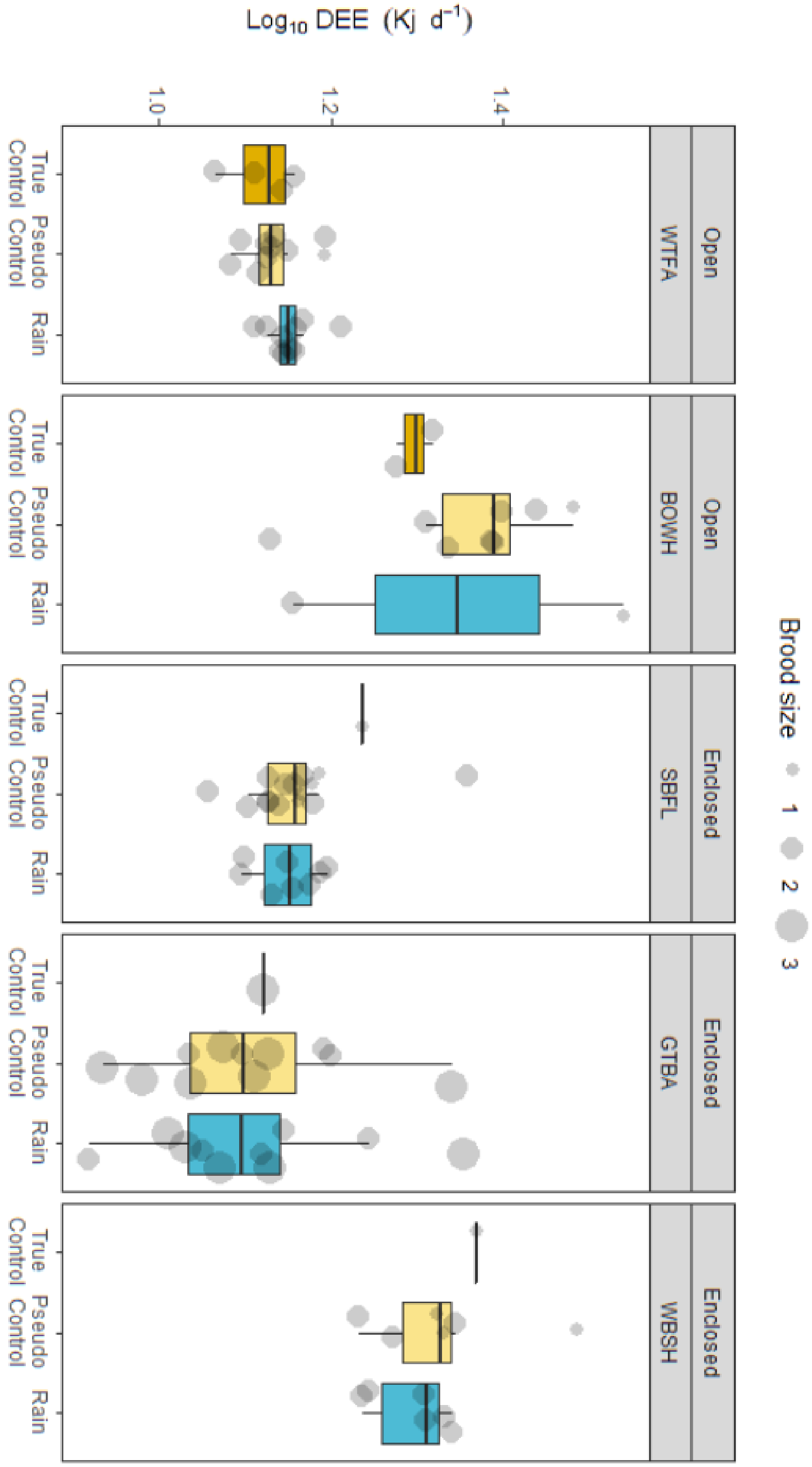

Log$_{10}$ DEE (Kj d^{-1})
1.0
1.2
1.4
Open
Open
Enclosed
Enclosed
Enclosed
WTFA
BOWH
SBFL
GTBA
WBSH
True Control
Pseudo Control
Rain
Brood size
1
2
3

Figure 3.

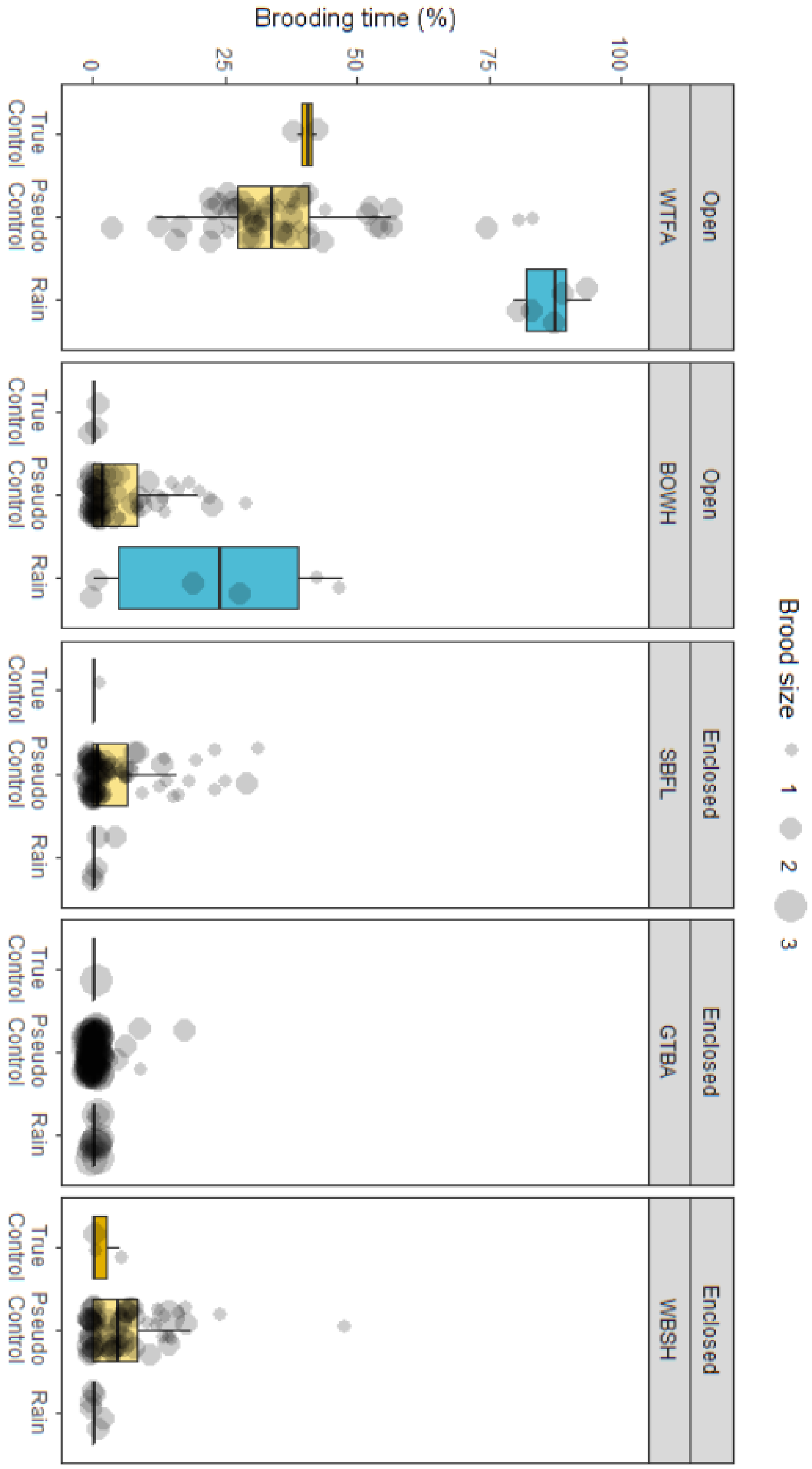

Brooding time (%)
0
25
50
75
100
Open
WTFA
Open
BOWH
Enclosed
SBFL
Enclosed
GTBA
Enclosed
WBSH
True Control
Pseudo Control
Rain
Brood size
1
2
3

Figure 4.

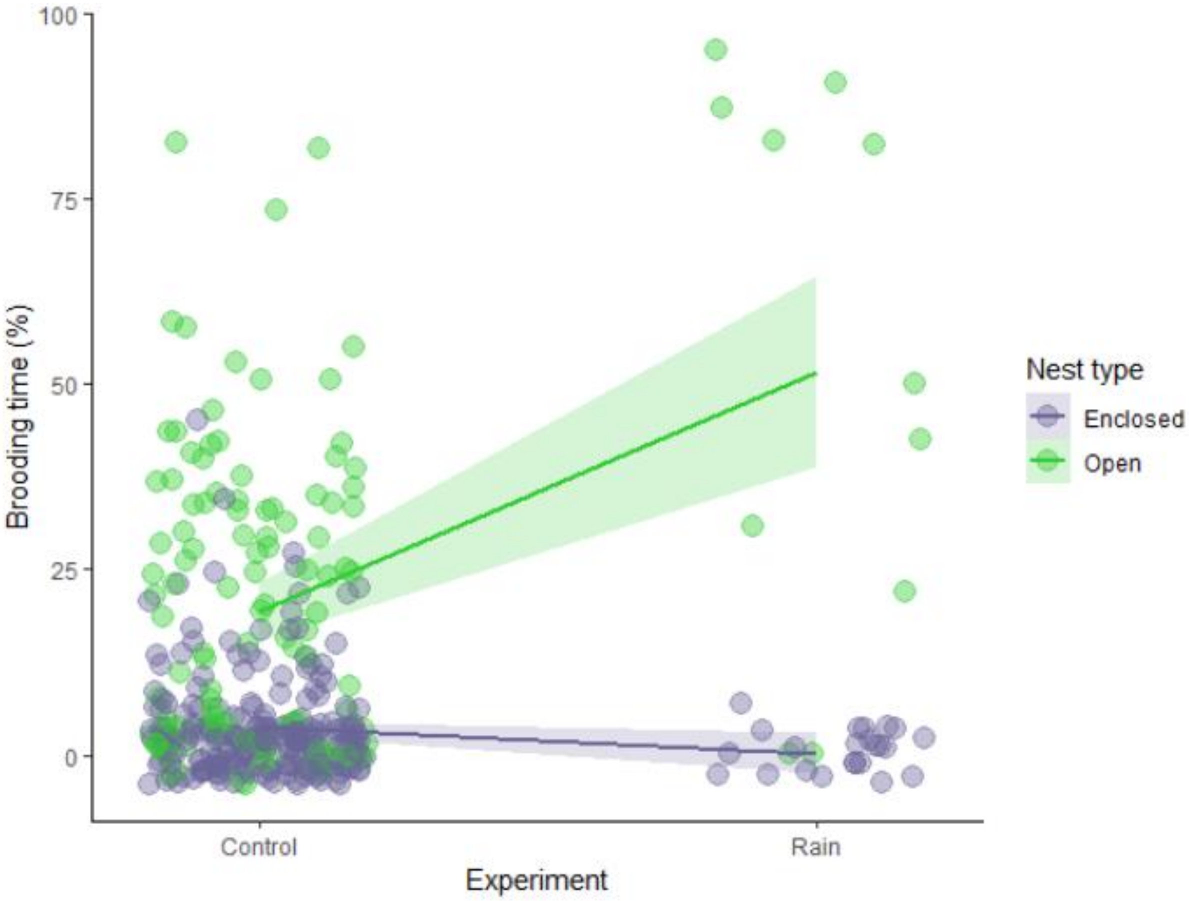

100
75
50
25
0
Brooding time (%)
Control
Rain
Experiment
Nest type
Enclosed
Open

Figure 5.

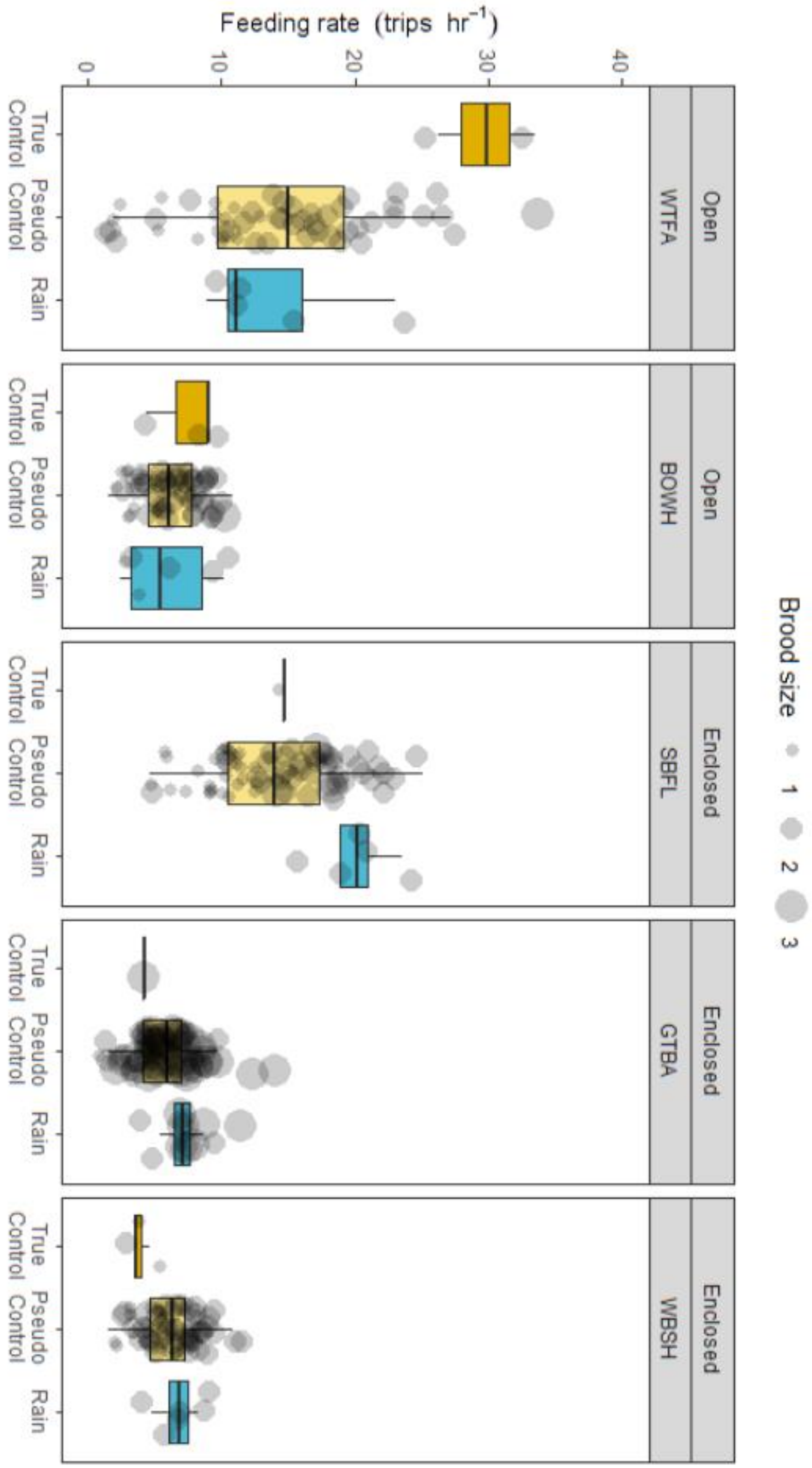
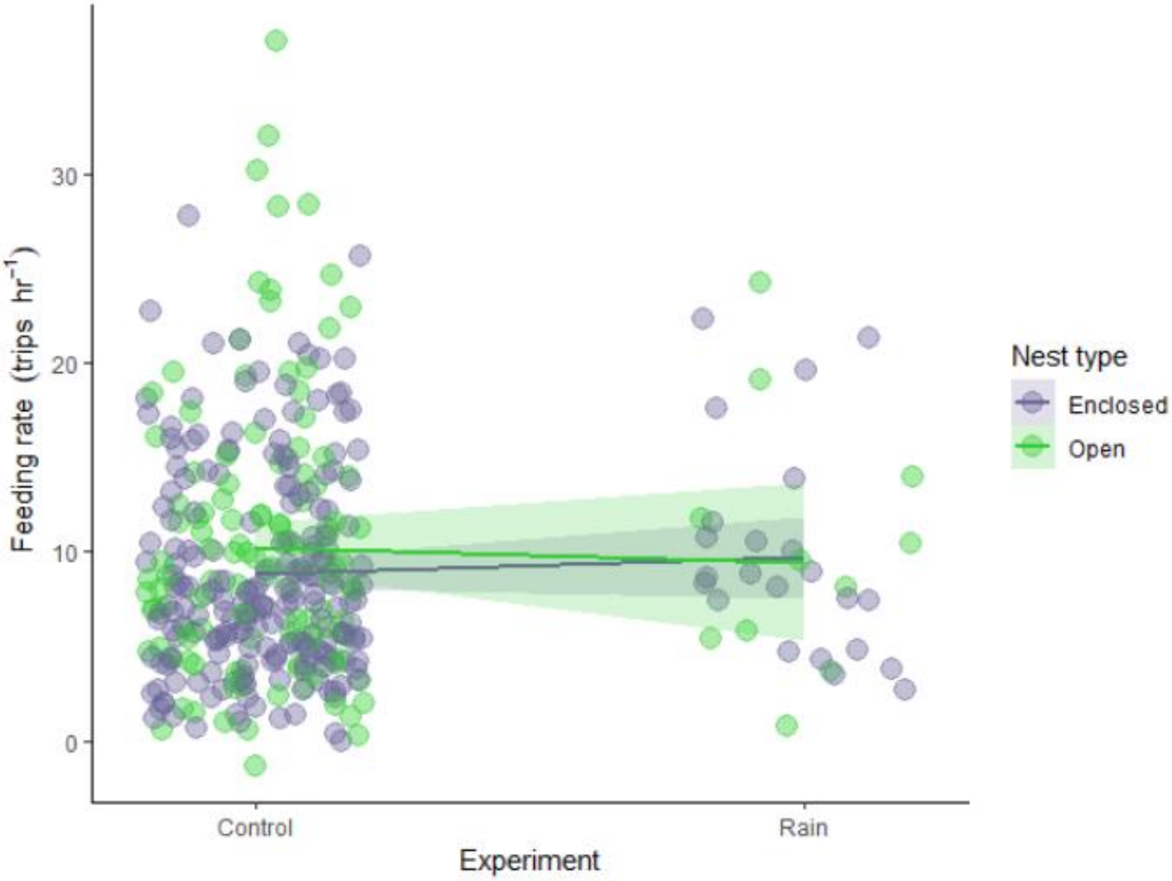

Feeding rate (trips hr⁻¹)
0
10
20
30
40
True Control
Pseudo Control
Rain
Open
WTFA
Open
BOWH
Enclosed
SBFL
Enclosed
GTBA
Enclosed
WBSH
Brood size
1
2
3

Figure 6.



Feeding rate (trips hr^{-1})
30
20
10
0
Control
Rain
Experiment
Nest type
Enclosed
Open

Figure 7.