

RESEARCH ARTICLE

Dry season intensity has equivocal effects on the nutritional condition of understory birds in a Neotropical forestElise T. Nishikawa,^{1,*} Henry S. Pollock,^{2,○} and Jeffrey D. Brawn^{2,○}¹ Program in Ecology, Evolution & Conservation Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA² Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA* Corresponding author: nishika2@illinois.edu

Submission Date: May 10, 2020; Editorial Acceptance Date: November 11, 2020; Published March 10, 2021

ABSTRACT

Rainfall regime, the amount and timing of annual precipitation, can influence the breeding phenology, individual fitness, and population dynamics of tropical birds. In Neotropical regions with rainfall seasonality (i.e. wet and dry seasons), the warm phase of the El Niño Southern Oscillation (ENSO) can exacerbate seasonal drought and negatively impact avian survival and reproduction. However, the mechanisms underlying associations between seasonal drought conditions and avian demography are largely unexplored. One hypothesis is that nutritional condition mediates demographic responses to seasonal drought: individuals in poor condition may be less capable of balancing their energy budgets and consequently suffer reduced survival, lower reproductive output, or both. We estimated nutritional condition (i.e. scaled mass index, percent hematocrit, plasma lipid metabolites) as a proxy of energy balance in understory forest birds with contrasting population-level responses to dry season length. This study took place across two dry seasons of differing intensity in central Panama: an El Niño dry season (2016, severe drought) and a more typical dry season (2017). Scaled mass index remained relatively constant throughout both dry seasons and across years for 5 common focal species and among 4 foraging guilds (22 additional species, 27 species total). Three of 5 focal species did exhibit reduced nutritional condition (i.e. lower hematocrit and/or higher β -hydroxybutyrate) during the El Niño dry season but not during the more typical dry season. However, foraging guilds did not show consistent nutritional responses to seasonal drought and we found little evidence of the reduced nutritional condition at the guild level, suggesting that many Neotropical forest bird species are capable of tolerating seasonal drought.

Keywords: body condition, hematocrit, metabolites, Neotropical birds, nutritional condition, seasonal drought

LAY SUMMARY

- The amount and timing of rainfall influences the ecology, phenology, and population dynamics of tropical organisms.
- Seasonal drought can negatively impact the survival, reproduction, and breeding phenology of tropical forest birds, although the mechanisms underlying these impacts remain unclear.
- We tested the hypothesis that seasonal drought negatively impacts the nutritional condition of resident forest birds in Central Panama.
- We estimated body condition, hematocrit, and plasma lipid metabolite concentrations in 27 bird species across two dry seasons of differing intensity—an El Niño year (2016, very dry) and a more typical year (2017).
- We found some evidence of reduced nutritional condition (i.e. lower hematocrit and greater concentrations of β -hydroxybutyrate) during the El Niño dry season in certain focal species, but little evidence of nutritional stress among foraging guilds.
- Our findings suggest that many tropical forest species can tolerate seasonal drought without exhibiting evidence of energetic stress.

La intensidad de la estación seca tiene efectos equívocos sobre la condición nutricional de las aves del sotobosque en un bosque neotropical**RESUMEN**

El régimen de lluvia, entendido como la cantidad y el momento de la precipitación anual, puede influir la fenología de cría, la adecuación biológica individual y las dinámicas poblacionales de las aves tropicales. En las regiones neotropicales con estacionalidad de lluvias (i.e. estaciones húmeda y seca), la fase cálida de la Oscilación del Sur El Niño (ENSO por sus siglas en inglés) puede exacerbar la sequía estacional e impactar negativamente la supervivencia y la reproducción de las aves. Sin embargo, los mecanismos que subyacen las asociaciones entre las condiciones de sequía estacional

y la demografía de las aves permanecen en gran medida inexplorados. Una hipótesis es que la condición nutricional determina las respuestas demográficas a la sequía estacional: los individuos en mala condición pueden ser menos capaces de balancear sus presupuestos energéticos y consecuentemente sufrir una menor supervivencia, un menor rendimiento reproductivo, o ambos. Estimamos la condición nutricional (i.e. índice de masa escalado, porcentaje de hematocritos, metabolitos de lípidos plasmáticos) como un indicador del balance energético en aves del sotobosque con respuestas poblacionales contrastantes a la duración de la estación seca. Este estudio fue realizado durante dos estaciones secas de diferente intensidad en el centro de Panamá: una estación seca El Niño (2016, sequía severa) y una estación seca más típica (2017). El índice de masa escalado permaneció relativamente constante a lo largo de ambas estaciones secas y a través de los años para cinco especies focales comunes y para cuatro gremios de forrajeo (22 especies adicionales, 27 especies en total). Tres de las cinco especies focales mostraron una condición nutricional reducida (i.e. hematocritos más bajos y/o β -hidroxibutirato más alto) durante la estación seca El Niño, pero no durante la estación seca más típica. Sin embargo, los gremios de forrajeo no mostraron respuestas nutricionales consistentes a la sequía estacional y encontramos poca evidencia de una condición nutricional reducida a nivel de gremio, sugiriendo que muchas especies de aves de bosques neotropicales son capaces de tolerar la sequía estacional.

Palabras clave: aves neotropicales, condición corporal, condición nutricional, hematocrito, metabolitos, sequía estacional

INTRODUCTION

The amount and timing of annual rainfall strongly impact the ecology and phenology of tropical organisms (Leigh et al. 1985). For example, rainfall patterns can affect leaf, flower, and fruit phenology (van Schaik et al. 1993, Wright et al. 1999); the activity and abundance of arthropods (Levings and Windsor 1985, Denlinger 1986, Silva et al. 2017); and the reproduction and survival of tropical birds (Brawn et al. 2017). Predicted changes in tropical rainfall regimes due to climate change (Karmalkar et al. 2011, Turner and Annamalai 2012, Feng et al. 2013) motivate a need to further understand possible associations between rainfall seasonality and the biology of tropical species. The magnitude, timing, and duration of rainfall have already been altered by climate change, with increased dry season length and intensity observed throughout both the Old World and New World tropics (Feng et al. 2013, Fu et al. 2013, Jiang et al. 2019).

Drought in the seasonal tropics can impact individual fitness and population dynamics of birds (Wunderle 1982, Faaborg et al. 1984, Wolfe et al. 2015, Brawn et al. 2017). For example, extended seasonal drought has been associated with depressed population growth rates and reduced abundance of tropical resident birds (Faaborg et al. 1984, Brawn et al. 2017). In particular, the warm phase of the El Niño Southern Oscillation (ENSO) can lead to severe seasonal droughts across much of Central America and the Caribbean (Lyon 2004, Malhi and Wright 2004, Jiménez-Muñoz et al. 2016). These severe seasonal droughts can have widespread negative effects on resident birds, including reduced survival (Wolfe et al. 2015) and delayed or inhibited reproduction (Duca and Marini 2011, Nesbitt-Styrsky and Brawn 2011, Opper et al. 2013).

Whereas the negative impacts of ENSO-induced seasonal drought on tropical bird populations are becoming evident, the mechanisms linking reduced rainfall to demographic responses remain poorly understood.

One possible mechanism is direct physiological sensitivity to the xeric conditions induced by ENSO events. However, recent studies have not found evidence of microclimate selectivity or avoidance of xeric microclimates among tropical forest birds (e.g., Patten and Smith-Patten 2012, Pollock et al. 2015), suggesting that more indirect mechanisms may be involved. For example, lack of rainfall could depress resource availability, indirectly affecting bird populations through a bottom-up trophic cascade. The availability of food resources, such as arthropods (Levings and Windsor 1985, Karr and Brawn 1990, Poulin et al. 1992, Poulin and Lefebvre 1996), is often reduced under xeric conditions associated with seasonal drought. Many tropical birds synchronize breeding with food availability, particularly arthropod abundance (Poulin et al. 1992, Aranzamendi et al. 2019), which may be especially important for raising nestlings and provisioning fledglings. Reduced food availability could negatively impact an individual's energy balance (i.e. the difference between an individual's energy intake and energy output), which may subsequently limit reproductive effort (Drent and Daan 1980) and/or reduce survival of adults or nestlings (Grant and Grant 1980, Wunderle 1982), with cascading population effects.

Because many tropical insectivorous birds have specialized diets (Poulin and Lefebvre 1996) or foraging strategies (e.g., obligate army ant followers), direct measures of overall arthropod abundance may not reflect food availability for insectivorous birds (Cooper and Whitmore 1990, Hutto 1990). Measuring nutritional condition is a common proxy for assessing an individual's energy state or balance. Indices of the condition can be morphological (e.g., body size, mass, composition) or physiological (e.g., metabolic rate, blood chemistry) and convey information about an organism's current energetic state. Thus, changes in nutritional condition should presumably reflect changes in food intake. However, very few studies have successfully linked changes in nutritional condition to the climate in

TABLE 1. Ecological characteristics of the 5 focal species and sample sizes collected in the 2 dry seasons. The predicted effect of seasonal drought is based on demographic data from [Brawn et al. 2017](#). Mass \pm SE calculated from birds captured on the study plot between 2016 and 2017.

Common name	Scientific name	Mass (g) \pm SE	Sexually dimorphic?	Length of breeding season	Foraging guild	Predicted effect of seasonal drought	Sample size	
							2016	2017
Red-capped Manakin	<i>Ceratopipra mentalis</i>	14.37 \pm 0.08	Yes	March-August	Frugivore	Negative	11	7
Bicolored Antbird	<i>Gymnopithys bicolor</i>	29.23 \pm 0.18	No	April-August	Ant-follower	None	15	20
Spotted Antbird	<i>Hylophylax naevioides</i>	16.77 \pm 0.10	Yes	May-October	Ant-follower	None	32	24
Chestnut-backed Antbird	<i>Poliocrania exsul</i>	27.28 \pm 0.25	Yes	April-November	Above-ground insectivore	No data	12	7
Song Wren	<i>Cyphorhinus phaeocephalus</i>	24.59 \pm 0.17	No	May-December	Ground insectivore	Negative	51	28

tropical birds. One study from Costa Rica found that seasonal storms negatively impacted the nutritional condition of White-ruffed Manakins (*Corapipo altera*), presumably via food limitation, and drove altitudinal migration ([Boyle et al. 2010](#)). Yet nutritional responses to seasonal drought remains, to our knowledge, virtually unexplored in tropical birds.

To explore the impact of seasonal drought on the energy balance of Neotropical forest birds in central Panama, we estimated 4 complementary indices of nutritional condition (scaled mass index [SMI]; hematocrit; and 2 plasma lipid metabolites, β -hydroxybutyrate and triglyceride) across 2 dry seasons. The El Niño dry season in 2016 was exceptionally long (172 days) and began with a precipitation deficit (>500 mm below the long-term average), whereas the 2017 dry season was more typical (157 days, no precipitation deficit). We made the general prediction that nutritional condition would decrease over the dry season and would decrease more during the longer El Niño dry season than in the subsequent 2017 dry season. We focused on 5 focal species (see [Table 1](#)) that were abundant and easily captured at the study site. Additionally, our focal species exhibit contrasting population-level responses to dry season length as previously shown by a 33 year mark-recapture study at our study site (see [Brawn et al. 2017](#)). Increased dry-season length was associated with negative population growth rates in 2 focal species: a ground insectivore (Song Wren [*Cyphorhinus phaeocephalus*]) and an understory frugivore (Red-capped Manakin [*Ceratopipra mentalis*]; [Brawn et al. 2017](#)). We, therefore, predicted that individuals of these species would exhibit greater decreases in nutritional condition in response to seasonal drought relative to the other 3 focal species, which either did not exhibit associations between dry season length and population growth rates or for which the effect of dry season length on population growth rate is unknown. In addition

to the 5 focal species, we also sampled 22 other understory species (27 species total; [Supplementary Material Table S1](#)) and compared nutritional responses to seasonal drought among 4 foraging guilds (ant-follower, frugivore, above-ground insectivore, ground insectivore). Increasing dry season length had the most significant negative impact on population growth rates in the frugivore guild at our study site ([Brawn et al. 2017](#)), we, therefore, predicted that frugivores would exhibit greater decreases in nutritional condition during seasonal drought relative to the other foraging guilds.

METHODS

Study Site, Focal Species, and Field Sampling

We sampled understory forest birds across the 2016 (hereafter “El Niño”) and 2017 dry seasons on a long-term 104 ha research plot (hereafter “Limbo Plot”) of lowland tropical moist forest in the 22,000 ha Soberanía National Park (9.15°N, 79.73°W) in the Republic of Panama (see [Robinson et al. 2000](#) for more details). The study site is classified as Tropical Monsoon (AM) under the Köppen climate classification system ([Croat 1978](#)) and is characterized by a distinct dry season that occurs between late December and mid-April, although its length is highly variable and can range from 66 to 177 days ([Paton 2019](#)). Approximately 90% of annual precipitation at the study site (\bar{x} = 2,600 mm) occurs during the rainy season.

Our sampling efforts focused on 5 of the most abundant understory species on Limbo Plot ([Table 1](#)): Red-capped Manakin, Bicolored Antbird (*Gymnopithys bicolor*), Spotted Antbird (*Hylophylax naevioides*), Chestnut-backed Antbird (*Poliocrania exsul*), and Song Wren. The Red-capped Manakin is a lekking frugivore for which increased dry season length has a significant negative

effect on population growth rate (Brawn et al. 2017). The Bicolored Antbird and Spotted Antbird are obligate and facultative army-ant followers, respectively (Willis and Oniki 1978), in which population growth rates are not significantly affected by increased dry season length (Brawn et al. 2017). While the effect of increased dry season length on population growth rate is unknown for the Chestnut-backed Antbird, this above-ground insectivore can persist in small forest fragments and may be able to tolerate more xeric conditions than most tropical insectivores (Visco and Sherry 2015). The Song Wren is a ground insectivore that is less abundant and exhibits greater physiological stress on the drier Pacific side of the rainfall gradient across the Panamanian isthmus (Busch et al. 2011), and its population growth rate decreases significantly with increasing dry season length (Brawn et al. 2017). All focal species typically initiate breeding at our study site near the transition between the dry and rainy season (April–May), except Red-capped Manakin, which can initiate breeding as early as March (Willis and Oniki 1972, Wikelski et al. 2003). Several studies have shown that tropical birds in seasonal environments often initiate breeding at the onset of the wet season when food resources are highest (Poulin et al. 1992, Aranzamendi et al. 2019), and at least one focal species at our study site (Spotted Antbird) delays breeding in particularly dry years (Nesbitt-Styrsky and Brawn 2011).

We captured birds using mist-nets and conspecific playback recordings within 4.5 hr after sunrise ($\bar{x} = 2.42 \pm 1.10$ h) to minimize the confounding effect of diel variation in food intake on plasma lipid metabolites (Guglielmo et al. 2002, Mandin and Vézina 2012). We marked birds with uniquely numbered aluminum bands to facilitate individual identification, weighed them to the nearest 0.5 g, and recorded several morphometric measurements (i.e. exposed culmen and right tarsus, ± 0.01 mm). We were able to recapture some but not all individuals throughout each dry season, so we were unable to track longitudinal changes in nutritional condition within individuals. Therefore, seasonal trends in nutritional condition represent species-level averages rather than individual reaction norms. We also collected blood samples (50–150 μ L) within 15 min ($\bar{x} = 5.20 \pm 2.17$ min) of capture (following recommendations of Jenni-Eiermann and Jenni 1996) because capture stress can influence plasma metabolite concentrations after only 15–20 min (Jenni-Eiermann and Jenni 1996, Guglielmo et al. 2002). We held blood samples on ice until centrifuging (ZIPocrit hematocrit centrifuge, LW Scientific Inc., Lawrenceville, GA). All samples used for metabolite assays were centrifuged on the day of capture. Plasma was stored at -20°C until laboratory analysis.

Rainfall Data

For each dry and rainy season, we used the start and end dates of each season (e.g., the dry season was defined

as day 1 of the dry season until the day before day 1 of the rainy season in a given year) as designated by the Panama Canal Authority (<https://micanaldepanama.com/nosotros/cuenca-hidrografica/anuario-hidrologico/>) and the Smithsonian Tropical Research Institution Physical Monitoring Program (http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado). These dates are determined each year based on multiple factors, such as the location of the Intertropical Convergence Zone, wind patterns on both coasts, and daily rainfall at multiple stations in the Gatun Lake watershed crossing threshold values. Because dry season length was negatively associated with population growth rates of certain species at our study site (Brawn et al. 2017), we used the day of the dry season as an index of seasonal drought. Thus, by capturing birds throughout the dry season, we were able to detect changes in nutritional condition as the season progressed. Moreover, during our study cumulative moisture deficit (i.e. the sum of daily rainfall minus daily evapotranspiration) from the start of the dry season and day of the dry season were highly correlated (Pearson correlation coefficient = -0.953 , $P < 0.0001$).

A strong El Niño event in 2015–2016 led to a substantial precipitation deficit (i.e. >500 mm below average May–November cumulative precipitation) at the start of the 2016 El Niño dry season in central Panama. Moreover, the El Niño dry season lasted 172 days (November 27, 2015, to May 18, 2016), 44 days longer than the Barro Colorado Island long-term average of 127.9 ± 23.25 days (Paton 2019). In contrast, there was not a precipitation deficit entering the 2017 dry season, which lasted for 157 days. Thus, we also used year as an index of seasonal drought. Estimates of soil moisture from environmental monitoring on nearby Barro Colorado Island (see Paton 2019) reveal that physical conditions were significantly drier from March to April 2016 than the same period in 2017 (paired t -test, $t = -7.6$, $df = 69$, $P < 0.001$).

Indicators of Nutritional Condition

SMI. We used the scaled mass index (SMI; Peig and Green 2009), calculated as

$$W_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}},$$

as a longer-term, integrated indicator of nutritional condition. We considered higher SMI as indicative of better nutritional condition, as greater relative mass adjusted for structural size, such as tarsal length, is expected to reflect accumulated energy reserves (Peig and Green 2009). To create species-specific SMIs, we calculated b_{SMA} , the scaling exponent, following Peig and Green (2009) using mass and tarsal measurements sampled from 10 or more individuals during previous work (e.g., long-term monitoring; 1998–1999, 2003, 2013–2015) at the study site (J. D. Brawn and

H. S. Pollock, personal observations) or during the 2016 and 2017 rainy seasons (E.T. Nishikawa, personal observation). We used the arithmetic mean tarsal length of individuals captured outside of the focal dry seasons as L_0 . W_i and L_i are individual mass and tarsal length, respectively. We then standardized each of these species-specific SMIs by subtracting the long-term mean SMI from each individual SMI and dividing by the long-term SMI standard deviation (e.g., setting the mean SMI for individuals captured outside of the focal dry seasons to zero and the standard deviation to one) to facilitate multi-species analyses.

Percent hematocrit. Hematocrit is the proportion of packed red blood cells in a blood sample (Fair et al. 2007), and reductions in hematocrit have been documented in response to low food intake, unpredictable food supply, or other forms of energetic stress (Piersma et al. 2000, Cucco et al. 2002, and reviewed in Fair et al. 2007). These changes can occur on a relatively rapid timescale (i.e. within days to weeks; Birkhead et al. 1998, Piersma et al. 2000) and are often due to reductions in erythropoiesis. Therefore, we interpreted individuals with lower hematocrit percentages as being in poorer nutritional condition, as anemic individuals may be unable to sustain normal daily activity (Glomski and Pica 2011). We calculated percent hematocrit by dividing the length of the packed red blood cells over the total length of the blood sample in the capillary tube.

Plasma lipid metabolites. Lipid metabolites are small molecules produced in one organ and transported via the bloodstream to another organ that are sensitive to variation in energy intake (Jenni-Eiermann and Jenni 1998, Zajac et al. 2006), respond rapidly to changes in food supply (i.e. within hours; Jenni-Eiermann and Jenni 1991, Landys et al. 2004, Khalilieh et al. 2012), and can be used to determine metabolic responses to extreme environmental conditions (Boyle et al. 2010). To characterize nutritional condition, we estimated circulating concentrations of 2 plasma lipid metabolites, triglyceride (hereafter “TRIG”) and β -hydroxybutyrate (hereafter “BUTY”). TRIG is derived from the diet and is indicative of the build-up of fat stores (Jenni-Eiermann and Jenni 1998). Circulating TRIG concentrations decline significantly within 2 hr of food deprivation in controlled and field settings (Jenni-Eiermann and Jenni 1991, Khalilieh et al. 2012); thus lower levels of TRIG are interpreted as indicative of poorer nutritional condition. Conversely, BUTY is a ketone body that largely replaces glucose as a fuel source when food intake is low (Jenni-Eiermann and Jenni 1998, McCue 2010). Controlled fasting studies of small passerines found BUTY concentrations reaching an average of 2.96 mMol L⁻¹ after 3–4 hr (Landys et al. 2004, Khalilieh et al. 2012) with average values ≥ 5 mMol L⁻¹ seen in individuals fasted for 6 hr (Khalilieh et al. 2012). Thus, higher levels of BUTY are interpreted as indicative of poorer nutritional condition.

If seasonal drought reduces nutritional condition, we expected to see lower average concentrations of TRIG and higher average concentrations of BUTY as the dry season progressed.

We conducted all metabolite assays at the Instituto de Investigaciones Científicas Y Servicios de Alta Tecnología (INDICASAT) in Panama (<http://indicat.org.pa/home/>). We used colorimetric-endpoint assays from Cayman Chemical to estimate concentrations of circulating TRIG (Item No. 10010303) and BUTY (Item No. 700190) following manufacturer instructions. Plates were read at 540 nm for TRIG and 450 nm for BUTY with a Biotek Synergy HT II reader (BioTek Instruments, Winooski, VT). We ran a standard curve in duplicate on all plates. Most plasma samples were assayed in duplicate or triplicate for both BUTY (intra-assay CV = 0.071) and TRIG (intra-assay CV = 0.066). For samples in which plasma volume was insufficient to conduct both metabolite assays in duplicate (9.06% of samples, $n = 30$), we assayed either BUTY or TRIG in duplicate. BUTY concentrations are stable for up to 180 days when stored at -20°C (Carragher et al. 2003) and TRIG concentrations are stable for up to 189 days when stored at -20°C (Tiedink and Katan 1989). Thus, we expected that samples frozen from the day of capture until laboratory analysis (range: 3–188 days) remained stable.

Statistical Analysis

We conducted all statistical analyses using R version 3.5.1 *Feather Spray* (R Core Team 2018). We constructed 2 sets of generalized linear mixed models (for focal species and for foraging guilds) using packages *lme4* (Bates et al. 2014), *glmmTMB* (Brooks et al. 2017), *stats* (R Core Team 2018), and *betareg* (Cribari-Neto and Zeileis 2010) to examine trends in 4 metrics of nutritional condition (body condition, hematocrit, and concentrations of both plasma lipid metabolites) in response to seasonal drought. We fit all models examining trends in lipid metabolite concentrations with a log-link function. Given that hematocrit is a proportional response variable (i.e. the proportion of red blood cells in a blood sample), we fit all hematocrit models using beta-regression (Ferrari and Cribari-Neto 2004).

For each of the 5 focal species, we ran a model for the 4 metrics of nutritional condition (5 focal species \times 4 metrics = 20 models), with the metric of interest as the response variable. Because the duration of the dry season and precipitation in the preceding rainy season both affect the intensity of seasonal drought, we included the year (i.e. El Niño vs. 2017) along with the day of the dry season and their interaction as fixed effects. Due to differences of scale among the predictor variables, we performed a linear transformation on the day of the dry season to facilitate model convergence and we report the back-transformed parameter estimates. To account for repeated sampling

TABLE 2. Associations between dry season length (e.g., per day of the dry season) and standardized SMI, hematocrit, β -hydroxybutyrate concentration, and triglyceride in 2016 (El Niño year) and 2017. Bullet (•) indicates models in which the 95% confidence interval around the estimated regression (beta) coefficient included zero. Down arrow (\downarrow) indicates models in which beta was negative and the 95% confidence interval did include zero. Up arrow (\uparrow) indicates models in which beta was positive and the 95% confidence interval did not include zero. Decreased nutritional condition is indicated by a \downarrow for SMI, hematocrit, or triglyceride and a \uparrow for β -hydroxybutyrate.

	SMI		Hematocrit		β -hydroxybutyrate		Triglyceride	
	2016	2017	2016	2017	2016	2017	2016	2017
Focal species								
Red-capped Manakin (<i>C. mentalis</i>)	•	•	•	•	•	•	•	•
Bicolored Antbird (<i>G. bicolor</i>)	•	•	\downarrow	•	•	•	•	•
Chestnut-backed Antbird (<i>P. exsul</i>)	•	•	\downarrow	•	•	•	•	•
Spotted Antbird (<i>H. naevioides</i>)	•	•	•	•	•	•	•	•
Song Wren (<i>C. phaeocephalus</i>)	•	•	\downarrow	•	\uparrow	•	•	•
Guild								
Frugivore	•	•	•	•	\uparrow	•	•	•
Ant-follower	•	•	\downarrow	•	\uparrow	\uparrow	•	•
Above-ground insectivore	•	•	\downarrow	•	\downarrow	\downarrow	\uparrow	•
Ground insectivore	•	•	\downarrow	•	•	•	•	•

of individuals, we included individual identity (i.e. band number) as a random effect for all focal species except Red-capped Manakins (none were recaptured). We initially included sex as an additional fixed effect in focal species models for the 3 sexually dimorphic focal species (Table 1) but found little evidence for the effect of sex on nutritional condition and subsequently pooled males and females. We excluded 2 female Bicolored Antbirds and 1 female Red-capped Manakin with clear evidence of breeding (e.g., vascularized brood patch or an egg present in the oviduct) from all analyses because body mass and plasma lipid metabolites are affected by egg production (Bryant 1988, Kern et al. 2005).

To assess guild level patterns, we ran models for all 4 condition metrics, with the metric of interest as the response variable. Models included fixed effects of foraging guild and the 2- and 3-way interactions of a guild with year and day of the dry season, as well as individual as a random effect. Similar to focal species models, we performed a linear transformation on the day of the dry season to facilitate model convergence and we report the back-transformed parameter estimates. To control for phylogenetic relationships among the focal species in the foraging guild models, we obtained 1,000 phylogenetic trees from birdtree.org using the Hackett tree backbone (Hackett et al. 2008, Jetz et al. 2012), built a phylogenetic consensus tree using package *ape* (Paradis et al. 2004), and estimated phylogenetic signal by calculating Pagel's λ (Pagel 1999) using package *phytools* (Revell 2012). We found little evidence of phylogenetic signal in median measures of nutritional condition ($\lambda < 0.001$ for all metrics). Nonetheless, we followed Wingfield et al. (2018) and included species nested in family as a random effect to account for phylogenetic inertia. We conducted post-hoc pairwise interaction analyses for estimated marginal means using a Bonferroni

correction to examine differences among the 4 guilds between years or across the dry season using package *emmeans* (Lenth 2018).

To further explore the importance of terms in the mixed-effects models, we calculated marginal and conditional R^2 values (Nakagawa and Schielzeth 2013). Marginal R^2 is an estimate of variance explained by the fixed effect terms whereas the conditional R^2 is a measure of variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). For generalized linear models without random effects, we report Nagelkerke's pseudo- R^2 -value, which compares the proportion of variance explained between the null (intercept only) versus the fitted models (Nagelkerke 1991). For the beta-regression models on hematocrit counts without random effects, we report the correlation between the logit link-transformed response and the linear predictor as a pseudo- R^2 (Ferrari and Cribari-Neto 2004). We considered a given effect to be important if the 95% confidence interval around the estimated regression coefficient did not include zero (Table 2).

RESULTS

Throughout the 2 dry seasons, we collected 380 blood samples from 27 species in 14 families (Supplementary Material Table S1). We assayed 320 samples from 277 individuals for plasma lipid metabolites, of which 208 were from the 5 focal species.

Focal Species Patterns

Seasonal drought did not strongly influence body condition in any focal species (Figure 1A, Table 2). Estimates of SMI throughout the El Niño and 2017 dry seasons were

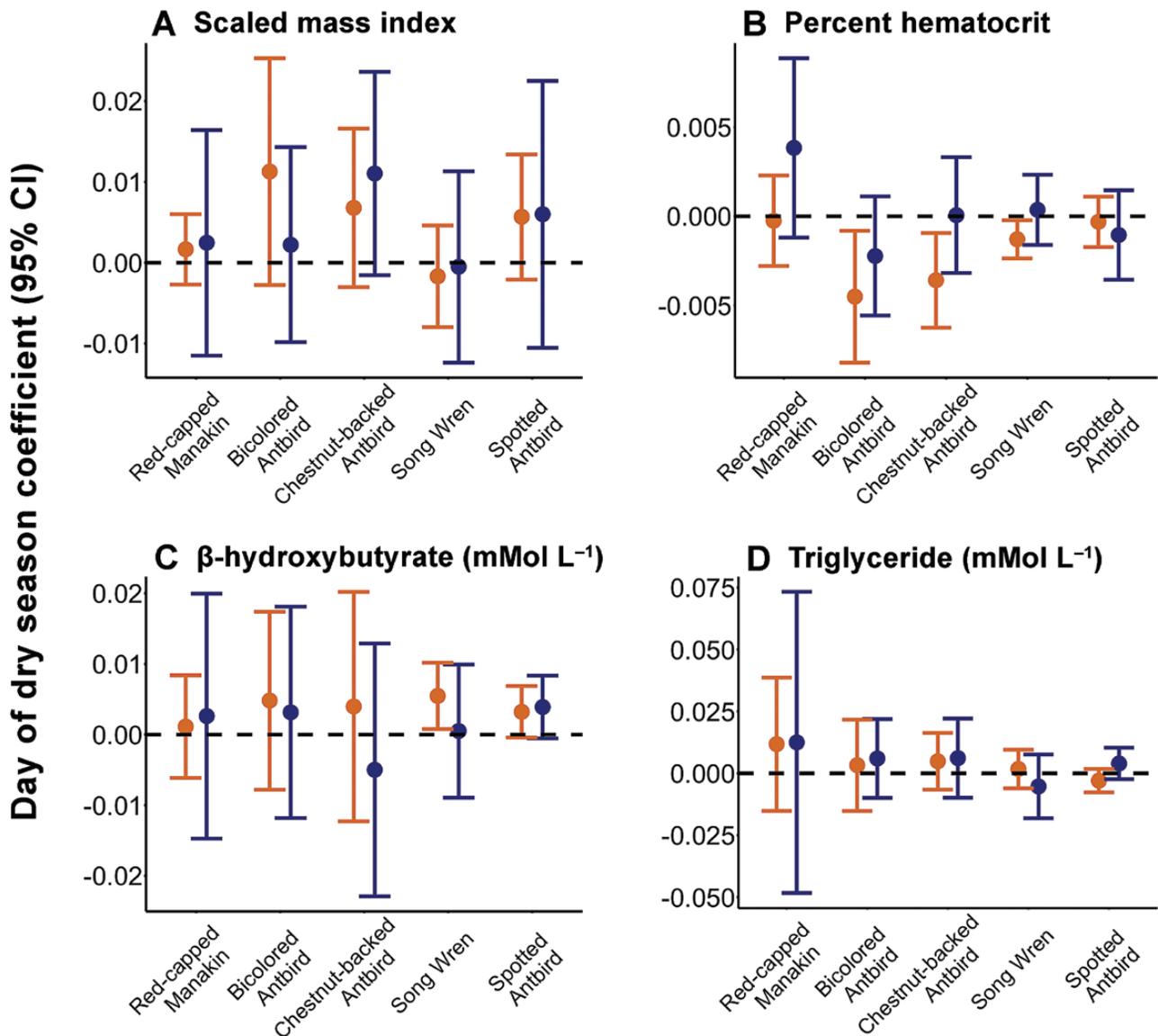


FIGURE 1. Estimated regression (β) coefficients and 95% confidence interval characterizing associations between dry season length (e.g., per day of the dry season) and (A) standardized scale mass index, (B) hematocrit, (C) β -hydroxybutyrate concentration, (D) triglyceride concentration in 2016 (orange) and 2017 (blue) for the 5 focal species. Coefficients are reported on the log-scale for β -hydroxybutyrate and triglyceride concentrations and on the logit-scale for hematocrit due to model link-functions. The figure was created with R package *ggplot2* (Wickham 2016).

similar to the long-term average SMIs for all 5 focal species (Supplementary Material Figure S1A–E).

We found a significant interaction between day of the dry season and year on hematocrit in 3 of the 5 focal species (Bicolored Antbird, Chestnut-backed Antbird, and Song Wren). These 3 focal species showed significant decreases in hematocrit concentrations, indicative of reduced nutritional condition, as the El Niño dry season progressed but not in the 2017 dry season (Figure 1B, Table 2). Specifically, throughout the El Niño dry season, average percent hematocrit decreased 12% (51.2% to 39.2%) in Bicolored Antbirds, 9.6% (50.3% to 40.7%) in Chestnut-backed Antbirds, and

3.4% (44.8% to 41.4%) in Song Wrens. We did not observe significant decreases in hematocrit concentrations in any of the focal species during the 2017 dry season.

Seasonal drought had little impact on the plasma lipid metabolites of the 5 focal species. TRIG concentrations did not vary significantly throughout the dry season or between years for any species (Figure 1D, Table 2). Plasma concentrations of BUTY were similarly invariable (Figure 1C, Table 2) with the exception of the Song Wren, which exhibited significant increases in BUTY as the El Niño dry season progressed. Estimated average BUTY concentrations in Song Wrens increased 115% (i.e. from

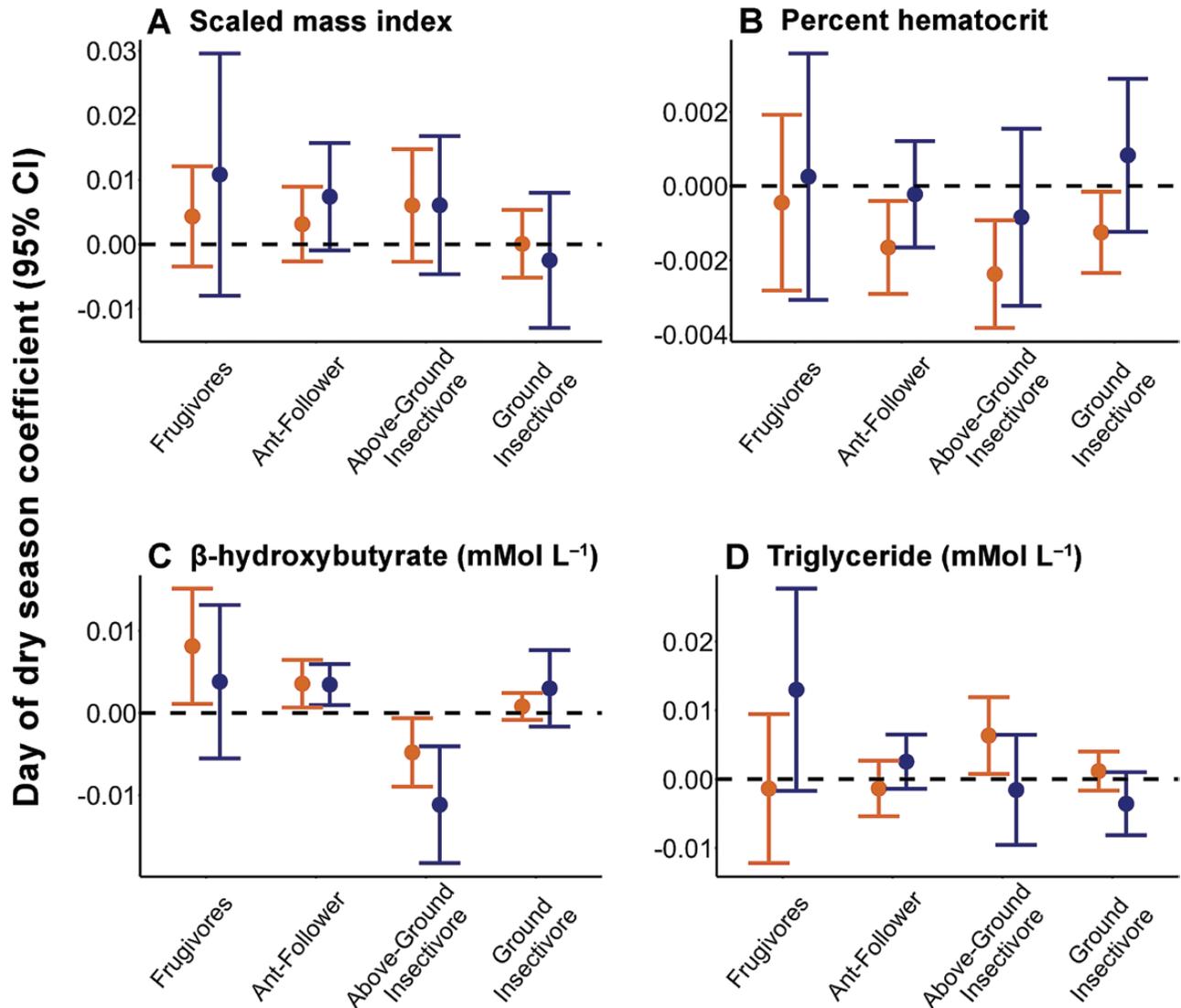


FIGURE 2. Estimated regression (β) coefficients and 95% confidence interval characterizing associations between dry season length (e.g., per day of the dry season) and (A) standardized scale mass index, (B) hematocrit, (C) β -hydroxybutyrate concentration, (D) triglyceride concentration in 2016 (orange) and 2017 (blue). Coefficients are reported on the log-scale for β -hydroxybutyrate and triglyceride concentrations and on the logit-scale for hematocrit due to model link-functions. The figure was created with R package *ggplot2* (Wickham 2016).

1.34 mMol L⁻¹ to 2.88 mMol L⁻¹) throughout the El Niño dry season (Supplementary Material Figure S4d), a trend suggestive of poor nutritional condition. We observed notably high BUTY concentrations (≥ 5 mMol L⁻¹) in 4 individuals, 2 pairs, captured in April and May of the El Niño dry season (Supplementary Material Figure S4d). One individual captured in May with BUTY concentrations ≥ 5 mMol L⁻¹ had strong influence (Cook's Distance $D_i = 0.39$); removal of this individual from the sample resulted in a parameter estimate with a 95% CI that spanned zero. We observed no trend in BUTY concentrations in Song Wrens during the 2017 dry season (Figure 1C, Table 2) nor

did we observe any individuals with notably high BUTY concentrations (≥ 5 mMol L⁻¹) during the 2017 dry season.

Guild-level Patterns

Mean SMI did not vary significantly among guilds (Supplementary Material Table S2), during the El Niño and 2017 dry seasons or between years in any of the 4 foraging guilds (post-hoc Bonferroni-adjusted $P > 0.05$ in all pairwise contrasts of estimated marginal means; Figure 2A, Table 2).

We found a significant 3-way interaction with year, day of the dry season, and guild on hematocrit (Supplementary

Material Table S3). As the El Niño dry season progressed, but not the 2017 dry season, average hematocrit decreased significantly in the 3 insectivorous foraging guilds but did not decrease in the frugivore guild ($p < 0.02$ in all Bonferroni-adjusted pairwise contrasts of estimated marginal means; Supplementary Material Table S3).

We also observed considerable heterogeneity in trends of circulating lipid metabolite concentrations among foraging guilds during the 2 dry seasons (Figure 2C, D; Table 2). In the ant-follower guild, BUTY concentrations increased significantly as the dry season progressed in both the El Niño and 2017 dry seasons (Figure 2C; Supplementary Material Figure S8b). Frugivores showed increased BUTY concentrations across the El Niño dry season, but not during the 2017 dry season (Figure 2C; Supplementary Material Figure S8a). Frugivores captured during the 2017 dry season had significantly lower BUTY concentrations than ground and above-ground insectivores (Bonferroni-adjusted $P < 0.05$ in both pairwise contrasts of estimated marginal means; Supplementary Material Table S3). TRIG concentrations in the frugivore and ant-follower guilds did not change across either dry season (Figure 2D; Supplementary Material Figure S7a, b), but frugivores maintained greater average TRIG concentrations compared to the 3 insectivorous guilds ($p < 0.03$, Bonferroni-adjusted contrasts; Supplementary Material Table S4) during the El Niño dry season. Average BUTY and TRIG concentrations in the ground-foraging insectivorous guild did not vary significantly throughout either dry season or between years (Figure 2C, D, Table 2). We found significant interactions between year and day of the dry season for both TRIG and BUTY in above-ground insectivores. Predicted average TRIG concentrations in above-ground insectivores increased threefold throughout the El Niño dry season (Supplementary Material Figure S7c), although TRIG concentrations were not associated with dry season length in 2017. Moreover, average BUTY concentrations of above-ground insectivores decreased twofold during the El Niño dry season and fourfold during the 2017 dry season (Supplementary Material Figure S8c).

DISCUSSION

We estimated seasonal changes in the nutritional condition of Neotropical forest birds in which seasonal drought (i.e. the length of the dry season) can lead to population declines (Table 1, see Brawn et al. 2017). Overall, we found mixed evidence that seasonal drought negatively impacts the nutritional condition and energy balance of these species. In short, the species we sampled appear largely capable of coping with seasonal drought and exhibited little evidence of reduced nutritional condition as the dry season progressed. The negative effects of

increased dry season length on population growth rates reported by Brawn et al. (2017) were driven largely by reduced recruitment, rather than reduced adult survival; results here are consistent in that adult birds were generally able to meet energetic requirements even during an El Niño dry season.

In contrast, Song Wrens showed some evidence of reduced nutritional condition in response to seasonal drought. Of the samples collected from Song Wrens, 9 (12.5%) showed BUTY concentrations at or above 2.96 mMol L^{-1} , which is indicative of prolonged fasting in small passerines (Landys et al. 2004, Khalilieh et al. 2012). Six of those samples were collected ≥ 95 days into the 2016 El Niño dry season. Notable declines in hematocrit levels of Song Wrens across the El Niño dry season are also suggestive of reduced food intake. These results are consistent with a previous study in Panama that found lower hematocrit levels in Song Wrens under more xeric conditions (Busch et al. 2011). Although our results do not establish a direct link between reduced nutritional condition and demography, they are consistent with the comparatively strong negative association between dry season length and Song Wren population growth rates reported by Brawn et al. (2017). Conceivably, Song Wrens that initiate breeding in relatively poor condition are less able to invest in reproduction.

However, Red-capped Manakins, a frugivore that also exhibited reduced population growth rates following longer dry seasons (Brawn et al. 2017), showed no evidence of reduced nutritional condition. Understory fruit can be conspicuous and abundant in the dry season (Morton 1973) and El Niño conditions in central Panama can lead to unusually high levels of dry-season fruit production (Wright et al. 1999). However, nestlings of frugivorous or omnivorous species consume $3\times$ to $5\times$ more arthropods than adults (Riehl and Adelson 2008, del Rosario Avalos 2015) and will starve when exclusively fed on fruit (Morton 1973, Dyrce 1983). Therefore, while Red-capped Manakins and perhaps other frugivores may be able to sustain positive energy balance in the dry season, other, as yet unknown, processes may reduce recruitment following relatively severe seasonal drought.

We also observed substantial variation in the nutritional responses to seasonal drought at the guild level. Whereas all 3 insectivorous guilds exhibited decreases in hematocrit across the El Niño dry season, frugivores did not. Similarly, frugivores maintained lower BUTY levels and higher TRIG levels than the insectivorous guilds across the El Niño dry season, indicative of greater resilience to seasonal drought. Studies in central Panama are generally consistent in reporting that arthropods are less abundant under dry conditions and that fruit availability is more constant throughout the wet and dry seasons (e.g., Poulin and Lefebvre 1996). Thus, frugivores may be less affected by seasonal food scarcity compared to insectivores that

rely on an invertebrate prey base (Levings and Windsor 1985). Nevertheless, unlike the ant followers and ground insectivores, the above-ground insectivores exhibited seasonal declines in BUTY in both years and increases in TRIG throughout the El Niño dry season. This suggests that above-ground insectivores not only tolerated seasonal drought but actually realized improved nutritional state under unusually dry conditions. The complex and variable responses among guilds suggest that, although food scarcity may be mediating population responses to seasonal drought for some species, the ecology of forest birds during seasonal drought merits more research. Our finding that insectivores with contrasting foraging substrates and behaviors can experience a negative, neutral, or positive energy balance during dry conditions motivates a comparison of the foraging efficiency, time budgets, and diet of insectivores during dry and wet seasons.

CONCLUSIONS

Whereas food availability and nutritional condition during the dry season are associated with the population dynamics of some species, our results highlight the variability among species and the need for further studies exploring the linkages between seasonal drought, availability and utilization of food resources, and recruitment and survival of Neotropical birds. The importance of seasonal rainfall regimes as a selective pressure is becoming increasingly recognized, though the factors dictating species' "hygric niches" still remain poorly understood (Boyle et al. 2020). Climate change and ocean warming are projected to increase the frequency and intensity of ENSO events (Cai et al. 2014, 2018) and increase annual variation in tropical rainfall regimes (Karmalkar et al. 2011, Turner and Annamalai 2012) and the intensity of seasonal drought (Feng et al. 2013, Fu et al. 2013, Jiang et al. 2019). Thus, it is urgent to understand the mechanisms (e.g., food availability, physiological tolerances, etc.) connecting rainfall to the demographic responses of resident tropical species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

ACKNOWLEDGMENTS

We thank S. Paton of the Smithsonian Tropical Research Institute Physical Monitoring Program for providing valuable access to the Barro Colorado Island weather record, D. Rincón, S. Brady, and K. Heath for assistance with fieldwork, D. Sambrano and V. Batista for access to INDICASAT for laboratory work, D. Rincón, C. A. Alfonso-Cuta, S. Brown,

and W. Brown for assistance conducting metabolite assays, and T. J. Benson and A. Luro for providing advice for statistical analysis.

Funding statement: The work was supported in part by the U.S. Department of Agriculture National Institute of Food and Agriculture Hatch Project # ILLU-875-956 and the National Science Foundation "Vertically Integrated Training with Genomics" Integrative Graduate Education and Research Traineeship #DGE-1069157.

Ethics statement: Field work in Panama was conducted under Ministerio de Ambiente permit numbers SE/A-88-14, SE/A-116-15, SE/A-78-16, and SE/A-70-17. These methods were approved under University of Illinois at Urbana-Champaign Institutional Animal Care and Use (IACUC) protocol 15234 and Smithsonian Tropical Research Institute IACUC numbers 2013-0101-2016 and 2015-1120-2018.

Author contributions: E.T.N. and J.D.B. conceived the idea and study design, E.T.N. and H.S.P. conducted fieldwork, E.T.N., J.D.B. and H.S.P. wrote the paper, E.T.N. and J.D.B. developed or designed the methods, E.T.N. conducted laboratory analyses and analyzed the data, J.D.B. contributed substantial materials, resources, and funding.

Data availability: Analyses reported in this article can be reproduced using the data provided by Nishikawa et al. (2021).

LITERATURE CITED

- Aranzamendi, N. H., M. L. Hall, S. A. Kingma, M. van de Pol, and A. Peters (2019). Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *The Journal of Animal Ecology* 88:1799–1811.
- Bates, D., M. Maechler, B. Bolker, and S. Walker (2014). lme4: Linear mixed-Effects Models Using Eigen and S4. R Package Version 1:1–23. <https://rdrr.io/cran/lme4/>
- Birkhead, T. R., F. Fletcher, and E. J. Pellatt (1998). Sexual selection in the Zebra Finch *Taeniopygia guttata*: Condition, sex traits and immune capacity. *Behavioral Ecology and Sociobiology* 44:179–191.
- Boyle, W. A., D. R. Norris, and C. G. Guglielmo (2010). Storms drive altitudinal migration in a tropical bird. *Proceedings Biological Sciences* 277:2511–2519.
- Boyle, W. A., E. H. Shogren, and J. D. Brawn (2020). Hygric niches for tropical endotherms. *Trends in Ecology & Evolution* 35:938–952.
- Brawn, J. D., T. J. Benson, M. Stager, N. D. Sly, and C. E. Tarwater (2017). Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change* 7:133–136.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker (2017). Modeling zero-inflated count data with glmmTMB. *BioRxiv* 132753. doi:10.1101/132753
- Bryant, D. M. (1988). Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology* 2:23–34.

- Busch, D. S., W. D. Robinson, T. R. Robinson, and J. C. Wingfield (2011). Influence of proximity to a geographical range limit on the physiology of a tropical bird. *The Journal of Animal Ecology* 80:640–649.
- Cai, W., S. Borlace, M. Lengaigne, P. Van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, and M. H. England (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111–116.
- Cai, W., G. Wang, B. Dewitte, L. Wu, A. Santoso, K. Takahashi, Y. Yang, A. Carréric, and M. J. McPhaden (2018). Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature* 564:201–206.
- Carragher, F. M., J. R. Bonham, and J. M. Smith (2003). Pitfalls in the measurement of some intermediary metabolites. *Annals of Clinical Biochemistry* 40:313–320.
- Cooper, R. J., and R. C. Whitmore (1990). Arthropod sampling methods in ornithology. In *Avian Foraging: Theory, Methodology, and Applications* (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Editors). *Studies in Avian Biology* 13:29–37.
- Cribari-Neto, F., and A. Zeileis (2010). Beta regression in R. *Journal of Statistical Software* 34:1–24.
- Croat, T. B. (1978). *Flora of Barro Colorado Island*. Palo Alto, CA, USA: Stanford University Press.
- Cucco, M., R. Ottonelli, M. Raviola, and G. Malacarne (2002). Variations of body mass and immune function in response to food unpredictability in magpies. *Acta Oecologica* 23:271–276.
- Del Rosario Avalos, V. (2015). Diet composition of nestlings and adults of the threatened Bolivian Swallow-tailed Cotinga *Phibalura flavirostris boliviana* (Aves: Passeriformes: Cotingidae) in Bolivia. *Journal of Threatened Taxa* 7:7649–7654.
- Denlinger, D. L. (1986). Dormancy in tropical insects. *Annual Review of Entomology* 31:239–264.
- Drent, R. H., and S. Daan (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- Duca, C., and M. A. Marini (2011). Variation in breeding of the Shrike-like Tanager in Central Brazil. *The Wilson Journal of Ornithology* 123:259–265.
- Dyrce, A. (1983). Breeding ecology of the Clay-coloured Robin *Turdus grayi* in lowland Panama. *Ibis* 125:287–304.
- Faaborg, J., W. J. Arendt, and M. S. Kaiser (1984). Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: A nine-year study. *The Wilson Bulletin* 96:575–593.
- Fair, J., S. Whitaker, and B. Pearson (2007). Sources of variation in haematocrit in birds. *Ibis* 149:535–552.
- Feng, X., A. Porporato, and I. Rodriguez-Iturbe (2013). Changes in rainfall seasonality in the tropics. *Nature Climate Change* 3:811.
- Ferrari, S., and F. Cribari-Neto (2004). Beta regression for modeling rates and proportions. *Journal of Applied Statistics* 31:799–815.
- Fu, R., L. Yin, W. Li, P. A. Arias, R. E. Dickinson, L. Huang, S. Chakraborty, K. Fernandes, B. Liebmann, R. Fisher, and R. B. Myneni (2013). Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America* 110:18110–18115.
- Glomski, C. A., and A. Pica (2011). *The Avian Erythrocyte: Its Phylogenetic Odyssey*. Boca Raton, FL: CRC Press.
- Grant, P. R., and B. R. Grant (1980). Annual variation in Finch numbers, foraging and food supply on Isla Daphne Major, Galápagos. *Oecologia* 46:55–62.
- Guglielmo, C. G., P. D. O'Hara, and T. D. Williams (2002). Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers (*Calidris mauri*). *The Auk* 119:437–445.
- Hackett, S. J., R. T. Kimball, S. Reddy, R. C. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K. L. Han, J. Harshman, et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* 320:1763–1768.
- Hutto, R. L. (1990). Measuring the availability of food resources. In *Avian Foraging: Theory, Methodology, and Applications* (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Editors). *Studies in Avian Biology* 13:20–28.
- Jenni-Eiermann, S., and L. Jenni (1991). Metabolic responses to flight and fasting in night-migrating passerines. *Journal of Comparative Physiology B* 161:465–474.
- Jenni-Eiermann, S., and L. Jenni (1996). Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. *Functional Ecology* 10:62–72.
- Jenni-Eiermann, S., and L. Jenni (1998). What can plasma metabolites tell us about the metabolism, physiological state, and condition of individual birds? An overview. *Biologia e Conservazione Della Fauna* 102:312–319.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers (2012). The global diversity of birds in space and time. *Nature* 491:444–448.
- Jiang, Y., L. Zhou, C. J. Tucker, A. Raghavendra, W. Hua, Y. Y. Liu, and J. Joiner (2019). Widespread increase of boreal summer dry season length over the Congo rainforest. *Nature Climate Change* 9:617–622.
- Jiménez-Muñoz, J. C., C. Mattar, J. Barichivich, A. Santamaría-Artigas, K. Takahashi, Y. Malhi, J. A. Sobrino, and G. v. Schrier (2016). Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. *Scientific Reports* 6:33130.
- Karmalkar, A. V., R. S. Bradley, and H. F. Diaz (2011). Climate change in Central America and Mexico: regional climate model validation and climate change projections. *Climate Dynamics* 37:605–629.
- Karr, J. R., and J. D. Brawn (1990). Food resources of understory birds in central Panama: quantification and effects on avian populations. In *Avian Foraging: Theory, Methodology, and Applications*. *Studies in Avian Biology*, Vol. 3. (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Editors). pp. 58–64.
- Kern, M., W. Bacon, D. Long, and R. J. Cowie (2005). Blood metabolite and corticosterone levels in breeding adult Pied Flycatchers. *The Condor* 10:665–677.
- Khalilieh, A., M. D. McCue, and B. Pinshow (2012). Physiological responses to food deprivation in the house sparrow, a species not adapted to prolonged fasting. *American Journal of Physiology Regulatory, Integrative and Comparative Physiology* 303:R551–R561.
- Landys, M. M., M. Ramenofsky, C. G. Guglielmo, and J. C. Wingfield (2004). The low-affinity glucocorticoid receptor regulates feeding and lipid breakdown in the migratory Gambel's white-crowned sparrow *Zonotrichia leucophrys gambelii*. *The Journal of Experimental Biology* 207:143–154.

- Leigh, E. G., A. S. Rand, and D. M. Windsor (1985). *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution, Washington, DC, USA
- Lenth, R. (2018). *Emmeans: Estimated Marginal Means, Aka Least-Squares Means*. R Package Version 1.2.4. <https://CRAN.R-project.org/package=emmeans>
- Levings, S. C., and D. M. Windsor (1985). Litter arthropod populations in a tropical deciduous forest: Relationship between years and arthropod groups. *Journal of Animal Ecology* 54:61–69.
- Lyon, B. (2004). The strength of El Niño and the spatial extent of tropical drought. *Geophysical Research Letters* 31:L21204.
- Malhi, Y., and J. Wright (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 359:311–329.
- Mandin, C., and F. Vézina (2012). Daily variation in markers of nutritional condition in wintering Black-capped Chickadees *Poecile atricapillus*. *Ibis* 154:791–802.
- McCue, M. D. (2010). Starvation physiology: Reviewing the different strategies animals use to survive a common challenge. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* 156:1–18.
- Morton, E. S. (1973). On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *The American Naturalist* 107:8–22.
- Nagelkerke, N. J. (1991). A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692.
- Nakagawa, S., and H. Schielzeth (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Nesbitt-Styrsky, J., and J. D. Brawn (2011). Annual fecundity of a Neotropical bird during years of high and low rainfall. *The Condor* 113:194–199.
- Nishikawa, E. T., H. S. Pollock, and J. D. Brawn (2021). Data from: Dry season intensity has equivocal effects on the nutritional condition of understory birds in a Neotropical forest. *Ornithology* 138:1–13. doi: [10.5061/dryad.66t1g1k18](https://doi.org/10.5061/dryad.66t1g1k18)
- Oppel, S., G. M. Hilton, R. Allcorn, C. Fenton, A. J. Matthews, and D. W. Gibbons (2013). The effects of rainfall on different components of seasonal fecundity in a tropical forest passerine. *Ibis* 155:464–475.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Paradis, E., J. Claude, and K. Strimmer (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Paton, S. (2019). *Monthly Summary_BCI*, horizontal. figshare. doi: [10.25573/data.10059455.v4](https://doi.org/10.25573/data.10059455.v4)
- Patten, M. A., and B. D. Smith-Patten (2012). Testing the microclimate hypothesis: Light environment and population trends of Neotropical birds. *Biological Conservation* 155:85–93.
- Peig, J., and A. J. Green (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891.
- Piersma, T., A. Koolhaas, A. Dekinga, and E. Gwinner (2000). Red blood cell and white blood cell counts in sandpipers (*Philomachus pugnax*, *Calidris canutus*): Effects of captivity, season, nutritional status, and frequent bleedings. *Canadian Journal of Zoology* 78:1349–1355.
- Pollock, H. S., Z. A. Cheviron, T. J. Agin, and J. D. Brawn (2015). Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. *Biological Conservation* 188:116–125.
- Poulin, B., and G. Lefebvre (1996). Dietary relationships of migrant and resident birds from a humid forest in Central Panama. *The Auk* 113:277–287.
- Poulin, B., G. Lefebvre, and R. McNeil (1992). Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73:2295–2309.
- R Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Revell, L. J. (2012). *Phytools: An R package for phylogenetic comparative biology (and other things)*. *Methods in Ecology and Evolution* 3:217–223.
- Riehl, C., and G. S. Adelson (2008). Seasonal insectivory by Black-headed Trogons, a tropical dry forest frugivore. *Journal of Field Ornithology* 79:371–380.
- Robinson, W. D., J. D. Brawn, and S. K. Robinson (2000). Forest bird community structure in central Panama: Influence of spatial scale and biogeography. *Ecological Monographs* 70:209–235.
- Silva, J. O., C. R. O. Leal, M. M. Espírito-Santo, and H. C. Morais (2017). Seasonal and diel variations in the activity of canopy insect herbivores differ between deciduous and evergreen plant species in a tropical dry forest. *Journal of Insect Conservation* 21:667–676.
- Tiedink, H. G. M., and M. B. Katan (1989). Variability in lipoprotein concentrations in serum after prolonged storage at -20°C . *Clinica Chimica Acta* 180:147–156.
- Turner, A. G., and H. Annamalai (2012). Climate change and the South Asian summer monsoon. *Nature Climate Change* 2:587–595.
- Van Schaik, C. P., J. Terborgh, and S. J. Wright (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- Visco, D. M., and T. W. Sherry (2015). Increased abundance, but reduced nest predation in the Chestnut-backed Antbird in Costa Rican rainforest fragments: surprising impacts of a pervasive snake species. *Biological Conservation* 188:22–31.
- Wickham, H. (2016) *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, NY, USA
- Wikelski, M., M. Hau, W. D. Douglas Robinson, and J. C. Wingfield (2003). Reproductive seasonality of seven neotropical passerine species. *The Condor* 105:683–695.
- Willis, E. O. and Y. Oniki (1972). Ecology and nesting behavior of the Chestnut-backed Antbird (*Myrmeciza exsul*). *The Condor* 74:87–98.
- Willis, E. O. and Y. Oniki (1978). Birds and army ants. *Annual Review of Ecology and Systematics* 9:243–263.
- Wingfield, J. C., M. Hau, P. D. Boersma, L. M. Romero, N. Hillgarth, M. Ramenofsky, P. Wrege, R. Scheibling, J. P. Kelley, B. Walker, and M. Wikelski (2018). Effects of El Niño and La Niña Southern Oscillation events on the adrenocortical responses to stress in birds of the Galapagos Islands. *General and Comparative Endocrinology* 259:20–33.

- Wolfe, J. D., C. J. Ralph, and P. Elizondo (2015). Changes in the apparent survival of a tropical bird in response to the El Niño Southern Oscillation in mature and young forest in Costa Rica. *Oecologia* 178:715–721.
- Wright, S. J., C. Carrasco, O. Calderon, and S. Paton (1999). The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. *Ecology* 80:1632–1647.
- Wunderle Jr, J. M. (1982). The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on the island of Grenada, WI. *Biotropica* 14:124–131.
- Zajac, R. M., D. J. Cerasale, and C. G. Guglielmo (2006). The rapid response of plasma metabolites to changes in feeding rate in a small passerine Wilson's Warbler *Wilsonia pusilla*. *Journal of Avian Biology* 37:405–408.