

Apparent survival of tropical birds in a wet, premontane forest in Costa Rica

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ABSTRACT. Despite the importance of tropical birds in the development of life history theory, we lack information about demographic rates and drivers of population dynamics for most species. We used a 7-year (2007–2013) capture-mark-recapture dataset from an exceptionally wet premontane forest at mid-elevation in Costa Rica to estimate apparent survival for seven species of tropical passerines. For four of these species, we provide the first published demographic parameters. Recapture probabilities ranged from 0.21 to 0.53, and annual estimates of apparent survival varied from 0.23 to 1.00. We also assessed the consequences of inter-annual variation in rainfall on demographic rates. Our results are consistent with inter-annual rainfall increasing estimates of apparent survival for two species and decreasing estimates for three species. For the three species where we could compare our estimates of apparent survival to estimates from drier regions, our estimates were not consistently higher or lower than those published previously. The temporal and spatial variability in demographic rates we document within and among species highlights the difficulties of generalizing life history characteristics across broad biogeographic gradients. Most importantly, this work emphasizes the context-specific role of precipitation in shaping tropical avian demographic rates and underscores the need for mechanistic studies of environmental drivers of tropical life histories.

RESUMEN. Factores que afectan la supervivencia aparente de aves tropicales en un bosque húmedo premontano

A pesar de la importancia de las aves tropicales en el desarrollo de teorías de historia de vida, aún no entendemos bien los patrones o factores causales en la dinámica de poblaciones para la mayoría de las especies tropicales. Usamos datos de una comunidad de aves paseriformes del sotobosque, marcando y recapturando individuos por siete años (2007–2013) en un bosque premontano altamente pluvial en Costa Rica con el fin de estimar las tasas de supervivencia aparente. Pudimos modelar la supervivencia aparente para siete especies, proporcionando los primeros parámetros demográficos publicados para cuatro de ellas. Las probabilidades de recaptura varían entre 0.21 y 0.53 mientras que las tasas de supervivencia aparente varían entre 0.23 y 1.00. También, evaluamos la relación entre precipitación y tasas demográficas. Se relacionó con la variación interanual en la supervivencia aparente en modelos competitivos de cuatro especies, pero el efecto de la precipitación varió, siendo positivo en dos especies y negativo en tres especies. Más aun, nuestras estimaciones de supervivencia aparente fueron a la misma vez mayores y mucho más bajas que otras estimaciones de poblaciones que experimentan regímenes de precipitación diferentes. La variabilidad en las tasas demográficas entre especies y poblaciones que encontramos demuestra la dificultad de generalizar a través de gradientes biogeográficos. Aún más importante, este trabajo destaca, en un contexto específico, el papel de la precipitación en los cambios de las tasas demográficas en aves tropicales, y destaca la necesidad de conducir estudios mecánicos de los factores ambientales que impulsan las historias naturales en el trópico.

Key words: abiotic effects, capture-mark-recapture, Central America, climate, montane, precipitation

Factors shaping population dynamics of tropical birds remain poorly understood. A prevailing view is that tropical species typically have slow life history strategies where individuals prioritize future reproductive efforts over success in a given year, have lower fecundity, extensive parental care, and high adult survival (Skutch 1967, Ghalambor and Martin 2001, Lloyd and Martin 2016,

Pizzaro Muñoz et al. 2018). However, few demographic data for testing these predictions are available for most tropical taxa (Martin et al. 2011, Martin 2015, Boyle et al. 2016, Boyce and Martin 2017). In particular, estimates of apparent survival of tropical birds vary widely and are often lower than expected (Karr et al. 1990, Sandercock et al. 2000, Blake and Loiselle 2013). However, variation in methods among studies (e.g., use of color band resighting, sampling effort, and estimation

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technique) and age distribution and site fidelity of populations may explain some of the differences among studies (Johnston et al. 1997, Martin et al. 2017). Robust estimates from a wide range of species and sites are needed to predict and understand the selective pressures that lead to biogeographic patterns in the life history traits of birds (Brawn et al. 1995, Pizzaro Muñoz et al. 2018).

Understanding the basis for taxonomic and spatial variation in survival is crucial not only from the perspective of testing fundamental questions in life history theory, but also to better understand the implications of global climate change for tropical animals. A long-standing paradigm for patterns of diversity in tropical bird communities emphasizes the importance of biotic interactions and downplays any potential role for direct abiotic sources of selection (Loiselle and Blake 1992, Stutchbury and Morton 2001). Unlike temperate ecosystems, periods of severe cold are unlikely to be a driver of variation in life history traits of tropical species (Martin and Wiebe 2004). However, precipitation creates seasonality in tropical regions, and both the amount and magnitude of seasonal variation in rainfall impose dramatic constraints on plant productivity and consumer responses (van Schaik et al. 1993, Prada et al. 2017). Variation in rainfall can have indirect effects on tropical animals via either reduced food availability (Wright et al. 1999) or access to food via foraging constraints (Boyle et al. 2010). Inter-annual variation in precipitation is recognized as an important driver of population dynamics of some tropical bird species, but the strength and direction of rainfall effects on demographic performance vary widely. For example, recruitment and population growth rates decreased during severe and extended dry seasons in Panama (Brawn et al. 2017), whereas reduced recruitment and apparent survival were associated with wetter years in Costa Rica and Ecuador (Wolfe et al. 2015, Ryder and Sillett 2016). In addition, precipitation can interact with phenotype, yielding different effects on behavior and demography depending on the environmental context and condition of individuals. For example, dispersal by Green-rumped Parrotlets (*Forpus passerinus*) both increased and decreased in years of higher rainfall, depending on natal environment and phenotype

(Tarwater and Beissinger 2012, 2013). Most tropical research efforts are not primarily designed to collect long-term data on survival and, except in a few systems (e.g., Wolfe et al. 2017), we currently lack sufficient data to predict how changes in rainfall may influence tropical avian populations or determine the degree to which shifts in demography mediated by abiotic conditions are caused by indirect drivers (e.g., food availability and foraging success) versus direct factors (e.g., mortality).

A mechanistic, bottom-up perspective predicts positive associations between above-average rainfall and demographic rates in drier and more seasonal environments where primary productivity is constrained by soil moisture (Meir and Woodward 2010). Conversely, negative relationships between demographic performance and rain might be predicted for wetter regions where solar energy is limiting (Esquivel-Hernández et al. 2017). Some evidence suggests that, in wet environments, tropical birds can experience direct negative consequences of heavy rain. For example, storm events are physiological stressors that induce short-term fasting and increase corticosterone levels in White-ruffed Manakins (*Corapipo altera*; Boyle et al. 2010). Birds also respond behaviorally to severe wet-season weather in montane regions by moving to lower elevations during the non-breeding season to escape the heaviest storms (Boyle et al. 2010, Boyle 2011). These results suggest that years with especially high rainfall could impose direct survival costs in wet environments. However, this prediction has not yet been tested. Insight into the nature and magnitude of such costs is important given that tropical rain events are projected to increase in intensity and frequency (Aguilar et al. 2005), and we need a better understanding of how climate change could affect survival of tropical birds.

Relatively few demographic estimates exist for birds in tropical communities. Low population densities of many tropical forest-dwelling bird species make recapturing large numbers of marked birds difficult (Ruiz-Gutiérrez et al. 2012). Additionally, maintaining the long time series and substantial effort necessary to gather adequate data for demographic studies of tropical vertebrates is logistically challenging, and relatively few

banding stations are located in the Neotropics (Karr et al. 1990, Sandercock et al. 2000, Parker et al. 2006). We collected mark-recapture data for forest-dwelling passerine birds over 7 breeding seasons in a mid-elevation primary forest on the Caribbean slope of Costa Rica subject to exceptionally wet conditions (i.e., pluvial forest; Holdridge 1967). We estimated apparent survival for as many species as our dataset allowed, then used our estimates to test relationships between annual survival and precipitation in a high-rainfall environment. We predicted that birds would experience reduced apparent survival in years of especially heavy rain. Rain could act directly by either increasing mortality due to exposure and short-term fasting during storms or by increasing permanent emigration from the site. If rain exerts direct negative effects, estimates of apparent survival should be lower in years with more precipitation across all species.

METHODS

We captured birds at a single elevation in primary forest owned by Rara Avis Rainforest Lodge and Selvatica Rainforestry (10°17'3"N, 84°02'47"W). Rara Avis and Selvatica are adjacent private reserves on the Caribbean slope of north-central Costa Rica, spanning elevations from 500 to 900 m, and are contiguous with nearly 50,000 ha of primary forest in Parque Nacional Braulio Carrillo. Daily rainfall was collected on site using a manual rain gauge from 1990 through the study period, and our study site averaged ~ 8300 mm of rain per year (Boyle 2010). Mean monthly precipitation ranged from 514 to 839 mm, and mean monthly temperatures vary negligibly during the year at this latitude (Boyle and Sigel 2015). Bird communities at low and middle elevations along this elevational gradient are some of the most diverse in Costa Rica (Blake and Loiselle 2000).

Each year from 2007 to 2013, we captured birds at 16 fixed-net locations in an 11.5-ha plot using 12-m mist-nets with 38-mm mesh (Ecotone, Gdynia, Poland). We opened nets from 06:00 to 13:00 for 4–6 d in a single week every month for a 2- to 5-mo period spanning the dry season and early wet season (February–July, a period corresponding to peak breeding season of most species). We

uniquely marked birds using numbered aluminum leg bands, and aged and sexed individuals by plumage coloration, molt patterns, and the presence of cloacal protuberances in males and brood patches in females (Bailey 1952, Wolfson 1952).

We constructed encounter histories for banded birds where 1 = captured and 0 = not captured in a given year; the interval between capture occasions was 1 yr. We did not assess within-year recaptures and included only one capture record per year when an individual was captured multiple times in a single year. For each capture history, we included covariates that varied annually, including precipitation in the preceding biological year (March–February) and year-specific capture effort measured in mist-net hours (one 12-m mist-net open for 1 h = 1 mist-net hour). We estimated apparent survival (ϕ) and recapture probability (p) for the seven species in our database with sufficient data for models to converge, fitting Cormack-Jolly-Seber (CJS) models for live-encounter data (Lebreton et al. 1992). Analyses were conducted in Program MARK (White and Burnham 1999) and using the R package RMark (Laake 2013; R Core Team 2018) as an interface to Program MARK. Apparent survival (ϕ) is the product of true survival and site fidelity (the probability an individual remains in the study area), whereas the probability of recapture (p) is the product of site propensity (the probability an individual does not temporarily leave the study area) and true detection (Sandercock 2006).

We constructed a set of seven candidate models to test relationships between apparent survival, recapture probability, and the z -score of annual covariates (precipitation and mist-net hours) for each species (Table 1). For all but one species, our datasets were too sparse to test for age or sex effects on apparent survival. Given the focus of our study, we opted to evaluate the influence of rain on estimates of apparent survival and did not include age or sex covariates for any species. We first considered a model where apparent survival and recapture probability were constant across all years, i.e., $\phi(\cdot) p(\cdot)$. We tested for a relationship between apparent survival and annual precipitation (precip) using z -transformed rainfall values from the preceding biological year, i.e., $\phi(\text{precip}) p(\cdot)$. We also assessed

models that accounted for variation in recapture probability due to differences in annual capture effort, i.e., $\phi(\cdot) p(\text{effort})$, measured as the z -transformed total number of mist-net hours (mnh) per season. Thus, precipitation and effort varied by year and were associated with each individual capture history. We did not assess models where precipitation influenced detection probability during the breeding season because (a) breeding is seasonal in our study area and occurred during the months we sampled, and (b) downhill altitudinal migration at our study site occurred after our sampling was concluded each year (Boyle 2008). In addition, we evaluated models including an effect of time-since-marking on apparent survival and constant recapture probability, i.e., $\phi(\text{tsm}) p(\cdot)$. The time-since-marking model separately estimates apparent survival for individuals following first capture (ϕ^1 ; potential transients or young individuals) and following subsequent capture (ϕ^{2+} ; individuals inferred to be residents; Pradel et al. 1997, Parker et al. 2006) because estimates of apparent survival can be negatively biased by inclusion of transient individuals and the characteristically low survival rates of young birds (Sandercock 2006). We considered models with annual covariates for both apparent survival and recapture probability, i.e., $\phi(\text{tsm}) p(\text{effort})$, $\phi(\text{precip}) p(\text{effort})$. Last, we included a model assessing an effect of time on estimates of apparent survival while holding recapture probability constant, i.e., $\phi(\text{time}) p(\cdot)$. We were unable to evaluate a fully time-dependent model ($\phi(\text{time}) p(\text{time})$) due to sparse capture histories and failure of models to converge. Table 1 contains the full set of models evaluated for each species.

We used the analysis of deviance (ANODEV) procedure in Program MARK to estimate the percentage of annual variation in apparent survival that is explained by precipitation (White and Burnham 1999). We ran the ANODEV procedure using the following models: $\phi(\text{precip}) p(\cdot)$, $\phi(\text{time}) p(\cdot)$, and $\phi(\cdot) p(\cdot)$. To adjust for possible overdispersion of the data and test goodness of fit, we estimated the overdispersion parameter \hat{c} by applying the median \hat{c} procedure in Program MARK to the global model, $\phi(\text{time}) p(\cdot)$ (White and Burnham 1999). For four species, the median \hat{c} procedure could not perform logistic regression with the $\phi(\text{time}) p(\cdot)$ model. We then

Table 1. List of all candidate models evaluated for each species, including combinations of parameters and annual covariates assessed to explain variation in apparent survival (ϕ) and recapture probability (p).

Candidate models	Apparent survival (ϕ)	Recapture probability (p)
$\phi(\cdot) p(\cdot)$	Constant	Constant
$\phi(\text{precip}) p(\cdot)$	Precipitation	Constant
$\phi(\cdot) p(\text{effort})$	Constant	Effort (mist-net hours)
$\phi(\text{tsm}) p(\cdot)$	Time-since-marking	Constant
$\phi(\text{tsm}) p(\text{effort})$	Time-since-marking	Effort (mist-net hours)
$\phi(\text{precip}) p(\text{effort})$	Precipitation	Effort (mist-net hours)
$\phi(\text{time}) p(\cdot)$	Time	Constant

performed additional goodness-of-fit tests in Program MARK (Bootstrap Goodness Of Fit, Program Release) to determine an appropriate correction for overdispersion. For two species, we were unable to calculate \hat{c} using the $\phi(\text{time}) p(\cdot)$ model and, therefore, used the overdispersion parameter \hat{c} calculated by the median \hat{c} procedure run on the less complex model $\phi(\text{tsm}) p(\cdot)$. We then ranked models using Akaike weights (w_i) and either Akaike's Information Criteria (AICc) or the Quasi-Akaike's Information Criteria (QAICc) corrected using the appropriate \hat{c} for each species.

RESULTS

Over our 7-year study, capture effort ranged from 286 to 1598 mist-net hours per year (mean = 970 ± 497 [SD] mnh/yr; Fig. S1). We recorded annual precipitation for the biological year preceding each sampling event (i.e., March–February), which ranged from 6990 to 8981 mm/yr (mean = 8130 ± 888 [SD] mm/yr; Fig. S2). We recorded a total of 2187 captures of 1674 individuals representing 79 species. Despite our extensive sampling effort, the median number of individuals captured per species was only five (range = 1–253). Across all years of sampling, the median number of recaptured individuals for each species was one (range = 0–85).

We were able to estimate apparent survival for seven species with a sufficient number of captures and recaptures for model convergence, including Wedge-billed Woodcreepers (*Glyphorhynchus spirurus*, Furnariidae), White-ruffed Manakins (*Corapipo altera*, Pipridae), White-breasted Wood-Wrens (*Henicorbhina leucosticta*, Troglodytidae), Tawny-crested Tanagers (*Tachyphonus delatrii*, Thraupidae), Orange-billed Sparrows (*Arremon aurantirostris*, Passerellidae), Carmiol's Tanagers (*Chlorothraupis carmioli*, Cardinalidae), and Tawny-capped Euphonias (*Euphonia annae*, Fringillidae). All seven species are small-bodied passerines (< 40 g) that inhabit low and mid-levels of forested regions. The manakin and euphonia are primarily frugivorous, whereas the tanagers and sparrow are omnivorous and consume substantial quantities of arthropod prey along with fruit. The wren and woodcreeper are insectivorous and forage exclusively on arthropods. Table S1 contains a complete summary of the model selection.

Estimates of \hat{c} for all species were < 3, indicating slight overdispersion of data in capture histories that was addressed by use of QAICc where appropriate. For four species (White-breasted Wood-Wrens, Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers), a model with constant probabilities of apparent survival and recapture was the best fit to the capture histories ($\phi(\cdot) p(\cdot)$; Table 2). For White-ruffed Manakins, time-since-marking influenced estimates of apparent survival for the top-ranked model, and an effect of time-since-marking was the second-ranked model within 2 AICc units for Orange-billed Sparrows. For both species, individuals had greater apparent survival following their second capture than following their initial capture (Table 3).

For Wedge-billed Woodcreepers and Tawny-capped Euphonias, the top-ranked model indicated that annual variation in precipitation affected estimates of apparent survival (Table 2). Additionally, the ANODEV results for both of these species were significant ($P < 0.05$) and estimated that 84% and 74% of annual variation in apparent survival of Wedge-billed Woodcreepers and Tawny-capped Euphonias, respectively, were explained by precipitation (Table 3). However, the nature of the relationship between precipitation and estimates of apparent survival seemed to vary, and

the small sample sizes and large confidence intervals limit the strength of our inference. We found a negative effect of increased precipitation for Wedge-billed Woodcreepers ($\beta = -8.67$, 95% CI = -20.81 – 3.46) and a slightly positive effect for Tawny-capped Euphonias ($\beta = 0.70$, 95% CI = -0.15 – 1.55 ; Tables 2 and 3). For an additional three species (Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers), a model including an effect of precipitation was ranked similar to the top model (≤ 2 (Q)AICc of the top model; Table 2). Orange-billed Sparrows and Carmiol's Tanagers show negative effects of precipitation on estimates of apparent survival, whereas Tawny-crested Tanagers showed a positive effect of additional rainfall (Table 2). For all three of these species, the ANODEV results indicated that precipitation accounted for > 50% of annual variation in estimates of apparent survival, but only Carmiol's Tanagers had a significant P value (Table 3).

We also summed the weights of models including rainfall effects for each species (Supplementary Information, Table S1). Although summed Akaike weights ought to be interpreted with caution (Galipaud et al. 2014, 2017), precipitation models accounted for > 0.25 of total model weight for four of our seven species (Wedge-billed Woodcreepers, Tawny-crested Tanagers, Carmiol's Tanagers, and Tawny-capped Euphonias).

DISCUSSION

Using data collected during an intensive field effort spanning 7 yr, we calculated demographic estimates for seven species of tropical birds, providing some of the first demographic data for four of those species. Across all seven species, annual recapture probabilities were low, as is often the case for systematic mist-netting efforts without additional resighting effort (Martin et al. 2017). For White-ruffed Manakins, estimates of apparent survival were lower following initial capture than after subsequent recapture in the top-ranked model. For species where precipitation was the strongest predictor of apparent survival, Wedge-billed Woodcreepers had widely varying estimates, perhaps driven by sparse capture histories, whereas demographic estimates for Tawny-capped Euphonias had not been published previously. For the remaining four species, estimates of apparent

Table 2. Model selection and parameter estimates for Cormack-Jolly-Seber models for seven Neotropical bird species captured in wet, premontane forest in Costa Rica, 2007–2013.

Species	C/R ^a	c ^b	Model ^c	$\Delta(Q)AICc^d$	w_i^e	p (95% CI) ^f	ϕ (95% CI) ^g	ϕ_1 (95% CI) ^h	ϕ_{2+} (95% CI) ⁱ	p β (95% CI) ^j	ϕ β (95% CI) ^k
Wedge-billed Woodcreeper	32/13	1.0	$\phi(\text{precip}) p(\cdot)$ $\phi(\cdot) p(\cdot)$ $\phi(\text{precip})$ $p(\text{effort})$	0.0 0.7 1.5 0	0.37 0.25 0.17 0.45	0.21 (0.11–0.37) 0.23 (0.09–0.46) 0.13–0.36 0.45 (0.33–0.58)	0.23–1.00 0.76 (0.42–0.93) 0.21–1.00 0.53 (0.44–0.62)				–8.67 (–20.81–3.46) –10.83 (–27.82–6.17)
White-ruffed Manakin	253/85	1.25	$\phi(\text{tsm}) p(\cdot)$ $\phi(\cdot) p(\cdot)$	0 1.9	0.17 0.53	0.37 (0.27–0.48) 0.27 (0.08–0.61)	0.53 (0.44–0.62) 0.71 (0.34–0.92)	0.39 (0.28–0.51)	0.62 (0.50–0.72)		
White-breasted Wood-Wren	15/6	1.06	$\phi(\cdot) p(\cdot)$	0	0.53	0.27 (0.08–0.61)	0.71 (0.34–0.92)				
Tawny-crested Tanager	35/14	2.63	$\phi(\cdot) p(\cdot)$ $\phi(\text{precip}) p(\cdot)$	0 1.3	0.40 0.21	0.49 (0.21–0.79) 0.56 (0.25–0.83)	0.50 (0.28–0.71) 0.28–0.63				0.68 (–0.13–1.48)
Orange-billed Sparrow	20/9	1.0	$\phi(\cdot) p(\cdot)$ $\phi(\text{tsm}) p(\cdot)$ $\phi(\cdot) p(\text{effort})$	0 1 1.3	0.34 0.21 0.18	0.53 (0.18–0.85) 0.66 (0.26–0.91) 0.30–0.92	0.56 (0.28–0.80) 0.55 (0.28–0.80)	0.37 (0.15–0.66)	0.76 (0.28–0.96)	–1.36 (–4.23–1.51)	
Carniol's Tanager	34/15	1.0	$\phi(\text{precip}) p(\cdot)$ $\phi(\cdot) p(\cdot)$ $\phi(\text{precip}) p(\cdot)$ $\phi(\cdot) p(\text{effort})$ $\phi(\text{precip})$ $p(\text{effort})$	0 1.3 1.3 1.3	0.29 0.23 0.15 0.15	0.23 (0.10–0.43) 0.23 (0.11–0.41) 0.13–0.30 0.11–0.34	0.78 (0.48–0.93) 0.49–1.00 0.77 (0.48–0.93)			0.42 (–0.44–1.28) 0.58 (–0.39–1.56)	–0.48 (–1.61–1.71) –2.80 (–14.34–8.74) –2.94 (–11.32–5.44)
Tawny-capped Euphonia	44/16	1.0	$\phi(\text{tsm}) p(\cdot)$ $\phi(\text{precip}) p(\cdot)$ $\phi(\cdot) p(\cdot)$	1.6 0 0.4	0.13 0.34 0.28	0.28 (0.11–0.53) 0.38 (0.17–0.64) 0.36 (0.16–0.61)	0.32–0.69 0.56 (0.34–0.75)	0.58 (0.20–0.80)	0.85 (0.40–0.98)		0.70 (–0.15–1.55)

^aC/R = numbers of individuals captured and recaptured for entire species including all years.

^bc^h = value calculated by median c-hat procedure and used to correct for overdispersion with QAICc model selection where > 1.

^cModel = models within 2 AICc or QAICc units.

^d $\Delta(Q)AICc$ = difference in QAICc units or AICc units (where appropriate) from top model.

^e w_i = model weights.

^f p (95% CI) = probability of recapture and 95% confidence interval, or range of probabilities for models that vary by year.

^g ϕ (95% CI) = estimate of apparent survival and 95% confidence interval, or range of estimates for models that vary by year.

^h ϕ_1 (95% CI) = estimate of apparent survival and 95% confidence interval in interval following first capture.

ⁱ ϕ_{2+} (95% CI) = estimate of apparent survival for intervals following recapture and 95% confidence interval for time-since-marking models.

^j p β (95% CI) = beta estimates for recapture probability that varies and 95% confidence interval for models that include an effect of effort.

^k ϕ β (95% CI) = beta estimates and 95% confidence interval for the effect of inter-annual variation in rainfall on apparent survival.

Table 3. Results of ANODEV procedure assessing what percent of annual variation in apparent survival can be explained by precipitation, using $\phi(\cdot)$ $p(\cdot)$, $\phi(\text{time})$ $p(\cdot)$, and $\phi(\text{precip})$ $p(\cdot)$ models. The nature of the relationship with precipitation from the $\phi(\text{precip})$ $p(\cdot)$ model (where competitive) and the significance of the ANODEV procedure are also shown.

Species	Total covariate ^a	Corrected total ^b	Percent variation from precipitation ^c	ϕ β (95% CI) ^d	<i>P</i> value ^e
Wedge-billed Woodcreeper	3.080	3.675	84	-8.67 (-20.81-3.46)	0.01
White-ruffed Manakin	0.024	9.288	0.26	—	0.92
White-breasted Wood-Wren	0.362	2.095	17	—	0.41
Tawny-crested Tanager	2.697	4.537	59	0.68 (-0.13-1.48)	0.07
Orange-billed Sparrow	0.691	1.363	51	-0.48 (-1.61-1.71)	0.11
Carmioli's Tanager	1.886	1.976	95	-2.80 (-14.34-8.74)	< 0.01
Tawny-capped Euphonia	3.049	4.140	74	0.70 (-0.15-1.55)	0.02

^aTotal covariate = the difference between deviance of $\phi(\cdot)$ and deviance of $\phi(\text{precip})$.

^bCorrected total = the difference between deviance of $\phi(\cdot)$ and deviance of $\phi(\text{time})$.

^cPercent variation from precipitation = the percent of annual variation explained by precipitation, calculated by dividing the total covariate by the corrected total and multiplying by 100.

^d ϕ β (95% CI) = the beta estimate and 95% confidence interval from the $\phi(\text{precip})$ $p(\cdot)$ models that were competitive with top models in estimating apparent survival.

^e*P* value = the significance of the ANODEV procedure result.

survival were constant across years in the top-ranked model. To our knowledge, estimates of apparent survival for three of these species, including Tawny-crested Tanagers, Orange-billed Sparrows, and Carmiol's Tanagers, had not been published previously. Although our results must be interpreted with caution due to the large confidence intervals surrounding these estimates, they provide difficult-to-obtain demographic data from an understudied avifauna and habitat type.

Quantitative comparison of demographic estimates is beyond the scope of this study, but where possible, we compared our results to published point estimates calculated using similar models and age classes. Although differences in estimated apparent survival among populations may be due in part either to site differences in field methods or the size of experimental plots, such comparisons provide an opportunity to assess what is known about species across geographic scales and under different environmental conditions. Our estimates of apparent survival were not

consistently lower than those of other studies conducted at sites with less rain. Our estimate of apparent survival for Wedge-billed Woodcreepers from the constant model ($\phi = 0.76$, 95% CI = 0.42-0.93) was at least 14% higher than estimates published from three other study sites in the Neotropics ($\phi = 0.36 \pm 0.06$ [SE], Jullien and Clobert 2000; $\phi = 0.41 \pm 0.03$ [SE], $\phi^{2+} = 0.62 \pm 0.02$ [SE], Blake and Loiselle 2013; $\phi = 0.56 \pm 0.12$ [SE], Wolfe et al. 2014). Conversely, our estimate of apparent survival for White-breasted Wood-Wrens ($\phi = 0.71$, 95% CI = 0.34-0.92) was 9% lower than an estimate from Ecuador ($\phi = 0.80 \pm 0.06$ [SE], Blake and Loiselle 2013). Our estimates of apparent survival for White-ruffed Manakins ($\phi^1 = 0.39$, 95% CI = 0.28-0.51, $\phi^{2+} = 0.62$, 95% CI = 0.50-0.72) were similar to those from a lower-elevation site along the same forested gradient as our study site ($\phi^1 = 0.37 \pm 0.25$ [SE], $\phi^{2+} = 0.59 \pm 0.18$ [SE], Blake and Loiselle 2002). However, these two estimates of apparent survival for

White-ruffed Manakins were dramatically lower than those reported from the drier Pacific Slope of Costa Rica in a population that does not migrate altitudinally ($\phi = 0.97 \pm 0.15$ [SE], Ruiz-Gutiérrez et al. 2008). Previous work in our population of manakins demonstrated that heavy rainfall causes short-term fasting and energetic stress, driving down-hill altitudinal migration during the non-breeding season (Boyle et al. 2010). Thus, although we found no evidence of inter-annual variation in precipitation influencing apparent survival for this species, variation in rainfall may affect behavior that mitigates survival costs and affect spatial variation in demography among populations.

The results of a growing body of studies suggest that abiotic factors play a greater role in shaping tropical population dynamics than previously appreciated (Whitfield et al. 2007, Wolfe et al. 2015, Ryder and Sillett 2016, Brawn et al. 2017). Our data were collected during a study designed to answer questions about the evolutionary ecology and behavior of a subset of the avifauna rather than a long-term research effort designed to generate survival data. However, we believe that our results can provide a starting point for future work and aid in developing novel hypotheses because it is integrated with other data, e.g., diet, behavior, and reproduction. Despite the sparseness of our dataset and low statistical power to detect the effects of covariates, in five of seven species, models that included rainfall were competitive with top models. Apparent survival was lower in wetter years for three of those species, including the insectivorous Wedge-billed Woodcreepers and omnivorous Orange-billed Sparrows and Carmiol's Tanagers. Conversely, apparent survival was higher in wetter years for Tawny-crested Tanagers, frugivores that vary their diet with a large proportion of arthropod prey, and highly frugivorous Tawny-capped Euphonias.

The differential response of multiple species at a single site to inter-annual variation in precipitation is intriguing, especially given both positive (Wolfe et al. 2015, Brawn et al. 2017) and negative (Ryder and Sillett 2016) demographic responses of birds during wet years in recent studies. However, our small sample sizes and wide confidence intervals make it difficult to draw conclusions.

Additional data would also have permitted us to assess more complex models. In particular, fitting a model that considers the effect of precipitation on the apparent survival of individuals following their second capture would have been especially informative because transients likely limit our ability to discern effects of precipitation on apparent survival. Nevertheless, the ANODEV procedure revealed a strong effect of precipitation that, despite our small sample size, suggests precipitation may be an important driver of tropical bird demography and should be explicitly considered in future studies.

Annual total precipitation is just one way to assess the effect of abiotic conditions on tropical birds. Other metrics can be biologically relevant and influence demography more strongly. For example, Wolfe et al. (2015) and Ryder and Sillett (2016) found that demographic rates were more strongly associated with the El Niño Southern Oscillation (ENSO) than to local variation in precipitation, suggesting that birds may respond more strongly to integrated or interactive consequences of climatic variation (e.g., including the timing and magnitude of rainfall events in combination with temperature) than to total rainfall amounts. Our sampling period of 7 yr spanned strong, moderate, and weak La Niña years and a moderate El Niño year. Thus, in preliminary analyses, we explored the potential influence of global climatic indices by replacing locally-measured annual variation in rainfall in our models with the ENSO index, but these models did not outperform the results we present here. Other metrics of rainfall, such as the duration of wet or dry seasons, number of extreme storm events, or variability in daily precipitation, may be equally or more important to birds as they breed, migrate, and forage (Boyle et al. 2010). However, making informed choices regarding which of these variables might be most appropriate requires a mechanistic understanding of how precipitation affects fitness, information currently lacking for most species of birds. We encourage investigators in future studies to develop this mechanistic understanding and evaluate associations between demographic rates and different precipitation metrics to help elucidate the direct and indirect links between rainfall and population dynamics in tropical regions.

We know little about what might explain species-level differences in responses to the same environmental conditions in the same community. Inter-annual variation in rainfall does seem to play a role in the survival and life history of a growing number of tropical bird species. This raises the question of how relationships with environmental covariates could affect population dynamics in the context of future changes to rainfall patterns in the Neotropics. Previous studies have demonstrated the complex selective effects that variation in rainfall can have on behavior and fitness (Boyle et al. 2010, Tarwater and Beissinger 2013, Ryder and Sillett 2016). Understanding the role that precipitation plays in the evolution of tropical species is critical because predictions for the Neotropics are complex. These involve locale-specific increases and decreases in mean annual precipitation and the intensity of rainfall events in many regions is predicted to increase and the temporal distribution of those storms is expected to change (Aguilar et al. 2005, Giorgi 2006, Whitfield et al. 2007). Thus, determining the role of environmental drivers of population dynamics will help identify conservation priorities as well as the evolutionary pressures shaping tropical avian life history. Our study helps elucidate fundamental life history characteristics of tropical birds and highlights both the temporal variability in demographic rates and the species-specific responses to environmental variability even within a single community. Improving our knowledge of demography across tropical environmental gradients is important to understanding the proximate and ultimate causes of variation in life histories within and across species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Cormack-Jolly-Seber model selection results for seven Neotropical bird species in Costa Rica.

Fig. S1. Variation in sampling effort across years measured in number of hours a 12-m mist-net was open during the sampling event.

Fig. S2. Variation in precipitation measured in millimeters during the biological year preceding sampling event (e.g., March 2007–February 2008).