

## Research



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# Hot temperatures during the dry season reduce survival of a resident tropical bird

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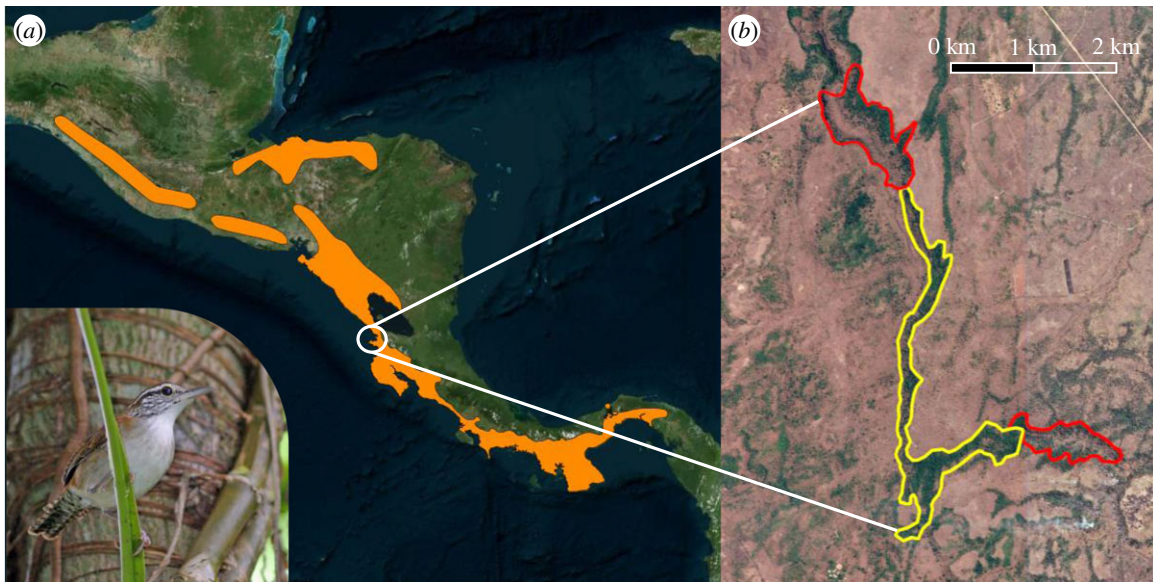
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Understanding how climate change will shape species distributions in the future requires a functional understanding of the demographic responses of animals to their environment. For birds, most of our knowledge of how climate influences population vital rates stems from research in temperate environments; even though most of the Earth's avian diversity is concentrated in the tropics. We evaluated effects of Southern Oscillation Index (SOI) and local temperature and rainfall at multiple temporal scales on sex-specific survival of a resident tropical bird, the Rufous-and-White Wren *Thryophilus rufalbus*, studied over 15 years in the dry forests of northwestern Costa Rica. We found that annual apparent survival of males was 8% higher than females, more variable over time, and responded more strongly to environmental variation than female survival, which did not vary strongly with SOI or local weather. For males, mean and maximum local temperatures were better predictors of survival than either rainfall or SOI, with high temperatures during the dry season and early wet season negatively influencing survival. These results suggest that, even for species adapted to hot environments, further temperature increases may threaten the persistence of local populations in the absence of distributional shifts.

## 1. Introduction

Knowledge of how climate influences survival and fecundity is necessary for understanding the factors that limit species abundance and shape their distributions. The ubiquity, diversity and wide-ranging life-histories and movement strategies of birds have made them model organisms for studies of the consequences of climate change for migration [1], population dynamics [2–4] and species distributions [5,6]. However, the overwhelming majority of these studies have focused on migratory species or residents of temperate environments. Considering that avian diversity is higher in the tropics than anywhere else on the Earth and that many tropical species are range-restricted [7,8], establishing a better understanding of how climate influences demography of tropical bird populations is essential for predicting consequences of future climate change for the persistence of local populations and species as a whole.

To date, the few long-term, longitudinal studies aimed at elucidating the effects of climate on demography of tropical bird species have revealed widely varying population-level responses to environmental variation both within and among species depending on habitat and species traits, such as diet and geography [9–14]. For example, adult White-collared Manakins *Manacus candei* in Costa Rica exhibited higher annual survival during cooler and wetter (positive) phases of the Southern Oscillation Index (SOI), but this effect was only apparent in young forests and not mature forest [10]. By contrast, adult male Wire-tailed Manakins *Pipra filicauda* in Ecuador exhibited higher annual survival during warmer and drier (negative) phases of SOI [12]. Two bird species in the Northern Mariana Islands showed a positive relationship between survival and relative dry-season greenness and a negative relationship between survival and relative wet-season greenness, suggesting that consistent moderate conditions favour



**Figure 1.** Distribution of Rufous-and-white Wrens in Central America and location of the study site. (a) Appearance and year-round distribution (orange) of Rufous-and-white Wrens in Central America, which also includes parts of Colombia and Venezuela not shown here (species distribution data from [19]). (b) The study site in Sector Santa Rosa of the Area de Conservación Guanacaste in northwestern Costa Rica ( $10^{\circ}52'N$ ,  $85^{\circ}36'W$ ). The study site encompassed an area of 125 ha from 2003 to 2005 (yellow) which was expanded by approximately 115 ha (red) in 2006. The background satellite image in (b) was taken at the end of the dry season in May 2013, highlighting the limited availability and patchiness of evergreen forest in comparison to seasonal scrub forest. Photo in (a) courtesy of David Bradley.

survival and that extreme rainfall events negatively affect survival [13]. Whereas these results revealed relationships between climate and survival, albeit in sometimes opposite directions, only one of 20 bird species analysed in Panama revealed a relationship between climate (length of the dry season) and adult survival [11]. Coupled with growing evidence of declines in tropical bird populations [15,16], the observed variation in results of these studies highlights the need for a clearer understanding of how the demography of tropical bird populations responds to climatic variation at different spatio-temporal scales.

Here, we evaluated the effects of climate (SOI) and local weather (temperature and rainfall) at annual, seasonal and monthly time scales on sex-specific annual apparent adult survival of a resident tropical bird, the Rufous-and-White Wren *Thryophilus rufalbus*. We collected 15 years of mark-recapture/re-sighting data from a population living in tropical dry forests in the Area de Conservación Guanacaste in northwestern Costa Rica. Tropical dry forests rank among the most imperilled terrestrial habitats globally and climate change threatens the persistence these forests [17] as well as some of the species that inhabit them [18]. Whereas most studies that have examined survival of tropical birds have generally only considered broad-scale climate indices, we also evaluated effects of local rainfall and temperature on survival and how rainfall influences vegetation greenness, a proxy for resource availability, to provide greater insight into the mechanisms mediating effects of climatic variation on survival.

## 2. Material and methods

### (a) Study species

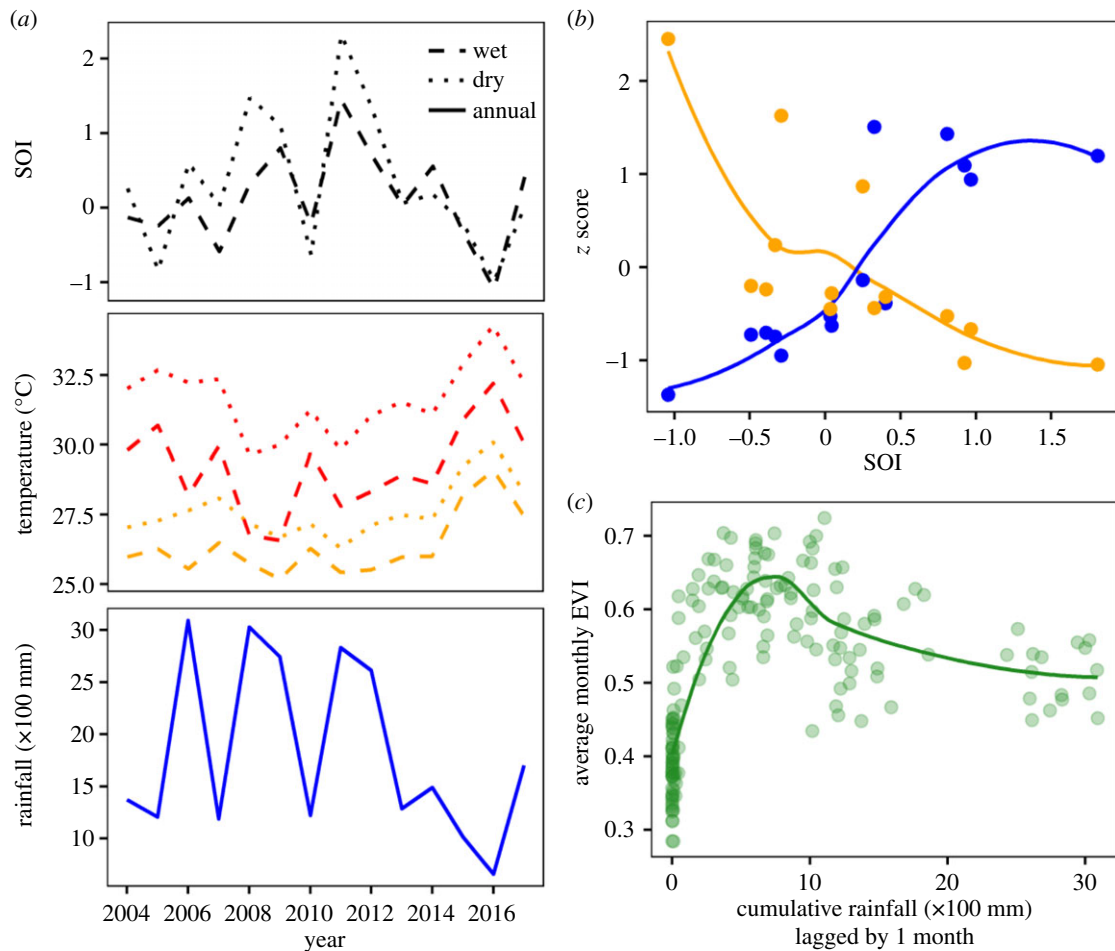
Rufous-and-white Wrens are resident, insectivorous Neotropical songbirds that inhabit the understory of tropical forests along the Pacific coast of southern Mexico to Panama (figure 1a) as well as parts of northern Colombia and Venezuela [19,20]. Annually, Rufous-and-white Wrens build nests several weeks in advance of

the rainy season and begin laying and incubating eggs following the first large rainfall, typically in early May in our study area. Owing to high levels of nest predation (greater than or equal to 50% of nests are depredated each year [21,22]), pairs will often attempt several nests per year, often continuing into August [23]. Rufous-and-white Wrens, like other understory insectivores, exhibit low levels of breeding dispersal [24]. Low mobility makes this species well-suited to demographic studies because measured (apparent) survival should closely approximate actual survival and because, with low levels of movement among populations (immigration and emigration) [24], survival and recruitment will be primary contributors to populations dynamics and persistence. Low mobility also makes insectivorous birds highly vulnerable to habitat disturbance and fragmentation [25,26], further emphasizing the need for expanded knowledge of environment–demography relationships for this and other tropical species.

### (i) Study site and field methods

Our study took place in Sector Santa Rosa of the Area de Conservación Guanacaste in northwestern Costa Rica ( $10^{\circ}52'N$ ,  $85^{\circ}36'W$ ; figure 1b). Habitat in Santa Rosa is characterized by a lowland tropical dry forest (elevation range = 225–290-m.a.s.l.) with a relatively open understory, especially during the dry season [27,28]. Within the dry forest, Rufous-and-white Wrens inhabit the more mature humid, evergreen sections (figure 1b). The dry season in Santa Rosa typically extends from December to April and the wet season from May to November, although the exact timing and duration of the seasons varies from year to year. Over the course of our study, the first 100 mm of rainfall in the calendar year was reached on 20-May (mean  $\pm$  s.d. ordinal date =  $141 \pm 12$  days) and all but the final 100 mm of rain had fallen by 06-November (mean  $\pm$  s.d. ordinal date =  $310 \pm 11$  days), resulting in an average ( $\pm$ s.d.) wet season length of  $170 \pm 18$  days. Annual rainfall ranged from 660 to 3090 mm over the course of our study, with 5 years exceeding 2500 mm of rain (figure 2a).

We conducted mark-recapture/re-sighting surveys of Rufous-and-white Wrens from 2003 to 2017. From 2003 to 2005, our study area was 125-ha in size (figure 1b). In 2006, we expanded the study area to 240 ha and continued to monitor this area through to 2017 (figure 1b). Beginning in April of each year,



**Figure 2.** SOI, local temperature and rainfall, and Enhanced Vegetation Index (EVI) measurements for Santa Rosa National Park, Costa Rica between 2003 and 2017. (a) Time-series of seasonally averaged monthly SOI (black), seasonally averaged daily maximum (red) and mean (orange) temperatures and total annual rainfall (blue). Monthly SOI and daily maximum and mean temperatures were averaged for the dry (April, December–March) and wet (May–November) seasons. Rainfall was summed from April to the following March. (b) Z-scores of average annual mean daily temperature (orange) and total annual precipitation (blue) in relation to annual average SOI. (c) Average monthly EVI in relation to cumulative rainfall from the previous month in the Santa Rosa study area. EVI plateaued between 500 and 1000 mm of cumulative rainfall, which was achieved in all but one of the study years. Curves in (b) and (c) were estimated from a local polynomial regression.

individuals were identified and captured using mist-nets. Each captured individual was marked with a unique combination of three plastic colour leg-bands and one aluminium leg-band and standard morphometric measurements were taken. Males and females were differentiated based on morphometric measurements, the presence or the absence of a brood patch, as well as sex-specific features of their songs [29–31]. Individuals that could not be captured, at least initially, were uniquely identified based on their consistent occupation of the same area or territory and their individually distinctive vocalizations [29,30,32]. All individuals in the population were identified by approximately mid-April of each year. Daily observations of the population continued until the end of June and included recording the territory centres of each bird using a hand-held Global Positioning System. Non-territorial floaters are rare in this population [33].

### (b) Environmental data

We used standardized monthly values of the SOI (downloaded from <http://www.cpc.ncep.noaa.gov/data/indices/soi>) to describe the climatic conditions at our study site, as with many locations in the northern neotropics, Santa Rosa experiences cooler and wetter conditions during positive phases of the Southern Oscillation (La Niña) and warmer and drier conditions (El Niño) during negative phases of the Southern Oscillation [34]. From the standardized monthly values, we calculated average annual (April–March), wet season (May–November) and dry season

(Apr, December–March) SOI for each year of the study. Climate and weather data were summarized beginning in April to coincide with the beginning of the mark–recapture/re-sighting period.

Daily maximum and minimum temperatures (°C) and rainfall (mm) measurements were obtained from weather stations within our study area operated by the Área de Conservación Guanacaste (2003–2015) and by L. Fedigan, A. Melin and K. Jack (2015–2017). Comparison of daily temperature and rainfall measurements from the two stations in 2015 revealed similar measurements (electronic supplementary material, figure S1), justifying the use of weather data from the latter station for the final 3 years of our study (2015–2017). Daily mean temperature was calculated as the mean of the daily minimum and maximum temperatures. Daily mean and maximum temperatures were then averaged at monthly, seasonal (wet/dry) and annual intervals (electronic supplementary material, table S1). Rainfall was summed over the same time intervals and we also calculated cumulative rainfall at monthly intervals, beginning in April and extending through to the following March (e.g. total rainfall for June was calculated as the sum of daily rainfall in June, whereas cumulative rainfall for June was calculated as the sum of daily rainfall in April, May and June; electronic supplementary material, table S1).

We also used the local rainfall data to measure the timing and duration of the wet season. Duration of the wet season was calculated as the number of days between when the first and last 50, 100 mm and 150 mm of rainfall occurred in each year. Timing of the onset (or end) of the wet season was measured as the ordinal

190 date on which the first (or last) 50, 100, 150, 200, 250 and 300 mm of  
191 rain had fallen. A full list of the eight climate and weather variables  
192 included in our analyses and the timescales over which they were  
193 summarized are presented in electronic supplementary material,  
194 table S1.

195 Lastly, we extracted monthly, 1-km<sup>2</sup> resolution Enhanced Veg-  
196 etation Index (EVI) measurements from the Terra MODIS dataset  
197 MOD13A3 [35] for the full 15-year study period to explore the  
198 relationship between local rainfall and vegetation greenness in  
199 our study area. MOD13A3 data were retrieved from the online  
200 DAAC2Disk download manager, courtesy of the NASA EOSDIS  
201 Earth Resources Distributed Active Archive Center and USGS/  
202 usgs.gov/data\_access/daac2disk). Similar to Saracco *et al.* [13],  
203 we removed cloud-contaminated pixels (pixel reliability code =  
204 3), extracted monthly EVI values for the six 1-km<sup>2</sup> pixels overlap-  
205 ping our study area using R [36] and package ‘raster’ [37], and then  
206 averaged values for the six pixels to acquire a monthly average  
207 EVI. We related monthly EVI to cumulative rainfall for the pre-  
208 vious month using local polynomial regression implemented  
209 using the ‘loess’ function in R with a smoothing parameter (or  
210 span) equal to 0.9 (figure 2c).

### 211 (c) Statistical analyses

212 We estimated sex-specific annual apparent survival and recap-  
213 ture/re-sighting probabilities using a Cormack–Jolly–Seber  
214 (CJS) model [38]. Hereafter, we use the word ‘survival’ in place  
215 of ‘annual apparent survival’, and ‘re-encounter probability’ in  
216 place of ‘recapture/re-sighting probability’. We analysed the  
217 CJS model in a Bayesian framework using Markov Chain  
218 Monte Carlo (MCMC) simulations, which we implemented in  
219 JAGS [39] from R [36] using the package ‘jagsUI’ [40]. The CJS  
220 model was formulated using a multinomial array [41,42].

221 To quantify temporal variability, survival  $\varphi$  and re-encounter  
222 probability  $p$  of each sex  $s$  was modelled on a logit scale as a  
223 function of its mean  $\mu$  and temporal residual  $\varepsilon_t$ :

$$224 \text{logit}(\varphi_{s,t}) \sim \mu_{\varphi_s} + \varepsilon_{\varphi_{s,t}} \quad \varepsilon_{\varphi_{s,t}} \sim N(0, \sigma_{\varphi_s}^2) \quad (2.1)$$

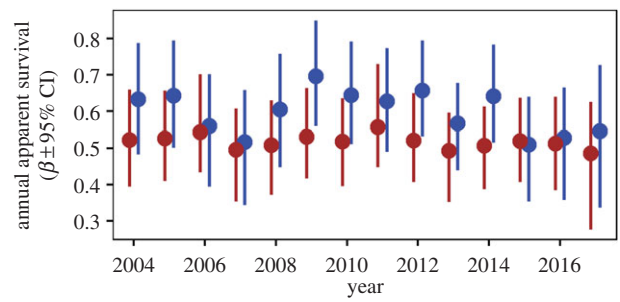
225 and

$$226 \text{logit}(p_{s,t}) \sim \mu_{p_s} + \varepsilon_{p_{s,t}} \quad \varepsilon_{p_{s,t}} \sim N(0, \sigma_{p_s}^2) \quad (2.2)$$

227 We evaluated effects of climate, local weather and seasonal  
228 timing and duration on survival by fitting a series of univariable  
229 models that included the climate and weather variables described  
230 above (see also electronic supplementary material, table S1).  
231 Relative variable importance was evaluated based on the magni-  
232 tudes of the standardized slope estimates ( $\beta_s$  in equation (2.3))  
233 and their uncertainty (95% credible intervals). We also evaluated  
234 the relative importance of variables using the indicator variable  
235 method [43], which can be an effective means of identifying influ-  
236 ential predictors under high estimation uncertainty [44]. By this  
237 method, each covariate  $\beta$  is multiplied by an indicator variable  $\gamma$   
238 that is drawn from a Bernoulli distribution with a prior probability  
239 of 0.5. At each MCMC iteration,  $\gamma$  takes a value of 1 or 0 causing  
240 the variable to be included or excluded from the model, respect-  
241 ively. If a variable is important for model fit, then  $\gamma$  will be  
242 included more times than not, causing the posterior mean of  $\gamma$   
243 to approach 1. By contrast, a variable that does little to improve  
244 model fit will often be excluded from the model, such that the  
245 posterior mean of  $\gamma$  will tend to 0. We only fitted models contain-  
246 ing a single predictor variable at a time due to SOI, temperature  
247 and rainfall being highly correlated (figure 2). The structure of  
248 the models was as follows:

$$249 \text{logit}(\varphi_{s,t}) \sim \mu_{\varphi_s} + \gamma_s \cdot \beta_s \cdot X_t + \varepsilon_{\varphi_{s,t}} \quad \gamma_s \sim \text{Bernoulli}(0.5) \quad (2.3)$$

250 Vague prior distributions were specified for all parameters:  
251  $\mu_{\varphi_s} \sim \text{Uniform}(0, 1)$ ;  $\mu_{p_s} \sim \text{Uniform}(0, 1)$ ;  $\sigma_{\varphi_s} \sim \text{Uniform}(0, 10)$ ;  
252



253 **Figure 3.** Sex-specific annual apparent survival probabilities of Rufous-and-  
254 white Wrens in Santa Rosa National Park, Costa Rica between 2003 and 2017.  
255 Male (blue) and female (maroon) survival were estimated using a Cormack–  
256 Jolly–Seber model.

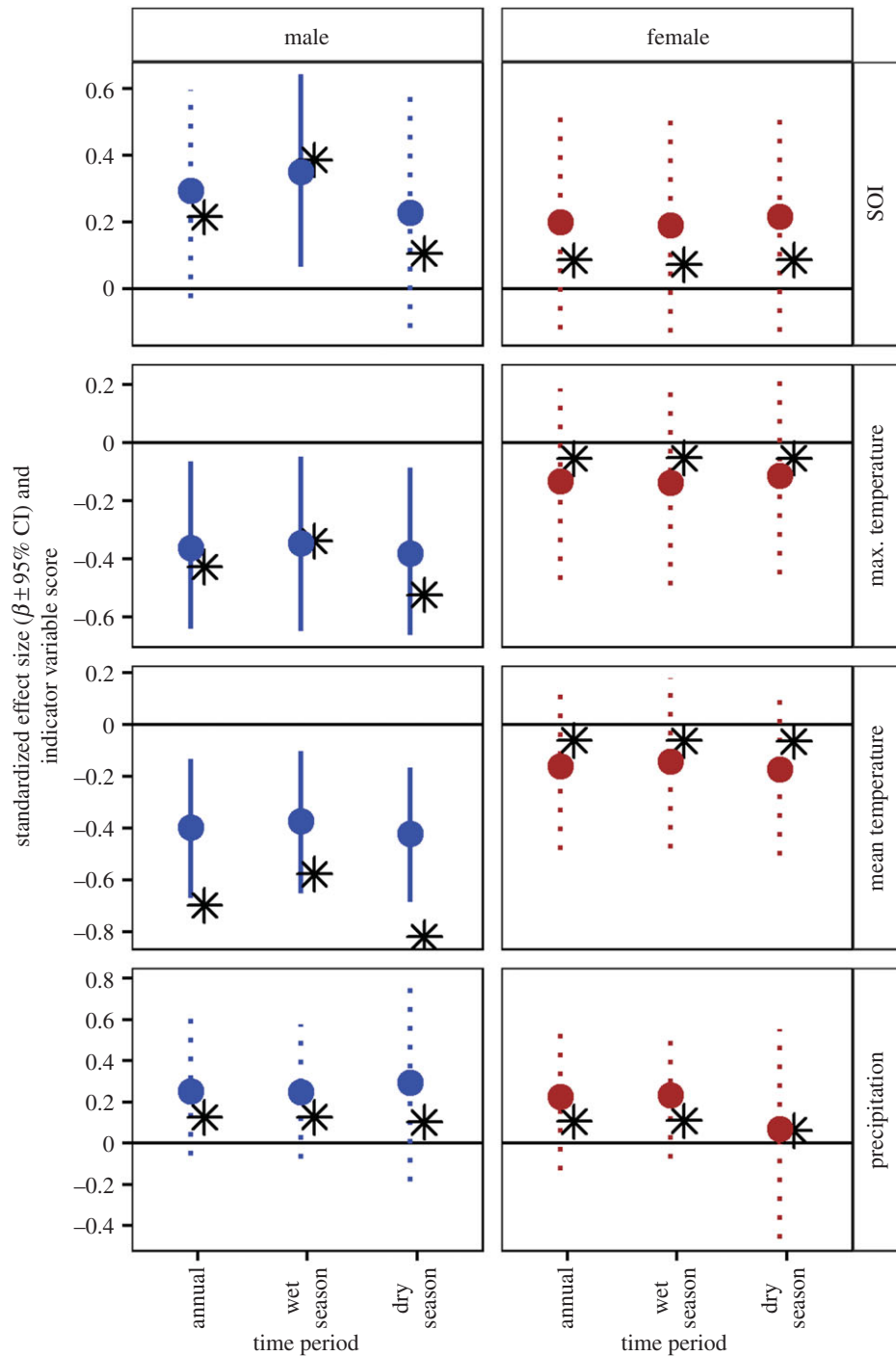
257  $\sigma_{ps} \sim \text{Uniform}(0, 10)$ ;  $\beta_s \sim N(0, 10^4)[-5, 5]$ . We ran three inde-  
258 pendent chains with different starting values for 250 000  
259 iterations. We used a burn-in of 50 000 iterations and kept every  
260 50th sample, resulting in 12 000 posterior samples for each  
261 model parameter. For modelling, climatic and weather variables  
262 were converted to z-scores by subtracting the mean of the variable  
263 across all years from the value for each year and dividing by the  
264 standard deviation of the variable across years, such that each vari-  
265 able had a mean of 0 and standard deviation of 1. Convergence of  
266 model chains was assessed using the Gelman-Rubin  $\hat{R}$  diagnostic  
267 statistic [45]. In the results, we present estimated survival and re-  
268 encounter probabilities on the real scale, whereas effect size and  
269 variance estimates are on the logit scale.

270 Goodness-of-fit of the CJS models was evaluated using the  
271 Freeman–Tukey statistic [46]. With this method, expected data  
272 simulated from the CJS model are compared to the observed data.  
273 Bayesian  $p$ -values greater than 0.5 indicate that the expected data  
274 are more variable than the observed data, whereas  $p$ -values less  
275 than 0.5 indicate that expected data are less variable than the  
276 observed data. A model that fits the data perfectly will result in a  
277 Bayesian  $p$ -value of 0.5. We found no evidence of lack of fit for  
278 any models. For the null model (equation (2.1)), Bayesian  $p$ -values  
279 were 0.58 for females and 0.41 for males (electronic supplementary  
280 material, figure S2). Across all models that contained environmental  
281 covariates, Bayesian  $p$ -values averaged 0.41 for males (range =  
282 0.32–0.60) and 0.58 for females (range = 0.51–0.62).

## 283 3. Results

284 From 2003 to 2017, we marked and monitored the survival of  
285 a total of 314 Rufous-and-white Wrens (175 males and 139  
286 females). The number of wrens monitored each year ranged  
287 from 22 to 70, with an average of 44. Mean annual survival  
288 probability of Rufous-and-white Wrens over the 15-year  
289 period was 0.60 [95% credible interval (CI) = 0.52, 0.68] for  
290 males ( $\hat{\mu}_{\varphi_m}$ ) and 0.52 [95% CI = 0.44, 0.59] for females ( $\hat{\mu}_{\varphi_f}$ ), a  
291 difference of 8% between the two sexes ( $\text{Pr}[\hat{\mu}_{\varphi_m} > \hat{\mu}_{\varphi_f}] =$   
292 0.94; figure 3). Survival of males was more variable over time  
293 compared to females ( $\hat{\sigma}_{\varphi_m} = 0.42$  versus  $\hat{\sigma}_{\varphi_f} = 0.22$ ;  
294  $\text{Pr}[\hat{\sigma}_{\varphi_m} > \hat{\sigma}_{\varphi_f}] = 0.79$ ). Of the 160 wrens encountered in more  
295 than 1 year of the study, 55% remained within 100 m of  
296 where they were initially encountered, 26% had a net dispersal  
297 of 100–400 m, and 14% had a net dispersal of 400–1000 m.  
298 Only 6% ( $n = 9$ ) dispersed greater than 1 km. Re-encounter  
299 probabilities were high for both sexes ( $\hat{\mu}_{p_m} = 0.96$  [95% CI =  
300 0.87, 0.99] versus  $\hat{\mu}_{p_f} = 0.93$  [95% CI = 0.80, 0.99]).

301 Annual survival of male Rufous-and-white Wrens was  
302 related to SOI during the wet season, whereas female survival  
303 was unrelated to annual or seasonal SOI (figure 4). Male

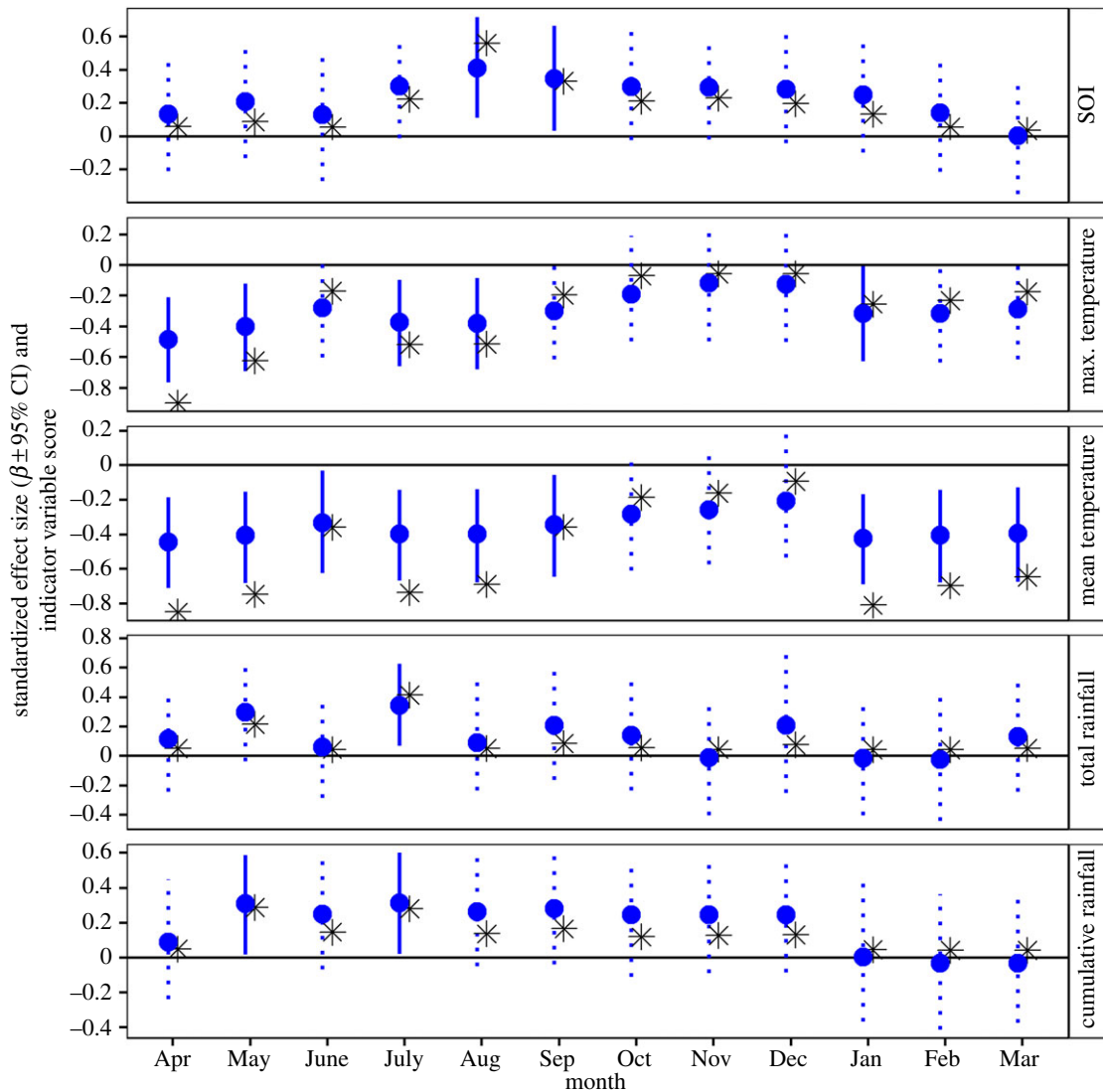


**Figure 4.** Effects of climate and local weather on annual survival of Rufous-and-white Wrens. Points show slope estimates ( $\pm$  95% CI) from Cormack–Jolly–Seber models relating annual survival to SOI or local weather (daily mean and maximum temperature and total precipitation) averaged over annual and seasonal (wet/dry) time periods. Asterisks show indicator variable scores, which range from 0 (unimportant) to 1 (important). For visualization, indicator variable scores were multiplied by  $-1$  if the corresponding effect size was negative. Credible intervals that overlap zero are represented with dotted lines. (Online version in colour.)

survival was positively related to wet-season SOI, primarily in August and September (figure 5). Consistent with positive phases of the SOI coinciding with cooler and wetter weather in Santa Rosa (figure 2*b*), male survival was negatively related to temperatures during the wet season (figure 4). Effects of rainfall on male survival were strongest for May and July (figure 5), but were overall weaker than effects of temperature. Female survival was unrelated to annual and seasonal temperatures and rainfall (figure 4). The only wet season weather variable for which there was some, albeit weak, evidence of a relationship to female survival was total September rainfall ( $\hat{\beta} = 0.33$ , 95% CI = 0.02, 0.66; electronic supplementary material, figure S3). In 2006, 2009 and 2011, over 500 mm of

rain fell in September compared to less than 400 mm in all other years. This coincided with an increase in female survival of 2.6%, 1.4% and 4.0% above the long-term average.

Although we did not find evidence for an effect of dry-season SOI on male survival, temperatures during this season had a strong negative effect on male survival (figure 4). In particular, mean and maximum temperatures in April, coinciding with the end of the dry season, had the strongest effects of any climatic or local weather variable on male survival (figure 5). The weakest temperature effects were in October, November and December, coinciding with peak rainfall, the end of the wet season and beginning of the dry season, respectively (figure 5). We found no evidence for



**Figure 5.** Effects of monthly SOI and local weather on annual apparent survival of male Rufous-and-white Wrens. Points show slope estimates ( $\pm$  95% CI) from Cormack–Jolly–Seber models relating annual apparent survival to monthly SOI and local weather. Months that occur during the dry season are indicated with bold text on the x-axis. Asterisks show indicator variable scores, which range from 0 (unimportant) to 1 (important). For visualization, indicator variable scores were multiplied by  $-1$  if the corresponding effect size was negative. Credible intervals that overlap zero are represented with dotted lines. (Online version in colour.)

effects of dry season temperature on female survival (figure 4). There was some evidence of a positive relationship between February precipitation and female survival ( $\hat{\beta} = 0.41$ , 95% CI = 0.04, 0.91; electronic supplementary material, figure S3), but this pattern was primarily due to 2 years (2006 and 2011) in which 10–15 mm of rain fell in February (compared to less than 2 mm in all other years). In those same years, female survival was 2.6 and 4.0% higher than the long-term average.

We found some evidence for timing of the onset of the wet season influencing annual survival of males. Male survival was higher when the first 150–250 mm of rain fell earlier in the year ( $\hat{\beta}_{150\text{mm}} = -0.28$ , 95% CI =  $-0.56, -0.01$ ;  $\hat{\beta}_{200\text{mm}} = -0.27$ , 95% CI =  $-0.56, 0.0$ ;  $\hat{\beta}_{250\text{mm}} = -0.29$ , 95% CI =  $-0.60, 0.00$ ; electronic supplementary material, figure S4), but, as with cumulative and total rainfall, timing of the onset of the wet season was a weaker predictor of male survival than temperature. Timing of the end of the wet season and total duration of the wet season were not strong predictors of Rufous-and-white Wren survival for either sex, nor was the start of the wet season for female survival (electronic supplementary material, figure S4).

## 4. Discussion

Our results show that local temperatures, particularly during the dry season and early wet season, are important predictors of annual apparent survival of adult male Rufous-and-white Wrens, with higher temperatures leading to lower survival. There was also evidence that average wet season SOI, rainfall during the early wet season and timing of the onset of the wet season influenced male survival, but generally these effects were weaker when compared with those of temperature. Similarly, length of the wet season did not strongly influence adult survival of either sex [11]. Although broad-scale climate indices are often better at predicting population processes than local weather [47], and have been shown to predict survival of several tropical birds [10,12], our results show the value of including both local and broad-scale climate and weather measurements when available.

In contrast to male survival, female survival was relatively insensitive to both local weather and broad-scale climatic variation. On average, female survival was 8% lower than male survival, a similar difference to that observed between male and female Buff-breasted Wrens *Cantorchilus leucotis* [48].

379 This, coupled with the result that survival of females was also  
 380 more constant over time relative to males, suggests a limiting  
 381 factor that was relatively constant among years, which may  
 382 have overridden local- and broad-scale climate effects. One  
 383 such possibility is that females suffer higher costs of reproduc-  
 384 tion compared with males. Tropical birds often exhibit high  
 385 nest predation rates and high re-nesting rates, both generally  
 386 [49–51] and in our study population specifically [21]. In species  
 387 where females perform all of the incubation and the majority  
 388 of nestling provisioning, such as Rufous-and-white Wrens  
 389 [31,52], this may result in females incurring high reproductive  
 390 costs which could lead to higher mortality after breeding com-  
 391 pared with males. However, identifying how differential costs  
 392 of reproduction between males and females could contribute to  
 393 sex differences in survival is complicated by the fact that costs  
 394 of reproduction may also vary with climate and other environ-  
 395 mental factors. Future studies examining drivers of the costs  
 396 of reproduction in tropical species and impacts of costs of  
 397 reproduction on other demographic processes are needed.

398 The positive relationship between SOI and annual survival  
 399 that we observed contributes to a growing understanding of  
 400 how climate influences demography of tropical bird species.  
 401 The pattern of higher survival during cooler and wetter (posi-  
 402 tive) phases of the SOI is consistent with that observed for  
 403 White-collared Manakins in young forest in northeastern  
 404 Costa Rica [10], but opposite to that observed for Wire-tailed  
 405 Manakins in Ecuador, which had higher survival during  
 406 warmer and drier (negative) phases of the SOI [12]. For  
 407 insectivores in dry forests, such as Rufous-and-white Wrens,  
 408 survival may be higher when conditions are cooler and  
 409 wetter due to reduced heat-induced thermoregulatory costs  
 410 [53]. Indeed, resident tropical species and insectivores have  
 411 lower basal metabolic rates compared with migrants and frugi-  
 412 vorous/granivorous species, respectively, suggesting their  
 413 ability to tolerate thermal fluctuations may be more limited  
 414 [8]. That temperature had a stronger influence on survival com-  
 415 pared with rainfall lends further support to thermoregulatory  
 416 costs as a contributor to the observed climate and weather  
 417 effects on survival. An important implication of this result is  
 418 that, even for species accustomed to living in hot environ-  
 419 ments, temperature increases may threaten the persistence of  
 420 local populations in the absence of distributional shifts.

421 Food availability is another mechanism that could explain  
 422 increased survival during cooler and wetter conditions.  
 423 Insect abundance in the understory has been shown to increase  
 424 with moisture in the Guanacaste region [54], suggesting that  
 425 conditions that are wetter, but not so wet as to limit access to  
 426 food by inhibiting foraging [55], could improve survival  
 427 through increased food availability [56]. However, evidence  
 428 from a comparative study of Rufous-and-white Wren and  
 429 Buff-breasted Wren reproductive biology in Columbia found  
 430 that insect abundance in the leaf litter, where Rufous-and-  
 431 white Wrens primarily forage, did not vary between wet and  
 432 dry seasons [22]. Moreover, we found that vegetation green-  
 433 ness, a proxy for resource availability, in Santa Rosa  
 434 plateaued between 600 and 1000 mm of cumulative rainfall  
 435 (figure 2c). This amount of rainfall was surpassed in all but  
 436 one of the study years (figure 2a), implying that, even in the  
 437 driest of years, conditions were sufficiently wet to provide  
 438 the resources necessary for survival. These two pieces of evi-  
 439 dence, coupled with the result that both the amount of  
 440 rainfall and the timing and duration of the wet seasons had  
 441 weaker effects on survival compared with temperature,

provide further evidence that higher thermoregulatory costs  
 associated with hot temperatures was likely the main mechan-  
 ism by which climate and weather limited survival.

The opposite effects of SOI on survival of two frugivorous  
 manakin species observed by Wolfe *et al.* [10] and Ryder &  
 Sillett [12] points to the importance of considering how vari-  
 ation in SOI manifests locally. Indeed, Wolfe *et al.* [10] found  
 little effect of SOI on manakin survival in mature forests  
 despite strong effects on survival in young forests, showing  
 that responses to climate can vary within species and over  
 small spatial scales. Vast differences in average annual rainfall,  
 which exceeds 5000 mm in northeast Costa Rica compared  
 with under 3000 mm in Ecuador, might explain the opposite  
 effects of SOI on manakin survival if manakins in Ecuador  
 are less adapted to cooler and wetter conditions compared  
 with those in northeast Costa Rica which experience almost  
 double the annual rainfall. Whatever the cause of the discre-  
 pancy, variation in responses to climate among and within  
 species seen by comparing our results with those of previous  
 studies [10–13], highlights the need to consider the local  
 environment, such as forest type (open versus closed and dry  
 versus wet), elevation [55] and species traits, such as their  
 diet and foraging behaviour [11], when predicting and inter-  
 preting effects of climate on the dynamics of tropical bird  
 populations. The observed diversity of responses to climatic  
 variation similarly highlights the need to study a broader  
 range of species that represent the range of life histories and  
 habitats in the tropics. Such studies are needed in order to  
 detect emergent patterns of how climatic variation shapes  
 population dynamics across tropical taxa.

In summary, our results provide much-needed infor-  
 mation on the demography of a tropical bird, including sex  
 differences in survival and the effects of climatic variables  
 at different spatio-temporal scales thereon. Although declines  
 of tropical bird species have primarily been attributed to  
 direct habitat loss and degradation caused by humans, the  
 observed negative effects of increased temperature on survi-  
 val in an undisturbed habitat reveals a mechanism by  
 which climate change could drive future population declines  
 in the tropics independent of habitat loss. That the distri-  
 bution and composition of tropical dry forest itself will  
 likely shift with climate change [17] is likely to only exacer-  
 bate the problem in the absence of concurrent distributional  
 shifts by the species that inhabit these forests. Future studies  
 that consider climate and local weather effects on all vital  
 rates simultaneously, and how those vital rates contribute  
 to population growth rate, will further clarify the popula-  
 tion dynamical consequences of short-term variation and  
 long-term trends in climate for tropical species.

**Ethics.** The long-term field study on Rufous-and-white Wrens was con-  
 ducted with permission of the Area de Conservación Guanacaste, the  
 government of Costa Rica (MINAE), and the University of Windsor  
 Animal Care Committee.

**Data accessibility.** Data and model code supporting this article are avail-  
 able on Dryad: <http://dx.doi.org/10.5061/dryad.k785p43> [57].

**Authors' contributions.** D.J.M. initiated the long-term study in 2003 and,  
 together with his students, collected and collated the mark–recapture  
 data; D.J.M. lead the field investigation from 2003 to 2010, B.A.G.  
 from 2011 to 2015 and Z.A.K. from 2015 to 2017. B.K.W., D.J.M.  
 and D.R.N. designed the survival analysis. B.K.W. analysed the  
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