


## PRIMARY RESEARCH ARTICLE

# Temperature-associated decreases in demographic rates of Afrotropical bird species over 30 years

Montague H. C. Neate-Clegg<sup>1</sup>  | Thomas R. Stanley<sup>2</sup> | Çağan H. Şekercioğlu<sup>1,3</sup> | William D. Newmark<sup>4</sup>

<sup>1</sup>School of Biological Sciences, University of Utah, Salt Lake City, UT, USA

<sup>2</sup>Fort Collins Science Center, US Geological Survey, Fort Collins, CO, USA

<sup>3</sup>Faculty of Sciences, Koç University, Istanbul, Turkey

<sup>4</sup>Natural History Museum of Utah, University of Utah, Salt Lake City, UT, USA

## Correspondence

Montague H. C. Neate-Clegg, School of Biological Sciences, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, USA.

Email: monte.neate-clegg@utah.edu

## Funding information

JRS Biodiversity Foundation, Grant/Award Number: 60708\_TAWIRI; DANIDA; Field Museum of Natural History; Chicago Zoological Society; Sophie Danforth Conservation Fund; National Geographic Society, Grant/Award Number: 524-94 and 977815; Earthwatch Institute; John D. and Catherine T. MacArthur Foundation; Critical Ecosystem Partnership Fund; World Wide Fund for Nature; US Geological Survey

## Abstract

Tropical mountains harbor globally significant levels of biodiversity and endemism. Climate change threatens many tropical montane species, yet little research has assessed the effects of climate change on the demographic rates of tropical species, particularly in the Afrotropics. Here, we report on the demographic rates of 21 Afrotropical bird species over 30 years in montane forests in Tanzania. We used mark-recapture analyses to model rates of population growth, recruitment, and apparent survival as functions of annual mean temperature and annual precipitation. For over one-half of focal species, decreasing population growth rates were associated with increasing temperature. Due to the trend in temperature over time, we substituted a time covariate for the temperature covariate in top-ranked population growth rate models. Temperature was a better explanatory covariate than time for 6 of the 12 species, or 29% of all focal species. Population growth rates were also lower for species found further below their elevational midpoint and for smaller-bodied species. Changes in population growth rates were more closely tied to changes in recruitment than to changes in apparent survival. There were no consistent associations between demographic rates and precipitation. This study demonstrates temperature-associated demographic impacts for 6 (29%) of 21 focal species in an Afrotropical understory bird community and highlights the need to incorporate the impacts of climate change on demographic rates into conservation planning across the tropics.

## KEYWORDS

body mass, climate change, Eastern Arc Mountains, elevational range, population growth rate, precipitation, recruitment, survival, temperature, tropical mountains

## 1 | INTRODUCTION

As global climate change alters temporal and spatial patterns of temperature and precipitation, many species must shift their geographic range, adapt or face extinction (Moritz & Agudo, 2013; Norberg et al., 2012; Radchuk et al., 2019). While changes in the phenology and geographic ranges of species are well documented in temperate regions (Parmesan, 2006), there are far fewer studies assessing the impact of climate change on species in the tropics

(Feeley et al., 2017; Rosenzweig et al., 2008; Sheldon, 2019) and particularly in the Afrotropics (Sheldon, 2019), despite low latitudes harboring the majority of the world's biodiversity. Furthermore, tropical plant and animal species may be at greater risk of extinction from climate change than their temperate counterparts (Deutsch et al., 2008) as they are thought to be more ecologically specialized, have lower dispersal ability (Salisbury et al., 2012; Sheard et al., 2020), and have narrower elevational ranges (Janzen, 1967; Şekercioğlu et al., 2008).

Previous studies in the tropics have demonstrated links between demographic rates of birds and various climatic parameters (Oro et al., 2010; Ryder & Sillett, 2016; Saracco et al., 2016; Wolfe et al., 2015; Woodworth et al., 2018). However, there has been little research conducted in the tropics on the demographic responses of birds to recent climate change at a community level (Sheldon, 2019). An important exception is a recent multi-species study of understory birds in the lowlands of Panama which reported a negative association between population growth rates and dry season length over a 33-year period for approximately one-third of the examined species (Brawn et al., 2017). Additionally, in the eastern Himalayas, temporal trends in apparent survival of understory bird species were shown to be related to the elevational distance of the study sites to species' elevational midpoint, with species found closer to their warm-edge elevational range limit having decreasing survival rates (Srinivasan & Wilcove, 2020). Such studies are important because of the unusually high diversity and endemism in the tropics and particularly in montane communities (Orme et al., 2005; Rahbek et al., 2019) where the threat of climate change is believed to be particularly great (Şekercioğlu et al., 2008). An understanding of the demographic responses of tropical birds to climate change is also central to assessing population viability, evaluating recent observed declines in tropical bird abundance (Blake & Loiselle, 2015; Latta et al., 2011; Lister & Garcia, 2018; Stouffer et al., 2020), and developing effective conservation interventions (Brawn et al., 2017).

In both high and low latitudes, temperature has been shown to be an important driver of the demographic rates of birds (Doyle et al., 2020; Dybala et al., 2013; Santisteban et al., 2012; Woodworth et al., 2018). While the magnitude of global warming—0.18°C per decade (NOAA, 2019)—has been comparatively small relative to the range of temperatures that most tropical birds typically experience over a lifetime, a year, or even a day, the impact of rapid change in mean annual temperature over the last half-century has, nonetheless, had marked effects on the distributions (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018; Neate-Clegg et al., 2020), community structure (Blake & Loiselle, 2015; Latta et al., 2011; Stouffer et al., 2020), and demographic rates (Srinivasan & Wilcove, 2020; Woodworth et al., 2018) of tropical birds. Most of these documented responses of tropical birds to global warming are almost certainly a result of temperature-induced changes in biotic interactions (Lister & Garcia, 2018; Santisteban et al., 2012) such as fruiting phenology (Chapman et al., 2005), prey availability (Lister & Garcia, 2018), or predator activity (Cox et al., 2013) rather than temperature *per se* (Londoño et al., 2017).

As with temperature, precipitation in both high and low latitudes has been shown to impact the demographic rates of birds (Blake & Loiselle, 2015; Brawn et al., 2017; Doyle et al., 2020; Saracco et al., 2016). Again, the mechanisms by which changes in precipitation affect bird demographic rates are very likely indirect, via changes in the growth patterns of plants (Hilker et al., 2014; Saracco et al., 2016) and food availability (Dybala et al., 2013) rather than changes in precipitation *per se*. Yet despite the importance of temperature

and precipitation on demographic rates of tropical birds, the combined impact of temperature and precipitation has to date received little attention, especially at a community level.

In this study, we report on the association between demographic rates of a forest-dependent understory bird community and temperature and precipitation over a 30-year period in the East (EUM) and West Usambara Mountains (WUM) in northeast Tanzania. We used mark-recapture analyses to model and estimate rates of realized population growth ( $\lambda$ ), recruitment ( $F$ ), and apparent survival ( $\varphi$ ) for 21 species using annual mean temperature and annual precipitation as climate covariates. We compared multiple species-specific demographic models containing climate covariates with associated models that assumed demographic rates remained constant, and used information-theoretic model selection procedures to identify the models best supported by the data for each species. Finally, we examined the association between demographic rates and species traits.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

The study was conducted in the East and West Usambara Mountains (EUM, WUM) in northeastern Tanzania, which are part of the Eastern Arc Mountains biodiversity hotspot (Myers et al., 2000). The two massifs are separated by a 17.5 km wide non-forested valley 290 m in elevation. The EUM and WUM have experienced extensive deforestation and fragmentation over the past two centuries (Newmark, 2002; Newmark & McNeally, 2018), with a 25% loss of forest cover between 1955 and 2000 (Hall et al., 2009).

Since 1987, understory bird communities have been monitored annually across 14 study sites in the EUM and WUM (see Fig 1. Korfanta, Newmark, & Kauffman, 2012). Here we restrict our analyses to the two largest forest blocks in our study system – 640 ha in the EUM and 908 ha in WUM, with mean elevations of 1037 m and 1301 m, respectively – to reduce the known spatial and temporal effects of fragmentation on understory bird species demography (Korfanta, Newmark, & Kauffman, 2012; Newmark, Jenkins, Pimm, McNeally, & Halley, 2017). Based on tea estate records, the ages of the two study sites (i.e., time since forest blocks were isolated through the clearing of adjacent forest), were 48 years in the EUM and c. 123 years in the WUM. Both forest blocks are bordered by small- and large-scale agriculture (tea) and Eucalyptus plantations (Korfanta et al., 2012)."

We assessed change over time in forest area and matrix habitat composition of the two forest blocks by comparing Google Earth historic aerial imagery (1987, 1988) having a spatial resolution of 30 m (Landsat/Copernicus) with more current aerial imagery (2002, 2017) having a spatial resolution of 0.5–1.5 m (CNES/Airbus; Figure S1). Aerial imagery was extensively ground-truthed during three decades of field work at the two study sites (Newmark & McNeally, 2018). Forest boundaries and adjacent matrix habitat types within

500 m of the forest edge of the two study sites were hand-digitized and matrix habitat types were classified as either forest, small-scale agriculture, large-scale agriculture (tea), or Eucalyptus plantation (Brodie & Newmark, 2019).

When we compared historic to current aerial imagery of the two study sites (Figure S1), we found that forest block area has not changed over the last three decades. Similarly, when we compared historic to current aerial imagery (Figure S1), we found that matrix habitat composition within 500 m of the forest edge has changed over the last three decades by <1.8% or 13.3 ha adjacent to the study site in the EUM, and has not changed adjacent to the study site in the WUM. The change in matrix habitat composition in the EUM was due to conversion of small-scale agriculture to Eucalyptus plantations. We can also exclude insecticide use in agricultural tea and in Eucalyptus plantations over the last three decades in matrix habitats because insecticides have not been used in the cultivation of these commercial crops at our study sites in the EUM and WUM.

## 2.2 | Bird sampling

Understory bird species were sampled annually between 1987 and 2016 in the EUM and between 1989 and 2016 in the WUM (with the exception of 2014 and 2015). All samples were collected with mist nets (12.0 × 2 m and 12.8 × 2 m, 36 mm mesh, four tier) during the cool, dry season from July to September, prior to the breeding season of most species. Sampling effort was constant between study locations and across years. Over all samples, we erected 988 m of mist nets in each forest block. Three mist net lines were operated within the EUM forest block, ranging in length from 208 to 442 m, and two mist net lines, each 494 m in length, were operated within the WUM forest block. The five mist net lines began at and ran perpendicular to the forest edge. Across all samples and years, mist nets were placed at the same location and were operated from dawn until dusk (12 h) for three consecutive days (36 h total) and were checked every 30 min. Forest blocks in the EUM and WUM were sampled in the same order over all years to maintain a constant 12-month interval between samples. The mean (±SE) temporal midpoint of a sample across all years in the EUM and WUM forest blocks was 12 August (±4.9 days) and 25 August (±4.3 days), respectively. During heavy rains, nets were closed and reopened for an equivalent duration on day four. All birds were banded (National Band and Tag Company, Newport, Kentucky, USA; I.Ö. Mekaniska AB, Bankeryd, Sweden) to allow re-identification.

## 2.3 | Climate data

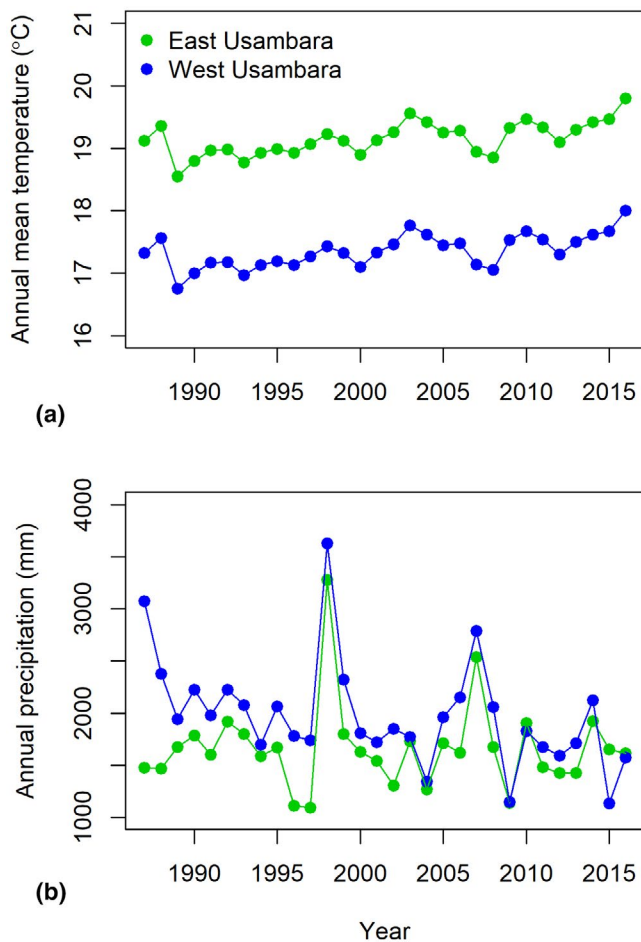
Annual mean temperature at the two study sites was derived from monthly mean temperature data available at half-degree grid cell resolution (cruts V 4.01) from the Climatic Research Unit (CRU),

University of East Anglia (Harris et al., 2014). It should be noted that the two study sites are 19 km apart, which is small relative to the half-degree grid cell resolution (55 km × 55 km) of the CRU data. Because of elevational differences between the EUM and WUM study sites, we estimated location-specific temperature based on the recorded lapse rate of 0.68°C per 100 m. The lapse rate was calculated by placing temperature loggers at 310, 600, 950, and 1265 m in the EUM and WUM and simultaneously recording temperature at 2-h intervals over a 22-month period between November 1997 and September 1999 (Newmark, 2002). On-site temperature logger data were also used to validate mean monthly temperature data from CRU, and temporal variation between study sites and CRU data and were highly correlated (Pearson's  $r = 0.96$ ;  $r = 0.92$ , respectively). As part of this analysis, we also compared CRU temperature data with CHELSAcruts data (Karger et al., 2017), having a much higher spatial resolution (~55-fold), and these were highly correlated ( $r = 0.95$ ). However, because the CHELSAcruts dataset only includes monthly minimum and maximum temperature rather than mean temperature we selected the CRU dataset.

Annual precipitation (October–September) at our study sites was calculated from on-site daily precipitation records at the Marikitanda Tea Research Station in the EUM and the Ambangulu Tea Estate in the WUM.

In our analyses, climate data are presented for the 12-month period (October–September) prior to and including the annual sampling period (July–September). In preliminary analyses, we considered multiple potential climate covariates. However, we found many of these covariates were highly correlated (e.g. annual mean temperature vs. breeding season temperature:  $r = 0.81$ ; annual precipitation vs number of rainy days:  $r = 0.73$ ). Consequently, so as to avoid multicollinearity issues, we narrowed the set of covariates to include only annual mean temperature and annual precipitation over the 12-month period prior to and including the sampling period. We chose these metrics because they (i) more effectively integrated annual demographic changes in bird populations than the other potential climate covariates and (ii) reduced the number of estimable parameters, hence reducing model degrees of freedom. Although the combined effects of temperature and precipitation on demographic rates of birds have also been assessed by collapsing multiple covariates in a PCA analysis (Grosbois et al., 2008), we chose to assess the effects of temperature and precipitation separately because it is easier to interpret and evaluate their independent effects on demographic rates.

Over the 30-year study period, annual mean temperature increased by 0.58°C (linear model:  $R^2 = 0.40$ ,  $p < 0.001$ ) across the two study sites, with a range of 1.25°C (Figure 1a). Annual precipitation over the study period was relatively constant in the EUM (Figure 1b,  $p > 0.20$ ) but decreased by ~670 mm or 29% in the WUM ( $R^2 = 0.16$ ,  $p < 0.03$ ). Over the study period, annual precipitation was 318 mm higher in the WUM than the EUM ( $p = 0.009$ ) and varied greatly between years (1090–3278 mm in the EUM; 1134–3632 mm in the WUM) (Figure 1b).



**FIGURE 1** Variation in (a) annual mean temperature and (b) annual precipitation (October–September) in the East and West Usambara Mountains (1987–2016). Temperature data were taken from the Climatic Research Unit (cruts V 4.01), University of East Anglia and precipitation data were recorded on-site

## 2.4 | Demographic analyses

In the demographic analysis, we included any species that had either >100 individuals or encounter probabilities >0.1. We also only included species if >10% of individuals were captured more than once. All remaining species for which we present results ( $n = 21$ ) had >70 individuals with >90 captures (Table S2). We used mark–recapture models implemented in program MARK (Cooch & White, 2006) to estimate demographic parameters and their associated 95% confidence intervals. Following Korfanta et al. (2012), we employed a two-step analysis. We first modeled and estimated apparent survival and encounter probabilities using Cormack–Jolly–Seber (CJS) models (Cormack, 1964; Jolly, 1965; Lebreton et al., 1992; Seber, 1965). We then conditioned on the best-supported model structure from the CJS analysis and used this structure in Pradel models (Pradel, 1996) to estimate recruitment and realized population growth rates. This approach was adopted because the number of permutations of model structures becomes extremely large and unwieldy when models for survival

and encounter probabilities are evaluated simultaneously with models for recruitment and population growth within the Pradel model framework.

A standard open population CJS model (Cormack, 1964; Jolly, 1965; Lebreton et al., 1992; Seber, 1965) estimates apparent survival ( $\phi$ ) and encounter probability ( $p$ ), where  $\phi$  is the product of true survival and the probability of remaining in the study area and available for capture. Under a constant model,  $\phi$  and  $p$  are constrained to be constant across all capture occasions and among all individuals. More general models relax these constraints by introducing covariates to assess their influence on estimated  $\phi$  and  $p$ . We used a logit link to model  $\phi$  as a linear function (on the logit scale) of annual mean temperature (hereafter “temperature”) and/or annual precipitation (hereafter “precipitation”). These covariates were based on annual temperature and precipitation values (October–September) rather than estimates derived from trend lines and thus the models explicitly incorporated interannual variation (Figures 1 and 3). To ensure the effect size of coefficients were comparable, we rescaled temperature and precipitation to have a mean of 0 and a standard deviation of 1. We also hypothesized that temperature could interact with precipitation (e.g., hotter weather may exacerbate the effect of drought on survival) and thus included the interaction term in the general model.

We included a binary location covariate to account for possible differences between the EUM and WUM not reflected by differences in the climate covariates. These differences could be due to a variety of factors including elevation, forest block area, habitat composition, matrix composition, predation pressure, etc. We did not include a location interaction term in the model set because we expected the effects of temperature and precipitation on demographic rates to be similar between locations, and we found little statistical support for an interaction of climate covariates with location in a preliminary analysis. We also modeled  $p$  as a function of location to account for possible differences in encounter probability between study locations.

Thus, for each species, the starting point for our two-step analysis was the general CJS model:

$$\phi (\text{temperature} + \text{precipitation} + \text{temperature}:\text{precipitation} + \text{location})$$

$$p (\text{location}).$$

For each species, we tested the goodness-of-fit of the general CJS model using the program RELEASE embedded within the program MARK. RELEASE tests several important assumptions of mark–recapture including issues relating to transient individuals. We found that we did not need to account for transient individuals in our data. We also tested for overdispersion using the *Median- $\hat{c}$*  routine in MARK. A model is overdispersed when  $\hat{c} > 1$ ;  $\hat{c}$  is used to scale the deviance when calculating  $AIC_c$  such that the quasi-likelihood adjusted  $AIC_c$  ( $QAIC_c$ ) is more heavily penalized by the number of parameters (Cooch & White, 2006). If the confidence intervals of the estimated  $\hat{c}$  for a general model did not overlap 1, the estimated  $\hat{c}$  was used in all subsequent model permutations. When the general

model failed to numerically converge onto reasonable point and error estimates (see below), we estimated  $\hat{c}$  using the most general nested model (Table S1) that successfully converged.

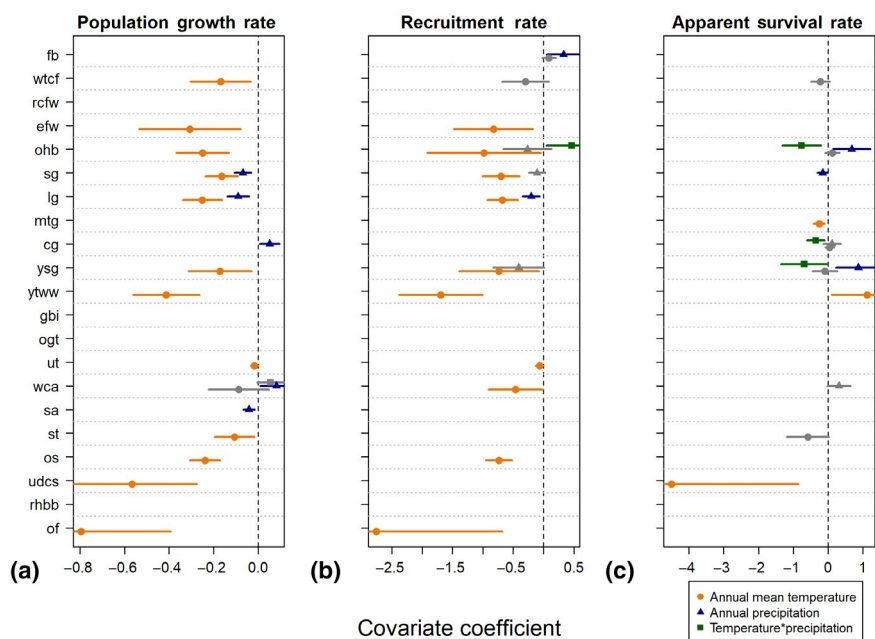
Next, we ran all model permutations nested within the general model (Table S1) yielding a total of 20 models (ten  $\varphi$  formulae  $\times$  two  $p$  formulae) per species including the general and constant models. For species found only in one of the two study locations, we omitted the location covariate and thus the candidate model set for these species included only five models (five  $\varphi$  formulae  $\times$  one  $p$  formula). We also censored models that failed to numerically converge onto reasonable point and error estimates—examples being models with an error estimate on coefficients of 0 or that were unrealistically large, or models with point estimates for  $\varphi$  or  $p$  whose confidence intervals converged toward both limit boundaries (i.e., 0 and 1). For some species with small sample sizes, certain models failed to converge, thus not all covariate coefficients in a model set could be estimated for these species. We excluded species from the analysis having identified problems within program outputs such as unrealistic point estimates or standard errors, or warning messages indicating failure of the numerical optimization routine.

We next used Pradel models (Pradel, 1996) implemented in program MARK to estimate recruitment rates ( $F$ ) and realized population growth rates ( $\lambda$ ). Pradel models take a reverse-time approach, estimating the rate at which individuals join, rather than leave the population (Nichols et al., 2000; Pradel, 1996).  $F$  incorporates additions to the population through both recruitment (i.e., born and survived) and immigration and is defined as the per capita rate of additions to the population (Cooch & White, 2006). For example, if  $F = 0.5$ , then the number of new individuals entering the population between time  $t$  and  $t + 1$  is half the number of individuals already in the population at  $t$ . Although estimates of  $F$  incorporated both births and immigration, out of >10,300 recaptures over the three-decade survey period we recorded only 13 instances of birds dispersing

within the two study systems from smaller to the larger study sites (see Figure 1, Korfanta et al. 2012), and we did not record any birds dispersing between the EUM and WUM study systems (Korfanta et al., 2012). Thus, we believe our estimates of recruitment largely reflect the contribution of births and juvenile survival rather than immigration.

Realized population growth,  $\lambda$ , is the sum of  $F$  and  $\varphi$  and represents the proportional change in population size between times  $t$  and  $t + 1$ . For example, if  $\lambda = 0.9$ , then the population size at time  $t + 1$  will be only 90% of the population size at time  $t$ . Importantly, changes in  $\lambda$  are not the same as changes in population size.  $\lambda$  can be constant over time (e.g., 0.9) and result in population declines (Figure S2[iv]). Conversely,  $\lambda$  can decrease over time without the population declining if  $\lambda$  remains greater than 1 (Figure S2[ii]). We used the same 10 formulae to model  $\lambda$  and  $F$  as were used to model  $\varphi$  in the CJS models (Table S1). Although Pradel models estimate  $\varphi$  and  $p$ , we constrained these parameters by conditioning on the formulae for  $\varphi$  and  $p$  from the top-ranked CJS model for each species (Korfanta et al., 2012). Consequently, in the Pradel candidate model set, formulae for  $\lambda$  or  $F$  varied across models but formulae for  $\varphi$  and  $p$  remained constant across models.

For each species, we selected the top-ranked model for  $\varphi$  (CJS models) and for  $F$  and  $\lambda$  (Pradel models) from the candidate model sets based on (Q)AIC<sub>c</sub> (Burnham & Anderson, 2002), and extracted the coefficient estimates and 95% confidence intervals from the top-ranked models. We also calculated  $R^2_{Dev}$  as a measure of the proportion of variation explained by the model covariates (Grosbois et al., 2008), as well as the model weight which gives the strength of evidence for that model relative to all the other models in the model set (Burnham & Anderson, 2002). We based our inferences on coefficients from the top-ranked model rather than model-averaged coefficients because coefficients cannot be validly averaged across models (Cade, 2015). Model rankings are provided in Table S6. We considered a



**FIGURE 2** The association between demographic rates and temperature and precipitation for 21 understory bird species between 1987 and 2016 in the East and West Usambara Mountains, Tanzania. The effects of climate covariates are displayed in relation to (a) realized population growth rates, (b) recruitment rates and (c) apparent survival rates. Coefficients and 95% confidence intervals (CI) are displayed for the top-ranked model for a given parameter. If the 95% CI on coefficients overlap 0, point estimates and CI are displayed in gray. If a top-ranked model for a species does not contain a climate covariate, point estimates and CI are not presented for the species. Species code follows Table 1



covariate to be an important predictor variable for a demographic parameter if the confidence interval on its coefficient did not overlap 0. We assessed the relative importance of covariates across species by tabulating the frequency that a covariate, with a confidence interval that did not overlap 0, appeared in the top-ranked model. When plotting species-specific coefficients (Figure 2), we display only the coefficients from the top-ranked model. If the top-ranked model for a given species did not contain a particular climate covariate, neither a point estimate nor confidence interval are presented. For species with smaller sample sizes, it was not always possible to estimate every covariate coefficient at least once, as indicated in the results. We also present average estimates for  $\lambda$ ,  $F$ , and  $\varphi$  from the constant models (Figure S3a; Table S2), as well as average estimates of  $\lambda$  by location (EUM vs. WUM) to compare locations (Figure S3b).

## 2.5 | Trait analyses

It has been hypothesized that in response to global warming the demographic rates of tropical montane bird species found further below their elevational range midpoint should be lower than the demographic rates of species found closer to their elevational range midpoint. This is because global warming should more adversely impact demographic rates of species found closer to their warm-edge elevational range limit than species found further from their warm-edge elevational range limit (Srinivasan & Wilcove, 2020). It has also been hypothesized that species with smaller body mass may be more sensitive than large-body mass species to changes over time in environmental temperature due to their higher surface-area-to-volume ratio and/or sensitivity to temperature-induced changes in food availability (Srinivasan & Wilcove, 2020).

We assessed these two hypotheses by regressing estimates of  $\lambda$  from the constant Pradel model ( $n = 21$ ) in a linear mixed model against the difference between mean elevation of the study locations (1169 m) and the elevational range midpoint of each species (hereafter “midpoint difference”) as well as against species’ log(body mass). Data for both explanatory variables were taken from a global dataset of bird traits (Şekercioğlu et al., 2019). Both variables were scaled to have a mean of 0 and a standard deviation of 1. We also included taxonomic family in the model as a random effect to account for possible phylogenetic differences. We then constructed a second model having the same structure, but in which the response variable was replaced with the temperature coefficients for  $\lambda$  from the top-ranked  $\lambda$  model that contained temperature. We again deemed explanatory variables to be statistically important if the 95% confidence intervals on the coefficients did not overlap 0.

## 2.6 | Post-hoc analysis

Because temperature generally increased over time (Figure 1a), associations between demographic rates and temperature may be spurious and artifacts of both being correlated with time. Consequently,

in a post-hoc analysis, we substituted a linear time covariate for the temperature covariate in the top-ranked  $\lambda$  models that contained temperature. We reasoned that if a linear trend over time was a better predictor than temperature, then there was insufficient evidence that temperature was a driver of the observed changes in the demographic rate; whereas if temperature was a better predictor than time, then this provided evidence that temperature likely either directly or indirectly drove changes in the demographic rate, because it explained additional variation that time alone could not explain.

All analyses were carried out in R version 3.2.4 (R Core Team, 2020) using the package RMark (Laake & Rexstad, 2006) for mark-recapture analyses which interfaces with program MARK (Cooch & White, 2006).

## 3 | RESULTS

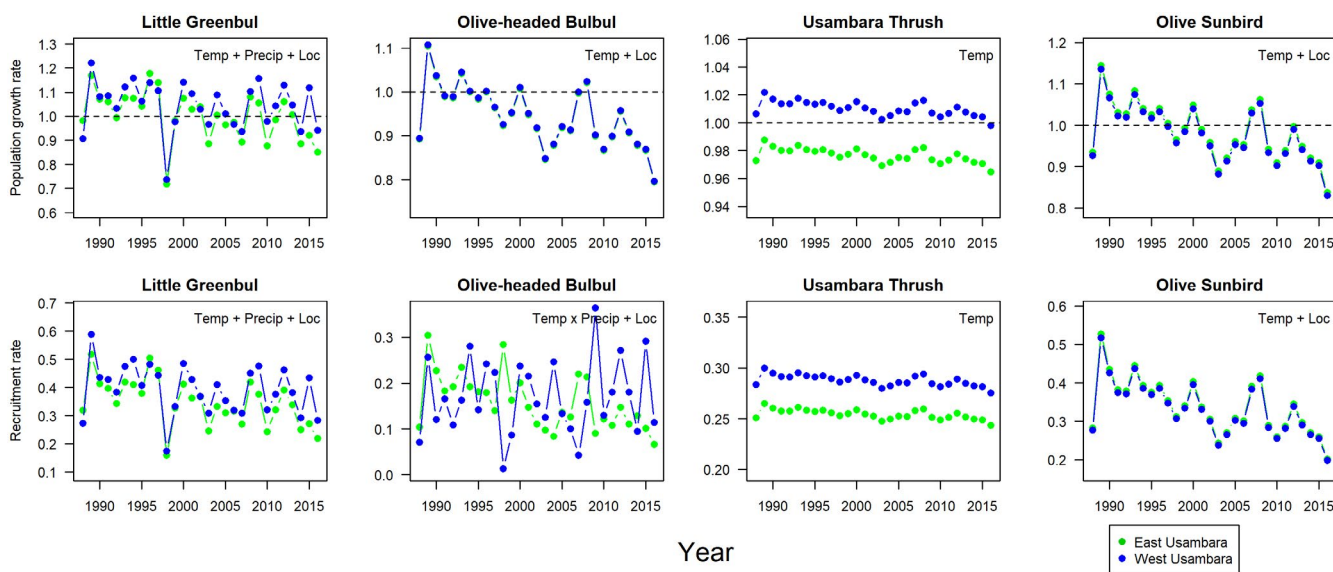
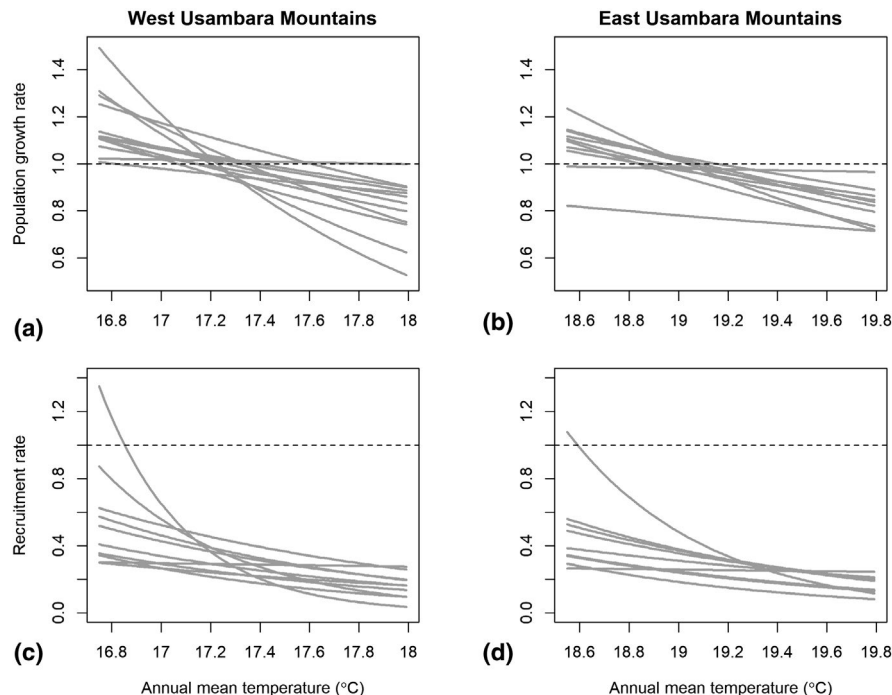
Over the 30-year study period, 16,624 birds of 63 species were captured of which there were sufficient sample sizes ( $>100$  individuals or encounter probability  $>0.1$ ) to estimate demographic rates for 21 species (Table 1). Of these 21 species, 18 species occurred both in the EUM and WUM (Table 1). Under a constant model for these 21 species (Table S2), population growth rates ( $\lambda$ ) ranged from 0.91 (Red-capped Forest-warbler) to 1.01 (Little Greenbul) with a mean of  $0.98 \pm 0.01$  ( $\pm$ SE; Figure S3a). Recruitment rates ( $F$ ) ranged from 0.17 (Olive-headed Bulbul) to 0.64 (Red-headed Bluebill) with a mean of  $0.31 \pm 0.02$  (Table S2). Apparent survival rates ( $\varphi$ ) ranged from 0.37 (Red-headed Bluebill) to 0.78 (Olive-headed Bulbul) with a mean of  $0.67 \pm 0.02$  (Table S2). Encounter probabilities ( $p$ ) ranged from 0.09 (Olive-headed Bulbul) to 0.63 (Red-headed Bluebill) with a mean of  $0.23 \pm 0.03$  (Table S2).

Across the 21 focal species, the most important climate covariate associated with  $\lambda$  was annual mean temperature, which appeared in the top-ranked model for 13 species (62%; Figure 2a; Table 1). For these 13 species, we also compared the top-ranked model with competing models that had similar support (i.e.,  $\Delta$ AICc  $<2$ ). For two of the 13 species, the top-ranked model was the only model for which  $\Delta$ AICc  $<2$ , while for eight species all models for which  $\Delta$ AICc  $<2$  also contained temperature (Table S3). These results indicate support for temperature across competing models. For 12 species (57%), the coefficient for temperature was negative and the confidence interval did not overlap 0, indicating that  $\lambda$  was negatively associated with temperature for more than one-half of all focal species (Figures 3 and 4, Figure S4). Because temperature generally increased over time (Figure 1) and thus is correlated with time, in a post-hoc analysis we replaced the temperature covariate with a time covariate (year) for the 12 species that contained temperature in their top-ranked  $\lambda$  model and for which the confidence interval on the temperature coefficient did not overlap 0. We then compared the two models (Table S4). For six species, the model containing temperature performed better than the model containing time ( $\Delta$ AICc  $>2$ ; Table S4); for three species, the models were equivocal ( $|\Delta$ AICc|  $\leq 2$ ); and for three species the model containing time performed better ( $\Delta$ AICc  $< -2$ ).

**TABLE 1** Top-ranked mark-recapture models for 21 focal understory bird species sampled between 1987 and 2016 in the East (EUM) and West (WUM) Usambara Mountains of Tanzania. Data are provided for the top-ranked CJS model (apparent survival,  $\phi$ , and encounter probability,  $p$ ), recruitment ( $F$ ) model, and population growth rate ( $\lambda$ ) model. The top-ranked model was the model with the lowest  $AIC_c$  in the model set. For each model, the covariates present in the model, the  $R^2_{Dev}$ , and the model weight are displayed. For the model covariates, T = temperature, P = precipitation, L = location, and c = constant

Species code	Species	Location	Survival model			Recruitment model			Population growth model		
			$\phi$	$p$	Model weight	$F$	$R^2_{Dev}$	Model weight	$\lambda$	$R^2_{Dev}$	Model weight
fb	<i>Batis mixta</i>	EUM,WUM	c	L	0.99	0.24	T + P	0.17	0.19	c	0.23
wicf	<i>Elminia albonotata</i>	EUM,WUM	T	L	0.17	0.11	T + L	0.20	0.33	T + L	0.39
rcfw	<i>Artisornis metopias</i>	EUM,WUM	c	c	0.36	0.40	c	c	0.23	c	0.22
efw	<i>Bradypterus lopezi</i>	EUM,WUM	c	c	0.25	0.25	T + L	0.19	0.46	T + L	0.44
ohb	<i>Arizelocichla striifacies</i>	EUM,WUM	T*P	c	0.37	0.18	T*P + L	0.20	0.19	T + L	0.64
sg	<i>Arizelocichla masukuensis</i>	EUM,WUM	P	L	0.24	0.20	T + P + L	0.17	0.42	T + P + L	0.68
lg	<i>Eurillas virens</i>	EUM,WUM	c	c	0.17	0.17	T + P + L	0.38	0.61	T + P + L	0.62
mtg	<i>Phyllastrephus albigula</i>	EUM,WUM	T	c	0.34	0.15	L	0.30	0.37	c	0.26
cg	<i>Phyllastrephus cabanisi</i>	EUM,WUM	T*P	c	0.25	0.25	c	c	0.36	P + L	0.18
ysg	<i>Phyllastrephus flavostriatus</i>	EUM,WUM	T*P	L	0.48	0.21	T + P + L	0.28	0.30	T + L	0.40
ytw	<i>Phylloscopus ruficapilla</i>	EUM,WUM	T + L	c	0.30	0.24	T + L	0.54	0.52	T + L	0.46
gbi	<i>Illadopsis distans</i>	EUM,WUM	c	c	0.20	0.20	c	c	0.25	c	0.25
ogt	<i>Geokichla gurneyi</i>	EUM,WUM	c	c	0.18	0.18	c	c	0.34	c	0.34
ut	<i>Turdus roehli</i>	EUM,WUM	c	c	0.21	0.21	T	0.12	0.22	T	0.22
wca	<i>Chamaetylas fuelleborni</i>	EUM,WUM	P	c	0.12	0.16	T + L	0.32	0.31	T*P + L	0.35
sa	<i>Sheppardia sharpei</i>	EUM,WUM	L	L	0.67	0.26	L	0.34	0.26	P	0.24
st	<i>Modulatrix stictigula</i>	EUM,WUM	T	c	0.17	0.24	c	c	0.25	T	0.34
os	<i>Cyanomitra olivacea</i>	EUM,WUM	c	L	0.09	0.13	T + L	0.48	0.46	T + L	0.40
udcs	<i>Cinnyris usambaricus</i>	WUM	T	c	0.35	0.38	c	c	0.37	T	0.61
rhhb	<i>Spermophaga ruficapilla</i>	EUM	c	c	0.49	0.49	c	c	0.51	c	0.51
of	<i>Linurgus olivaceus</i>	WUM	c	c	0.52	0.52	T	0.37	0.64	T	0.67

**FIGURE 3** The relationships between demographic rates and temperature for understory bird species in the East and West Usambara Mountains, Tanzania. Population growth rates ( $\lambda$ ) are plotted as a function of temperature in the (a) West Usambara Mountains and the (b) East Usambara Mountains. Recruitment rates ( $F$ ) are also plotted as a function of temperature in the (c) West Usambara Mountains and the (d) East Usambara Mountains. Each line represents the predicted values of a demographic rate as a function of temperature for a species whose top-ranked model contained temperature. Values are presented over the range of temperatures observed at each study location

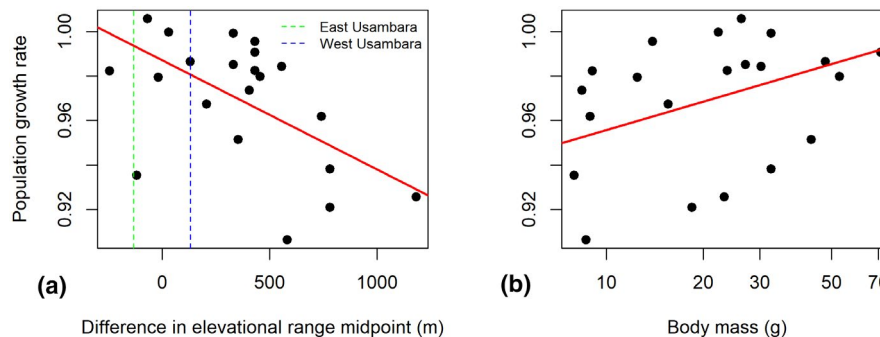


**FIGURE 4** Interannual variation in point estimates of realized population growth rate ( $\lambda$ ) and recruitment rate ( $F$ ) as a function of the climate covariates and location in the top-ranked Pradel models for four representative species in the East and West Usambara Mountains. Results for apparent survival rates are not displayed because apparent survival was relatively unaffected by either temperature or precipitation. Similar plots for other focal species are provided in Figures S4, S5, and S6

Annual precipitation appeared in the top-ranked  $\lambda$  model for five species (24%; Figure 2a; Table 1) and in all cases the confidence interval on the coefficient did not overlap 0. For these species, population growth rates fluctuated with precipitation (Figure 4; Figure S4), although the coefficients were on average a third of the size of the temperature coefficients. The precipitation coefficient was positive for two species and negative for three. The interaction term between temperature and precipitation did not appear in any of the top-ranked  $\lambda$  models.

Temperature was also the most important climate covariate associated with recruitment ( $F$ ). Across focal species, temperature appeared in the top-ranked model for 12 species (Figure 2b; Table 1). For 10 species (48%), the confidence interval on the coefficient for temperature did not overlap 0 and  $F$  was negatively associated with temperature (Figures 3 and 4; Figure S5). Precipitation appeared in the top-ranked  $F$  model for five species (29%), although the effect sizes were again much smaller than for temperature (Figure 2b; Table 1). For two species (17%), the confidence interval on the coefficient for





**FIGURE 5** The relationships between population growth rates and elevational range and body mass for understory bird species in the Usambara Mountains, Tanzania. Estimates of  $\lambda$  from constant models ( $n = 21$ ) were regressed against (a) the difference between the mean elevation of the study sites and the elevational midpoint of species and (b) log(body mass) in a linear mixed model. Dashed vertical lines illustrate the elevation of the study locations in the East and West Usambara Mountains

precipitation did not overlap 0, and the coefficient was positive for one species (Figure S5). The interaction term appeared in the top-ranked model for one species (Olive-headed Bulbul), where the confidence interval on the coefficient did not overlap 0.

The association of temperature and precipitation with  $\varphi$  was inconsistent across species (Figure 2c; Table 1). Although temperature appeared in the top-ranked models for eight species (38%), for only three species did the confidence intervals for coefficients not overlap 0 and these coefficients were positive for one species and negative for two (Figure S6). Similarly, precipitation appeared in the top-ranked  $\varphi$  models for five species (20%) of which the confidence intervals on the coefficients did not overlap 0 for three species and the coefficients were positive for two species and negative for one (Figure S6). The interaction term appeared in 3 of 19 top-ranked models (14%) and in all cases the confidence interval on the coefficient did not overlap 0 and the coefficient was negative.

For the 18 focal species that occurred in both the EUM and WUM, differences in average  $\lambda$  between locations varied inconsistently across species (Figure S3b). However, for the 10 species found both in the EUM and WUM and for which the temperature covariate was contained within the top-ranked  $\lambda$  model,  $\lambda$  was 2% higher on average in the WUM than the EUM (Figure S3b). The location covariate appeared in the top-ranked  $\lambda$  model for 10 species (57%; Table 1). For nine species (48%), the confidence interval on the location coefficient did not overlap 0. For eight of these species, the location covariate appeared in combination with the temperature covariate in the top-ranked model. Without the location covariate, average  $\lambda$  would have been much higher in the WUM due to the cooler temperatures. However, the presence of the negative location coefficient reduced the average difference in  $\lambda$  between locations (Figure S3b). Thus,  $\lambda$  estimates were more similar between locations (Figures 3 and 4; Figure S4) than predicted by the absolute difference in temperature alone (Figure 1a).

The location covariate appeared in the top-ranked  $F$  model for 11 species (52%; Table 1) and in all cases the confidence intervals on the coefficient did not overlap 0. For nine of these species, the location covariate appeared in combination with the temperature

covariate in the top-ranked model. Again, the presence of the negative location coefficient reduced average differences in  $F$  between sites. Thus,  $F$  estimates were more similar between the EUM and WUM study locations (Figures 3 and 4; Figure S5) than predicted by the absolute difference in temperature between locations (Figure 1a). The location coefficient associated with  $\varphi$  appeared in the top-ranked model for two species (10%), and in both cases the coefficients had confidence intervals that did not overlap 0, and  $\varphi$  was higher in the WUM. For encounter probability ( $p$ ), the location coefficient appeared in the top-ranked model for seven species (38%) and in all cases the confidence intervals on the coefficients did not overlap 0 (Table S5).

Estimates of  $\lambda$  from the constant models were negatively associated with midpoint difference ( $-0.017$ , 95% CI:  $-0.027$  to  $-0.007$ ), indicating that species in the EUM and WUM occurring further below their elevational midpoint had lower population growth rates on average than species found closer to their elevational midpoint (Figure 5a). Estimates of  $\lambda$  from the constant models were also positively associated with body mass ( $0.012$ , 95% CI:  $-0.022$  to  $-0.002$ ), indicating that smaller-bodied species had lower population growth rates on average than larger-bodied species (Figure 5b). Temperature coefficients for  $\lambda$  from the top-ranked  $\lambda$  models were not significantly associated with body mass ( $0.092$ , 95% CI:  $-0.023$  to  $0.207 \pm 0.115$  CI) or the midpoint difference ( $-0.062$ , 95% CI:  $-0.167$  to  $0.043$ ).

## 4 | DISCUSSION

As global climate changes, species may find themselves in increasingly unfavorable environments. Knowledge of demographic rates is key to understanding population-level responses of species to climate change yet few studies have investigated this across communities in the tropics, especially in montane regions or in Africa (Sheldon, 2019). Here we report a negative association between realized population growth rates and annual mean temperature for 57% of focal species (Figures 2a and 3) meaning that, for these species, population growth rates averaged lower in warmer years. As temperatures increased over time, population growth rates

consequently decreased over time for these species (Figure 4; Figure S4). Of the 12 species having this negative association, the population growth rates of nine species averaged below 1 (Figure S3a), meaning that their population sizes also declined over the 30-year period and at an accelerating rate as  $\lambda$  decreased. The remaining three species may also see shrinking population sizes in the future if population growth rates continue to decrease.

Estimates of  $\lambda$  under the constant models were negatively associated with the difference between the mean elevation of the study sites and the elevational midpoint of species (Figure 5a). This result indicates that species at our study locations found below their elevational midpoint and closer to their warm-edge elevational range limit had on average lower population growth rates than species found closer to their elevational midpoint, resulting in declining population sizes (Figure 5a). This result also corroborates findings from a recent study from the eastern Himalayas (Srinivasan & Wilcove, 2020) that found temporal trends in apparent survival rates of understory bird species were negatively associated with the difference between study location elevation and the elevational range midpoint of species. In the Usambara Mountains, bird species with smaller body masses also tended to have lower population growth rates (Figure 5b) than bird species having larger body masses. We suspect this observed positive relationship between  $\lambda$  and body mass is most likely a result of the greater sensitivity of smaller-bodied species to temperature-induced changes in food availability (see below; Srinivasan & Wilcox, 2020). While results were very similar in direction of effect when we replaced  $\lambda$  estimates under the constant model with the temperature coefficients from the top-ranked  $\lambda$  model, the 95% confidence intervals did overlap 0. This latter result, however, is not particularly surprising due to the comparatively smaller sample size ( $n = 13$ ).

The negative association between population growth rate and temperature was shared among species that also varied widely in terms of other species traits. Population growth rates were negatively associated with temperature for both common (Olive Sunbird) and uncommon (Oriole Finch) species; edge-tolerant (Little Greenbul) and edge-averse (Spot-throat) species; terrestrial (Usambara Thrush) and midstory (Yellow-streaked Greenbul) species; and among multiple feeding guilds—insectivores (Yellow-throated Woodland-warbler), nectarivores (Usambara Double-collared Sunbird), granivores (Oriole Finch), and frugivores (Olive-headed Bulbul). These patterns indicate that associations between population growth rates and increasing temperatures over the last three decades were widespread across the Usambara understory bird community.

While 21 species were included in the analysis presented here—one of the largest such community-wide mark–recapture analyses to be conducted in the tropics—an additional 42 species were captured over the course of the study for which sample sizes were too small or encounter probabilities too low to estimate demographic rates. However, we believe that, based on the species traits of the more common temperature-sensitive species in the Usambara understory bird community, temperature-associated declines have very likely

also occurred among many of the rarer species in this same community as well as among many of the common and uncommon understory bird species occurring in other nearby Eastern Arc Mountains (see Figure 1, Newmark & McNeally, 2018) that share similar bird communities. Elsewhere in the tropics, there is evidence that recent climate change has contributed to community-wide declines of bird species in lowland (Blake & Loiselle, 2015; Lister & Garcia, 2018; Stouffer et al., 2020) and in other montane communities (Latta et al., 2011), to elevational range contractions (Neate-Clegg et al., 2020), and to mountaintop extinctions (Freeman, Scholer, et al., 2018).

For 12 of the 21 focal species for which population growth rates were not associated with temperature, three of these species' population growth rates were associated with annual precipitation (Figure 2a). However, the association of precipitation with  $\lambda$  was inconsistent in terms of the direction of the effect. This result contrasts with that observed in lowland Panama where population growth rates for approximately one-third of species in the observed community ( $n = 20$ ) were found to be negatively associated with the length of the dry season (Brawn et al., 2017). Annual precipitation in the EUM and WUM (Figure 1) is, however, less seasonal than in Panama. In Panama, 10% of the annual precipitation falls on average in the dry season which extends from mid-December to late April (Kupers et al., 2019). In contrast, at the study sites in the EUM and WUM 28% and 30%, respectively, of annual mean precipitation (Figure 1b) fell during the two dry seasons (January–February; July–October) over the course of this study. Thus, we suspect resource availability during the dry seasons for understory birds in the Usambara Mountains is less constraining than in Panama.

In a post-hoc analysis, we replaced the temperature covariate with a time covariate (year) for the species that contained temperature in their top-ranked  $\lambda$  model ( $n = 12$ ). For six of these species, a temperature covariate performed better than a time covariate, for three species results were equivocal, and for another three species the time covariate performed better than the temperature covariate. These results indicate there is strong support for an association between decreasing population growth rates and rising temperature for over one-quarter of the focal understory species. For the species for which results were equivocal ( $|\Delta AIC_c| \leq 2$ ), additional data may provide evidence for even broader community-wide impacts. Furthermore, even when the time model performed better than the temperature model, temperature cannot be ruled out as the driver behind decreases in  $\lambda$ . It is possible, for example, that temperature-driven changes in habitat and resource availability accrue very slowly over time (Feeley et al., 2011) and consequently changes in demographic rates may not closely track interannual fluctuations in temperature (Neate-Clegg et al., 2020; Srinivasan & Wilcove, 2020).

Yet could other confounding factors affect population growth rates and recruitment rates among understory bird species over time? We can exclude two of the more likely confounding factors for observed declines in  $\lambda$ : change in forest block area and matrix habitat composition. Based on a comparison of historic and current aerial imagery of the two study sites, forest block area has not changed in the EUM and WUM while matrix habitat composition has

changed minimally (<1.8%) in the EUM and has not changed in the WUM (Figure S1). To our knowledge, the only anthropogenic-driven change during the study period has been the increase in temperature. Thus, because temperature tended to predict population growth rates better than time, and because of the lack of plausible alternative hypotheses, we believe that temperature-mediated effects are the most parsimonious explanation for the negative association we observed between temperatures and the demographic rates of over one-quarter of all focal species in the Usambara Mountains. We expect that climate change will exacerbate the negative effects of increasing temperature we observed through continued global warming.

Changes in the population growth rates of focal species were driven largely by changes in recruitment rates rather than apparent survival rates which is consistent with findings in the Neotropics (Blake & Loiselle, 2015; Brawn et al., 2017). Apparent survival rates were relatively unaffected by changes in temperature or precipitation (Figure 2c), contrary to results from Himalayan birds that linked temperature increases to decreases in survival over time (Srinivasan & Wilcove, 2020). On the other hand, recruitment rates for understory bird species in the Usambara Mountains had a pronounced negative association with temperature for almost one-half of all focal species (Figure 2b). Although little is known about the direct effects of increased temperature on juvenile tropical birds, there is evidence from higher latitudes that altricial chicks may be vulnerable to warming (Greño et al., 2008). Yet, there is also evidence that adult birds in the tropics are not constrained by their physiological tolerance to temperatures (Freeman, 2016; Londoño et al., 2017). Moreover, parents can thermally buffer eggs and nestlings through nest site selection, nest structure, and nest materials (Heenan, 2013). Hence, we believe indirect effects are a more likely mechanism for the negative association between recruitment and temperature as a result of potential changes in food supply (Chapman et al., 2005; Ferger et al., 2014; Lister & Garcia, 2018; Powell et al., 2015), breeding season length (Brawn et al., 2017), and/or predation pressure (Ghalambor et al., 2013), which, in turn, may be climate sensitive (Blake & Loiselle, 2015; Williams & Middleton, 2008).

In montane habitats in the Afrotropics, temperature has been shown to influence fruit and flower productivity (Potts et al., 2020) and phenology (Chapman et al., 2005), and thus changes in temperature could indirectly impact food availability for frugivores, nectivores, and granivores. Changes in temperature could also affect food availability for insectivores as evidenced by recent temperature-associated declines of arthropods in the Neotropics. In Puerto Rico, mean maximum temperatures increased by 2.0°C between 1976 and 2012. During this same time period, dry weight biomass of arthropods decreased by 4 to 8 times in sweep samples and 30 to 60 times in sticky traps (Lister & Garcia, 2018). Changes in temperature may also alter the phenology of peak insect abundance (Ovaskainen et al., 2013), leading to mismatches in food availability (Renner & Zohner, 2018; Visser & Gienapp, 2019). When resources are scarce, adult birds may provide less food to their young (Ghalambor &

Martin, 2001; Tieleman et al., 2008), and this under-provisioning could extend into the post-fledging period (Tarwater & Brawn, 2010). Additionally, newly independent juveniles may have greater difficulty locating and acquiring food for themselves (Tarwater et al., 2011; Weathers & Sullivan, 1989; Wheelwright & Templeton, 2003), also reducing post-fledging survival.

Changes in temperatures may also mediate competitive interactions. The elevational ranges of many tropical montane species are influenced by congeneric competitors (Boyce & Martin, 2019; Freeman et al., 2016; Jankowski et al., 2010; Srinivasan et al., 2018). Climate-induced changes in the abundance of species may potentially alter patterns of competition among species affecting nest-site selection, parental energy expenditure, or food provisioning, and thus recruitment (Martin & Martin, 2001). However, in our study system, there were only two focal species—Sharpe's Akalat and Montane Tiny Greenbul—that have congeners with partially overlapping ranges. Yet for neither of these two focal species were recruitment rates associated with temperature.

Finally, increased temperatures may increase nest predation pressures and/or predation risk which, in turn, can influence provisioning rates (Ghalambor et al., 2013) and juvenile survival (Tarwater et al., 2011), thus impacting recruitment. In our study system, nest predation accounts for >97% of all nest failures (Newmark & Stanley, 2011) with snakes being the dominant nest predator (Newmark, 2018). Annual snake activity patterns are also highly seasonal at our study locations (1037 and 1301 m) with considerably lower activity levels during the cold season (March–September) than the hot season (October–February; Newmark, personal observation) and this is consistent with reported activity patterns for snakes elsewhere in montane habitat in the tropics (Marques et al., 2006). Locomotor performance, movement, and length of annual activity period of snakes have been shown to be associated with increased temperatures (Gerald et al., 2008; Moreno-Rueda et al., 2009; Peterson et al., 1993) and increased movement of snakes, in turn, has been shown to be positively associated with increased nest predation rates in birds (DeGregorio et al., 2015; Sperry et al., 2008, 2012). Furthermore, nest predation by snakes and birds in temperate regions is also shown to be positively associated with increasing temperature over a recent decadal period (1997–2010; Cox et al., 2013).

Although population growth rates were higher on average in the WUM, the higher elevation location, differences in population growth and recruitment rates of temperature-sensitive bird species between the EUM and WUM (Figure 4) tended to be smaller (Figure S3b) than predicted based on the absolute difference in temperature between study locations (Figure 1a). There are a number of reasons why average demographic rates may be more similar than expected between study locations. First, the location covariate in the general model captures unmeasured differences between the locations (e.g., resource availability, fragment isolation, predation pressure), distinct from temperature and precipitation, that may affect average demographic rates. Consequently, these other location-specific differences may be masking the effect of temperature on demographic rates between locations.

Second, most tropical montane bird species can physiologically tolerate a much broader range of temperatures than they currently experience (Khaliq et al., 2014; Londoño et al., 2017; Pollock et al., 2020). In the Usambara Mountains, the elevational range for most of the 21 focal species extends from 600 to 2100 m (Stuart, 1983). Thus, most of our focal species can tolerate a wide range of temperatures. Moreover, these spatial temperature gradients have existed for tens of thousands of years in the Eastern Arc Mountains of Tanzania and Kenya (Lovett & Wasser, 2008), providing ample time for species to adapt. By contrast, small annual changes in average temperature as a result of global warming have accrued at a rapid rate over recent decades (NOAA, 2019), and can have large effects on tropical bird populations (Latta et al., 2011; Stouffer et al., 2020) and distributions (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018) as a result of indirect biotic interactions. For example, increasing temperatures over time could drive declines in invertebrate abundance (Lister & Garcia, 2018) at both study locations, reducing the provisioning rates of adults to nestlings and fledglings. Alternatively, increasing temperatures could increase snake activity (DeGregorio et al., 2015; Gerald et al., 2008; Moreno-Rueda et al., 2009; Sperry et al., 2008, 2012) and as a result nest predation rates at both locations (Cox et al., 2013). In summary, our results emphasize the importance of comparatively sudden annual increases in temperature over time as drivers of demographic rates of understory birds in the Usambara Mountains as opposed to spatial variation in temperature between locations.

In this study, we found temperature-associated decreases in population growth rates for 6 (29%) of 21 focal species in an Afrotropical understory bird community, driven largely by changes in recruitment rates. In addition, population growth rates were lower, and populations therefore declined more, for species occurring further below their elevational midpoint and for species with smaller body mass. However, our knowledge of how increases in temperature are integrated into vital rates of tropical bird species clearly remains poor. Understanding the proximate mechanisms mediating demographic changes in tropical understory bird species is critical for developing effective conservation interventions and thus should be a high priority in future research in the tropics. Over the next four decades, annual mean temperature across Tanzania is predicted to increase by 1.0–2.7°C while annual precipitation is also projected to increase (McSweeney et al., 2013). Thus, the effects of climate change on tropical bird species demography will almost certainly continue to increase over time.

## ACKNOWLEDGEMENTS

We thank DANIDA, Field Museum of Natural History, Chicago Zoological Society, Sophie Danforth Conservation Fund, National Geographic Society (#524-94, #977815), Earthwatch Institute, John D. and Catherine T. MacArthur Foundation, Critical Ecosystem Partnership Fund, World Wide Fund for Nature, JRS Biodiversity Foundation (#60708\_TAWIRI), and US Geological Survey for support; the Tanzania Wildlife Research Institute and Tanzania Commission for Science and Technology for permission to conduct this study; V. Mkongewa, A. Mkongewa, D. Barua, H. Pombekali, and

J. Ayubu for their assistance in the field; and D. Mtui for administrative and logistical support. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## DATA AVAILABILITY STATEMENT

The data supporting this study will be deposited in Dryad upon acceptance of the manuscript.

## ORCID

Montague H. C. Neate-Clegg  <https://orcid.org/0000-0001-9753-6765>

## REFERENCES

- Blake, J. G., & Loiselle, B. A. (2015). Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. *PeerJ*, 2015(8). <https://doi.org/10.7717/peerj.1177>
- Boyce, A. J., & Martin, T. E. (2019). Interspecific aggression among parapatric and sympatric songbirds on a tropical elevational gradient. *Behavioral Ecology*, 30(2), 541–547. <https://doi.org/10.1093/behec/ory194>
- Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D., & Tarwater, C. E. (2017). Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change*, 7(2), 133–136. <https://doi.org/10.1038/nclimate3183>
- Brodie, J. F., & Newmark, W. D. (2019). Heterogeneous matrix habitat drives species occurrences in complex, fragmented landscapes. *American Naturalist*, 193(5), 748–754. <https://doi.org/10.1086/702589>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Retrieved from [http://cds.cern.ch/record/1608735/files/9780387953649\\_TOC.pdf](http://cds.cern.ch/record/1608735/files/9780387953649_TOC.pdf)
- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96(9), 2370–2382.
- Chapman, C. A., Chapman, L. J., Struhsaker, T. T., Zanne, A. E., Clark, C. J., & Poulsen, J. R. (2005). A long-term evaluation of fruiting phenology: Importance of climate change. *Journal of Tropical Ecology*, 21(1), 31–45. <https://doi.org/10.1017/S0266467404001993>
- Cooch, E. G., & White, G. C. (2006). *Program MARK: A gentle introduction* (17th ed.). <https://doi.org/10.1080/00063659909477239>
- Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, 51(3/4), 429. <https://doi.org/10.2307/2334149>
- Cox, W. A., Thompson, F. R., & Reidy, J. L. (2013). The effects of temperature on nest predation by mammals, birds, and snakes. *The Auk*, 130(4), 784–790. <https://doi.org/10.1525/auk.2013.13033>
- DeGregorio, B. A., Westervelt, J. D., Weatherhead, P. J., & Sperry, J. H. (2015). Indirect effect of climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation. *Ecological Modelling*, 312, 239–246. <https://doi.org/10.1016/j.ecolmodel.2015.05.031>
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105(18), 6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Doyle, S., Cabot, D., Walsh, A., Inger, R., Bearhop, S., & McMahon, B. J. (2020). Temperature and precipitation at migratory grounds influence demographic trends of an Arctic-breeding bird. *Global Change Biology*, 26(10), 5447–5458. <https://doi.org/10.1111/gcb.15267>
- Dybala, K. E., Eadie, J. M., Gardali, T., Seavy, N. E., & Herzog, M. P. (2013). Projecting demographic responses to climate change: Adult and



- juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Global Change Biology*, 19(9), 2688–2697. <https://doi.org/10.1111/gcb.12228>
- Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R., & Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, 38(4), 783–791. <https://doi.org/10.1111/j.1365-2699.2010.02444.x>
- Feeley, K. J., Stroud, J. T., & Perez, T. M. (2017). Most 'global' reviews of species' responses to climate change are not truly global. *Diversity and Distributions*, 23(3), 231–234. <https://doi.org/10.1111/ddi.12517>
- Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M., & Böhning-Gaese, K. (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, 23(5), 541–549. <https://doi.org/10.1111/geb.12151>
- Freeman, B. G. (2016). Thermal tolerances to cold do not predict upper elevational limits in New Guinean montane birds. *Diversity and Distributions*, 22(3), 309–317. <https://doi.org/10.1111/ddi.12409>
- Freeman, B. G., Class Freeman, A. M., & Hochachka, W. M. (2016). Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient. *Ibis*, 158(4), 726–737. <https://doi.org/10.1111/ibi.12384>
- Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, 27(11), 1268–1276. <https://doi.org/10.1111/geb.12774>
- Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V., & Fitzpatrick, J. W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences of the United States of America*, 115(47), 11982–11987. <https://doi.org/10.1073/pnas.1804224115>
- Gerald, G. W., Mackey, M. J., & Claussen, D. L. (2008). Effects of temperature and perch diameter on arboreal locomotion in the snake *Elaphe guttata*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 309(3), 147–156. <https://doi.org/10.1002/jez.443>
- Ghalambor, C. K., & Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, 292, 494–497.
- Ghalambor, C. K., Peluc, S. I., & Martin, T. E. (2013). Plasticity of parental care under the risk of predation: How much should parents reduce care? *Biology Letters*, 9(4), 20130154. <https://doi.org/10.1098/rsbl.2013.0154>
- Greño, J. L., Belda, E. J., & Barba, E. (2008). Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. *Journal of Avian Biology*, 39(1), 41–49. <https://doi.org/10.1111/j.0908-8857.2008.04120.x>
- Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A. P., & Weimerskirch, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, 83(3), 357–399. <https://doi.org/10.1111/j.1469-185X.2008.00047.x>
- Hall, J., Burgess, N. D., Lovett, J., Mbilinyi, B., & Gereau, R. E. (2009). Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. *Biological Conservation*, 142(11), 2510–2521. <https://doi.org/10.1016/j.biocon.2009.05.028>
- Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations – The CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3), 623–642. <https://doi.org/10.1002/joc.3711>
- Heenan, C. B. (2013). An overview of the factors influencing the morphology and thermal properties of avian nests. *Avian Biology Research*, 6(2), 104–118. <https://doi.org/10.3184/003685013X13614670646299>
- Hilker, T., Lyapustin, A. I., Tucker, C. J., Hall, F. G., Myneni, R. B., Wang, Y., Bi, J., Mendes de Moura, Y., & Sellers, P. J. (2014). Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, 111(45), 16041–16046. <https://doi.org/10.1073/pnas.1404870111>
- Jankowski, J. E., Robinson, S. K., & Levey, D. J. (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology*, 91(7), 1877–1884. <https://doi.org/10.1890/09-2063.1>
- Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, 101(919), 233–249.
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, 52(1/2), 225–247. <https://doi.org/10.2307/2333826>
- Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4. <https://doi.org/10.1038/sdata.2017.122>
- Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K., & Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 1–8. <https://doi.org/10.1098/rspb.2014.1097>
- Korfanta, N. M., Newmark, W. D., & Kauffman, M. J. (2012). Long-term demographic consequences of habitat fragmentation to a tropical understory bird community. *Ecology*, 93(12), 2548–2559. <https://doi.org/10.1890/11-1345.1>
- Kupers, S. J., Wirth, C., Engelbrecht, B. M. J., & Rüger, N. (2019). Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama. *Scientific Data*, 6(1), 1–9. <https://doi.org/10.1038/s41597-019-0072-z>
- Laake, J., & Rexstad, E. (2006). RMark - an alternative approach to building linear models in MARK. In E. G. Cooch, & G. C. White (Eds.), *Program MARK: A gentle introduction* (pp. 1–111). [http://www.phidot.org/software/mark/docs/book/pdf/app\\_3.pdf](http://www.phidot.org/software/mark/docs/book/pdf/app_3.pdf)
- Latta, S. C., Tinoco, B. A., Astudillo, P. X., & Graham, C. H. (2011). Patterns and magnitude of temporal change in avian communities in the Ecuadorian andes. *Condor*, 113(1), 24–40. <https://doi.org/10.1525/cond.2011.090252>
- Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62(1), 67–118.
- Lister, B. C., & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the United States of America*, 115(44), E10397–E10406. <https://doi.org/10.1073/pnas.1722477115>
- Londoño, G. A., Chappell, M. A., Jankowski, J. E., & Robinson, S. K. (2017). Do thermoregulatory costs limit altitude distributions of Andean forest birds? *Functional Ecology*, 31(1), 204–215. <https://doi.org/10.1111/1365-2435.12697>
- Lovett, J. C., & Wasser, S. K. (2008). Biogeography and ecology of the rain forests of eastern Africa. In J. C. Lovett & S. K. Wasser (Eds.), *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge University Press.
- Marques, O. A. V., Almeida-Santos, S. M., & Rodrigues, M. G. (2006). Activity patterns in coral snakes, genus *Micrurus* (Elapidae), in south and southeastern Brazil. *South American Journal of Herpetology*, 1(2), 114–120. [https://doi.org/10.2994/1808-9798\(2006\)1\[114:A PICSG\]2.0.CO;2](https://doi.org/10.2994/1808-9798(2006)1[114:A PICSG]2.0.CO;2)
- Martin, P. R., & Martin, T. E. (2001). Ecological and fitness consequences of species coexistence: A removal experiment with wood warblers. *Ecology*, 82(1), 189–206. [https://doi.org/10.1890/0012-9658\(2001\)082\[0189:EAFCS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0189:EAFCS]2.0.CO;2)
- McSweeney, C., New, M., & Lizcano, G. (2013). *UNDP climate change country profiles: Tanzania* (pp. 1–27). UNDP Country Profiles.
- Moreno-Rueda, G., Pleguezuelos, J. M., & Alaminos, E. (2009). Climate warming and activity period extension in the Mediterranean snake



- Malpolon monspessulanus. *Climatic Change*, 92(1–2), 235–242. <https://doi.org/10.1007/s10584-008-9469-y>
- Moritz, C., & Agudo, R. (2013). The future of species under climate change: Resilience or decline. *Science*, 341(6145), 504–508.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Neate-Clegg, M. H. C., O'Brien, T. G., Mulindahabi, F., & Şekercioğlu, Ç. H. (2020). A disconnect between upslope shifts and climate change in an Afrotropical bird community. *Conservation Science and Practice*, 2(11), 1–11. <https://doi.org/10.1111/csp2.291>
- Newmark, W. D. (2002). *Conserving biodiversity in East African forests: A study of the Eastern Arc Mountains*. Springer.
- Newmark, W. D. (2018). *Habitat fragmentation and Afrotropical avian nest predators in the East Usambara Mountains, Tanzania*. Final report on Grant 9778-15 to the National Geographic Society.
- Newmark, W. D., & McNeally, P. B. (2018). Impact of habitat fragmentation on the spatial structure of the Eastern Arc forests in East Africa: Implications for biodiversity conservation. *Biodiversity and Conservation*, 27(6), 1387–1402. <https://doi.org/10.1007/s10531-018-1498-x>
- Newmark, W. D., & Stanley, T. R. (2011). Habitat fragmentation reduces nest survival in an Afrotropical bird community in a biodiversity hotspot. *Proceedings of the National Academy of Sciences of the United States of America*, 108(28), 11488–11493. <https://doi.org/10.1073/pnas.1104955108>
- Newmark, W. D., Jenkins, C. N., Pimm, S. L., McNeally, P. B., & Halley, J. M. (2017). Targeted habitat restoration can reduce extinction rates in fragmented forests. *Proceedings of the National Academy of Sciences*, 114(36), 9635–9640. <https://doi.org/10.1073/pnas.1705834114>
- Nichols, J. D., Hines, J. E., Lebreton, J.-D., & Pradel, R. (2000). Estimation of contributions to population growth: A reverse-time capture-recapture approach. *Ecology*, 81(12), 3362–3376. [https://doi.org/10.1890/0012-9658\(2000\)081\[3362:EOCTPG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3362:EOCTPG]2.0.CO;2)
- NOAA. (2019). *Global climate report – Annual 2019*. In *State of the Climate: Global Climate Report*. <https://www.ncdc.noaa.gov/sotc/global/201913>
- Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2, 747–751. <https://doi.org/10.1038/NCLIMATE1588>
- Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J., & Owens, I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436(7053), 1016–1019. <https://doi.org/10.1038/nature03850>
- Oro, D., Torres, R., Rodríguez, C., & Drummond, H. (2010). Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology*, 91(4), 1205–1214. <https://doi.org/10.1890/09-0939.1>
- Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., & Delgado, M. D. M. (2013). Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 110(33), 13434–13439. <https://doi.org/10.1073/pnas.1305533110>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Peterson, C. R., Gibson, A., & Dorcas, M. (1993). Snake thermal ecology: The causes and consequences of body-temperature variation. In J. T. Seigel & R. A. Collins (Eds.), *Snakes: Ecology and behavior* (pp. 241–314). McGraw-Hill.
- Pollock, H. S., Brawn, J. D., & Cheviron, Z. A. (2020). Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. *Functional Ecology*, 35(1), 93–104. <https://doi.org/10.1111/1365-2435.13693>
- Potts, K. B., Watts, D. P., Langergraber, K. E., & Mitani, J. C. (2020). Long-term trends in fruit production in a tropical forest at Ngogo, Kibale National Park, Uganda. *Biotropica*, 52(3), 521–532. <https://doi.org/10.1111/btp.12764>
- Powell, L. L., Cordeiro, N. J., & Stratford, J. A. (2015). Ecology and conservation of avian insectivores of the rainforest understory: A pan-tropical perspective. *Biological Conservation*, 188, 1–10. <https://doi.org/10.1016/j.biocon.2015.03.025>
- Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, 52(2), 703. <https://doi.org/10.2307/2532908>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M. P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K. S., Borrás, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A. A., ... Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, 10(3109), 3109. <https://doi.org/10.1038/s41467-019-10924-4>
- Rahbek, C., Borregaard, M. K., Colwell, R. K., Dalsgaard, B. O., Holt, B. G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R. J., & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365(6458), 1108–1113. <https://doi.org/10.1126/science.aax0149>
- Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 49, 165–182. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453(7193), 353–357. <https://doi.org/10.1038/nature06937>
- Ryder, T. B., & Sillett, T. S. (2016). Climate, demography and lek stability in an Amazonian bird. *Proceedings of the Royal Society B*, 283(1823), 1–9. <https://doi.org/10.1007/s13398-014-0173-7.2>
- Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters*, 15(8), 847–855. <https://doi.org/10.1111/j.1461-0248.2012.01806.x>
- Santisteban, L., Benkman, C. W., Fetz, T., & Smith, J. W. (2012). Survival and population size of a resident bird species are declining as temperature increases. *Journal of Animal Ecology*, 81(2), 352–363. <https://doi.org/10.1111/j.1365-2656.2011.01918.x>
- Saracco, J. F., Radley, P., Pyle, P., Rowan, E., Taylor, R., & Helton, L. (2016). Linking vital rates of landbirds on a tropical island to rainfall and vegetation greenness. *PLoS One*, 11(2), 1–18. <https://doi.org/10.1371/journal.pone.0148570>
- Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika*, 52(52), 249–259. <http://www.jstor.org/stable/2333827>
- Şekercioğlu, Ç. H., Mendenhall, C. D., Oviedo-Brenes, F., Horns, J. J., Ehrlich, P. R., & Daily, G. C. (2019). Long-term declines in bird populations in tropical agricultural countryside. *Proceedings of the National Academy of Sciences of the United States of America*, 116(20), 9903–9912. <https://doi.org/10.1073/pnas.1802732116>
- Şekercioğlu, Ç. H., Schneider, S. H., Fay, J. P., & Loarie, S. R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, 22(1), 140–150. <https://doi.org/10.1111/j.1523-1739.2007.00852.x>
- Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J.

- A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, 11, 2463. <https://doi.org/10.1038/s41467-020-16313-6>
- Sheldon, K. S. (2019). Climate change in the tropics: Ecological and evolutionary responses at low latitudes. *Annual Review of Ecology, Evolution, and Systematics*, 50, 303–333. <https://doi.org/10.1146/annurev-ecolsys-110218>
- Sperry, J. H., Barron, D. G., & Weatherhead, P. J. (2012). Snake behavior and seasonal variation in nest survival of northern cardinals *Cardinalis cardinalis*. *Journal of Avian Biology*, 43(6), 496–502. <https://doi.org/10.1111/j.1600-048X.2012.05632.x>
- Sperry, J. H., Peak, R. G., Cimprich, D. A., & Weatherhead, P. J. (2008). Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology*, 39(4), 379–383. <https://doi.org/10.1111/j.0908-8857.2008.04451.x>
- Srinivasan, U., Elsen, P. R., Tingley, M. W., & Wilcove, D. S. (2018). Temperature and competition interact to structure himalayan bird communities. *Proceedings of the Royal Society B: Biological Sciences*, 285(1874). <https://doi.org/10.1098/rspb.2017.2593>
- Srinivasan, U., & Wilcove, D. S. (2020). Interactive impacts of climate change and land-use change on the demography of montane birds. *Ecology*, <https://doi.org/10.1002/ecy.3223>
- Stouffer, P. C., Jirinec, V., Rutt, C. L., Bierregaard, R. O., Hernández-Palma, A., Johnson, E. I., Midway, S. R., Powell, L. L., Wolfe, J. D., & Lovejoy, T. E. (2020). Long-term change in the avifauna of undisturbed Amazonian rainforest: Ground-foraging birds disappear and the baseline shifts. *Ecology Letters*, 24(2), 186–195. <https://doi.org/10.1111/ele.13628>
- Stuart, S. N. (1983). *Biogeographical and ecological aspects of forest bird communities in eastern Tanzania*. University of Cambridge. Ph.D. dissertation.
- Tarwater, C. E., & Brawn, J. D. (2010). The post-fledging period in a tropical bird: Patterns of parental care and survival. *Journal of Avian Biology*, 41(4), 479–487. <https://doi.org/10.1111/j.1600-048X.2010.05006.x>
- Tarwater, C. E., Ricklefs, R. E., Maddox, J. D., & Brawn, J. D. (2011). Pre-reproductive survival in a tropical bird and its implications for avian life histories. *Ecology*, 92(6), 1271–1281. <https://doi.org/10.1890/10-1386.1>
- Tieleman, B. I., Dijkstra, T. H., Klasing, K. C., Visser, G. H., & Williams, J. B. (2008). Effects of experimentally increased costs of activity during reproduction on parental investment and self-maintenance in tropical house wrens. *Behavioral Ecology*, 19(5), 949–959. <https://doi.org/10.1093/beheco/arn051>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3, 879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Weathers, W. W., & Sullivan, K. A. (1989). Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs*, 59(3), 223–246. <https://doi.org/10.2307/1942600>
- Wheelwright, N. T., & Templeton, J. J. (2003). Development of foraging skills and the transition to independence in juvenile savannah sparrows. *The Condor*, 105(2), 279–287. <https://doi.org/10.1093/condor/105.2.279>
- Williams, S. E., & Middleton, J. (2008). Climatic seasonality, resource bottlenecks, and abundance of rainforest birds: Implications for global climate change. *Diversity and Distributions*, 14(1), 69–77. <https://doi.org/10.1111/j.1472-4642.2007.00418.x>
- Wolfe, J. D., Ralph, C. J., & Elizondo, P. (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(3), 715–721. <https://doi.org/10.1007/s00442-015-3256-z>
- Woodworth, B. K., Norris, D. R., Graham, B. A., Kahn, Z. A., & Mennill, D. J. (2018). Hot temperatures during the dry season reduce survival of a resident tropical bird. *Proceedings of the Royal Society B: Biological Sciences*, 285(1878), 1–8. <https://doi.org/10.1098/rspb.2018.0176>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Neate-Clegg MH, Stanley TR, Şekercioğlu ÇH, Newmark WD. Temperature-associated decreases in demographic rates of Afrotropical bird species over 30 years. *Glob Change Biol*. 2021;27:2254–2268. <https://doi.org/10.1111/gcb.15567>