PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

# Does climate variability influence the demography of wild primates? Evidence from long-term life-history data in seven species

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## Abstract

Earth's rapidly changing climate creates a growing need to understand how demographic processes in natural populations are affected by climate variability, particularly among organisms threatened by extinction. Long-term, large-scale, and cross-taxon studies of vital rate variation in relation to climate variability can be particularly valuable because they can reveal environmental drivers that affect multiple species over extensive regions. Few such data exist for animals with slow life histories, particularly in the tropics, where climate variation over large-scale space is asynchronous. As our closest relatives, nonhuman primates are especially valuable as a resource to understand the roles of climate variability and climate change in human evolutionary history. Here, we provide the first comprehensive investigation of vital rate variation in relation to climate variability among wild primates. We ask whether primates are sensitive to global changes that are universal (e.g., higher temperature, large-scale climate oscillations) or whether they are more sensitive to global change effects that are local (e.g., more rain in some places), which would complicate predictions of how primates in general will respond to climate change. To address these questions, we use a database of long-term life-history data for natural populations of seven primate species that have been studied for 29–52 years to investigate associations between vital rate variation, local climate variability, and global climate oscillations. Associations between vital rates and climate variability varied among species and depended on the time windows considered, highlighting the importance of temporal scale in detection of such effects. We found strong climate signals in the fertility rates of three species. However, survival, which has a greater impact on population growth, was little affected by climate variability. Thus, we found evidence for demographic buffering of life histories, but also evidence of mechanisms by which climate change could affect the fates of wild primates.

### KEYWORDS

climate change, demographic buffering, El Niño Southern Oscillation, environmental stochasticity, population dynamics, rainfall, temperature, vital rates, weather

# 1 | INTRODUCTION

As evidence mounts that the Earth's changing climate will create unprecedented climate states and patterns around the world (Garcia, Cabeza, Rahbek, & Araújo, 2014; Taylor, Stouffer, & Meehl, 2011; Xie et al., 2015), there is a growing need to understand how natural populations are affected by extreme weather events and climate variability (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Boyce, Haridas, & Lee, 2006; Jenouvrier, 2013; Stenseth et al., 2002). This is particularly true for organisms that are threatened by extinction because their effective conservation may hinge on anticipating how their populations and their ecosystems will respond to changing climates (Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Araújo & Rahbek, 2006; Stein et al., 2013). The relationship between climate variability and vital rates, such as survival and fertility, has long been a central topic in population ecology, and there is a large body of knowledge about how climate variables can drive population processes by acting on vital rates (Benton, Plaistow, & Coulson, 2006; Boyce et al., 2006; Frederiksen, Lebreton, Pradel, Choquet, & Gimenez, 2014; Stenseth et al., 2002). Although much of this research relates to temporal variation in the vital rates of single populations of short-lived organisms, there is increasing recognition that long-term, large-scale, and/or cross-taxon studies in this domain are especially valuable because they may reveal generalized or synchronized environmental drivers that can affect multiple, geographically disparate communities (Gaillard et al., 2013; Hansen et al., 2013; Pardikes, Shapiro, Dyer, & Forister, 2015; Parmesan & Yohe, 2003; Post & Forchhammer, 2002; Post et al., 2009).

Large-scale climate patterns, including the El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD), are of particular interest because they produce correlated weather events and climate anomalies around the world that can synchronize population processes in multiple species and over extensive regions (Halkka, Halkka, Halkka, Roukka, & Pokki, 2006; Hallett et al., 2004; Jenouvrier et al., 2009; Marchant, Mumbi, Behera, & Yamagata, 2007; Pardikes et al., 2015; Post & Forchhammer, 2002; Roland & Matter, 2013; Stenseth et al., 2003), thus creating the potential for widespread conservation challenges that require coordinated actions. In addition to acting more broadly than local weather, indices of large-scale climate phenomena can be more accurate than local weather at predicting population dynamics and vital rates, perhaps because the large-scale indices integrate information about multiple linked climate variables over long time periods (Hallett et al., 2004; Stenseth et al., 2002). Nonetheless, these large-scale phenomena must act on organisms through local processes, and so the stronger correlations sometimes observed with global indices might be due to unidentified or unmeasured local covariates, or failure to identify the appropriate time window in which local covariates act (Stenseth & Mysterud, 2005; van de Pol et al., 2013). Climate change models for the 21st century predict increases in the intensity and frequency of ENSO activity (Cai et al., 2014, 2015; Latif & Keenlyside, 2009), a shift in mean climate conditions toward a positive IOD state (Cai et al., 2013), and increases in local climate extremes (Orlowsky &

Seneviratne, 2011; Tebaldi, Hayhoe, Arblaster, & Meehl, 2006). The study of how natural populations respond to both local and large-scale climate variability can therefore provide important information about which species may be put at risk by anomalous climate states, and whether those risks are likely to be present at other locations and in other species.

Most studies that have investigated effects of climate variability on the demography of multiple widespread populations have been carried out in circumpolar or temperate regions where the timing of climate seasonality in all the populations is strongly synchronized by the Earth's axial tilt. In such studies, there is often a critical period of sensitivity to climate variability (a "climatic time window") during which population regulation by weather or climate variability occurs; for example, winter rain is a key determinant of population dynamics in a variety of northern vertebrates (Coulson et al., 2001; Hansen et al., 2013). If such effects are confined to specific lags or time periods, then the relationship may be weakened or obscured by taking the annual average of climate conditions. It is therefore important to consider different possible critical climatic time windows, which can differ among sites and species (Bailey & van de Pol, 2016; McLean, Lawson, Leech, & van de Pol, 2016; Sims, Elston, Larkham, Nussey, & Albon, 2007; van de Pol, Cockburn, Gaillard, & McPeek, 2011; van de Pol et al., 2016). Comparatively few studies have examined the effects of climate variability on demographic rates of long-lived vertebrates in the tropics, where climate seasonality is more asynchronous than in circumpolar and temperate zones, and where many endemic and endangered species reside. Specifically, climate seasonality in tropical regions is characterized by complex seasonal rainfall regimes that vary in magnitude, timing, and interannual variability from one place to another (Feng, Porporato, & Rodriguez-Iturbe, 2013).

The nonhuman primates have been singled out among terrestrial mammals as one of the groups least capable of keeping pace with climate change by moving to track suitable climates because of their limited dispersal capacities and highly fragmented ecosystems (Schloss, Nuñez, & Lawler, 2012). Moreover, primates have low potential for rapid evolutionary responses via genetic changes because of their slow life histories and low reproductive rates. Thus, for many primate populations in rapidly changing environments, the only viable option to stave off extinction is resilience in situ by behavioral, physiological, and demographic plasticity. In this study, we use an extraordinary archive of nonhuman primate life-history data, the Primate Life History Database (Strier et al., 2010), to investigate how local and large-scale climate conditions affect vital rates in seven geographically dispersed wild populations that include species from the four major radiations of nonhuman primates and that all reside in the tropics. A previous study found low interannual variation in vital rates in these populations, with relatively high adult and juvenile survival rates in all species, and undetectable "process variance" in fertility for most species (i.e., any true variability in fertility rates was obscured by sampling variability) (Morris et al., 2011). That study also found that rainfall variability at each site, measured as the coefficient of variation, was not an informative predictor of

variance in survival rates, but the analysis was crude, and other climate variables were not considered. Other studies have found evidence of demographic variation in response to local climate variability in single populations among these species (Carnegie, Fedigan, & Melin, 2011; Fedigan, Carnegie, & Jack, 2008; Fitzpatrick, Altmann, & Alberts, 2014; Lawler et al., 2009; Richard, Dewar, Schwartz, & Ratsirarson, 2000; Strier, 1999). There is also evidence that abundance in some primate populations varies in response to large-scale climate phenomena or to extreme weather events, but this evidence involves single populations (Campos, Jack, & Fedigan, 2015; Dunham, Erhart, Overdorff, & Wright, 2008; Dunham, Erhart, & Wright, 2011; Milton & Giacalone, 2014), or several populations that are geographically or taxonomically proximal (Wiederholt & Post, 2010, 2011). No previous study has examined the relative effects of local climate variability and large-scale climate oscillations on vital rates within and across primate species using life-history data as large and comprehensive as that contained in the Primate Life History Database, nor have any of these studies explicitly evaluated the role of distinct climatic time windows on inferences about such effects.

We aimed specifically to investigate the following questions. First, does climate variability predict stage-specific survival rates and adult female fertility rates in each species? Second, are there detectable cross-site patterns that suggest similar demographic responses to the same environmental drivers or seasons, despite climate asynchrony among the study populations? Third, if vital rates are affected by climate variability, are they more accurately predicted by local conditions or by large-scale climate phenomena? Fourth, how do inferences about these questions change depending on different definitions of critical climatic time windows?

## 2 | MATERIALS AND METHODS

### 2.1 | Vital rates

We analyzed individual life-history data collected on wild populations of seven nonhuman primate species that span the primate order: one prosimian, Verreaux's sifaka (*Propithecus verreauxi*); two New World Monkeys, white-faced capuchin (*Cebus capucinus imitator*) and northern muriqui (*Brachyteles hypoxanthus*); two Old World Monkeys, blue monkey (*Cercopithecus mitis stuhlmanni*) and yellow baboon (*Papio cynocephalus*); and two great apes, eastern chimpanzee (*Pan troglodytes schweinfurthii*) and mountain gorilla (*Gorilla beringei beringei*). The study populations have all been subjects of long-term continuous study for 28.6–51.9 years (Table 1). The locations of these study populations are shown in Figure 1. Strier et al. (2010) provide a detailed description of how the data were standardized and compiled in the Primate Life History Database (http://demo.plhdb.org/). The database includes complete biographical information for thousands of individual animals, including the date and way in which each animal entered and departed the study, as well as the animal's sex, birth date, and mother's identity. The database also includes a table of reproductive information, which consists of time periods during which each female's fertility was monitored.

Using these data, we estimated survival rates for three life-history stages—infants, juveniles, and adults—as well as fertility rates for adult females, following the methods described in Morris et al. (2011) with a few changes noted below (Figure 2). In brief, we defined a series of hypothetical censuses at one-year intervals spanning the duration of each study, and for each vital rate and interval, we converted the life-history data to a set of binary trials that represent each individual present during the interval. The hypothetical censuses occurred on 1 January of each year for which life-history data were available. For survival rates, the outcome of each trial is a success if an animal present during the intercensus interval survived to the next census. For fertility rates, the outcome of each trial is a success if an animal present during the intercensus interval reproduced before the next census. We adjusted the numbers of trials and successes to account for left and right censoring following the procedure detailed in the Appendix of Morris et al. (2011). We defined infants as individuals either born during the intercensus interval or who were alive at the first census of an intercensus interval but were younger than the median weaning age for that species, which we defined as the median successful interbirth interval (i.e., an interbirth interval in which the preceding infant survived at least until the subsequent infant's birth) minus the gestation length. We defined juveniles as individuals who entered an intercensus interval aged older than an infant but younger than the minimum age at first reproduction for females of that species. We defined adults as all older individuals.

### 2.2 | Climate data

We compiled monthly values of total rainfall and mean temperature for each study site using data from several sources (Figs S1–S3). At some sites, accumulated rainfall was measured at daily or subdaily intervals using rain gauges or weather stations located near the study population. Reliable rain gauge data were not available for two of the sites, Gombe (chimpanzees) and Beza Mahafaly (sifaka). For these sites, and for any gaps in the rain gauge data for the other sites, we used data from two sources. First, for 1998 to the near present, we filled gaps using data from the Tropical Rainfall Measuring Mission (TRMM) satellite, which estimates accumulated rainfall over 0.25° grid cells (27.83 km at the equator) at subdaily intervals using satellite-borne precipitation radar (Kummerow, Barnes, Kozu, Shiue, & Simpson, 1998). Second, because TRMM data are not available before 1998, we filled gaps before 1998 using rainfall data from the Global Precipitation Climatology Centre (GPCC V7), which uses interpolated weather station data to estimate monthly rainfall totals over 0.5° grid cells (55.66 km at the equator) (Schneider et al., 2015). Reliable locally measured temperature data were not available for all but one of the study sites. We therefore used the Monthly Land Average Temperature dataset from Berkeley Earth (http://berkeleyearth.org/) to represent temperature conditions for all seven sites. The Berkeley Earth dataset uses bias-corrected weather station data and other data sources to estimate monthly average surface temperature over a global 1.0° grid (111.32 km at the equator;

**TABLE 1** Summary of life-history data for the seven primate species analyzed in this study

| Species | First observation | Last observation | N animals | Dataset duration (years) | Accrued animal-years[a] |
|---|---|---|---|---|---|
| *Biographical data for estimating survival rates* | | | | | |
| Verreaux's sifaka | 1984-07-15 | 2013-08-18 | 993 | 29.1 | 4,557.7 |
| White-faced capuchin | 1986-06-08 | 2014-12-31 | 308 | 28.6 | 1,324.0 |
| Northern muriqui | 1983-06-25 | 2014-12-31 | 562 | 31.5 | 4,331.9 |
| Blue monkey | 1979-07-27 | 2014-09-30 | 599 | 35.2 | 3,086.5 |
| Yellow baboon | 1971-08-01 | 2013-06-28 | 1324 | 41.9 | 7,440.3 |
| Eastern chimpanzee | 1963-01-15 | 2014-12-31 | 313 | 51.9 | 3,172.8 |
| Mountain gorilla | 1967-09-15 | 2014-12-31 | 337 | 47.3 | 3,142.5 |
| *Adult female reproductive data for estimating fertility rates* | | | | | |
| Verreaux's sifaka | 1983-07-15 | 2013-08-18 | 242 | 30.1 | 1,656.6 |
| White-faced capuchin | 1986-06-15 | 2014-12-31 | 125 | 28.6 | 348.8 |
| Northern muriqui | 1983-06-25 | 2014-09-30 | 133 | 31.3 | 624.5 |
| Blue monkey | 1997-02-15 | 2014-09-30 | 221 | 17.6 | 1,091.1 |
| Yellow baboon | 1971-08-01 | 2013-06-28 | 618 | 41.9 | 1,903.7 |
| Eastern chimpanzee | 1963-05-15 | 2014-12-31 | 144 | 51.7 | 1,032.9 |
| Mountain gorilla | 1967-09-15 | 2014-12-31 | 151 | 47.3 | 949.1 |

[a]The sum of each animal's exact time contribution to the study measured in years.
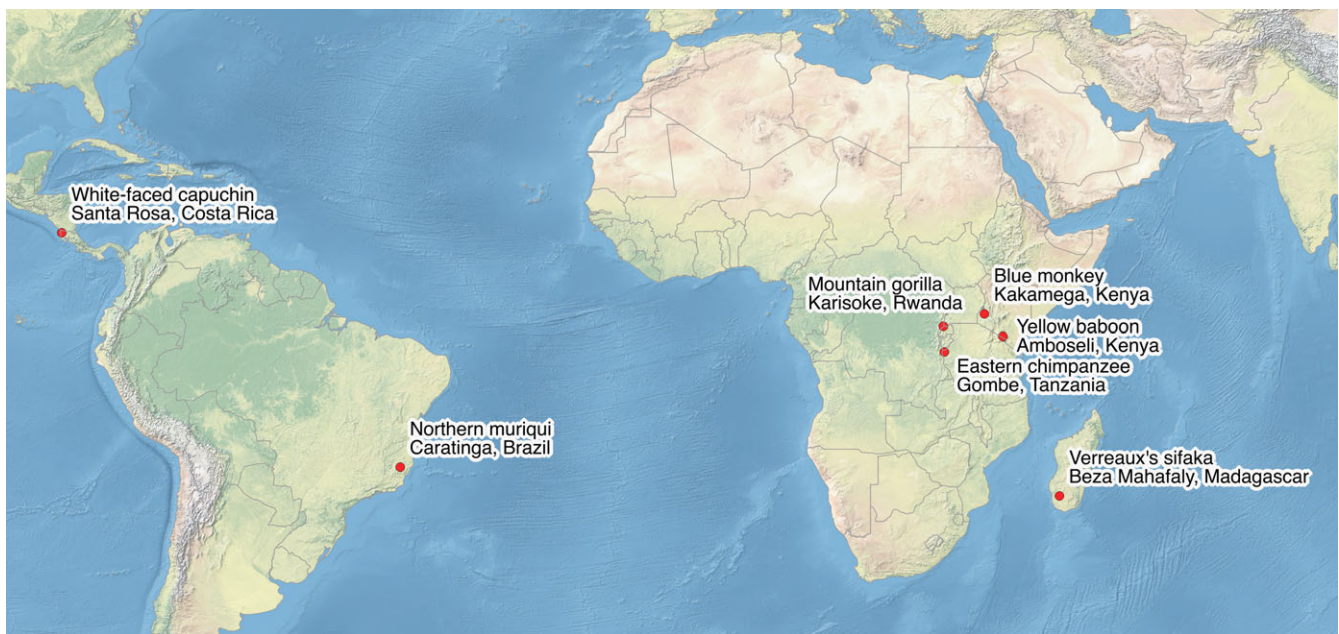


**FIGURE 1** Locations of the study sites for the seven primate species included in this study

Rohde et al., 2013). For all gridded climate variables, we extracted monthly values for the grid cell whose center was located nearest to the center of the study area.

The relatively coarse TRMM and GPCC rainfall data and the Berkeley Earth temperature data may be consistently different from the "true" weather values on site due to, for example, elevation differences that shift the baseline conditions of the site relative to the average conditions in the large grid cell. Problematic mismatches might occur if uncorrected coarse-scale data were mixed with locally measured data because the two source's real baselines would differ, creating systematic false variation in the mean conditions. To address this problem, whenever we used coarse-scale data to fill gaps in local-scale data (which occurred in the rainfall dataset only; Fig. S2), we first corrected the coarse-scale data by creating a regression model between the two data sources based on times of overlap when both coarse-scale and local-scale rainfall were measured on the same dates. We then used the regression model to predict the missing local-scale data from the measured coarse-scale
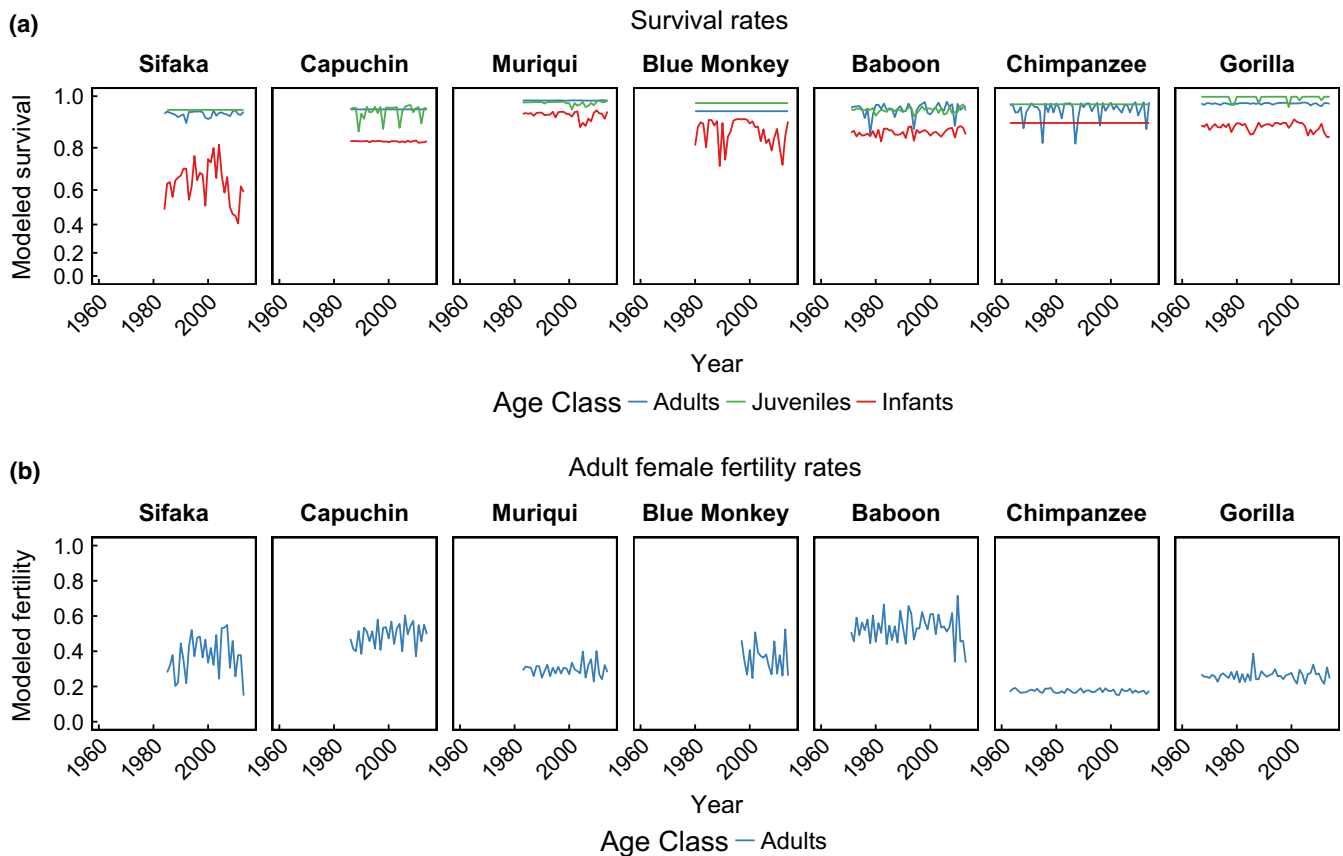
**FIGURE 2** Estimated vital rates. Estimates are corrected for sampling variation following Morris et al. (2011). Flat lines indicate cases where the estimate for the random effects variance component is zero, which means that year-to-year variability in the vital rate ("process" variation) was not distinguishable from sampling variability. (a) Survival rates for infants, juveniles, and adults of all species. (b) Fertility rates for adult females of all species. Fertility rates express the mean number of new offspring produced by an adult female during the following year

values, effectively correcting the baseline in the coarse-scale data to match that of the local-scale data. In the case of Gombe (chimpanzees) and Beza Mahafaly (sifaka), where we had no reliable local-scale rainfall data, there was no mixing and gap-filling—all the data were coarse-scale. Likewise, all of the temperature data were coarse-scale. Whether the coarse-scale data were baseline-corrected to fill gaps or used entirely in lieu of local-scale data, we believe that the coarse-scale data are valid approximations of local-scale weather because variation around each source's baseline should be comparable, even if the absolute baselines differ due to factors such as elevation. We subtracted out the baselines when we rescaled the climate variables to standardized anomalies.

In addition to these local climate variables, we obtained monthly time series of ENSO and IOD conditions. ENSO is the dominant driver of interannual climate variability throughout the tropics, including Central and South America as well as East Africa, where our study populations were located (Aceituno, 1988; Nicholson & Entekhabi, 1986; Nicholson & Kim, 1997). The IOD is a distinct mode of interannual climate variability that can influence weather in East Africa, and can also interact with ENSO to modulate its effects (Marchant et al., 2007; Saji, Goswami, Vinayachandran, & Yamagata, 1999). As an index of ENSO activity, we used monthly ERSST.v4 SST

anomalies in the Niño 3.4 region (http://www.cpc.ncep.noaa.gov/data/indices/ersst4.nino.mth.81-10.ascii), hereafter called the Niño3.4 Index. As an index of IOD activity, we used monthly values of the Dipole Mode Index (DMI) (http://www.jamstec.go.jp/frcgc/research/d1/iod/DATA/dmi.monthly.txt). Because the vital rates were calculated on a yearly timescale, we aggregated monthly values of the climate predictors as detailed below to obtain a single value for each climate variable and census year during the time windows of interest for each study population.

## 2.3 | Variable climatic time windows

We used a moving window approach (van de Pol et al., 2016) to test hypotheses about the importance of all possible climatic time windows in the 24 months leading up to each census date. We chose to consider lagged effects up to 24 months prior to the census because the vital rate data assessed at each census represent all individual "trials" of survival or fertility during the preceding 12 months, and those demographic events could be affected by climate variability before the start date of the intercensus interval, which is 12 months prior to the census. Moreover, other studies have found lagged effects of similar length of weather or climate

variability on the demography of primates (Wiederholt & Post, 2011), other animals (Hansen et al., 2013), and plants (Teller, Adler, Edwards, Hooker, & Ellner, 2016). We used an absolute time window method in which the climatic time windows are measured in months (ranging in duration from 0 to 24 months) before the hypothetical censuses on 1 January of each year. We aggregated each climate variable by taking the mean of all monthly values contained within the climatic time window. We carried out this analysis using the R package CLIMWIN (Bailey & van de Pol, 2016).

## 2.4 | Statistical analyses

We used generalized linear mixed models (GLMMs) to investigate the effects of climate variability on vital rates. For each model, the individual "trials" assessed annually at each hypothetical census served as the response variable. Because the response variables were binary (success or failure), we specified a binomial error distribution with a logit link function for all the models. Before fitting the models, we rescaled each climate predictor by converting to $Z$ scores within study sites. This rescaling standardized climate anomalies at different sites so that they were comparable to one another even though their magnitudes differed considerably due to different means or variances. We examined pairwise correlations among the climate variables within sites during all time windows (Figs S4e–S10e). Multicollinearity among these variables was not a concern for fitting the models, as we included only one climate variable in each model, but correlations among the climate variables may be important for interpreting the model results.

The moving window approach implemented in climwin systematically evaluates climate models in each time window by comparing Akaike's information criterion corrected for sample size (AIC$_c$; Burnham & Anderson, 2002) in climate models to that of a null model with no climate variable included. We used GLMMs with a random year effect and no fixed effects (for each species and vital rate separately) as a null model that measures random variation not tied to any climate variable. We then fit a temperature model, a rainfall model, an ENSO model, and an IOD model to the same vital rate data—each model included one climate predictor and a random year effect. Although weather patterns at some of the sites were not clearly related to cycles of either ENSO or IOD, we nonetheless included these models for all sites as a check against false positives (e.g., a "significant" IOD model for the site in Costa Rica, where weather is not directly linked with IOD phases, would cast doubt on other findings). All of the models were fit in R (R Development Core Team, 2016) using the LME4 package (version 1.1-12; Bates, Mächler, Bolker, & Walker, 2015).

The moving window approach is exploratory and involves evaluating many climate models for each vital rate, and so there is a risk of false positives where spurious relationships are interpreted as true climate signals. To evaluate the reliability of the purported climate signals, we carried out randomizations using the climwin package by reordering the date variable paired to the response variable (survival/reproduction) while keeping the climate data intact to preserve climate autocorrelation. We then refit the models on randomized data in each iteration of the procedure. The large number of models and the need for many randomizations resulted in a computational bottleneck. To overcome this problem, van de Pol et al. (2016) have proposed a statistic (P$_C$) that is based on comparisons of the number of models in the 95% confidence set in observed vs. randomized data. P$_C$ performs well at discriminating true signals from type I and type II errors with as few as five iterations of the randomization procedure (van de Pol et al., 2016), with the caveat that the performance metrics reported in that study are based on simulated data with errors in the response variables assumed to follow a normal distribution, whereas we assume that the errors in our binary response variables follow a binomial distribution. For each vital rate, we carried out 10 randomizations on the full set of models, and following van de Pol et al. (2016), we consider P$_C$ < 0.5 as indicating that the climate signal is likely to be real, although we interpret cases near the upper end of this range with caution.

## 3 | RESULTS

### 3.1 | Survival

We found little evidence that climate variables were informative predictors of survival rates for most species and age classes (Figs S4a–S10a). The randomization procedure revealed that only the model of survival in infant sifaka showed strong evidence of a true climate signal (P$_C$ < 0.01). The best model of infant sifaka survival (ΔAIC$_c$ = −14.1 compared to null model) included rainfall from 8 to 4 months prior to census (Figure 3a). This time period—May to September—coincides with the dry season (April to September) at the sifaka research site Beza Mahafaly (Fig. S11), as well as the birth season for sifaka (July to August; Figure 4). More rainfall during this time predicted higher infant survival (β = 5.13, Figure 3b). The P$_C$ statistic for models of adult baboon survival that included rainfall (P$_C$ = 0.48) barely met the threshold of 0.5, indicating that the climate signal is more likely than not to be true, although this finding should be treated with caution (Fig. S8a). Here, several time windows varying in duration received about equal support (ΔAIC$_c$ ranging from −9.15 to −8.65 compared to null model). All of these time windows occurred from 8 to 4 months prior to the census. As in the case of sifaka, this time period—May to September—coincides with the dry season (June to October) at the baboon research site, Amboseli, with more rain predicting higher adult survival in all of the well-supported models (Fig. S11).

### 3.2 | Fertility

Climate variables were informative predictors of adult female fertility rates in some species but not in others (Figure 5). The randomization procedure identified likely true climate signals in three species: sifaka, blue monkey, and northern muriqui. In sifaka, the IOD models with time windows from 9 to 7 months prior to the census received strongest support (ΔAIC$_c$ = −10.1 compared to null model). This
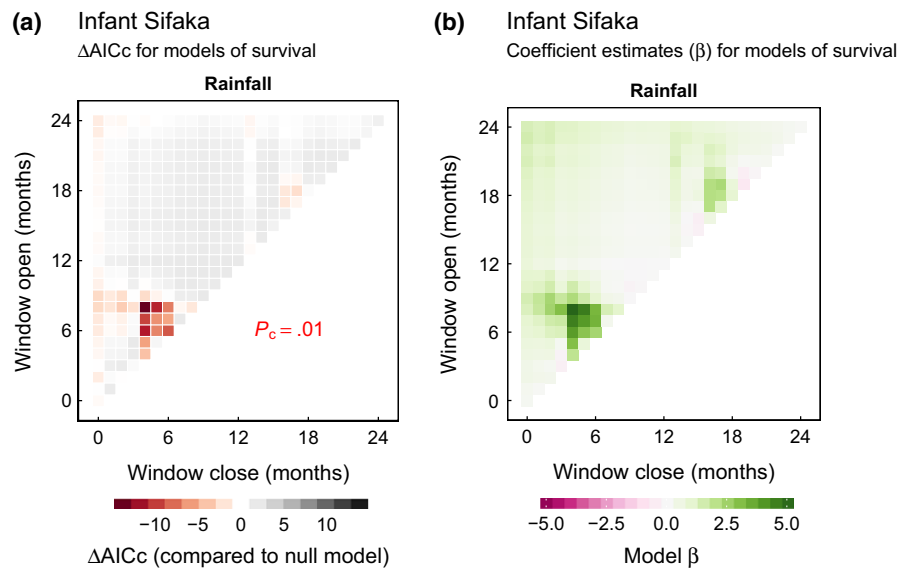
**(a)** Infant Sifaka
ΔAICc for models of survival

**(b)** Infant Sifaka
Coefficient estimates (β) for models of survival

**FIGURE 3** (a) $\Delta AIC_c$ values for climate models of Verreaux's sifaka infant survival rates for each time window. Each grid cell represents the $\Delta AIC_c$ value of the model for that particular climatic time window relative to a null model fit to the same vital rate data but excluding the climate variable. Deeper red shading indicates more informative models, while deeper gray shading indicates less informative models. The inset text indicates the $P_C$ value, which is an indication of the likelihood of a "true" climate signal in the observed data based on comparisons to randomized data (see text). Climate model sets with $P_C < 0.5$ are shown in red. (b) Coefficient estimates for the climate variable term for survival models in each time window

time period corresponds to the start of the dry season (Fig. S11) and also closely precedes the peak of the birth season for sifaka at Beza Mahafaly (Figure 4). Positive IOD values, corresponding to warmer and wetter conditions during this time period (Fig. S4e), were associated with increased fertility rates (β = 0.44, Fig. S4d). In blue monkeys, climate models including rainfall, temperature, and ENSO all showed some evidence of a climate signal (Figure 5). This finding is consistent with a true climate signal producing multiple apparent effects, some spurious, that arise from collinearity among the climate variables. There were two distinct "regions" of time windows that predicted blue monkey fertility: one from 24 to 18 months prior to the census (period 1), and another from 7 to 3 months prior to the census (period 2). For each climate variable in the blue monkey models of fertility, the model coefficients for the climate variable terms in periods 1 and 2 have opposite signs. This arises from significant 1-year lagged negative autocorrelation in blue monkey fertility rates (Fig. S12). Births are seasonal in blue monkeys, with most births occurring from January to March (12 to 10 months prior to the census; Figure 4). Because period 2 is after the birth season in each intercensus interval, only period 1 could realistically influence the fertility trials registered in the census. The apparent climate signal in period 2 is therefore probably a result of the autocorrelation with fertility rates in period 1, for example, a depression in fertility the year after many females in the population give birth following favorable conditions in period 1.

Period 1 encompasses January to July of the year before the census year; this includes the dry-to-wet season transition as well as the warmest and wettest months of the year (Fig. S11). The rainfall and temperature models during period 1 received similarly high

support that exceeded that received by the ENSO models (best rainfall model $\Delta AIC_c = -7.6$; best temperature model $\Delta AIC_c = -8.0$; best ENSO model $\Delta AIC_c = -5.7$). Increased fertility in blue monkeys was associated with greater rainfall (β = 0.83) and cooler temperatures (β = −0.54) during this time (Fig. S7d). In northern muriquis, ENSO models of varying window lengths within the period from 7 months to 1 month prior to the census (June to December) received moderately strong support (best model $\Delta AIC_c = -6.1$ compared to null model, Figure 5). Muriqui births are seasonal and match this time window closely: There is a sharp onset of births in June followed by a peak in mid-July, and births continue to occur with decreasing frequency until early December (Figure 4). This time period includes the driest and coldest months of the year as well as the start of the rainy season (Fig. S11). Positive ENSO values, corresponding to warmer conditions during this time period (Fig. S6e), were associated with decreased fertility rates (β = −0.27, Fig. S6d).

## 4 | DISCUSSION

### 4.1 | Climate variability was a poor predictor of stage-specific survival rates in most species, whereas adult female fertility rates showed species-dependent responses to climate variability

The overarching message that emerged from this study is that the effects of climate variability on primate vital rates are context-dependent for different species and age classes, with overall weak evidence that vital rates in most species respond strongly to climate variability. This was particularly true for the 21 distinct survival rates
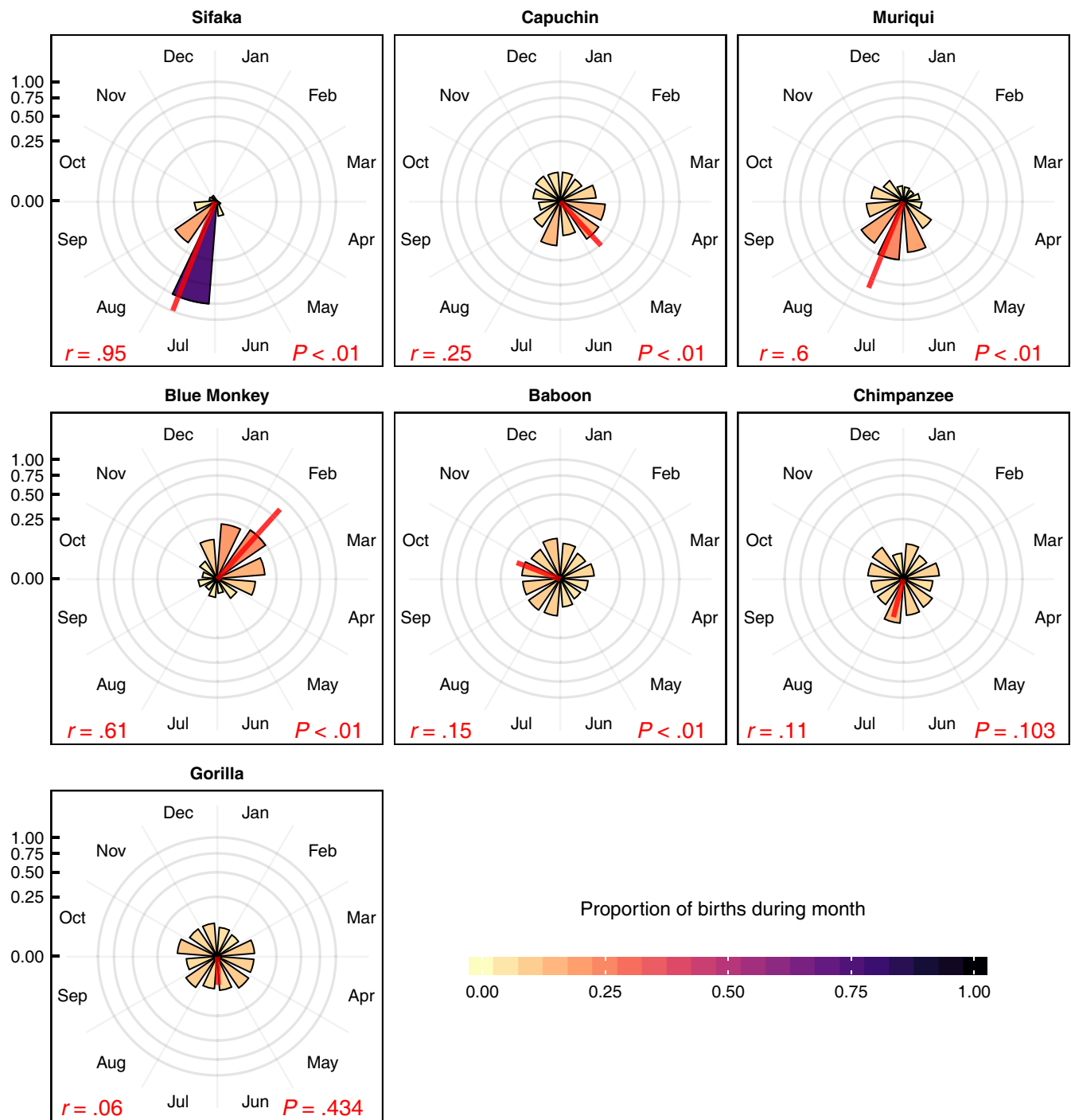
**FIGURE 4** Circular histograms showing the proportion of births in each month in each study population. Note that the radial axis is square-root-transformed to exaggerate differences in the lower end of the scale. The red lines show the mean vector ($r$). The orientation of $r$ indicates the average birth day of year in the population, and the length of $r$ indicates how unevenly observations are spread across the annual cycle. When $r = 1$, all births occur on the same day of year, and when $r = 0$, the births are evenly distributed across the 12 months. The $p$ values show the results of a Rayleigh test for nonuniformity of circular data. Significant results indicate seasonal reproduction. See also Table S1

that we considered. Here, we found strong evidence in support of a true climate signal only in infant sifaka, for which the evidence was much stronger than all other climate signals in the fertility rates we analyzed ($P_C < 0.01$ for infant sifaka survival compared to $P_C$ between 0.11 and 0.3 in other cases). We found only weak evidence

in support of a second true climate effect on the survival rates of adult baboons ($P_C = 0.48$), but this result is about as likely to be a statistical artifact as a "real" result. The lack of robust and detectable climate signals in most survival rates reinforces previous findings that variance in survival rates in these populations was not predicted by
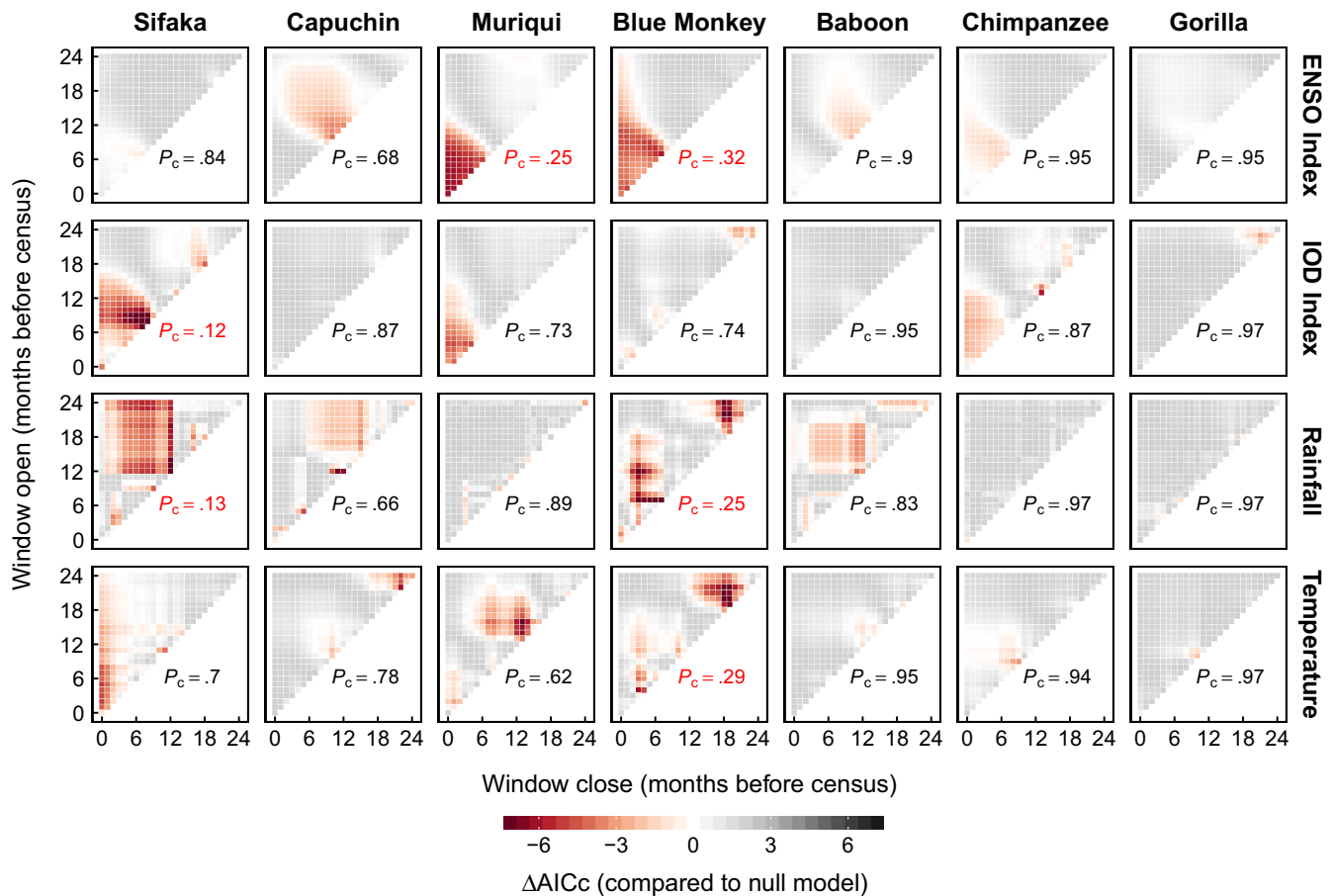
**FIGURE 5** ΔAIC_c values for climate models of adult female fertility rates for each species and climatic time window. The components of the plot are as described in Figure 3a

the coefficient of variation of annual rainfall (Morris et al., 2011). Morris et al. (2011) offered the cautious statement that the lack of an association between survival rate variance and climate variability in that study could be due to other environmental variables that were not considered or to differences among species (not modeled in that analysis) in the slope of the relationship between vital rates and climate variability. Our analysis explores that possibility and indicates that it is unlikely. Nonetheless, our relatively small sample sizes suggest that our study may be underpowered to detect moderate-to-weak climate signals in survival rates that might still be important for long-term species persistence.

In the study by Morris et al. (2011), process variance in fertility rates (i.e., true variability rather than sampling variability) was undetectable for all species except sifaka. Here, using a similar method but with seven additional years of life-history data for each species and a small change to the definition of adult females (minimum rather than median age at first reproduction) that increased sample size, we could detect process variance in fertility rates for all species (Figure 2b). When we modeled these fertility rates as functions of climate variables, we found reasonably strong evidence that fertility rates were affected by climate variability during one or more critical climatic time windows in three of seven primate species. Taken in combination with the lack of strong climate effects on survival in

most species, our findings also suggest that the mechanism underlying previously described cross-species synchrony of primate demography by large-scale climate oscillations (Wiederholt & Post, 2010) is probably linked to changes in fertility rates rather than to changes in survival rates.

Pfister (1998) hypothesized that vital rates that contribute more to fitness should show less temporal variability. For the primate species and vital rates considered here, deterministic population growth rates are most sensitive to adult survival and least sensitive to infant survival, with female fertility and juvenile survival somewhere in between (Morris et al., 2011). If some of the vital rate variability can be attributed to climate, then one might predict from Pfister's hypothesis that infant survival should have shown greatest responsiveness to climate variables in our analyses. Thus, the broad pattern here, in which female fertility seemed to show greater sensitivity to climate variability than infant survival in several species, is not entirely consistent with Pfister's hypothesis. One possible reason for this discrepancy is that infant survival in many of our study species can be strongly affected by other factors, particularly infanticide (capuchins: Fedigan, 2003; sifaka: Littlefield, 2009; blue monkeys: Cords & Fuller, 2010; chimpanzees: Wilson et al., 2014; gorillas: Robbins et al., 2013; baboons: Zipple et al., 2017). If infanticide or other processes that are largely unrelated to climate are important

determinants of infant survival, then any direct effects of climate variability on infant survival may be obscured by such semistochastic events, and climate variables may appear to be uninformative. Loss of an infant can also affect female fertility rates by reducing inter-birth intervals (baboons: Altmann, Altmann, & Hausfater, 1978; capuchins: Fedigan & Rose, 1995; gorillas: Czekala & Robbins, 2005; blue monkeys: Cords & Chowdhury, 2010; chimpanzees: Jones, Wilson, Murray, & Pusey, 2010; muriquis: Strier & Ives, 2012), potentially weakening true climate signals in fertility rates per se.

## 4.2 | The three species that showed evidence of climate-dependent changes in female fertility are the species in our study with the most seasonal breeding patterns

The three species in which fertility rates showed strong evidence of sensitivity to climate variables—sifaka, blue monkeys, and northern muriquis—are the most seasonal breeders in our dataset (Figure 4). In these species, more than 50% of births occurred in the top 3 months, and fewer than 5% of births occurred in the bottom 3 months (Table S1). Births in the other species in our study are either nonseasonal (eastern chimpanzees and mountain gorillas) or more weakly seasonal (yellow baboons and white-faced capuchins), meaning they are significantly more common during certain months but regularly occur year-round (Figure 4, Table S1). In Verreaux's sifaka, previous research has shown that poor rainfall years are associated with reduced body mass in adult females, and subsequently, with reduced reproductive output (Richard et al., 2000). This finding is consistent with our results regarding the positive relationship between the IOD and fertility rates in female sifaka (positive IOD phases bring warmer and wetter conditions to Madagascar). Our results for Verreaux's sifaka also provide an interesting comparison to previous research on Milne Edward's sifaka (Propithecus edwardsi) in Ranomafana National Park, Madagascar. Fecundity rates in this strongly seasonal breeder are markedly lower during El Niño years, which are associated with wetter and warmer conditions at that site (Dunham et al., 2008, 2011). Ranomafana is located in a rainforest biome that receives 3,000 mm of annual rainfall on average (Wright et al., 2012), an amount over four times greater than the rainfall received in the dry spiny forest biome of Beza Mahafaly. Thus, while both populations show strongly seasonal breeding that is modulated by climate, they show roughly opposite functional relationships between climate variability and reproduction: wetter and warmer conditions increase female reproductive rates at the drier site but reduce female reproductive rates at the wetter site.

The limitations of our data and research design do not allow us to make causal inferences about a general relationship between breeding seasonality and the sensitivity of fertility rates to climate variability. Nonetheless, our findings suggest the hypothesis that fertility rates in primate species with more seasonal breeding may be more sensitive to climate variability than in species with less seasonal breeding. If climate effects on fertility rates were random with respect to seasonal breeding, the probability that these three species and no others would be the exact subset to exhibit strong evidence

of a climate signal is equal to 1 divided by the number of unique combinations of species, or $1/2^7 = 0.0078$. If we had started this study with an a priori hypothesis about the proposed relationship, then our findings would be taken as strong evidence in support of this hypothesis. However, as we formed this hypothesis after the results were known, a valid test must remain a task for future studies. Moreover, we do not have enough species in our study to consider potentially confounding factors such as phylogeny, geography, body mass, and diet that could invalidate the proposed relationship (Janson & Verdolin, 2005); these possibilities merit further study.

Reproductive seasonality in primates and other animals is understood to be a strategy to align critical life-history stages to periodic favorable conditions, such as dependable food abundance during particular seasons (Brockman & van Schaik, 2005). Holding other factors constant, primate species with more pronounced reproductive seasonality (i.e., a narrower birth peak) tend to rely on more seasonal food resources (Janson & Verdolin, 2005; Strier, Mendes, & Santos, 2001). Why might fertility rates in strongly seasonal breeders have shown greater apparent sensitivity to climate variability? One possibility is that highly seasonal breeding may be favored by selection when intra-annual climate variability is relatively large compared to interannual climate variability—that is, seasonality is strong but predictable. In highly seasonal breeders, selection has acted to focus breeding at the time of year that is most predictably suitable for offspring production/survival. With all reproductive effort concentrated into a single critical period, climate variability leading up to this critical period could produce strong and consistent climate effects on reproduction. This may explain the strong climate effects on the vital rates of sifaka, which experience very high but predictable intra-annual climate variation (Fig. S13). Muriquis appear to fit this pattern to a lesser degree, but blue monkeys do not (Fig. S13).

Alternatively, why might fertility rates in less seasonal breeders have shown greater apparent buffering against climate variability? One possibility is that some nonseasonal breeders may simply never see unfavorable climatic conditions, leading to a lack of reproductive seasonality and making climate variability irrelevant to reproductive function in these species. For example, mountain gorillas experience relatively invariant climates over annual and interannual timescales (Fig. S13), and they show no evidence of breeding seasonality or of climate signals in fertility rates. Other weakly seasonal breeders, including baboons and capuchins, did experience highly seasonal climates that were also highly variable across years. This low interannual predictability of favorable climatic conditions may work against the evolution of highly seasonal breeding. In such species, reproductive function could be affected by weather and climate conditions preceding birth, but if those periods occur at inconsistent times across years, there might be little sign of a climate signal during any particular absolute time window because the asynchronous births average over these effects. This may be the case for the baboons and capuchins, both of which experience relatively high intra-annual and interannual rainfall variability but show only weak breeding seasonality and little evidence of climate signals in their vital rates. In these species, climate signals may be revealed using individual-based

relative time windows that count backward from the critical life-history stage that limits reproduction in that species. However, an approach employing relative time windows could be biased unless it were supplemented with hormonal evidence of pregnancy failure, as the precise timing of the relative time window in such cases would be unknown from observational data alone.

## 4.3 | Large-scale climate phenomena were not consistently better predictors of primate vital rates than locally measured climatic conditions

We did not find a general pattern supporting the idea that indices of large-scale climate oscillations are more informative predictors of vital rates than locally measured climate variability. Many studies that have found evidence that large-scale climate phenomena predict demographic variation in their study populations have been carried out in areas that are strongly affected by such oscillations, such as subarctic ecosystems (Halkka et al., 2006; Post & Forchhammer, 2002) and the Southern Ocean (Forcada, Trathan, Reid, & Murphy, 2005; Leaper et al., 2006; Nevoux, Forcada, Barbraud, Croxall, & Weimerskirch, 2010). Differences among species and populations in apparent sensitivity to large-scale climatic indices can depend on the degree to which those indices predict local weather and climate patterns (van de Pol et al., 2013). Given that temperature and rainfall variability at some of our study sites were only weakly correlated with ENSO and IOD phases, and that the timing and direction of the correlations differed among sites, it is unsurprising that these indices were not dependably better predictors of vital rate variation than locally measured climatic variability. We did find ENSO and IOD conditions to be good predictors of *some* fertility rates, albeit without a consistent pattern for which time windows were most critical. The overall impression that emerges from these results is that large-scale climate indices may not be broadly accurate or reliable guides for conservation planners to assess risks across multiple primate species.

The lack of a cross-site synchronizing effect of ENSO or IOD in this study contrasts somewhat with a previous study that found ENSO to be an important driver of synchronized changes in abundance of primates of the genus *Ateles* (Wiederholt & Post, 2010). Compared to the present study, the primate populations analyzed by Wiederholt and Post (2010) were relatively close both taxonomically and geographically—a pattern of broad homogeneity, not present in our study, that may have contributed to the observed synchronous changes in population size.

In our study, inferences about the effects of climate variability on vital rates depended heavily on when the climate variables were measured. As others have noted, this complex "time window" component is often overlooked by studies that use fixed time windows, and this may explain why large-scale climate indices often outperform locally measured variables at predicting demographic variation when using fixed time windows (Hallett et al., 2004; Stenseth & Mysterud, 2005; van de Pol et al., 2013). Specifically, local weather and climate variability measured during a fixed time window may fail to capture a critical period, such as a severe weather event, if the occurrence and timing

of such periods vary from 1 year to the next. Because large-scale climatic indices combine features of multiple weather components over longer time periods, they are often better predictors of whether the critical period will occur or not compared to any single weather component measured during the same fixed time window (Hallett et al., 2004). Large-scale climate indices appear to be less useful as integrative proxies for local climate in studies such as ours, in which local weather and climate variability at the different sites show highly differentiated associations with the large-scale indices.

## 4.4 | Conclusions and implications for climate change-integrated primate conservation

Our findings add to a relatively small but growing body of knowledge about the implications of climate change for nonhuman primates (Estrada et al., 2017; Graham, Matthews, & Turner, 2016; Korstjens & Hillyer, 2016). Much of the research in this area has focused on activity budget constraints (Korstjens, Lehmann, & Dunbar, 2010; Lehmann, Korstjens, & Dunbar, 2010; Majolo, McFarland, Young, & Qarro, 2013; McFarland, Barrett, Boner, Freeman, & Henzi, 2014) or species distribution models (Gouveia et al., 2016; Sesink Clee et al., 2015; Struebig et al., 2015). Few studies have examined climate effects on primate demography with the aim of understanding implications of future climate change (Campos et al., 2015; Dunham et al., 2008, 2011; Wiederholt & Post, 2010), and none with the level of individual-based detail and cross-taxon scope of the present study. Our findings of strong climate signals in the vital rate variation of several species provide a quantitative basis for predicting the demographic consequences of future climate change scenarios on the long-term outlook of these populations.

Nonetheless, most of the species included in our study evinced robust buffering of life histories—a process in which the demographic rates that most influence population growth (e.g., adult survival) show low variation due to buffering against environmental fluctuations (Morris & Doak, 2004). Selection for life-history buffering that prioritizes individual survival over fertility or offspring survival during any single reproductive cycle may be expected in long-lived iteroparous organisms such as nonhuman primates. Given the relative insensitivity of most primate vital rates to climate variability, our findings suggest that moderate changes in mean climate conditions per se are unlikely to be the primary drivers of extinction risk for most primate species. Rather, it is likely that the most serious risks associated with climate change to the long-term survival of primate populations are synergisms between changing climates and other extinction drivers such as habitat loss, anthroponotic disease, hunting, loss of critical mutualisms, phenological shifts and nutritional mismatches, and declining ecosystem health (Brook, Sodhi, & Bradshaw, 2008; Butt et al., 2015; Estrada et al., 2017; Laurance & Useche, 2009; Ockendon et al., 2014).

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