Climate oscillations and conservation measures regulate white-faced capuchin population growth and demography in a regenerating tropical dry forest in Costa Rica

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ABSTRACT

Tropical dry forests are among the world's most imperiled biomes, and most long-lived and large-bodied animals that inhabit tropical dry forests persist in small, fragmented populations. Long-term monitoring is necessary for understanding the extent to which such populations can cope with changing climate conditions and recover after the elimination of human disturbances. We investigated how conservation measures, local rainfall patterns, and large-scale climate oscillations have affected the population dynamics of white-faced capuchins (*Cebus capucinus*) in a Costa Rican tropical dry forest over a 42-year period after the elimination of most human disturbances. The population's rapid initial growth and later stabilization suggests that it was below the habitat's carrying capacity at the time of the conservation area's establishment. Management practices, such as aggressive fire suppression, may have played an important role in promoting this growth. Rainfall patterns were strongly coupled with phases and intensity conditions of the El Niño Southern Oscillation. The population experienced two distinct growth phases after the conservation area's establishment, a period of rapid growth through the 1980s and 1990s and a subsequent period of stability from about 2000 to the present. El Niño-like conditions in the three years preceding a census year were associated with declines in reproductive output and/or offspring mortality during the rapid growth phase. The sensitivity of this ecosystem to global climatic phenomena suggests that some animals will be negatively affected if drought years become more common as the global climate warms.

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1. Introduction

Long-term monitoring is vital for understanding the biological requirements and conservation outlook of threatened animal populations (Clutton-Brock, 2012; Sinclair and Byrom, 2006). A major aim of long-term population monitoring is to describe trends in demographic variables over time (Clutton-Brock and Sheldon, 2010). By documenting such trends, it may be possible to link population fluctuations with changes in climate and habitat (Wright, 2007), thereby improving predictions about how the population will fare in projected disturbance or climate change scenarios (Lawler et al., 2006). The demographic structure of relatively small or isolated populations may be especially sensitive to anomalous events such as human disturbance, natural disasters, prolonged extreme climatic episodes, and disease outbreaks. These dependencies may be impossible to detect without concurrent and

systematic data on climate and population trends over a multi-generational time frame (Clutton-Brock, 2012). Most studies of long-lived nonhuman primates have not been lengthy enough to investigate these important questions, and consequently, there have been few studies on the long-term dynamics of primate populations in relation to quantitative data on ecosystem change (for some notable exceptions, see chapters in Kappeler and Watts, 2012). Nonetheless, primate taxa may be particularly useful for quickly gauging conservation risks and establishing conservation priorities because primates are often abundant and easily censused compared to many other vertebrates in tropical habitats, and they may play key roles in ecological communities as ecosystem engineers (Chapman et al., 2013). Conservation approaches focused on primates are therefore likely to confer protection to many other sympatric organisms and their ecological dependencies (Lambert, 2011).

With few exceptions (e.g. Robbins et al., 2011; Strier and Boubli, 2006; Strier and Ives, 2012), our current knowledge about the long-term effects of climate and ecosystem change on primates comes from declining populations of lemurs (Dunham et al.,

2011; Jolly, 2012; Sussman et al., 2012; Wright et al., 2012) and Old World monkeys (Chapman et al., 2010, 2005, 2000; Lwanga et al., 2011). Thus, most studies on primates' responses to environmental change have focused on their capacity to cope with diminishing and/or deteriorating ecosystems. This focus pragmatically reflects the dire situation faced by many primate populations around the world (Cowlishaw and Dunbar, 2000). However, it is also important to know how primate populations fare in conservation areas that are "succeeding" (Laurance et al., 2012); that is, areas in which the major anthropogenic detriments to primates—deforestation, logging, live-capture, hunting, and fire (Chapman and Peres, 2001)—have been effectively and lastingly eradicated. Conservation strategies that target large, long-lived animals in profoundly disturbed habitats may be predicated on the belief that dwindling populations will recover over time if their habitats can be adequately restored. Globally, there are very few study sites that both support primates and meet the reserve-health criteria for investigating these important questions, and even fewer sites with a sufficiently long record of continuous demographic, climatic, and ecological monitoring to draw meaningful conclusions.

Several studies that have examined the dynamics of primate populations have implicated global weather patterns as a key driver (Dunham et al., 2011, 2008; Milton and Giacalone, 2014; Wiederholt and Post, 2011, 2010). The El Niño Southern Oscillation (ENSO) is one of the most globally consequential large-scale climate oscillators: extreme phases of ENSO have geographically widespread and diverse effects on local weather. Although relatively few studies have examined the effects of ENSO phases on nonhuman populations, there is evidence from geographically widespread locations that extreme ENSO phases can trigger significant population dynamic events, including changes in fecundity and mass mortality. For example, warm phases of ENSO ("El Niño") are associated with reduced fecundity in Milne Edward's sifaka (*Propithecus edwardsi*), perhaps due to the greater severity of cyclones that strike Madagascar during such periods (Dunham et al., 2011, 2008). El Niño phases also coincide with or closely precede synchronous population declines, delayed birth seasons, and reduced birth rates in various geographically-dispersed primates of the Neotropical family Atelidae, perhaps due to the disruption of food tree phenology (Wiederholt and Post, 2011, 2010). Extraordinarily high rainfall associated with strong episodes of the cool phase of ENSO ("La Niña") may have been responsible for a mass mortality event among the white-faced capuchins (*Cebus capucinus*) on Barro Colorado Island, Panama (Milton and Giacalone, 2014). In light of these widespread and diverse effects on primate populations, there is an urgent need to assess the risks that large-scale climatic oscillations pose to primates in order to make informed conservation decisions.

Here, we examine demographic changes of a population of white-faced capuchins (*Cebus capucinus*) in northwestern Costa Rica over a 42-year period in relation to local weather patterns and large-scale climate oscillations during the same period. Previous studies have documented the rapid growth of this capuchin population since the early 1970s (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976). These studies indicate that the population was well below its carrying capacity when the conservation area was established, and they point to the elimination of fire damage and other anthropogenic detriments as the key conservation measures that enabled this growth (Fedigan and Jack, 2001). The study area is situated in the core of a well-studied and thriving endeavor in ecosystem restoration that was initiated in 1971 (Allen, 2003; Janzen, 2000, 1987; Woodworth, 2013). Our study offers a unique perspective on the factors that promote or limit primate population growth, and it sheds light on their potential for recovery after the

elimination of human disturbances. Our objectives are to: (1) describe historical trends in our study site's population of capuchins from 1971 to 2013, extending previously published records (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976); (2) assess the relationship between local rainfall patterns and indices of large-scale climate oscillations; and (3) model the relationship between population trends and both local and large-scale climate patterns.

2. Materials and methods

2.1. Study System

Our study area is Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10.84°N, 85.62°W), a UNESCO World Heritage site and a global model of tropical dry forest restoration ecology (Allen, 2003; Janzen, 1987). Janzen (2000) gives a thorough history of the anthropogenic disturbance of this region, the creation and expansion of the ACG, and the ecological recovery that has occurred after decades of aggressive fire suppression. Land owners in the Guanacaste province of Costa Rica set fires annually to manage overgrown cattle pastures, and throughout the 1970s and early 1980s (and presumably for centuries before), these fires routinely swept into the park and burned large tracts of forest (Janzen, 2000). Since the park's founding, there were nascent efforts to limit fire damage, but effective fire control was not realized in SSR until 1984 (Janzen, 1988). Subsistence hunting of white-faced capuchins is historically uncommon in Costa Rica (Gonzalez-Kirchner and Maza, 1998) and is absent today in SSR, but capuchins (particularly capuchin males) probably faced regular harassment by ranchers before SSR's establishment (Fedigan and Jack, 2001). The ACG was classified as "succeeding" in a recent global assessment of 60 representative tropical forest reserves, ranking second in overall reserve health (Laurance et al., 2012). The geographic boundaries of SSR, which contain 108 km^2 of varied habitat, were formed with the establishment of Santa Rosa National Park in 1971. SSR is situated in a dry tropical forest biome that experiences stark rainfall seasonality, with nearly all the annual rain falling between mid-May and late-November. The 6-month-long dry season triggers total leaf shedding in many plant species. SSR supports three primate species, the white-faced capuchin, the mantled howler (*Alouatta palliata*), and the black-handed spider monkey (*Ateles geoffroyi*). This paper focuses on the population of white-faced capuchins.

2.2. Data collection

2.2.1. Park-wide censuses

The population demographic data consist of 14 censuses carried out between 1971 and 2013 (Fedigan, 1986; Fedigan et al., 1996, 1985; Fedigan and Jack, 2012, 2001; Freese, 1976). Most of the censuses were carried out between late April and June, a time period that corresponds to the dry-to-wet season transition in SSR. Beginning with the 1983 census, teams of observers employed a "modified quadrat" technique in which separate pairs of searchers walked transects and all trails, roads, fence lines, and stream beds in a chosen sampling area. Any capuchins encountered were followed until multiple observers could agree on a consistent, complete group count and composition, or until the group was lost. Distinctive individuals in each group were described (e.g., those with noticeable scars, pelage markings, or missing digits/tail portions), and these notes were used to avoid repeat counts of the same group. In later years, straight-line transects were discontinued as census-takers became increasingly proficient at relocating

known groups and discovering newly established groups. From 1983 forward, our knowledge of the different capuchin groups living in the park was sufficiently complete that we could calculate true count estimates with reasonably high confidence. Sampling effort varied among censuses, and in some years it was necessary to supplement actual count data with "replacement counts" in cases when particular groups were not found but were known to still exist. All replacement counts were set to the population mean group size for that particular census year. In addition, we replaced a small number of actual counts that were known to be incomplete. Most such cases involved difficult terrain or highly unhabituated animals that fled before a good-quality count could be obtained. The census count data are summarized in Table A1.

2.2.2. Climate data

Daily measurements of accumulated rainfall were collected by ACG personnel between July 1979 and February 2007 (Janzen and Hallwachs, unpublished data) and by members of our research team from January 2005 to the present. The ENSO is a coupled oceanic-atmospheric oscillation in central Pacific Ocean surface temperatures and air surface pressures, respectively. The "warm" phase of ENSO (El Niño) brings warm and dry conditions to Central America during the normally wet months of June to August, whereas the "cool" phase (La Niña) brings increased rainfall during approximately the same months (Ropelewski and Halpert, 1987). There are a variety of indices that are commonly used for monitoring ENSO activity. Based on data exploration with several indices of ENSO (see Appendix A.1), we determined that the Multivariate ENSO Index (MEI) was most strongly correlated with rainfall patterns in SSR, and we use the MEI hereafter to represent ENSO conditions. The MEI is a composite index calculated as the first principle component of six distinct meteorological processes measured over the tropical Pacific (Wolter and Timlin, 1993, 2011). We obtained the MEI data from the National Oceanic and Atmospheric Administration Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/enso/mei/table.html, accessed 2014-11-24).

2.3. Data analysis

2.3.1. Population changes

Previous studies have examined a variety of demographic parameters for the capuchin population as a whole. Here, we extend this record by including two additional censuses (2011 and 2013). Although we consider the population estimate from Freese's (1976) census in 1971/1972 for comparative purposes, we excluded this census from all analyses due to major methodological differences; specifically, animals of different age/sex categories were not distinguished during this census and the total search area may have differed from subsequent censuses. Following Fedigan and Jack (2012), we estimated the total population size in 1972 as 297 individuals in total, based on Freese's (1976) data. For the other census years, we calculated the total number of animals, total number of groups, mean group size, and the ratio of small immature animals to adult females (IFR) as an index that integrates female fertility and offspring mortality (Fedigan and Jack, 2001). Mean group size and IFR were based on high-quality counts only (i.e., we excluded the "replacement counts"). Small immature animals were defined as 0–3 years of age. Experienced observers can distinguish animals of this age category easily based on body size and shape. We focused on small immature animals rather than infants ($\leqslant$1 year) because the number of infants at any particular time can be strongly influenced by irregular waves of infanticide following male take-overs (Fedigan, 2003), whereas the number of small immature animals—consisting

of multiple infant cohorts—should be less sensitive to such irregular pulses.

The total population size from 1983 to 2013 had an asymptotic form (see Section 4.1) that is characteristic of logistic-based growth under resource limitation. To investigate this relationship in greater detail, we modeled the total population size estimates between 1983 and 2013 with a logistic growth model,

$$y = \frac{\theta_1}{1 + e^{[-\theta_2 + \theta_3]t]}} + \varepsilon$$

where y is the population size, t is the year, θ_1 is the carrying capacity, and the parameters θ_2 and θ_3 control the shape of the curve (following Fox and Weisberg, 2010). We obtained parameter estimates via nonlinear least-squares using the function "nls" in R (R Development Core Team, 2014).

2.4. Climate trends

The MEI time series data were organized into 12 annual sliding bimonthly seasons (Dec/Jan, Jan/Feb, ..., Nov/Dec) (Wolter and Timlin, 2011). To analyze the relationship between ENSO conditions and rainfall, we first restructured the monthly rainfall time series into the same sliding bimonthly seasons as the MEI time series by averaging the two values of accumulated rainfall in each bimonth. We performed a seasonal decomposition of the bimonthly rainfall time series by locally weighted scatterplot smoothing (LOESS) in R. This procedure models the time series as the combination of three different components: a periodic (i.e., annual) seasonal effect, a slowly varying trend, and an irregular remainder (Cleveland et al., 1990). We set the span of the LOESS window for rainfall trend extraction to 17 months based on data exploration with window lengths ranging from 3 to 36 months (see Appendix A.2). The MEI data were already normalized to adjust for seasonal effects. We calculated the cross correlation between MEI and the seasonally adjusted rainfall trend, as well as the lag which resulted in maximum correlation. To assess the significance of the cross-correlation, we calculated critical values using a permutation test under the null hypothesis of zero correlation. This involved comparing the actual cross-correlation to the 0.025 and 0.975 quantiles of the empirical distribution obtained by randomly reordering one of the time series, computing the new cross-correlation, and repeating these steps 10,000 times.

2.5. Statistical models

Based on data exploration, previous findings in our study system (Fedigan et al., 2008), and results from other primate populations (Dunham et al., 2008; Wiederholt and Post, 2011), we had reason to suspect that IFR might vary as a function of time-lagged rainfall and/or MEI. To analyze this relationship, we fit linear models of census groups' IFR to a variety of rainfall and MEI "influence period" scenarios. We considered lags from 1 to 4 years before the census date as plausible influences on IFR for two reasons: (1) most rainfall recorded during the census year itself (0-year lag) typically falls during June to November, which is later in the year than most censuses were carried out; and (2) small immature animals were aged 0–3 years, and so conditions more than 4 years previous should not be strongly reflected in the IFR. We calculated simple rolling means of total rainfall and MEI for influence period scenarios with window lengths ranging from 1 to 4 years prior to the census year (in one year increments). We also considered the possibility that rainfall/MEI in recent years could affect IFR in a weighted fashion whereby climate conditions in more recent years would be stronger influences on IFR than conditions in more distant years. However, the weighted rolling means were generally poorer predictors of IFR than simple rolling means,

and we do not consider these weighted models further. We also considered that the influence of MEI/rainfall might have changed over time due to changing density-dependent effects as the population saturated its available habitat. We therefore defined two population growth periods: the early growth period from 1983 to 1998, and the recent stable period from 1999 to the present (see Section 4.1). We fit separate full models for the 1-, 2-, and 3-, and 4-year influence-period scenarios. The predictor variables in these full models included the rolling mean of MEI or rainfall during the appropriate influence period, the population growth period as a categorical variable, and an interaction effect. After fitting the models, we confirmed visually that the residuals were homogeneous. We chose the climate index/influence period combination that best predicted IFR based on the log-likelihood values from the full models. Given the most likely full model, we then generated a set of models with combinations of terms from the chosen best full model (i.e., the full model, an intercept-only null model, two models with each predictor variable in isolation, and a model with both predictor variables but without the interaction term), and we applied information-theoretic model selection based on sample-size corrected Akaike's Information Criterion (AICc) (Burnham and Anderson, 2002).

3. Results

3.1. Demographic trends

As of 2013, the total number of capuchins in the conservation area approximately doubled since the first reliable population estimate in 1983 (Fig. 1a). Changes in the total population size of capuchins in SSR from 1983 to 2013 were well described by the logistic growth model (Fig. 2, Table 1). In the last decade, the total population size appears to have reached an asymptote ($\theta_1 \pm$ std. error) at 628 ± 15.2 animals (Fig. 2). The estimated population size in 1972 (which did not contribute to the model) clearly did not fit the model (census estimate: 297 animals, model prediction: 80 animals). The IFR showed high inter-annual volatility with a trough through the early and middle 1990s that coincides with slowing population growth (Fig. 1d). Since monitoring began, there have been two relatively long periods of stasis in the number of capuchin groups (Fig. 1b). There were approximately 28 capuchin groups in the park from the first intensive census in 1983 until the early 1990s. There is a gap in monitoring between the 1992 and 1999 censuses, but when monitoring resumed, the total number of groups had increased to 35. Within a few more years, there were approximately 40 capuchin groups in the park, and this number has remained relatively constant since 2003. Mean group size also fluctuated over the study period (Fig. 1c). From a low of 11.7 animals per group when monitoring began, mean group size increased rapidly and peaked at 17–18 in the late 1980s and early 1990s. Mean group size has since decreased, and in the last decade, appears to have stabilized at about 15 animals.

3.2. Climate trends

Total yearly rainfall was highly variable over the study period (annual median: 1497 mm; range: 818–3498 mm) (Fig. 3a) and showed strong correspondence with phases and intensity conditions of the ENSO (Fig. 3b). The cross-correlation between the smoothed rainfall and MEI time series was significantly negative for lags between −6 and +12 months, and the lag that maximized the cross-correlation function ($r = -0.639$) was 2 months (Fig. 4a and b). This indicates that ENSO conditions as reflected by the MEI are inversely related to rainfall to within roughly one half-year in either direction, and changes in MEI precede
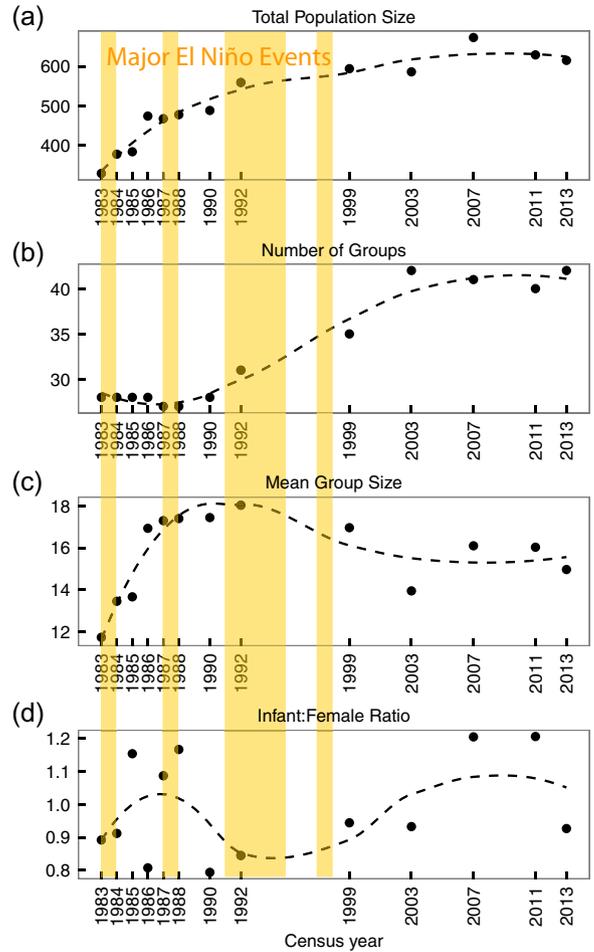
Fig. 1. Trends in the capuchin population from 1983 to 2013, including (a) total population size, (b) the total number of groups, (c) mean group size, and (d) small immature to adult female ratio. LOESS smoothers added to aid visual interpretation of the trends. Shaded periods indicate major El Niño episodes.
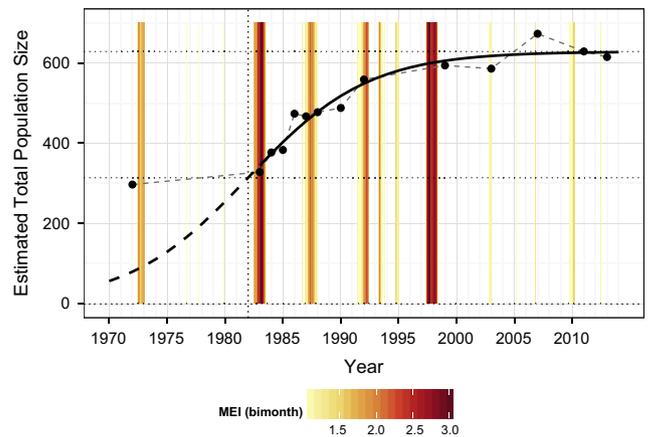
Fig. 2. Changes in total population size during the study period (points) fit by the logistic growth model (solid black line), which is based on counts from 1983 to 2013. Based on this growth, the dashed black line indicates predicted population size before the implementation of fire control in 1984. The point from 1972 clearly does not fit the model. Dotted lines indicate the population size at zero, at the asymptote $\theta_1 = 628$, and at the half-maximum (predicted in 1982, vertical dotted line). The vertical shading indicates the amplitude of El Niño-like conditions (Multivariate ENSO Index $\geqslant$ 1).

Table 1
Summary and parameter estimates for the logistic model of population growth.

Parameter	Estimate	Std. error	t-Value	P
θ_1	628.4	15.16	41.445	1.60×10^{-12}
θ_2	−382.7	73.83	−5.184	0.000411
θ_3	0.1931	0.0372	5.190	0.000407

Residual standard error: 27.32 on 10° of freedom.
Number of iterations to convergence: 5.
Achieved convergence tolerance: 9.412×10^{-06}.

associated changes in rainfall most congruently by about 2 months. The most severe dry periods, which occurred during 1983, 1987, 1991 to 1995, and 1997 coincided with unusually intense ENSO activity (i.e., positive MEI values). By increasing the temporal span of the smoother, it is apparent that rainfall shows an increasing long-term trend since the mid-1990s (Fig. 4a) in conjunction with an ENSO regime dominated recently by frequent La Niña phases (Fig. 3b). When bimonthly rainfall anomalies are separated into La Niña-like (MEI $\leqslant$ −1), neutral (−1 < MEI < 1), and El Niño-like (MEI $\geqslant$ 1) phases, it is evident that Niña-like phases bring much wetter conditions from July to October, but they have no noticeable effects on rainfall patterns during the dry-to-wet season transition from April to June, when water stress on the monkeys is most severe (Fig. 5). El Niño-like phases, in contrast, cause two noticeable rainfall deficits: one during the dry-to-wet season transition in April to June, and another during the peak of the normal wet season from August to October (Fig. 5).

### 3.3. Links between population dynamics and climate

In the first round of model selection involving the full models, the rainfall or MEI influence period that best predicted IFR was a rolling mean of MEI values during the 3 years prior to the census year (Table 2). Given the 3-year MEI model, the second round of model selection provided strong empirical support for the full model over the other candidate models (ΔAICc > 14, Table 3), including the null model. In this best model, higher MEI (i.e., more El Niño-like conditions) during the previous three years predicted
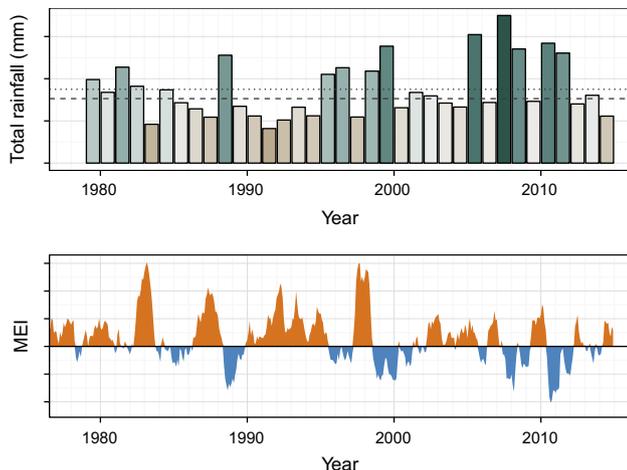
Fig. 3. (a) Yearly rainfall totals from 1979 to 2013. The dashed line is the annual median and the dotted line is the annual mean. (b) Bimonthly values of the Multivariate ENSO Index (MEI) over the same time period. The positive phase of ENSO (orange shading) corresponds to El Niño-like conditions whereas the negative phase (blue shading) corresponds to La Niña-like conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lower IFR during the early growth period but not the recent stable period ($F_{(3,251)}$ = 7.105, p: 0.000134; Fig. 6a and b).

Four notable population dynamic trends were coincident with significant environmental changes that occurred in SSR during our study's timeframe. First, the apparent switch in population growth dynamics that occurred between the 1972 census and those from the 1980s coincides with the implementation of successful large-scale fire control in SSR around 1984 (Fig. 2). Second, over-prediction of total population size by the logistic growth model in 1985, 1990, and 1999 to 2003 follows exceptionally strong El Niño episodes in 1983, 1987, and 1998 (Fig. 2). All three of these episodes were associated with acute rainfall deficits during the critical April/May and May/June bimonths during which rainfall normally begins after approximately five consecutive months without significant rain (Fig. A3). Third, an unusually prolonged El Niño episode from 1991 to 1994 occurred during six consecutive years of below-average rainfall in SSR, including the driest (1991) and third-driest (1992) years on record (Fig. 3a). During this time, mean group size decreased, IFR declined, and the total number of groups increased, perhaps as a result of large groups dissolving (Fig. 1a and b). In the dry season of 1993, there was unusually high mortality and apparent illness in our study groups that led to one of only two group extinctions that we have observed in our 30-
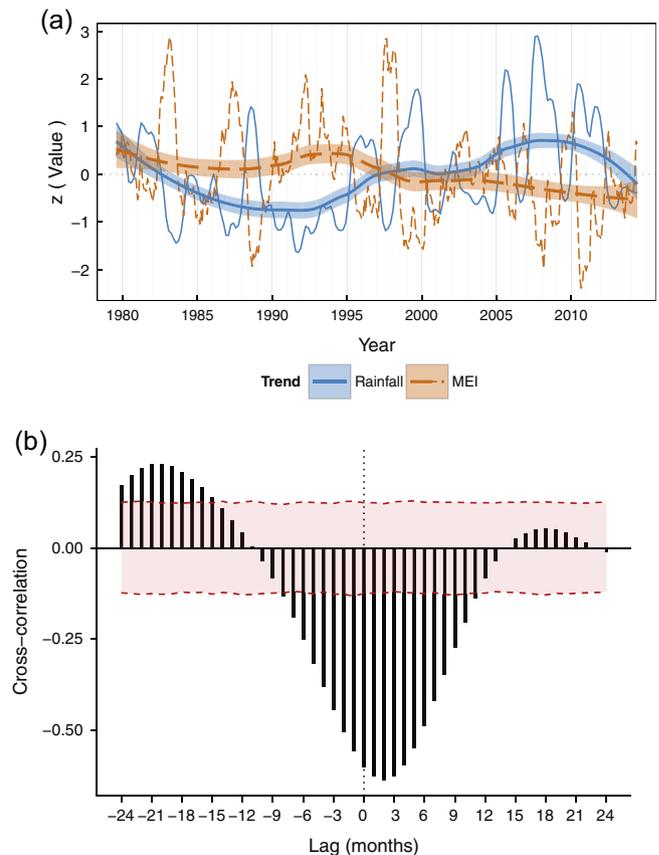
Fig. 4. (a) Relationship between seasonally adjusted bimonthly rainfall totals (solid lines) and Multivariate Enso Index (MEI) values (dotted lines). The thin lines show LOESS-smoothed (with 17-month span) and scaled (z-transformed) bimonthly time series for seasonally adjusted rainfall trend and MEI. The thick line shows a 20-year LOESS smooth with 95% confidence interval. (b) Permutation test of the significance of the cross-correlation between bimonthly Multivariate ENSO Index (MEI) values and seasonally adjusted bimonthly rainfall time series for lags between −24 and 24 months. Dashed lines show the 0.025 and 0.975 quantiles of the empirical distribution obtained by a permutation test with 10,000 replicates. These values provide a two-tailed test of the null hypothesis that the cross correlation is zero, conditional on the data. Positive values outside this envelope (shaded region) indicate a significant cross-correlation between MEI and rainfall.
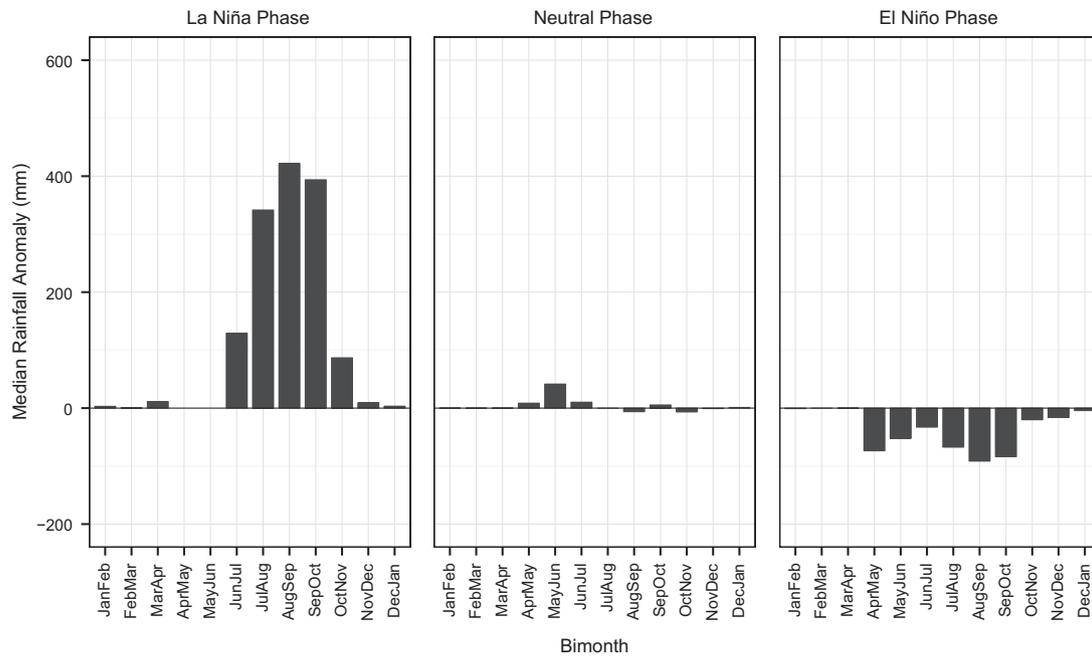
Fig. 5. Median bimonthly rainfall anomalies associated with phases of ENSO as measured by the Multivariate ENSO Index (MEI). The phases were defined as follows: La Niña phase: MEI ⩽ −1; neutral phase: −1 < MEI < 1; El Niño phase: MEI ⩾ 1.

Table 2
Summary of first round of model selection to identify the full model on which to concentrate further. Each full model included the mean annual value of rainfall or Multivariate ENSO Index (MEI) during the corresponding influence period, the population's growth period ("rapid growth period" or "recent stable period"), and an interaction effect.

Model	Variable	Influence period	logLik
m1	Rainfall	1 year	−94.12
m2	Rainfall	2 years	−90.61
m3	Rainfall	3 years	−92.09
m4	Rainfall	4 years	−96.33
m5	MEI	1 year	−97.21
m6	MEI	2 years	−96.22
m7	MEI	3 years	−87.32
m8	MEI	4 years	−90.61

year study and that may have resulted from, or been exacerbated by, the drought of the previous years. Fourth, 1998 marked the end of an approximately 22-year long "warm" phase of the Pacific Decadal Oscillation (Bond, 2003; Chavez et al., 2003), which is associated with reduced rainfall in Central America (Mantua and Hare, 2002). This coincides with or closely precedes inflection points in the smoothed trends for mean group size and IFR that reverse the negative, drought-associated demographic shifts of the early 1990s.

Table 3
Summary of second round of model selection applied to subsets of the full 3-year Multivariate ENSO Index (MEI) model (m7). Aside from the full model (m7), candidate models included a null model (m7a), models with each predictor variable in isolation (m7b and m7c), and a model with both predictor variables but no interaction effect (m7d).

Model	Terms	AICc	ΔAICc	Akaike weight
m7a	Intercept only	199.5	14.59	0.001
m7b	MEI	199.3	14.43	0.001
m7c	GrowthPeriod	200.9	15.98	0
m7d	GrowthPeriod + MEI	201.4	16.47	0
m7	GrowthPeriod * MEI	184.9	0	0.998

4. Discussion

This study's cardinal finding is that environmental stressors have played an important role in regulating the population growth dynamics of white-faced capuchins in SSR. This conclusion centers around two key results. First, the population has experienced two distinct growth phases since the conservation area's establishment, a period of rapid growth through the 1980s and 1990s and a subsequent period of stability from about 2000 to the present. Second, the effects of climate on the population's IFR differed during the two phases in conjunction with a switch in the dominant ENSO regime. Below, we consider causes and implications these two findings in greater detail.

4.1. Changes in capuchin population size and structure

Our data show that in the last decade the capuchin population of SSR has entered a period of relative stasis with close to zero population growth. If the population has indeed reached the habitat's carrying capacity, then its size at the time of the conservation area's establishment was half of its eventual maximum, which was reached after about 20 years of logistic-based growth. Previous studies have documented a similar but accelerated trajectory of rapid increase and eventual leveling-off among sympatric howler monkeys, but the howler population apparently reached saturation around the late 1980s and has increased little since then (Fedigan et al., 1998; Fedigan and Jack, 2012, 2001). Given the probable influence of habitat destruction by fire in mediating these growth curves (Fedigan and Jack, 2001), the availability of suitable (i.e., unburned) habitat is likely to have been the key resource limiting both howler and capuchin population growth. The slow increase of suitable habitat via forest regeneration in recently cleared or burned areas (Janzen, 1988) may also have contributed to this population growth. As previously cleared or burned areas of tropical dry forest continue to regenerate in SSR (Janzen, 1988), we expect the capuchin population to continue growing slowly as more habitat becomes available. However, because the pace of forest regeneration will limit this future growth, it should occur along
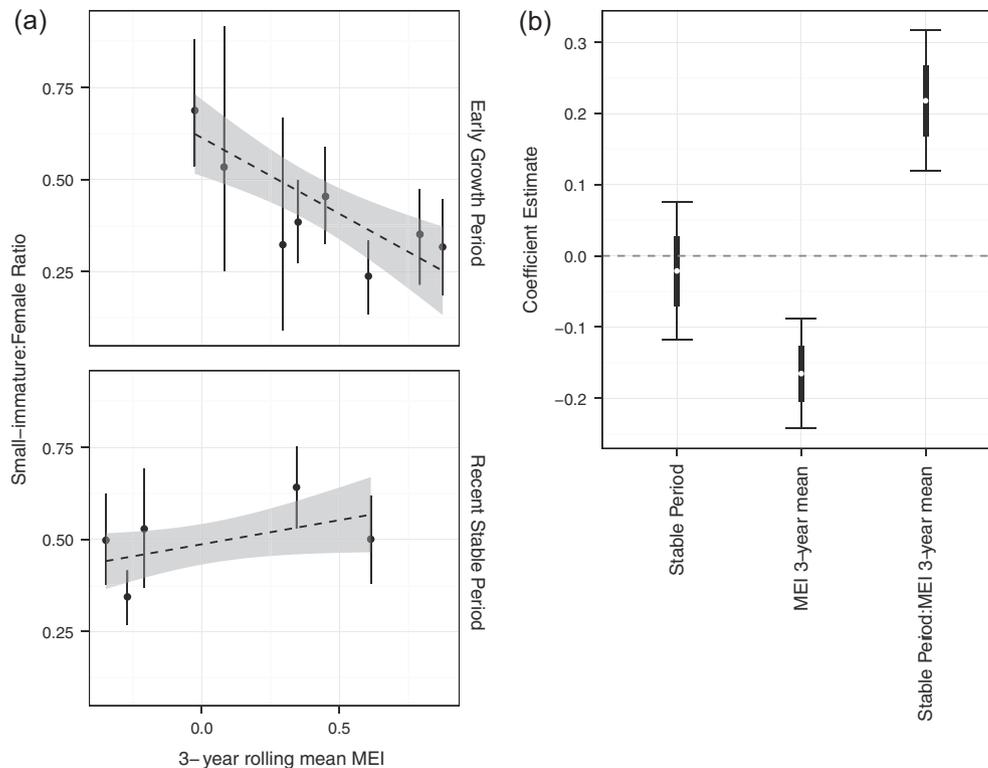
Fig. 6. (a) Relationship between small-immature-to-female ratio (IFR) and a rolling mean of Multivariate ENSO Index (MEI) values in the three years prior to the census year during the population's early growth period (pre-1999) and during the recent stable period (1999 and after). Each point corresponds to one census year, and the vertical bars show 95% confidence limits for the population mean value for that census year calculated by nonparametric bootstrapping. (b) Regression coefficients for the linear model of IFR as a function of 3-year mean MEI and growth period. Thin error bars show 95% confidence intervals, and thick bars show ± 1 SD. For the categorical variable "growth period", the early growth period is defined as zero.

a markedly slower trajectory than the rapid growth we observed through the late 1980s and 1990s.

4.2. Effects of variable climate

More El Niño-like conditions over a multi-year timeframe were associated with lower IFR in subsequent years during the period of relatively rapid population growth. The fundamental process that drove this relationship was likely to be the close link between ENSO conditions and local rainfall. Phenological changes in tropical dry forest trees, such as leaf flushing or flowering, are often induced by rehydration after the first heavy rains at the beginning of the wet season (Borchert, 1994; Borchert et al., 2004). Therefore, altered rainfall patterns are likely to affect the timing and performance of fruit production among many fruit-bearing trees on which capuchins rely heavily. In particular, rainfall deficits associated with El Niño-like conditions during the period of time when the first heavy rains of the wet season normally fall may have cascading effects downstream on food availability, female body condition, and ultimately on female reproductive output and/or offspring mortality. At Barro Colorado Island, Panama, a nearby but wetter Neotropical ecosystem, strong El Niño episodes are associated with increased fruit production but are often followed by widespread fruit crop failure in the following year (Wright et al., 1999). Altered rainfall patterns in SSR could also produce downstream changes in IFR in a variety of other ways. For example, some of our study groups go without drinking water for the last 2–3 months of the dry season after their natural sources are exhausted (Childers, 2008). In these groups, the delayed onset of significant rainfall in the early wet season could increase mortality in immature animals, which may be particularly sensitive to dehydration. Alternatively, widespread fruit crop failure and scarce

surface water might bring neighboring groups into more frequent and aggressive contact over the remaining resources, which may increase the risk of male takeovers and subsequent waves of infanticide. Further individual-based studies of vital rates in relation to climate indices and available fruit biomass are needed to elucidate the proximate mechanisms at work.

Why might the effects of ENSO conditions on IFR have changed after the population entered its recent stable period? One possible reason is that smaller populations tend to have more unstable dynamics and show greater sensitivity to environmental stochasticity than larger, stable populations. For example, butterfly species with more volatile population dynamics are more strongly affected by ENSO conditions than species with more stable population dynamics (Harrison et al., 2015). A second possible reason is that there has not been a historically powerful El Niño episode after 1997/1998, which approximately marked the end of the "rapid growth period" for our population, whereas there were four strong El Niño episodes between 1983 and 1998. Indeed, much of the variability in the MEI values since 1998 relates to frequent oscillations between strong La Niña episodes and either neutral conditions or mild El Niño-like conditions. It may be that the downstream ecological effects associated with these oscillations do not meaningfully affect IFR in the same way that strong El Niño episodes do. For example, fruit crop failure may be more likely when normally wet periods become drier (as with a strong El Niño episode) than when normally wet periods become wetter (as with a strong La Niña episode). A cross-site analysis of annual census data from several ateline populations has shown that strong El Niño episodes are followed by immediate or one-year-lagged population declines (Wiederholt and Post, 2010) as well as reduced birth rates (Wiederholt and Post, 2011). Our irregularly spaced census data do not permit such a year-by-year analysis, but they

do suggest that strong El Niño phases are likely to have both geographically and taxonomically widespread negative effects on primate populations. Wiederholt and Post's (2010) study implicated changes in food tree phenology as an important driver of this pattern. The rainfall-associated effects on capuchin population dynamics in SSR provide an interesting comparison with the capuchin population on Barro Colorado Island. This capuchin population suffered a period of catastrophic mortality, with greater than 70% loss of the population, following unprecedented high rainfall in December 2010 in association with a powerful La Niña phase of ENSO (Milton and Giacalone, 2013). Although relatively near to SSR, Barro Colorado Island is a lowland rainforest ecosystem with very different ecological dynamics. Nonetheless, the combined results from SSR and Barro Colorado Island indicate that rainfall extremes in either direction can have profound negative impacts on white-faced capuchin populations in Central America.

4.3. Conservation and management implications

Greenhouse warming in the coming century will produce more frequent extreme El Niño episodes (Cai et al., 2014; Timmermann et al., 1999), such as those that caused catastrophic damage in 1982/83 and 1997/98. Our study adds to the small but growing literature that provides cause for concern about the effects of increasing strong El Niño episodes on primate populations in the near future (Dunham et al., 2011, 2008; Milton et al., 2005; Milton and Giacalone, 2013; Wiederholt and Post, 2011, 2010). These studies indicate that primate populations in widely separated locations may suffer simultaneous negative consequences from greater frequency and/or amplitude of large-scale climate oscillations. Primates often make up a major proportion of the vertebrate biomass in their ecosystems (Kamilar and Beaudrot, 2013) and may play key roles in structuring plant communities via seed dispersal, nutrient cycling, and folivory (Chapman et al., 2013). Therefore, conservation strategies that promote the survival of primates are likely to be beneficial for many other members of the ecological community.

From a regional perspective, several empirical studies have reported a long-term drying trend in Central America (Borchert, 1998; Fleming, 1986; Vargas and Trejos, 1994); climate models bear out these observations and predict continued drying in the future (Christensen et al., 2007; Neelin et al., 2006). For example, using global warming simulations, Xie et al. (2010) predict mean annual precipitation decreases of 5–10 mm per month over the next 50 years for this region of Central America. If drought years become increasingly common as the global climate warms, we expect that not only capuchins but also many other animals in affected regions with seasonally dry forests may suffer declines in fecundity. Conservation planners in highly seasonal ecosystems with scarce surface water should evaluate whether providing sources of drinking water during the late dry season can mitigate these effects. Nonetheless, it is striking that most of our study population's growth occurred during the late 1980s and 1990s, a time of recurrent droughts dominated by frequent and powerful El Niño episodes. The major change that occurred in SSR at the beginning of the rapid growth period was the elimination of extensive annual burning. As in the study by Dunham et al. (2008), this suggests that anthropogenic pressures related to habitat loss or degradation were considerably more important constraints on primate population dynamics compared to climate oscillations. This suggests a markedly greater capacity in primates to cope with even extreme climate stressors compared to anthropogenic stressors, and it supports the idea that fire control can be a particularly efficacious method of promoting conservation in tropical dry forests (Janzen, 2000).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.03.017.

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