Tropical warming and the dynamics of endangered primates

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Many primate species are severely threatened, but little is known about the effects of global warming and the associated intensification of El Niño events on primate populations. Here, we document the influences of the El Niño southern oscillation (ENSO) and hemispheric climatic variability on the population dynamics of four genera of ateline (neotropical, large-bodied) primates. All ateline genera experienced either an immediate or a lagged negative effect of El Niño events. ENSO events were also found to influence primate resource levels through neotropical arboreal phenology. Furthermore, frugivorous primates showed a high degree of interspecific population synchrony across Central and South America attributable to the recent trends in large-scale climate. These results highlight the role of large-scale climatic variation and trends in ateline primate population dynamics, and emphasize that global warming could pose additional threats to the persistence of multiple species of endangered primates.

Keywords: ateline primates; El Niño southern oscillation; global climate change; population synchrony; neotropics

1. INTRODUCTION

Climate change has resulted in an increase in global temperatures of 0.74°C over the last century, with an additional increase of 1.8–4°C expected over the next century (IPCC Climate Change 2007). Given that such a warming may alter the frequency of El Niño events (Timmermann et al. 1999), it is critical to understand the effects of large-scale climate factors on wildlife populations. The impacts of climatic variability and El Niño events have been studied for numerous species and ecosystems (Walther et al. 2002), including neotropical forests. These ecosystems have undergone multiple changes in response to global climate change and El Niño events, which could have direct effects on primate populations (Wright et al. 1999). Nonetheless, very few investigations of the implications of El Niño events for population dynamics have been conducted on primate species in general (Dunbar 1998; Dunham et al. 2008), or on platyrhine (New World) monkeys (Milton et al. 2005). Quantifying the role of climate change in the dynamics of primates is crucial because, globally, up to one-third of primate species are threatened with extinction. The subfamily Atelinae (large-bodied New World primates) is of particular conservation interest as it is a highly threatened group (Campbell et al. 2007). If there is a climate signal in their dynamics, there may be a potential for large-scale climate change to synchronize their fluctuations or population trends (Post & Forchhammer 2002), which may furthermore exacerbate the extinction risk of multiple populations (Heino et al. 1997).

Here, we aimed to quantify the effects of large-scale climate and resource availability (tree phenology) on ateline primate population dynamics using one species from each of the four declining ateline genera. We then examined the level of interspecific synchrony among these populations and quantified the role of large-scale climatic variability in synchrony.

2. MATERIAL AND METHODS

(a) Study species and areas

Data on primate annual abundances and resource phenology were used from four neotropical sites. The muriqui (Brachyteles arachnoides), currently classified as endangered on the IUCN red list, was censused in Minas Gerais, Brazil (19°44’ S, 41°49’ W), from 1982 to 2005 (Stirri 2005). The Colombian red howler monkey (Alouatta seniculus), classified as declining but of least concern on the IUCN red list owing to its wide distribution, was studied in Guárico State, Venezuela (9°34’ N, 67°35’ W), from 1970 to 1999 (Rudran & Fernandez-Duque 2003). The woolly monkey (Lagothrix lagotricha), currently appearing on the IUCN red list as vulnerable, was censused in Meta, Colombia (2°40’ N, 74°10’ W), from 1987 to 1998 (Nishimura 2003). Geoffroy’s spider monkey (Ateles geoffroyi), classified as endangered on the IUCN red list, was studied on Barro Colorado Island, Panama (9°10’ N, 79°51’ W), from 1964 to 2003 (Milton & Hopkins 2006). All population counts were log-transformed to normalize residuals.

(b) Phenology data

Tree phenology data from Barro Colorado Island, Panama (a lowland, moist tropical forest), were available from 1987 to 2004 (Wright & Calderon 2006). Intersite variation is likely to exist, however, as lowland moist to wet tropical forests are the dominant vegetation form of northern South America (Daly & Mitchell 2000). BCI vegetation data represent an approximate index of resource availability. We used the monthly maximum and minimum number of species fruiting and flowering for each year as an index of resource availability, along with the annual values of flower and seed production for a subset of 44 mammalian-dispersed species. These values were log-transformed to normalize residuals.

(c) Climate data

The southern oscillation index (SOI), the El Niño southern oscillation (ENSO), and ENSO indices (http://www.cdc.noaa.gov/data/climateindices/list) were used to represent large-scale ENSO conditions along with the Southern Hemisphere temperature anomaly index (http://data.giss.nasa.gov/gistemp). Regional annual rainfall data from Venezuela, the northeast Brazil rainfall anomaly index (http://jisao.washington.edu/data_sets/brazil) and the mean annual temperature, annual rainfall, and dry and wet season length from Barro Colorado Island, Panama (http://strirsi.si.edu/esp/physical_monitoring/summary_bci.htm), were used to quantify more regional weather conditions. In order to compare local climatic conditions between sites, we used annual, wet season, dry season and three-month quartiles values for temperature and rainfall data interpolated to a 0.5° by 0.5° grid resolution for each site from 1960 to 1990 (http://climate.geog.udel.edu/~climate/html_pages/archive.html).

(d) Population models

In order to assess the influence of ENSO and climatic conditions on primate abundances, we used autoregressive density-dependent models (Royama 1992). The general form of the model was as follows:

\[ X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(\gamma_1) + b_2(\gamma_{t-1}) + b_3(\gamma_{t-2}) + b_4(\gamma_{t-3}) + e_t \]  

(2.1)
where $X_i$ are the log of population densities in year $t$, $a_i$ is a constant representing the intrinsic rate of population increase, $a_i$ are the estimates of the strength of density dependence at the lags of $i$ years, $b_i$ are the estimates of the effects of climate or phenology on population density, in year $t$, $y_i$ is the SOI, ENSO3 index, rainfall or phenology value in year $t$, and $e_i$ is the random error component in year $t$. The year was also included as a covariate in all models to account for any temporal trends in the data. First-, second- and third-order models were first examined to determine the most parsimonious skeleton model of density-dependent dynamics without covariates. We then included the climate variables (SOI, ENSO3 index and rainfall) or phenology of density-dependent dynamics with the exception of annual flower production which displayed second-order density dependence.

Next, we modelled the potential climatic effects on primate population dynamics to identify the best overall model describing the dynamics of each species based on a Bayesian information criterion score (Burnham & Anderson 1998).

We included the climate variables (SOI, ENSO3 index and rainfall) or phenology indices with lags up to three years in the best skeleton model of primate population dynamics to identify the best overall model describing the dynamics of each species based on a Bayesian information criterion score (Burnham & Anderson 1998).

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Table 1. Best-fit primate population models quantifying the effect of climate or phenology on log density.

<table>
<thead>
<tr>
<th>genus</th>
<th>model equations$^a$</th>
<th>climate or phenology coefficient ± s.e.</th>
<th>BIC$^b$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alouatta</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + b_1(\text{SOI}) + y_t + e$</td>
<td>$0.013 \pm 0.019$</td>
<td>$-3.059$</td>
<td>$0.823$</td>
</tr>
<tr>
<td><em>Ateles</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + y_t + e$</td>
<td>$-0.052 \pm 0.032$</td>
<td>$-3.176$</td>
<td>$0.857$</td>
</tr>
<tr>
<td><em>Lagothrix</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + y_t + e$</td>
<td>$-0.04 \pm 0.051$</td>
<td>$-3.352$</td>
<td>$0.604$</td>
</tr>
<tr>
<td><em>Brachyteles</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{SOI}) + y_t + e$</td>
<td>$0.02 \pm 0.011$</td>
<td>$-4.917$</td>
<td>$0.975$</td>
</tr>
<tr>
<td><em>Ateles</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_3(\text{minfrt}_{t-2}) + y_t + e$</td>
<td>$0.302 \pm 0.042$</td>
<td>$-3.642$</td>
<td>$0.984$</td>
</tr>
<tr>
<td><em>Lagothrix</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_3(\text{minfrt}_{t-2}) + y_t + e$</td>
<td>$0.009 \pm 0.010$</td>
<td>$-4.327$</td>
<td>$0.946$</td>
</tr>
<tr>
<td><em>Brachyteles</em></td>
<td>$X_t = a_0 + a_1(X_{t-1}) + b_3(\text{minfrt}) + y_t + e$</td>
<td>$-0.004 \pm 0.011$</td>
<td>$-4.339$</td>
<td>$0.681$</td>
</tr>
</tbody>
</table>

$^a$Seed = annual seed production, mxfrt = monthly maximum number of species flowering per year, minfrt = monthly minimum number of species fruiting per year.

$^b$Bayesian Information criterion.

Table 2. Best-fit model coefficients quantifying the influence of climate on phenology.

<table>
<thead>
<tr>
<th>phenology indices$^a$</th>
<th>climatic factor</th>
<th>coefficient ± s.e.</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>monthly max. number of spp. fruiting</td>
<td>ENSO3$^3_t$</td>
<td>$9.057 \pm 2.094$</td>
<td>$4.325$</td>
<td>$0.001$</td>
</tr>
<tr>
<td>monthly min. number of spp. fruiting</td>
<td>ENSO3$_{t-1}^3$</td>
<td>$-5.29 \pm 2.009$</td>
<td>$-2.632$</td>
<td>$0.02$</td>
</tr>
<tr>
<td>monthly max. number of spp. flowering</td>
<td>BCI temperature</td>
<td>$6.608 \pm 2.953$</td>
<td>$2.237$</td>
<td>$0.042$</td>
</tr>
<tr>
<td>monthly min. number of spp. flowering</td>
<td>ENSO3$_{t-2}^3$</td>
<td>$-3.974 \pm 2.343$</td>
<td>$-1.696$</td>
<td>$0.112$</td>
</tr>
<tr>
<td>annual seed production</td>
<td>ENSO3$_{t-1}$</td>
<td>$-0.248 \pm 0.115$</td>
<td>$-2.158$</td>
<td>$0.05$</td>
</tr>
<tr>
<td>annual flower production</td>
<td>BCI dry season length$_{t-1}$</td>
<td>$-0.003 \pm 0.002$</td>
<td>$-2.163$</td>
<td>$0.051$</td>
</tr>
</tbody>
</table>

$^a$All the phenology indices were characterized by first-order density dependence with the exception of annual flower production which displayed second-order density dependence.

3. RESULTS

The more frugivorous ateline populations (muriquis, spider and woolly monkeys) declined one year following El Niño events, while howler monkeys declined in the same year that El Niño events occurred (table 1). Resource availability (our phenology index) had either a lagged positive, lagged negative or immediate negative effect on population density; the differences among phenology indices entering the best-fitting models may reflect variation in ateline diet (Campbell et al. 2007) or the indices’ abilities to track important resources. The immediate influence of resources could indicate the more seasonal environment of muriquis, while the negative effect may denote increased resource competition during the wet season, a time of seasonal scarcity. Indeed, woolly monkeys can have a high dietary overlap with other sympatric primates (Campbell et al. 2007).

For the phenology analysis, the resource indices included either an ENSO index or a local weather effect (which are indicative of El Niño events) in the best-fitting models of phenological dynamics (table 2). The phenology indices exhibited either a positive immediate effect or a lagged negative effect of an El Niño event (continuing up to two years afterwards).

A high degree of synchrony was found among the more frugivorous primate populations for the untransformed time series (figure 1). Smaller correlations among the detrended time series underline the contribution of large-scale climatic trends to population synchrony. Correlations between primate synchrony and pairwise local climate correlations were mainly negative, indicating that population synchrony was not linked to the proximal drivers of dynamics. On the other hand, correlations between primate synchrony and pairwise model coefficient correlations were mainly positive, indicating that synchronous population dynamics were associated with similar population level responses to ENSO events or large-scale temperature anomalies (figure 2).
4. DISCUSSION

Our multi-species analysis indicates a strong relationship between large-scale climate and primate population dynamics: populations of ateline primates of conservation concern representing widely dispersed locations in Central and South America are affected by the ENSO and El Niño events. Spider, woolly, muriqui and howler populations experienced either an immediate or a one year lagged negative effect of an El Niño event. Furthermore, the more frugivorous and threatened genera (muriquis, woolly and spider monkeys) experienced the greatest declines following El Niño events.

We hypothesized that the effects of El Niño and seasonal weather on primate populations are probably mediated through food availability. Our analyses indicated either an immediate or a lagged effect of resource availability on primate populations, and a strong effect of climatic variability and El Niño events on the potential primate resource levels. These results, along with the more frugivorous genera’s decline one year after an El Niño event, are consistent with other ecological research from BCI. A cycle of high then low fruit production during El Niño and La Niña years, respectively, has been documented, the latter can cause famines in frugivorous mammals (Wright et al. 1999; Milton et al. 2005).

Finally, the more frugivorous primate populations exhibited a high degree of population synchrony over considerable distances. Notably, howler monkeys, the more folivorous and distantly related ateline genus, were the only primates to show asynchronous dynamics (Campbell et al. 2007). Furthermore, we documented that as the populations’ responses to ENSO events and temperature changes were more similar, they exhibited a higher degree of synchrony. The ability of climate to synchronize populations has been well documented in the neotropics (Jaksic 2001); it poses an additional threat for primates as metapopulation theory suggests that multiple populations have a greater extinction risk when exhibiting
synchronous versus asynchronous population dynamics (Heino et al. 1997).

Our results indicate that global climate change and increased El Niño events could pose a serious threat to ateline primates. Given that the status of many primate species is already precarious, in the face of continued global change, further studies to quantify the effects of climate and environmental variability on primate species are needed.

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