Tropical warming and the dynamics of endangered primates

Ruscena Wiederholt^{1,*} and Eric Post²

¹Program in Ecology, Pennsylvania State University, 409 Carpenter Building, University Park, PA 16802, USA

²Department of Biology, Pennsylvania State University, 208 Mueller Laboratory, University Park, PA 16802, USA

*Author for correspondence (rpw143@psu.edu).

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 over large scales 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 platyrrhine (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 (Strier 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 (8°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)3, ENSO34, ENSO4 and ENSO12 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, dry and wet season length from Barro Colorado Island, Panama (http://striweb.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:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(\gamma_t) + b_2(\gamma_{t-1}) + b_3(\gamma_{t-2}) + b_4(\gamma_{t-3}) + \varepsilon_t \quad (2.1)$$

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

genera	model equations ^a	climate or phenology coefficient $\pm$ s.e.	BIC ^b	R ²
<i>Alouatta</i>	$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + b_1(\text{SOI}_t) + \text{yr} + \varepsilon$	0.013 ± 0.019	-3.059	0.823
<i>Ateles</i>	$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + \text{yr} + \varepsilon$	-0.052 ± 0.032	-3.176	0.857
<i>Lagothrix</i>	$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + \text{yr} + \varepsilon$	-0.04 ± 0.051	-3.352	0.604
<i>Brachyteles</i>	$X_t = a_0 + a_1(X_{t-1}) + b_2(\text{SOI}_{t-1}) + \text{yr} + \varepsilon$	0.02 ± 0.011	-4.917	0.975
<i>Alouatta</i>	$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + b_3(\text{seed}_{t-2}) + \text{yr} + \varepsilon$	0.302 ± 0.042	-3.642	0.984
<i>Ateles</i>	$X_t = a_0 + a_1(X_{t-1}) + b_3(\text{mxflwr}_{t-2}) + \text{yr} + \varepsilon$	0.009 ± 0.010	-4.327	0.946
<i>Lagothrix</i>	$X_t = a_0 + a_1(X_{t-1}) + b_3(\text{minfrt}_{t-2}) + \text{yr} + \varepsilon$	-0.009 ± 0.002	-4.339	0.681
<i>Brachyteles</i>	$X_t = a_0 + a_1(X_{t-1}) + b_1(\text{minflwr}) + \text{yr} + \varepsilon$	-0.004 ± 0.001	-6.482	0.982

^aSeed = annual seed production, mxflwr = monthly maximum number of species flowering per year, minfrt = monthly minimum number of species fruiting per year, minflwr = monthly minimum number of species fruiting per year.

^bBayesian information criterion.

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

phenology indices ^a	climatic factor	coefficient $\pm$ s.e.	t-value	p-value
monthly max. number of spp. fruiting	ENSO3 _t	9.057 ± 2.094	4.325	0.001
monthly min. number of spp. fruiting	ENSO3 _{t-2}	-5.29 ± 2.009	-2.632	0.02
monthly max. number of spp. flowering	BCI temperature	6.608 ± 2.953	2.237	0.042
monthly min. number of spp. flowering	ENSO4 _{t-2}	-3.974 ± 2.343	-1.696	0.112
annual seed production	ENSO3 _{t-2}	$-0.248 \pm .115$	-2.158	0.05
annual flower production	BCI dry season length _{t-1}	$-0.003 \pm .002$	-2.163	0.051

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

where X_i are the log of population densities in year i , a_0 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 quantifies the effects of climate or phenology on population density in year i , γ_i is the SOI, ENSO3 index, rainfall or phenology value in year t , and ε_t 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 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).

Next, we modelled the potential climatic effects on primate resource levels in the same manner as primate abundances. Climate terms (BCI weather indices, SOI and ENSO indices) at lags up to three years were added to the models that had the strongest correlation coefficients with the phenology indices. Parameter coefficients were obtained by using ARIMA in SPSS (SPSS Inc., Chicago, IL).

In order to assess the patterns of population synchrony, we quantified all pairwise lag-0 correlations between the raw time series of yearly primate abundances, and repeated this using the detrended time series. We also conducted correlation analyses between the local climatic conditions for each pair of sites and between the ENSO3 index, SOI and temperature anomaly coefficients with lags up to three years from the primate population models. Then, to investigate whether primate population synchrony could be attributed to climatic factors, we conducted correlation analyses between the local climatic conditions or climate index coefficients at each pair of sites and synchrony (pairwise correlation) between pairs of primate populations at those sites (*sensu* Post & Forchhammer 2002).

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).

Figure 1. Pairwise primate population synchrony for the untransformed and detrended time series plotted against the distance between populations. Howlers indicates correlations of the howler population with the frugivorous genera, while frugivores indicates correlations between the frugivorous genera only. Filled square, untransformed howlers; filled triangle, untransformed frugivores; filled diamond, detrended howlers; filled cross, detrended frugivores.

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

Figure 2. Pairwise primate population synchrony (for untransformed time series) plotted against pairwise site correlations for the population model coefficients quantifying contributions to population dynamics of (a) the southern oscillation index; (b) the ENSO3 index and (c) the Southern Hemisphere temperature anomaly index.

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.

We thank two anonymous reviewers and the PSU Graduate Fellowship program for the financial support to R.W.

- Burnham, K. & Anderson, D. 1998 In *Model selection and inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.
- Campbell, C., Fuentes, A., MacKinnon, K., Panger, M. & Bearder, S. (ed.) 2007 In *Primates in perspective*. New York, NY: Oxford University Press.
- Daly, D. & Mitchell, J. 2000 Lowland vegetation of tropical South America. In *Imperfect balance: landscape transformations in the precolumbian Americas* (ed. D. Lentz), pp. 391–454. New York, NY: Columbia University Press.
- Dunbar, R. 1998 Impact of global warming on the distribution and survival of the gelada baboon: a modelling approach. *Global Change Biol.* **4**, 293–304. (doi:10.1046/j.1365-2486.1998.00156.x)
- Dunham, A., Erhart, E., Overdorff, D. & Wright, P. 2008 Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur. *Biol. Conserv.* **141**, 287–297. (doi:10.1016/j.biocon.2007.10.006)
- Heino, M., Kaitala, V., Ranta, E. & Lindström, J. 1997 Synchronous dynamics and rates of extinction in spatially structured populations. *Proc. R. Soc. Lond. B* **264**, 481–486. (doi:10.1098/rspb.1997.0069)
- IPCC Climate Change. 2007 In *Fourth assessment report of the intergovernmental panel on climate change*. Cambridge, UK: Cambridge University Press.
- Jaksic, F. 2001 Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* **24**, 241–250.
- Milton, K. & Hopkins, M. 2006 Growth of a reintroduced spider monkey population on Barro Colorado Island, Panama. In *New perspective in the study of mesoamerican primates* (eds A. Estrada, P. Garber, M. Pavelka & L. Luecke), pp. 489–511. New York, NY: Springer.
- Milton, K., Giacalone, J., Wright, S. & Stockmayer, G. 2005 Do frugivore population fluctuations reflect fruit production? In *Tropical fruits and frugivores* (eds J. Dew & J. Boubli), pp. 5–35. Dordrecht, The Netherlands: Springer.
- Nishimura, A. 2003 Reproductive parameters of wild female *Lagothrix lagotricha*. *Int. J. Primatol.* **24**, 707–722. (doi:10.1023/A:1024681703616)
- Post, E. & Forchhammer, M. 2002 Synchronization of animal population dynamics by large-scale climate. *Nature* **420**, 168–171. (doi:10.1038/nature01064)
- Royama, T. 1992 In *Analytical population dynamics*. London, UK: Chapman & Hall.
- Rudran, R. & Fernandez-Duque, E. 2003 Demographic changes over thirty years in a red howler population in Venezuela. *Int. J. Primatol.* **24**, 925–947. (doi:10.1023/A:1026241625910)
- Strier, K. 2005 Reproductive biology and conservation of muriquis. *Neotrop. Prim.* **13**, 41–46.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. 1999 Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–697. (doi:10.1038/19505)
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Wright, S. & Calderon, O. 2006 Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* **9**, 35–44.
- Wright, S., Carrasco, C., Calderón, O. & Paton, S. 1999 The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* **80**, 1632–1647.