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EFFECTS OF ENVIRONMENTAL VARIATION
ON ATELINE PRIMATE POPULATION DYNAMICS

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by

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ABSTRACT

Assessing the effects of environmental stress and variation on primates is crucial as globally, up to one-third of primate species are threatened with extinction. The subfamily Atelinae (large-bodied New World primates) is of particular conservation concern because it is a highly threatened group. Little work has been done on the impacts of global warming and climate change on primate species in general, or on their reproduction and population viability. However, an understanding of the role of extrinsic, environmental factors on primate population dynamics and reproduction is needed to assess the effects of global climate change on these species. In addition, overexploitation of neotropical wildlife populations has been increasing over the last several decades and poses a serious threat to the long-term survival of large-bodied primate species. Therefore, the goal of my research was to examine the effects of environmental change on ateline primate populations and the nature and capacity of these genera to respond to ecological stress. I examined this topic from three different aspects. First, I investigated the effects of harvest rates and reserve area on primate population persistence, hunting yields and sustainability, and social dynamics using a spatially explicit, individual-based model. My results showed a prominent role of reserve area in population persistence and hunting sustainability. Under harvesting pressure, only in scenarios with no reserve areas did the population go extinct, and when reserve area decreased, population losses and losses per unit area increased disproportionately. Hunting also disrupted the social structure, and these alterations in social dynamics could have a synergistic effect causing further reductions in population growth in addition to hunting mortality. Finally, it was
found that reserve area could improve hunting yields (kgs. of biomass). Thus, I found that spatial control of hunting via a reserve system holds merit as an effective conservation strategy for hunted species and a useful tool for wildlife management.

My second project examined the effects of the El Niño southern oscillation, hemispheric climatic variability, and global warming on ateline primate population dynamics using time series analyses. I found significant negative impacts of global warming on all ateline primates examined. Ateline genera experienced either an immediate or a lagged negative effect of El Niño events. Furthermore, the more frugivorous primates (muriquis, woolly, and spider monkeys) exhibited a high level of interspecific population synchrony across considerable distances found to be attributable to large-scale climatic trends. This ability of large-scale climate change to synchronize population trends is problematic because it can exacerbate the extinction risk of multiple populations.

Lastly, I investigated the impacts of the El Niño southern oscillation and hemispheric climatic variability on the reproduction and infant sex ratios of ateline primates. El Niño years were characterized by reduced birth rates, which were indirectly affected by climate through alterations in reproductive seasonality. The annual birth season was delayed and shortened during El Niño years, and delayed birth seasons were linked to lower birth rates. Additionally, El Niño years were characterized by male-biased offspring sex ratios, which could slow population growth rates. These results highlight the role of large-scale climatic variation and trends in ateline primate population dynamics and reproduction, and emphasize that global warming could pose additional threats to the persistence of ateline primate species.
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Chapter 1

Introduction

Periods of environmental change and ecological stress have a prominent influence on species and a considerable evolutionary role (Rosenberger and Strier, 1989; Strier, 1992; Vrba, 1992, 1996). For instance, global climate changes have been hypothesized to play a large role in the evolution and speciation of diverse taxa (e.g. African micromammals and bovids), are associated with large-scale evolutionary events such as the great American interchange of mammals between South and North America, and are linked to primate radiations and hominid evolution (including increased encephalization) (Vrba, 1992, 1996). A species’ adaptations and survival mechanisms for these periods are therefore of great significance from both an ecological and evolutionary perspective. Interspecific variation in life history strategies, diet, mobility, social structure, and other traits are likely to affect species’ ability to respond to environmental change and stress.

Ateline primates (large-bodied, New World monkeys) encompass divergent life history strategies, and, therefore, it is expected that the four ateline primate genera would respond to environmental stress and resource variation differently. The ateline primates represent a continuum of dietary preferences, varying from highly folivorous to predominantly frugivorous. Ateline primates differ in their behavior, social structure, and mating patterns, and these characteristics are linked to their diet and the spatial distribution of food resources (Strier, 1992). Such variations raise the question of whether
one of the evolutionary strategies (folivory or frugivory) is more susceptible to environmental change than the other, or conversely, if both strategies are equally able to cope with environmental stress. Furthermore, it is of interest how the nature of each species’ response, in terms of population trends, social behavior, reproduction, population synchrony, and distribution, differs in a quantitative or qualitative manner. For instance, in response to an environmental perturbation, one species may decline more than another species while they exhibit disparate changes in behavior. Finally, these questions are relevant today because the neotropics are undergoing rapid change from anthropogenic disturbances (including habitat destruction, fragmentation, overharvesting, and climate change) that is likely to continue in the future. Under such conditions, it is important for conservation related efforts to be informed of whether one life history strategy will be affected more than another, and how the nature of these genera’s responses may vary.

Knowledge of primate life history characteristics allows for generation of hypotheses concerning the different genera’s responses in times of stress but no definitive conclusions. For instance, among African primates, it has been posited that species capable of exploiting folivorous resources are better able to survive of periods of low fruit availability, while the degree of folivory among ateline primates increases in more seasonal environments (Strier, 1992; Tutin et al., 1997). Such observations suggest that folivory may be an adaptation for more environments with more variable resource bases and, based on this surmise, one might postulate that the more folivorous primates are more resilient and able to cope with to environmental and resource variation. However, other factors such as social structure, behavioral patterns, or competition should also be considered.
*Alouatta*, the most folivorous ateline genus, is often sympatric with another ateline species and may experience a high degree of interspecific competition. This genus also experiences overt intrasexual reproductive competition among both sexes including infanticides, which could hinder population growth and recovery. In contrast, frugivorous ateline genera tend to be specialist feeders and have lower biomasses per unit area than *Alouatta*, from which I might predict a disadvantage in coping with variation in resource levels. Nonetheless, these genera are capable of foraging over larger areas, experience less intrasexual reproductive competition, lack infanticides, and have greater relative brain sizes than *Alouatta*. Therefore, it remains unknown how the capacity and nature of the different genera to respond to environmental change will vary (Rosenberger and Strier, 1989; Di Fiore and Campbell, 2007).

**Primate dietary variation**

For primates, dietary variation is likely to be an important determinant of their response to ecological stress. Resource availability, distribution, and defensibility, as well as conspecific feeding competition are hypothesized to constitute some of the main components determining primate behavior and social dynamics, including dispersal patterns, group composition and size, reproduction, and dominance hierarchies (Rosenberger and Strier, 1989; Strier, 1992; Di Fiore and Campbell, 2007). Such life history traits would evidently influence the capacity and manner of a species to respond
to environmental perturbation. Moreover, resource abundance and distribution play a crucial role in structuring primate communities. For instance, simple measures of resource availability such as plant productivity and fruit abundance are strong predictors of Neotropical primate abundance and species richness (Kay et al., 1997; Stevenson, 2001). The latter factor explains a large proportion of variability in both biomass (80%) and species richness (64%; Stevenson, 2001). Dietary variation also has been linked to Old World primate biomass, whereas dietary quality has been proposed as the ultimate factor limiting folivorous New World primate population abundances (genus Alouatta) and is positively correlated with the biomass of Old World folivorous primates (Ganzhorn, 1992; Milton, 1996; Tutin et al., 1997).

The seasonal distribution of food resources also is an important factor for primate evolution and community structure. The abilities of primates to cope with seasonal food shortages are posited to have a strong influence on morphology, behavior, and dietary variation (Strier, 1992). In addition, the seasonal distribution of resources is most likely an important determinant of the carrying capacity since a species’ survival may depend on the availability of keystone resources during such times of scarcity (Terborgh, 1983; 1986; Oates et al., 1990). Seasonality in resource abundance also may have influenced the evolution of feeding niches in primate communities; potential greater seasonality in leaf and fruit abundance in the Neotropics versus the Paleotropics may be an important explanatory factor for the variation between Old and New World primate feeding guilds, body size ranges, and overall biomass (Terborgh, 1983).

In addition, multi-annual periods of environmental perturbation, such as El Niño events, can affect tropical forest dynamics and food resource availability for primates.
For instance, El Niño events can influence tree and leaf phenology by increasing tree mortality rates and augmenting leaf shedding; such events could have direct or indirect effects on primate populations (Laurance and Williamson, 2001; Itioka and Yamauti, 2004). More drastically, El Niño events can alter fruit production by causing a cycle of high then low fruit production during El Niño and La Niña years respectively, which can cause famines in frugivorous mammals during La Niña years (Wright et al., 1999).

**Overview of Ateline Primates**

Large-bodied, New World primates constitute the subfamily Atelinae. Ateline primates inhabit a variety of forest ecosystems and their distribution extends from eastern Mexico to Northern Argentina. Four genera compose the subfamily: howler monkeys, (*Alouatta*), woolly monkeys (*Lagothrix*), spider monkeys (*Ateles*), and muriquis (*Brachyteles*). The genera can be placed into two tribes, Alouattini, containing *Alouatta*, and Atelini containing the other three genera. Most treatments of phylogenetic relationships place *Alouatta* as the basal taxon. *Alouatta* is the most widespread of the genera and is sympatric with at least one other ateline primate species throughout most of its range (Di Fiore and Campbell, 2007).
The diets of all ateline genera include fruits, flowers, and leaves. *Alouatta* and *Brachyteles* eat predominantly immature and mature leaves but of the two genera *Brachyteles* is more frugivorous. Species of the *Ateles* and *Lagothrix* genera have primarily frugivorous diets, whereas *Lagothrix* consumes more animal prey. To exploit widely distributed fruit resources, *Ateles* and *Lagothrix* species have rapid, suspensory locomotion with large day- and home ranges. In contrast, *Alouatta* employs quadrupedal locomotion, a slower and less energy demanding form of movement. Consequently, *Alouatta* species have small home- and day ranges which allows for energy conservation since long-distance foraging is relatively expensive energetically. *Brachyteles* also employs suspensory locomotion but has smaller day and home ranges than *Ateles* and *Lagothrix* species (Strier, 1992; Di Fiore and Campbell, 2007).

Group size and behavior varies among ateline primates, ranging from cohesive troops where all members forage together, to fluid grouping patterns where troops may subdivide into smaller parties during foraging. *Alouatta* has cohesive social groups that contain only a small number (three or fewer) of adult males per troop for most species. The cohesive nature of *Alouatta* groups can be attributed to the ubiquitous nature of their predominantly folivorous diet, which reduces levels of intragroup feeding competition. *Ateles* has fission-fusion societies, in which larger groups disperse into smaller parties, with flexible membership, to forage during the day. Such grouping patterns are presumably an adaptation to avoid feeding competition among conspecifics with patchily distributed resources. Both *Brachyteles* and *Lagothrix* have more flexible grouping patterns. Southern populations of *Brachyteles* have been reported to have fission-fusion societies; however, some northern populations of *Brachyteles* have been observed to
range in cohesive social groups at low population densities and to subdivide into smaller
parties at high population densities. For *Lagothrix*, it seems that troops usually exist as
cohesive groups, with subdividing occurring only occasionally (Strier, 1992; Di Fiore and
Campbell, 2007).

Mating systems also differ among the ateline genera. *Alouatta* is polygynous, and
breeding is controlled by socially dominant males. Males are dominant to females, and
reproductive competition among both males and females can be intense. Dispersing
males may attempt to displace the alpha male of a troop and, if successful, oftentimes kill
existing infants. The male dominated societies found among *Alouatta* may be related to
the higher level of sexual dimorphism in this genus and the consequent ability of males to
monopolize females. The other ateline genera are characterized by a more promiscuous
mating system that is not controlled as much by dominant males, and exhibits less overt
intrasexual reproductive competition. Males of these genera have not been observed to
commit infanticide, and exhibit little aggression in mating situations. Similar to *Alouatta*,
*Ateles* and *Lagothrix* males are dominant to females, whereas *Brachyteles* is marked by
egalitarian societies. The nature of *Brachyteles*’ societies may be linked to their sexual
monomorphism since males may be unable to monopolize females through aggression.
In contrast, *Lagothrix* is sexually dimorphic, whereas *Ateles* exhibits little sexual
dimorphism in body size but is dimorphic in canine size, which may permit them to
monopolize females. Nonetheless, in all three genera, female choice is an important
component of the mating systems. Therefore, males may employ less overt methods of
reproductive competition than *Alouatta*, such as mate guarding and sperm competition
(Strier, 1994; Di Fiore and Campbell, 2007).
Lastly, the pace of life history strategies varies among the genera. *Alouatta* evolved to have faster rates of reproduction than the other ateline primates. The age of sexual maturation for females is younger and their interbirth intervals are shorter than in the other genera. *Alouatta’s* interbirth intervals are typically between 1.5 to 2 years whereas other genera have interbirth intervals of $\geq 3$ years (Di Fiore and Campbell, 2007). In concordance with their reduced level of investment in offspring and a low energy diet, relative brain size also is reduced in *Alouatta* compared to the remaining three genera (Rosenberger and Strier, 1989).

Ateline primates also provide important ecosystem services. In addition, to the effects of herbivory, they are important seed dispersers in neotropical forests. An estimated 80% of tree and shrub species in tropical wet forests rely on frugivorous animals for seed dispersal and ateline primates are the dispersers for a large number of plant species (Levey et al., 1994). For instance, long-haired spider monkeys *Ateles belzebuth* were found to disperse 133 different plant species while common woolly monkeys *Lagothrix lagothricha* were found to disperse 147 plant species (Link and Di Fiore, 2006; Stevenson, 2007). Even the more folivorous red howler monkeys *Alouatta seniculus* have been documented to disperse 86 plant species (Julliot, 1996). Mean seed dispersal distances appear to be similar between *Alouatta* and the more frugivorous ateline species, no significant differences were found between seed dispersal distances for common woolly monkeys *Lagothrix lagothricha* and red howler monkeys *Alouatta seniculus* (Yumoto et al., 1999). Moreover, ateline primates are effective seed dispersers, dispersal distances were long enough to escape the effects of parent trees, dispersed seeds were found to be largely undamaged, and, in some cases seed deposition occurred in
favorable locations for germination (e.g. gaps) (Julliot, 1996; Yumoto et al., 1999; Link and Di Fiore, 2006). Reduced and modified seed dispersal patterns are a cause for concern as this could potentially alter the future species composition in tropical forests. Comparisons of hunted sites with reduced primate and mammalian abundances to unhunted sites with healthy mammal populations have corroborated this idea. Hunted sites were found to have greatly reduced seed dispersal rates, shorter seed dispersal distances, reduced species richness of seedlings dispersed by medium and large-bodied primates, reduced tree species gene flow, and increased densities of abiotically dispersed plants (Pacheco and Simonetti, 2000; Wright et al., 2000; Nunez-Iturri et al., 2008; Brodie et al., 2009; Holbrook and Loiselle, 2009).

In sum, the ateline primates can be viewed as adopting two distinct life history strategies, one of minimization of energy expenditure minimization, and one of maximizing energy intake. Species of the genus *Alouatta* feed on abundant, yet energy-poor resources, whereas species of the genera *Ateles*, *Lagothrix*, and *Brachyteles* forage for energy-rich resources patchily distributed in space. The diet of *Brachyteles* species is similar to *Alouatta*, but their social structure, grouping patterns, and ranging behavior are similar to the other ateline genera. Folivory in *Brachyteles* may be an adaptation to fruit shortages in a more seasonal environment (Brazilian Atlantic forests) in what is otherwise a general strategy of maximizing energy intake (Rosenberger and Strier, 1989; Strier, 1992).

Two explanations are offered for the evolutionary divergence of these life history strategies. *Alouatta* occupies a wide range of habitats and is regarded as more of a generalist and pioneering species. Thus, they may have undergone selection for an energy
minimizing strategy, relying on a diet of predominantly leaves to be successful in seasonal or marginal environments with less abundant fruit. Alternatively, because *Alouatta* is frequently sympatric with other ateline primates, their strategy may be the result of feeding competition with the more frugivorous ateline primates. From this perspective, possible niche divergence between *Alouatta* and the other ateline genera may have been the more important evolutionary factor behind the divergence of these life history strategies (Rosenberger and Strier, 1989; Strier, 1992).

**Summary**

The aim of this dissertation is to investigate the susceptibility of the two evolutionary strategies of ateline primates (folivory and frugivory) to environmental stress, resource variation, and anthropogenic disturbances, their abilities to adapt to such change, and how the nature of their responses varied in quantitative and qualitative manners. These issues are relevant from evolutionary biology, ecological, and conservation standpoints. First, I examine the effects of anthropogenic disturbance in the form of human exploitation on ateline primate population persistence, population size, and social dynamics using the red howler monkey, *Alouatta seniculus*, as a case study species. Human exploitation poses a threat to the long-term survival of large-bodied
primate species across the humid tropics and enforcing harvest quotas is difficult, at best (Mittermeier, 1991; Redford, 1992; Peres, 2000b; 2001; Thoisy et al., 2009). Consequently, I investigate the role of refugia (undisturbed, un-hunted areas) in sustaining populations because they have been postulated to result in sustainable harvests and their design is an important conservation issue (Knowlton 1972; Novaro 1995; Hill and Padwe 2000; Novaro, Redford et al. 2000; Peres 2001). However, the benefits or effects of refugia may be difficult to test empirically. Thus, I created a spatially explicit, individual-based model to simulate a red howler monkey population and investigate the capacity of reserve areas where human harvest did not occur to sustain primate populations. In the second chapter, I examine the influences of climatic variability on primate population dynamics using time series analyses. The impacts of climate change on primates and the potential risks of global warming to primate population viability have been little studied (Dunbar 1998; Milton, Giacalone et al. 2005; Dunham, Erhart et al. 2008). Therefore, I investigated the effects of the El Niño Southern Oscillation (ENSO), hemispheric climatic variability, and global warming on species of the four genera of ateline primates. The potential for large-scale climate change to synchronize population trends can increase the global extinction risk for multiple populations (Heino et al. 1997). For this reason, I quantified population synchrony among species and assessed the role of climatic variability in population synchrony. In the last chapter, I examine the influences of the El Niño Southern Oscillation (ENSO) and hemispheric climatic variability on reproduction in ateline primates. Understanding the effects of climate change on ateline primates is conditional on a comprehension of the effects of extrinsic, environmental influences on reproduction. If climate change adversely affects reproduction, then it will
have direct implications for the population viability of these species. Using linear and logistic regression analyses, I investigated the effects of large-scale climatic variability on birth rates, birth seasonality, and infant sex ratios of species of the two ateline primate genera, *Brachyteles* and *Lagothrix*.
References


Chapter 2

Modeling the impacts of hunting on the population dynamics of red howler monkeys (*Alouatta seniculus*)

Abstract

Overexploitation of wildlife populations occurs across the humid tropics and is a significant threat to the long-term survival of large-bodied primates. To investigate the impacts of hunting on primates and ways to mitigate them, I developed a spatially explicit, individual-based model for a landscape that included hunted and un-hunted areas. I used the large-bodied neotropical red howler monkey (*Alouatta seniculus*) as my case study species because its life history characteristics make it vulnerable to hunting. I modeled the influence of different rates of harvest and proportions of landscape dedicated to un-hunted reserves on population persistence, population size, social dynamics, and hunting yields of red howler monkeys. In most scenarios, the un-hunted populations maintained a constant density regardless of hunting pressure elsewhere, and allowed the overall population to persist. Therefore, the overall population was quite resilient to
extinction; only in scenarios without any un-hunted areas did the population go extinct. However, the total and hunted populations did experience large declines over 100 years under moderate and high hunting pressure. In addition, when reserve area decreased, population losses and losses per unit area increased disproportionately. Furthermore, hunting caused some changes in the social structure of troops; the number of male turnovers and infanticides increased slightly in hunted populations, while birth rates decreased. Finally, my results indicated that when more than 55% of the landscape was harvested at high (30%) rates, hunting yields, as measured by kilograms of biomass, were less than those obtained from moderate harvest rates. Additionally, hunting yields, expressed as the number of individuals hunted/yr/km², increased in proximity to un-hunted areas, and suggested that dispersal from un-hunted areas may have contributed to hunting sustainability. These results indicate that un-hunted areas serve to enhance hunting yields, population size, and population persistence in hunted landscapes. Therefore, spatial regulation of hunting via a reserve system may be an effective management strategy for sustainable hunting, and I recommend it because it may also be more feasible to implement than harvest quotas or restrictions on season length.

Introduction

Hunting remains one of the greatest mortality factors for large-bodied mammals inhabiting tropical rainforests, and is one of the most widespread forms of resource
extraction in Amazonia (Redford, 1992; Peres, 2000b; 2001). Furthermore, harvest rates have increased over the last several decades due to loss of forested habitat, human population growth, increased accessibility to forests, commercialization of hunting, and use of new hunting technologies (Milner-Gulland and Bennett, 2003). As a result, overharvesting has often extirpated or reduced densities of mammals around neotropical settlements, and on an ecosystem scale, can precipitate even more serious problems such as trophic cascades and loss of ecosystem functions and services (Redford, 1992; Alvard, 1995; 2000; Bennett et al., 2000; Peres, 2000b; Borgerhoff Mulder and Coppolillo, 2005; Peres and Nascimento, 2006; Thoisy et al., 2009). Yet, hunting provides an important source of protein, calories, and essential nutrients for indigenous and rural people living in South American tropical rainforests (Redford, 1992). Therefore, national governments have tried to encourage sustainable wildlife harvests. Despite this effort, sustainable hunting of neotropical primates may be hard to achieve because even low harvest rates and subsistence hunting by an increasing number of people can cause severe population declines; and hunting often interacts with other threats in neotropical habitats (Thoisy et al., 2009). Furthermore, primate hunting varies according to local factors, can be difficult to quantify, and its effects on population densities can be confounded by habitat heterogeneity and quality. Therefore, hunting’s impacts on primate populations can be unclear (Peres, 1990; Mittermeier, 1991; Peres, 1991; Redford, 1992; Peres, 2000a; de Thoisy et al., 2005; Di Fiore and Campbell, 2007; Thoisy et al., 2009; Arroyo-Rodriguez and Dias, 2010), and difficult to monitor in the neotropics, making it a challenge to regulate harvests effectively (Robinson et al., 1999; Novaro et al., 2000; Peres, 2000b; 2001).
Overcoming the above challenge is important because as much as one third of all primate species are threatened with extinction (Chapman and Peres, 2001; Strier, 2007). Among neotropical primates, the majority of ateline species are listed as vulnerable, endangered, or critically endangered (IUCN, 2010). Atelines are particularly vulnerable to anthropogenic disturbances because they are large bodied (3-15 kg) and long-lived species with low reproductive rates (Di Fiore and Campbell, 2007; Thoisy et al., 2009). Declines in their abundance have the potential to trigger significant changes in forest ecology. An estimated 80% of tree and shrub species in tropical wet forests rely on frugivorous animals for seed dispersal, and atelines are dispersers for many plant species (Levey et al., 1994; Julliot, 1996; Link and Di Fiore, 2006). Red howler monkeys *Alouatta seniculus* in particular have been documented to disperse 86 plant species (Julliot, 1996). Moreover, dispersal distances were long enough to escape the effects of parent trees and dispersed seeds were found to be largely undamaged (Julliot, 1996; Yumoto et al., 1999). Comparisons of hunted and un-hunted sites suggest changes in ateline abundance and distribution could alter seed dispersal patterns, and consequently, plant species composition and distribution in tropical forests (Wright et al., 2000; Nunez-Iturri et al., 2008; Brodie et al., 2009; Holbrook and Loiselle, 2009). The role of Atelines in tropical forest conservation and the endangered status of numerous primates underscore the importance of developing an effective strategy for their conservation and long-term sustainable management.

A strategy proposed by several empirical studies suggests that in order to sustain harvestable mammalian populations it is important to maintain refugia, areas where hunting does not occur (Knowlton, 1972b; Novaro, 1995; Hill and Padwe, 2000; Novaro
et al., 2000; Peres, 2001). However, these studies do not consider the dynamics of populations in a spatial context. Modeling studies also have estimated hunting sustainability but they use traditional wildlife management ideas (e.g. maximum sustainable yield) and assume that harvests are spatially uniform (Caughley, 1977; Robinson and Redford, 1991; Robinson, 2000). Studies with non-uniform spatial harvests have shown that protecting a harvestable resource in part of its range would garner maximum sustainable yields (Joshi and Gadgil, 1991; McCullough, 1996), whereas other research indicate that source populations and size and shape of hunted areas are important for sustainable hunting and population persistence (McCullough, 1996; Gaona et al., 1998; Salas and Kim, 2002). However, such models are theoretical, rely on estimates of maximum rates of increase to provide indications of minimum reserve area (Joshi and Gadgil, 1991; McCullough, 1996), are specific for ungulates or felids (Gaona et al., 1998; Salas and Kim, 2002), and do not account for complex life histories and potential disruptions to a species’ social structure from hunting.

Keeping the above issues in mind, I developed a spatially explicit model to examine the influence of hunting and un-hunted reserves on population persistence and hunting sustainability. The amount of reserve area in a landscape was of particular interest because the influence of refugia is an important conservation issue; albeit one that may be difficult to test empirically. Nonetheless, in hunted and disturbed landscapes, reserve areas promise to be a useful conservation strategy that merits further investigation.

For this spatially explicit model, I used an individual-based framework because it can incorporate individual variations, complex life histories, and dynamics commonly
found on a local scale among social animals (Grimm and Railsback, 2005). Only a few spatially explicit, individual-based models have investigated the role of reserve areas on hunting sustainability (Salas and Kim, 2002), or hunting’s influence on social structure and dynamics (Kenney et al., 1995; Whitman et al., 2004; Whitman et al., 2007). Nevertheless, these effects may be particularly important for the sustainable management of a social species such as the red howler monkey (Alouatta seniculus), a large bodied (4-11 kg.), long-lived (>22 yrs), polygynous primate (Eisenberg and Redford, 1999), that exhibits behaviors such as male-male reproductive competition, infanticide, and turnover of troop males that could make the species vulnerable to human hunting.

**Site description**

I parameterized the model using primarily a 30-year data set collected from a Venezuelan red howler population (Neville, 1972; Rudran and Fernandez-Duque, 2003) between 1969–1999 at Hato Masaguaraal, a wildlife preserve and cattle ranch, in the Guárico State of Venezuela (8° 34’ N, 67° 35’W). The ranch contains two major habitat types consisting of a continuous gallery forest found along the Guárico river, and a tropical savanna composed of matas, or forest patches, surrounded by seasonally inundated grassland (Troth, 1979). Annual rainfall is seasonal with a wet season from May to October and a dry season from November to April (Crockett and Rudran, 1987). The vegetation is semi-deciduous with many species of trees and shrubs losing their
leaves in the late dry season. The elevation is approximately 70 m ASL, and average monthly temperatures vary from a minimum of 19-22 °C during the wet season to a maximum of 33-38 °C during the dry season (Troth, 1979).

Model Description

The Model’s purpose

The purpose of constructing a spatially explicit, individual-based model was to incorporate the life history traits and troop dynamics of *Alouatta seniculus* adequately so I could examine the effects of hunting and un-hunted reserves on population dynamics and the options for sustainable hunting. I conducted simulations using NetLogo, an individual-based modeling program (Center for Connected Learning and Computer-Based Modeling, Northwestern University, version 4.0.2, 1999).

The Model’s variables and scales

I created a model that included a 101 × 101 grid representing a 20.2 km × 20.2 km landscape (408 km²) with hunted and un-hunted areas. I assumed a uniform habitat, and
to simulate empirical evidence that the majority of hunting in the neotropics occurs around permanent settlements (Hames, 1980b; Alvard et al., 1997; Novaro et al., 2000; Koster, 2007), the model used circular hunted areas of five km radius. Harvest rates within these areas were also based on reported indigenous neotropical hunting yields and varied with distance from the center of the hunted patch (Hames, 1980b; Koster, 2007).

To determine the harvest rates within the hunted patches, the ring that had the highest yield based on the reported hunting patterns (1 - 2 km from the center of the patch) was set at a 100% harvest rate and the other rings' harvest rates were then set in proportion to this harvest rate. Thus, starting at the center of the patch and moving to the edge, harvest rates within rings encompassing 1/5 of the patch radius were set at 35%, 100%, 84%, 93%, and 58% respectively of the overall model’s harvest rate to correspond to the indigenous harvest yields. If there were one or two hunted patches in the landscape, they were placed randomly, and if there were three, four, or five hunted patches, they were placed equidistant from each other. If there were five patches, the outer rings of different patches overlapped by 9% of their area, but in all other cases hunted patches were completely surrounded by reserve area. Harvest rates, which remained constant over time, corresponded to hunter effort and represented the probability of hunting mortality for howler monkeys. An individual’s chance of being hunted depended on its location within a hunted patch, its age class, and the model’s overall harvest rate.

This spatial harvest pattern was chosen to model indigenous hunting patterns as accurately as possible. However, the model does represent a simplification of real hunting patterns. For instance, indigenous populations may undertake hunting expeditions and treks that extend long distances from their settlements. Therefore, reserve areas are
unlikely to be completely undisturbed by harvesting. However, my objective was to
examine the effect of undisturbed reserve areas on red howler population dynamics, so
hunting was not included in these areas. Also hunting can occur farther away than 5 km
away from a settlement, but due to logistical constraints of the software and computing
time required, models of a smaller spatial extent were necessary. Finally, this model
simulated only one harvest pattern, the one that occurs nearby settlements. Other spatial
patterns of hunting can occur (e.g. along roads or rivers), and these various patterns could
have different effects on harvest yields and population persistence.

Furthermore, the carrying capacity of the habitat (44.8 individuals/km²) was based
on the mean density of eleven red howler populations (Chapman and Balcomb, 1998).
Incorporating density dependence in both survival and birth rates hindered population
growth rates. Therefore, I modeled birth rates to be density-independent, whereas
survival rates were density–dependent, which produced logistic growth in the population.
For the estimation of density-dependent survival rates, the model assumed that
individuals could only detect conspecifics that were within one km of themselves. This
distance, which corresponds to the mean maximum day range (Di Fiore and Campbell,
2007), is used as an approximation of the number of conspecifics with which an
individual would be interacting and competing most frequently. I incorporated different
sex and age classes (adults, sub-adults, juveniles, and infants) of red howler monkeys in
the model in proportion to the age distribution of the undisturbed population that
contributed the 30-year data set (Rudran and Fernandez-Duque, 2003). I classified
juvenile sizes into large, medium, and small categories for males and large and small
categories for females. For each scenario, I ran the model with annual time steps for 100 years.

**Overview of Processes**

In each time step, individuals of the model population underwent the six life history processes given below (see Appendix A for a complete description of processes).

1. Adults aged one year, whereas immature individuals advanced to the next age class.

2. Natural mortality, which varied according to the age and sex of the individual, could occur.

3. Adults of both sexes reproduced. Females whose infants experienced infanticide in the previous time step had a greater likelihood of reproducing than females whose infants did not experience an infanticidal event.

4. Troops changed social status. Bisexual extra-troop associations, consisting of dispersing individuals, could become established troops if they produced an infant.

5. Individuals of both sexes dispersed and searched for suitable troops or associations to join. Adult and subadult males could also enter troops in this process, which could result in infanticides and the death or eviction of the resident and invading males.

6. Hunting occurred in hunted areas. The model reflected indigenous hunting patterns by placing the majority of hunting pressure on older individuals, but it did not include a hunting bias between the sexes. Nevertheless, more adult females than adult males were
hunted because they comprised a larger segment of the population (see Appendix B for a complete list of the model input parameters).

**Design concepts**

Emergence: Several model outcomes emerged from individual traits and behaviors. Patterns of population loss, hunting yields, and social dynamics emerged under various hunting scenarios that were not imposed by the model structure.

Collectives: Individuals belonged to troops, and only one troop could occur in a cell (representing an area of 0.04 km\(^2\)), which corresponds to a minimum home range estimate for *Alouatta seniculus* (Crockett and Eisenberg, 1987).

Sensing and Fitness: Individuals of both sexes could assess troop characteristics (including their status and composition), but did not recognize differences between hunted and un-hunted areas. They also sought to improve their fitness by dispersing from large troops where reproductive opportunities may have been limited. Dispersing males associated with dispersing females and tried to establish new troops or attempted to take over the established troops they encountered.

Interactions: Individuals interacted during reproduction, turnovers, and dispersal (i.e. during eviction from or entry into troops and during new troop formation).

Stochasticity: I incorporated stochastic processes into birth, dispersal, survival, turnovers, and hunting rates. For stochastic functions, the model generated a uniform (0, 1) random number, and if it was less than the specified probability of the process, the action
occurred. I also included logical rules in the processes of dispersal and reproduction to account for troop composition and females’ past reproductive history.

**Initialization**

I created the initial population’s sex-age structure in proportion to the mean age and sex distribution of the undisturbed population that contributed the 30-year data set (Rudran and Fernandez-Duque, 2003). The initial population density was at carrying capacity. The model grouped individuals into unimale or multimale troops, with initial multimale troops having two or three adult males. Approximately 46% of the initial troops were multimale and 54% unimale, which corresponded to the mean composition of the undisturbed population. Initial multimale and unimale troops varied in size from four to 18 and from three to 18 individuals, respectively. The distribution of individuals among sex and age classes within troops varied and there were ≤18 individuals and ≤4 adult females per troop (Rudran and Fernandez-Duque, 2003). The model grouped some immature individuals of an appropriate age into bisexual associations (non-established troops consisting of dispersing individuals). Each troop was placed in a randomly selected cell (without replacement) within the hunted or un-hunted areas.

I used the 30-year data set to estimate fecundity, survival, and dispersal rates, and to obtain information on the mean age distribution, sex ratio at birth, troop composition, and howler lifespan (see Appendix B for a complete list of the model input parameters). I estimated mean birth rates from the inter-birth intervals of 556 infants born to 124
females in the population. Using a known fate analysis, I estimated maximum and minimum annual survival and dispersal rates based on a nine-year portion of the long-term dataset. I obtained information from the literature on the possible causes of dispersal, dispersal distance, extra-troop associations, new troop formation, likelihood of male turnovers and infanticides, and factors governing turnover success (Rudran, 1979; Sekulic, 1983; Crockett, 1984; Crockett and Sekulic, 1984; Agoramoorthy and Rudran, 1993; Crockett and Pope, 1993).

Sensitivity analyses and simulation experiments

I measured the sensitivity of the model to variation in the input parameters. For each analysis, I recorded the following output parameters: end and average population size, mean annual growth rate, population persistence for 100 years (time steps), and mean number of turnovers, births, and infanticides per year. I altered ten input parameters which I hypothesized would strongly influence population growth, or for which estimates in the literature were either lacking or based on studies with small sample sizes (Table 1). I assessed the model’s sensitivity to the maximum and minimum values of a parameter when a range of estimates was available. If few empirical estimates were available, I assessed model sensitivity by varying parameters by ± 50% of the best estimate. I also conducted a control run using the best estimates for each parameter. For each sensitivity analysis and the control run, I ran the model for 100 time steps (years) for 100 iterations.
The model’s output included the total population size, population sizes in the hunted and un-hunted areas, population persistence for 100 years (time steps), mean annual population growth rate, total number of individuals hunted, location of hunting, biomass hunted, and the number of turnovers, births, infanticides, and male deaths that occurred during turnovers. I calculated the total biomass hunted using the mean weights of the different sex and age classes (Thorington et al., 1979; Di Fiore and Campbell, 2007). I measured population sizes as both the size after 100 years (end population size) and mean size during the 100 years (average population size). For technical reasons related to the simulation software, population extinction was assumed to have occurred when population size declined to <1% of carrying capacity before the 100 years (time steps) of the model run were completed.

To elucidate the effects of hunting on population dynamics I used three different rates of harvest and five different sizes of hunted areas in the model. Preliminary analyses indicated that annual harvest rates of 1%, 5%, and 30% of the population corresponded to light, moderate, and heavy hunting intensities. Thus, I ran each model with a light (1%), moderate (5%), and heavy (30%) harvest rate for simulations with 18%, 55%, 74%, 83%, and 100% of the landscape in hunted areas. The first four simulations represented 1, 3, 4 and 5, hunted patches respectively in the landscape. I also ran a simulation with a moderate harvest rate and 2 hunted patches (37%) in the landscape. For each scenario, I ran the model for 100 time steps (years) and 500 iterations.
Results

Sensitivity analyses

The model was robust to variations in parameter values as shown by the sensitivity analyses (Fig. 1). The mean population growth rate varied little from the control run of the model for the majority of parameters (<2% difference from the control run’s value, Fig. 1a). Still, lower values of adult female reproduction and survival reduced the mean population growth rate by as much as 14.7% from the control run’s value. Similarly, average population size was also significantly altered when rates of female survival, reproduction, or male survival during turnovers were varied (as much as a 81% difference from the control run’s population size), whereas variations in other parameters resulted in only moderate changes to population size (<9% difference from the control run’s population size, Fig. 1b).

Population dynamics and population persistence

The populations were quite resilient to extinction, and in all but one scenario persisted for 100 years (Fig. 2a). The only case of population extinction (i.e. a population decline to <1% of carrying capacity) occurred when the entire landscape was hunted at high (30%) harvest rates (Fig. 2a). In this scenario, populations went extinct, on average,
in 13.8 years (s.d. = 0.7). In all other scenarios, populations persisted despite, in some
cases, quite large reductions in total size. For instance, light (1%) harvest rates reduced
the total end population size after 100 steps (years) between 5-33% in models with 18-
100% hunted area, and moderate (5%) harvest rates reduced it between 16-94% in
models with 18-100% hunted area (Fig. 2a). These declines in total population size were
the result of large losses in the hunted subpopulation, which is reflected by the fact that
moderate (5%) harvest rates reduced the hunted subpopulation size by 86-91%, while
high (30%) harvest rates reduced it by >98% (Fig. 2b). In contrast, the size of the un-
hunted population remained relatively constant when the hunted area and harvest rate
increased elsewhere (Fig. 2c); and it was the stability of the un-hunted subpopulation that
allowed the total population to persist despite large losses, and avoid overall population
extirpation.

Increasing the area hunted within a landscape also caused larger proportional
decreases in the hunted subpopulation and total population (Figs. 2b and 3). To compare
the different models, I standardized the decline in overall population size as number of
individuals lost per km² of area hunted. When the hunted area increased at a moderate
(5%) harvest rate, the decline per unit area of the total population increased from 38.9 to
42.1 individuals lost per km² hunted (Fig. 3). The variance associated with these losses
also decreased with greater amounts of hunted area, indicating that the size of population
losses were more consistent with less reserve area in the landscape. This may be due to
the larger numbers of hunted patches in the landscape with less reserve area and
effectively a larger sample size. In addition, at a moderate (5%) harvest rate, the
proportional decline of the hunted subpopulation was greater as the amount of hunted
area increased. For instance, declines of hunted subpopulations in landscapes with 83% hunted area were 5.3% greater than in landscapes with 18% hunted area (Fig. 2b). Furthermore, in models where 55% or more of the landscape was hunted at a high (30%) rate or 83% was hunted at a moderate (5%) rate, the un-hunted population actually increased beyond its initial value (Fig. 2c).

**Demographic parameters**

Increasing the harvest rate or hunted area caused declines in the number of male deaths per turnover and in the total turnover-related deaths per 1000 individuals (Table 2). For instance, when harvest rates increased from 1% to 30% in a landscape with 83% hunted area, turnover parameters dropped from 0.35 to 0.16 and 9.9 to 6.2 for male and total turnover-related deaths, respectively. The numbers of births, infanticides, or turnovers did not exhibit clear trends when the harvest rate increased, but they did undergo some changes when the area hunted increased. For example, when the area hunted at a moderate (5%) rate increased from 18% to 100%, the annual number of infanticides per 1000 individuals increased slightly (from 3.4 to 3.8) along with turnovers per 1000 individuals (from 16.8 to 21.4). Under the same scenario, the annual number of births per 1000 individuals declined (from 144.7 to 139). Thus, when the hunted area increased, reproduction and infant survival declined while the number of turnovers increased.
Demographic parameters exhibited the greatest changes when the entire landscape was hunted at a high (30%) rate (Table 2). As harvest rates increased from 1% to 30%, the number of infanticides increased from 3.7 to 4.1 and the number of births decreased from 143.8 to 124.2. The number of turnovers and turnover-related deaths also increased sharply from 18.4 to 39.3 and from 9.7 to 17.7, respectively.

**Hunting yields**

Hunting yields, expressed as mean annual biomass (kgs) obtained from all hunted areas, increased when hunting was maintained at low (1%) or moderate (5%) rates while increasing the proportion of the hunted area (Table 3). For instance, at a moderate (5%) harvest rate, hunting yields increased from 203 kg to nearly 890 kg as the hunted area increased from 18% to 100%, and each additional percent of the landscape hunted translated into a mean gain of 10.2 kg of biomass hunted/yr (Table 3). However, at a 5% harvest rate, the yield per unit area hunted declined as the size of the hunted area increased; thus, the additional gain from hunting larger areas declined with reduced reserve area. Furthermore, when harvest rates increased, annual yields varied according to the amount of reserve area in the landscape. If 55% or less of the landscape was hunted, annual yields increased with higher harvest rates. However, when more than 55% of the landscape was hunted at high (30%) rates, annual yields were less than those obtained at moderate (5%) harvest rates. When the entire landscape was hunted at a high (30%) rate, the annual yield was very high. However, because the population was
extirpated quickly (on average within 14 yrs), the total yield (69,839 kgs) over 100 years was less than the total yield obtained at a moderate harvest rate (88,944 kgs) over the same period.

Hunting yields, expressed as the number of individuals hunted/yr/km², varied according to harvest rate and the location of hunting (Fig. 4). For instance, at a low (1%) harvest rate in a landscape with 74% hunted area, the yields obtained in the different rings of a hunted patch followed the pattern set by the model’s hunting rates, i.e., they were greater in the three middle rings than in the inner- and outer-most rings (Fig. 4). However, as harvest rates increased, the outer-ring, which abutted un-hunted reserve areas, produced a greater yield than all other rings. This result indicated that maintaining un-hunted reserves will increase hunting yields obtained at moderate and high harvest rates adjacent to these areas.

Discussion

Population dynamics and population persistence

The results showed that harvest rates and size of reserves had important independent and synergistic effects on sustainable hunting and population persistence. In all scenarios where the landscape included any reserve areas, the population persisted for
100 years and hunting was sustainable; the population was extirpated only when the entire landscape was hunted at a high (30%) rate (Fig. 2a). The overall population’s persistence was due to the un-hunted population size, which remained constant or increased in all scenarios (Fig. 2c). The un-hunted population maintained this fairly stable size due to the logistic growth of the population and absence of additional mortality factors in reserve areas. These findings are consistent with theoretical and experimental studies which concluded that if a certain minimum area was set aside as a reserve, the population would be protected from extinction (Salas and Kim, 2002; Chapron et al., 2003; Fryxell et al., 2006). Also, I found that population losses increased disproportionately when reserve area decreased (Fig. 2b, 3), indicating that landscapes containing larger reserves had greater capacities to mitigate the effects of hunting. These results support McCullough’s (1996) finding that spatial control of hunting via the establishment of reserves was more effective than numerical control through hunting quotas at preventing overharvesting and population extirpation. However, while others estimated that a minimum of 65% - 100% reserve area was needed to ensure population viability (Joshi and Gadgil, 1991; Novaro et al., 2000), I found that red howlers could persist indefinitely in landscapes with smaller reserves. This difference may have been the result of others using a model that assumed complete mixing of hunted and un-hunted populations, and thus increased individuals exposure to hunting mortality, which did not occur in the model. Therefore, reduced dispersal into hunted areas in the model may have allowed the population to persist in a landscape with smaller refugia.
These results are congruent with Robinson and Redford’s (1991) estimate that a maximum of 2.52 kg/km² can be harvested sustainably for Alouatta species. Assuming a uniform spatial harvest, when the entire landscape was harvested at a 30% rate, the yield was 12.39 kg/km². This exceeds their 2.52 kg/km² threshold, and in this scenario, the population was extirpated. When the entire landscape was harvested at 5% or 1% rates, the yields obtained were 2.18 kg/km² and 1.57 kg/km² respectively; the populations in both these scenarios persisted. Robinson (2000) estimated the maximum annual sustainable offtake of a population (expressed as the percent of the standing population or biomass) was 3% for Alouatta species. In the models used here, if the entire landscape was hunted at a 30% harvest rate the population was extirpated but not at a 5% harvest rate. This discrepancy arises from the fact that 5% was the model’s overall harvest rate, but it was modified according to the actual location of hunting within the hunted area. In the majority of cases, the location of hunting lowered the harvest rate. Therefore, the mean harvest rate was actually 3.6%, which slightly exceeds their estimate of a 3% maximum sustainable offtake of the total population. However, Robinson’s estimate is based on maximum rates of increase and proposed levels of sustainable human offtake (defined according to categories of short-, medium-, and long-lived taxa). Thus, these parameter estimates likely involve some uncertainty and also lack species-specific detail for levels of sustainable harvesting. Finally, in my model, the reserve subpopulation actually increased beyond its initial value when hunting occurred at moderate or high rates over large areas (Fig. 2c). This unexpected increase was likely due to dispersing individuals moving into reserves from extensively hunted areas because of declining numbers, or remaining in un-hunted areas to improve their chances of joining a troop.
Thus, the behavior of dispersing individuals would have exacerbated the population losses in extensively hunted areas. This explanation is consistent with findings of others who have noted limited dispersal into areas with suppressed population densities (Porter et al., 1991; Porter et al., 2004).

**Demographic parameters**

Although the model considered many aspects of red howler social structure, it may not have captured all aspects of the complex life history of this species. Despite these limitations, the model results indicated several demographic changes with respect to hunting and red howler social dynamics (Table 2). Although the changes in overall rates are slight to moderate, they present an interesting result, as to my knowledge, no previous studies have examined of the effects of hunting on primate social dynamics. Therefore, they are suggestive of changes that may be occurring in wild populations under human exploitation. The decline of adult male deaths and total deaths (male deaths plus infant mortality) per turnover was most likely due to hunting mortality resulting in fewer males per troop. This decrease would also reduce the likelihood that dispersing males would leave their troops with a partner, and therefore, single invading males would have been less capable of killing resident males during a turnover. In addition, the increases in the rate of turnovers as hunted area increased were also probably due to hunting, which
would have reduced the number of resident males per troop and increased the success rate of turnovers. This increase in turnovers with increased hunted area would also cause the higher number of infanticides, since a larger number of turnovers augments the chance that invading males can commit infanticide (Table 2). The drop in birth rates observed under the same scenario likely reflected the hunters’ preference to harvest the larger-bodied adult females rather than younger age classes, as prescribed by the model. Therefore, in my model of social dynamics, the effects of hunting extended beyond the number of individuals harvested, and led to some disruptions in the social structure.

**Hunting yields**

I found that in landscapes with large reserves the yield increased as harvest rates increased, but when hunted areas exceeded 55% of the landscape, yields declined at high harvest rates (Table 3). These results are similar to those presented for tapirs, where an increase in the un-hunted subpopulation increased the maximum sustainable harvest rate of a hunted subpopulation (Salas and Kim, 2002). Hunting yields also increased in areas adjacent to reserves, suggesting that dispersal from un-hunted areas may help promote sustainable hunting (Fig. 4). Empirical observations of marine reserves in more than a dozen countries support this conclusion, and for a variety of species fishing effort was concentrated around reserve boundaries (Gell and Roberts, 2003). In most scenarios of the model, the circular hunted patches were completely surrounded by reserve area. This patch design should have maximized immigration rates into hunted patches and most
likely sustained hunting yields as well. This inference is consistent with empirical studies that hypothesized nearby un-hunted areas permitted high rates of hunting (Hill and Padwe, 2000; Knowlton, 1972; Novaro, 1995; Novaro et al., 2000; Peres, 2001). Although I did not explicitly examine other landscape geometries, different spatial configurations of hunted areas may have influenced hunting yields and population persistence. Finally, I assumed that hunting mortality was additive to natural mortality rates. If I had assumed hunting mortality was compensatory, this would have influenced the results by likely augmenting yields and lessening population declines.

**Reserves as a management tool**

Both empirical and modeling studies, including this one, have shown that reserves promote population persistence, and establishing them could help sustainable management of hunted populations (Knowlton, 1972a; Joshi and Gadgil, 1991; Novaro, 1995; McCullough, 1996; Gaona et al., 1998; Hill and Padwe, 2000; Novaro et al., 2000; Peres, 2001; Salas and Kim, 2002). Such management is needed since ateline primates are important seed dispersers and their extirpation could affect future forest compositions in the Neotropics (Levey et al., 1994; Julliot, 1996; Link and Di Fiore, 2006). In the neotropics, where monitoring and management capabilities are limited, reserves provide opportunities for spatial control of hunting, which could perhaps be more easily enforced than restrictions on hunting quotas (Novaro et al., 2000). Spatial control of hunting may also be desirable because continued increases in human populations and the easy
accessibility of the Amazon basin are likely to make passive forms of reserve protection (through religious or social taboos, etc.) ineffective (Milner-Gulland and Bennett, 2003; Peres and Lake, 2003; Borgerhoff Mulder and Coppolillo, 2005; Diefenbach et al., 2005). Therefore, active management of reserve areas, with the help or direction of local communities becomes important to ensure sustainable primate populations (Borgerhoff Mulder and Coppolillo, 2005).

The results indicated that even small reserve areas were sufficient to promote hunting sustainability and prevent population extirpation. Notably, reserve areas in this model were undisturbed by anthropogenic influences; however, modern-day realities such as hunting and poaching can undermine the effectiveness of small reserves. Furthermore, this model did not consider habitat heterogeneity, or other factors such as climate change, pollution, or habitat fragmentation and degradation, all of which could affect primate population dynamics (Wiederholt and Post, 2010). Also as environmental variation was not included, the only form of stochasticity present in the model was demographic. This most likely contributed to the logistic growth and stability of the un-hunted subpopulation, and the high level of population persistence with only small reserve areas. Incorporating such variation would strengthen the model and represent a more realistic model of Alouatta population dynamics. Therefore, due to these assumptions of the model, reserves larger than those prescribed by this model may be essential to ensure population persistence.
Suggestions for future research

The model discussed here simulated a naturally occurring hunting pattern that reflected high adult female mortality, but other patterns such as preferential hunting of adult or subadult males could be examined to elucidate further the impacts of hunting on primate populations. In addition, changing the spatial configurations of the landscape could help determine if this factor has any effect on hunting sustainability and population viability. Modeling the simultaneous effects of multiple variables such as hunting, climate change, and habitat loss could also be useful in designing and implementing primate conservation strategies since such a study would effectively address the potential for several environmental variables to decrease population viability synergistically (Mora et al., 2007; Brook et al., 2008).

Conclusions

Due to hunter preference for large-bodied individuals, adult female red howler monkeys, which constituted the largest segment of the population, were most often the victims of hunting. Thus, hunting had the greatest negative impact on individuals that were essential for reproduction and population viability. These results also showed that hunting causes some disruption of troop social structure, by increasing rates of infanticides and turnovers while decreasing birth rates. Effective strategies for sustainable
hunting are urgently needed because existing regulations based on restricting harvest quotas or season length are difficult to enforce. Spatial regulation of hunting via a reserve system may be easier to enforce, and these results indicated that appreciably high harvest rates were sustainable even with relatively small refugia. However, these models did not consider impacts other than hunting (e.g. climate change, habitat fragmentation) on primate populations, that may require larger reserve areas than my model recommends to ensure population viability.

Notes

This project was completed in collaboration with Drs. Eduardo Fernandez-Duque and Rasanayagam Rudran. I completed the individual-based model and analyses, while they contributed a long-term dataset to the project, provided advice on the species biology, and aided in the manuscript preparation. This chapter is published in Ecological Modelling.

Table 2-1. Model input parameters altered in the sensitivity analysis. Parameters were tested at their maximum or minimum values (when a range of estimates was available), or plus or minus 50% of their values in the model (when few estimates were available). An extreme parameter value was also tested in two cases.

<table>
<thead>
<tr>
<th>Parameter probabilities</th>
<th>Baseline values</th>
<th>Sensitivity analysis (min value, max value, extreme value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproduction with surviving infant</td>
<td>0.35</td>
<td>0.17, 0.57</td>
</tr>
<tr>
<td>Reproduction after infanticide</td>
<td>0.42</td>
<td>0.19, 0.78</td>
</tr>
<tr>
<td>Turnover success</td>
<td>0.12</td>
<td>0.06, 0.17</td>
</tr>
<tr>
<td>Male death during turnovers</td>
<td>0.002</td>
<td>0.001, .004, .01</td>
</tr>
<tr>
<td>Infanticide</td>
<td>0.50</td>
<td>0.45, 0.56</td>
</tr>
<tr>
<td>Ability of 1 invading male to evict or kill resident males</td>
<td>0.25</td>
<td>0.13, 0.38</td>
</tr>
<tr>
<td>Ability of 2 invading males to evict or kill resident males</td>
<td>1.00</td>
<td>0.50, 1.00</td>
</tr>
<tr>
<td>Invading males join troop or are evicted from troop after unsuccessful turnover</td>
<td>0.50</td>
<td>0.25, 0.75</td>
</tr>
<tr>
<td>Adult female survival</td>
<td>0.90</td>
<td>0.75, 0.95, 0.59</td>
</tr>
<tr>
<td>Subadult female survival</td>
<td>0.81</td>
<td>0.53, 0.89</td>
</tr>
<tr>
<td>Juvenile female survival</td>
<td>0.87</td>
<td>0.64, 0.93</td>
</tr>
<tr>
<td>Infant female survival</td>
<td>0.92</td>
<td>0.67, 0.94</td>
</tr>
</tbody>
</table>
Table 2-2. Effects of hunted area and harvest rate on demographic parameters expressed as mean annual rates.

<table>
<thead>
<tr>
<th>Hunted area (%)</th>
<th>Harvest Rate (%)</th>
<th>Number of infanticides/1000 ind. ± 1 s.d.</th>
<th>Number of births/1000 ind. ± 1 s.d.</th>
<th>Number of turnovers/1000 ind. ± 1 s.d.</th>
<th>Male deaths per turnover ± 1 s.d.</th>
<th>Total turnover deaths/1000 ind. ± 1 s.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control 0</td>
<td>3.4 ± 0.1</td>
<td>145.2 ± 1.6</td>
<td>16.6 ± 0.1</td>
<td>0.4 ± 0.0</td>
<td>10.4 ± 0.1</td>
<td></td>
</tr>
<tr>
<td>18 5</td>
<td>3.4 ± 0.1</td>
<td>144.7 ± 1.8</td>
<td>16.8 ± 0.1</td>
<td>0.4 ± 0.0</td>
<td>9.7 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>37 5</td>
<td>3.5 ± 0.1</td>
<td>144.1 ± 2.0</td>
<td>17.2 ± 0.2</td>
<td>0.3 ± 0.0</td>
<td>9.0 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>55 5</td>
<td>3.5 ± 0.1</td>
<td>143.3 ± 2.3</td>
<td>17.7 ± 0.2</td>
<td>0.3 ± 0.0</td>
<td>8.4 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>74 5</td>
<td>3.6 ± 0.1</td>
<td>142.1 ± 2.8</td>
<td>18.6 ± 0.3</td>
<td>0.2 ± 0.0</td>
<td>7.9 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>83 5</td>
<td>3.6 ± 0.1</td>
<td>141.8 ± 3.1</td>
<td>19.0 ± 0.4</td>
<td>0.2 ± 0.0</td>
<td>7.6 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>100 5</td>
<td>3.8 ± 0.2</td>
<td>139.0 ± 4.0</td>
<td>21.4 ± 0.5</td>
<td>0.2 ± 0.0</td>
<td>8.0 ± 0.3</td>
<td></td>
</tr>
<tr>
<td>18 1</td>
<td>3.4 ± 0.1</td>
<td>145.0 ± 1.7</td>
<td>16.8 ± 0.1</td>
<td>0.4 ± 0.0</td>
<td>10.3 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>18 5</td>
<td>3.4 ± 0.1</td>
<td>144.7 ± 1.8</td>
<td>16.8 ± 0.1</td>
<td>0.4 ± 0.0</td>
<td>9.7 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>18 30</td>
<td>3.4 ± 0.1</td>
<td>145.0 ± 1.9</td>
<td>16.6 ± 0.1</td>
<td>0.4 ± 0.0</td>
<td>9.3 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>55 1</td>
<td>3.5 ± 0.1</td>
<td>144.6 ± 1.9</td>
<td>17.4 ± 0.2</td>
<td>0.4 ± 0.0</td>
<td>10.1 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>55 5</td>
<td>3.5 ± 0.1</td>
<td>143.3 ± 2.3</td>
<td>17.7 ± 0.2</td>
<td>0.3 ± 0.0</td>
<td>8.4 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>55 30</td>
<td>3.4 ± 0.1</td>
<td>144.9 ± 2.4</td>
<td>16.7 ± 0.2</td>
<td>0.2 ± 0.0</td>
<td>7.3 ± 0.2</td>
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<tr>
<td>74 1</td>
<td>3.6 ± 0.1</td>
<td>144.4 ± 2.0</td>
<td>17.7 ± 0.2</td>
<td>0.4 ± 0.0</td>
<td>10.0 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>74 5</td>
<td>3.6 ± 0.1</td>
<td>142.1 ± 2.8</td>
<td>18.6 ± 0.3</td>
<td>0.2 ± 0.0</td>
<td>7.9 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>74 30</td>
<td>3.4 ± 0.1</td>
<td>145.1 ± 3.3</td>
<td>16.9 ± 0.3</td>
<td>0.2 ± 0.0</td>
<td>6.4 ± 0.2</td>
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<tr>
<td>83 1</td>
<td>3.6 ± 0.1</td>
<td>144.2 ± 2.1</td>
<td>18.0 ± 0.2</td>
<td>0.3 ± 0.0</td>
<td>9.9 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>83 5</td>
<td>3.6 ± 0.1</td>
<td>141.8 ± 3.1</td>
<td>19.0 ± 0.4</td>
<td>0.2 ± 0.0</td>
<td>7.6 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>83 30</td>
<td>3.5 ± 0.1</td>
<td>145.9 ± 3.5</td>
<td>17.2 ± 0.3</td>
<td>0.2 ± 0.0</td>
<td>6.2 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>100 1</td>
<td>3.7 ± 0.1</td>
<td>143.8 ± 2.4</td>
<td>18.4 ± 0.2</td>
<td>0.3 ± 0.0</td>
<td>9.7 ± 0.2</td>
<td></td>
</tr>
<tr>
<td>100 5</td>
<td>3.8 ± 0.2</td>
<td>139.0 ± 3.9</td>
<td>21.4 ± 0.5</td>
<td>0.2 ± 0.0</td>
<td>8.0 ± 0.3</td>
<td></td>
</tr>
<tr>
<td>100 30</td>
<td>4.1 ± 0.4</td>
<td>124.2 ± 5.2</td>
<td>39.3 ± 2.1</td>
<td>0.3 ± 0.0</td>
<td>17.7 ± 1.3</td>
<td></td>
</tr>
</tbody>
</table>

*Male deaths and infanticides due to turnovers*
Table 2-3. Changes in hunting yields for different harvest rates and amounts of hunted area.

<table>
<thead>
<tr>
<th>Hunted area (%)</th>
<th>Harvest rate (%)</th>
<th>Mean annual biomass hunted (kgs) ± 1 s.d.</th>
<th>Mean annual biomass hunted (kgs) / percent hunted area</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>5</td>
<td>203.2 ± 7.3</td>
<td>11.0</td>
</tr>
<tr>
<td>37</td>
<td>5</td>
<td>399.7 ± 11.4</td>
<td>10.8</td>
</tr>
<tr>
<td>55</td>
<td>5</td>
<td>583.8 ± 12.5</td>
<td>10.5</td>
</tr>
<tr>
<td>74</td>
<td>5</td>
<td>770 ± 16</td>
<td>10.4</td>
</tr>
<tr>
<td>83</td>
<td>5</td>
<td>804.6 ± 17.7</td>
<td>9.7</td>
</tr>
<tr>
<td>100</td>
<td>5</td>
<td>889.4 ± 17.4</td>
<td>8.9</td>
</tr>
<tr>
<td>18</td>
<td>1</td>
<td>108.7 ± 3.5</td>
<td>5.9</td>
</tr>
<tr>
<td>18</td>
<td>5</td>
<td>203.2 ± 7.3</td>
<td>11.0</td>
</tr>
<tr>
<td>18</td>
<td>30</td>
<td>230.8 ± 5.3</td>
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</tr>
<tr>
<td>55</td>
<td>1</td>
<td>326 ± 5.8</td>
<td>5.9</td>
</tr>
<tr>
<td>55</td>
<td>5</td>
<td>583.8 ± 12.5</td>
<td>10.5</td>
</tr>
<tr>
<td>55</td>
<td>30</td>
<td>600.9 ± 10.2</td>
<td>10.8</td>
</tr>
<tr>
<td>74</td>
<td>1</td>
<td>435.6 ± 6.9</td>
<td>5.9</td>
</tr>
<tr>
<td>74</td>
<td>5</td>
<td>770 ± 16</td>
<td>10.4</td>
</tr>
<tr>
<td>74</td>
<td>30</td>
<td>759.3 ± 12.2</td>
<td>10.3</td>
</tr>
<tr>
<td>83</td>
<td>1</td>
<td>503.3 ± 7.8</td>
<td>6.1</td>
</tr>
<tr>
<td>83</td>
<td>5</td>
<td>804.6 ± 17.8</td>
<td>9.7</td>
</tr>
<tr>
<td>83</td>
<td>30</td>
<td>724.3 ± 9.5</td>
<td>8.7</td>
</tr>
<tr>
<td>100</td>
<td>1</td>
<td>638.7 ± 9.5</td>
<td>6.4</td>
</tr>
<tr>
<td>100</td>
<td>5</td>
<td>889.4 ± 17.4</td>
<td>8.9</td>
</tr>
<tr>
<td>100</td>
<td>30</td>
<td>5054.2 ± 2.5</td>
<td>50.5</td>
</tr>
</tbody>
</table>
Figure 2-1. Sensitivity analyses results for (a) mean population growth rate (b) and mean population size over 100 years expressed as percent deviation from the control run’s value. Each altered input parameter was run for 100 iterations, + or – signs indicate positive or negative alterations from the base model’s values. Codes are as follows: Reprod = probability of reproduction; Ad f survival = adult female survival probability; Juv f survival = Juvenile female survival probability; Subad f survival = subadult female survival probability; Trnvr death = probability of male death during turnovers; Kill or evict = probability of invading males being able to either evict or kill resident males; Turnover = turnover probability; Infanticide = probability of infanticide; Join or evicted = probability of unsuccessful invading males being evicted or joining the troop; Inf f survival = infant female survival probability.
Figure 2-2. End population sizes as percent of initial population sizes for (a) the total population, (b) hunted subpopulation, (c) and un-hunted subpopulation at the various harvest rates (1%, 5%, and 30%) after 100 time steps (yrs). Error bars show ± 1 s.d.
Figure 2-3. Total population losses after 100 years, expressed as individuals lost per km$^2$ hunted, for various amounts of hunted area at a 5% harvest rate. Error bars show ± 1 s.d.
Figure 2-4. Hunting yields (individuals/yr/km²) obtained in different rings of the hunted patches for various harvest rates with 74% hunted area. Error bars show ± 1 s.d.
References


Peres, C., 2000a. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In: J. Robinson and E. Bennett (Editor), Hunting


Appendix A, Submodel Descriptions

Aging and Growth

The first step of the model was aging and growth. Adults (> 4 yrs for females, > 5yrs for males) aged one year, whereas immature individuals advanced to the next age class. Infancy lasts approximately one year, females are juveniles for slightly more than two years, males are juveniles for three years, females are subadults for slightly less than one year, and males are subadults for one year (Rudran and Fernandez-Duque, 2003).

Natural Mortality

In the next step, individuals had a probability of dying from natural causes which varied according to age and sex. I modeled survival rates to be density-dependent and follow a pattern of logistic growth with a carrying capacity of 44.8 individuals/km². The model considered that individuals could only detect other conspecifics within a five patch radius (corresponding to a distance of one km) of themselves. This distance, which
corresponds to the mean maximum day range (Di Fiore and Campbell, 2007), is used as an approximation of the number of conspecifics with which an individual would be interacting and competing most frequently. The probability of survival was determined by the equation below,

\[ P_{\text{survival}} = S_{\text{min}} + S_{\text{diff}} \times (\frac{K - N}{K}) \]

where \( S_{\text{min}} \) = the age and sex-specific minimum survival rate, \( S_{\text{diff}} \) = the difference between the age and sex-specific minimum and maximum survival rates, \( K \) = the carrying capacity of a five patch radius, and \( N \) = the number of howlers in a five patch radius. An infant’s fate was dependent on that of its mother, if its mother died, the infant also died. Infants’ chances of dying in this step were from natural, non-infanticidal events. All adults died after reaching 22 years of age because this was the oldest age to which red howler monkeys were known to have lived.

**Reproduction**

Adult females had a probability of reproducing if an adult male was present in their troop. Birth rates were density-independent and adult females had an equal chance of giving birth to male or female infants as the mean percent of males born, 50.69%, is not greatly different from 50%. Females whose infants experienced infanticide in the previous time step had a greater likelihood of reproducing than females whose infants
did not experience an infanticidal event. The mean interbirth interval for these females is significantly shorter (16.3 months) than for females with surviving infants (21.8 months) \((t(140) = -6.33, p < .001)\).

**Creation of established troops**

Established troops were either newly-formed bisexual troops consisting of dispersing individuals that had recently produced their first crop of infants, or long-established bisexual troops, that had already produced several sets of infants. If a bisexual, extra-troop association produced infants it became a newly formed, established troop in this step.

**Dispersal**

Individuals of all age/sex classes except infants, small, and medium male juveniles had a probability of dispersing and entering bisexual troops or associating with extra-troop individuals. Rules for dispersal varied according to the age and sex of the individual. In addition, the probability of dispersal varied for individuals living in established troops and those found in extra-troop associations. If an individual was found alone, that individual was taken as a disperser who had failed to become a troop member.
or whose troop mates had died. This category included medium-sized male juveniles, who disperse only rarely (Crockett and Sekulic, 1984; Agoramoorthy and Rudran, 1993).

In general, when individuals started dispersing, they moved from one patch to another in a random direction. Upon arrival at the new patch, they searched for a suitable troop or extra-troop association to join. If none were found, they continued their search in the surrounding eight patches (excluding their original patch). They repeated this process until they found a suitable troop or association, or until they reached their maximum dispersal distance per time step. In the former case, they moved to the troop or association and gained membership. In the latter case, they continued dispersing in the next time step. Individuals were allowed to search the neighboring patches as the average day range of red howlers from four different sites is 559 m, and the longest possible distance between the corners of two patches corresponded to 565 m (Di Fiore and Campbell, 2007).

Female dispersal

For immature females living in established troops, the likelihood of dispersing was contingent upon her troop’s size and the number of adult females already present in it. If there were less than two adult females, the female would stay in her natal troop, and if there were four adult females, she would disperse. A female’s probability of dispersing was 5% when two adult females were present in the troop and 9% when three adult females were present. Additionally, an immature female would disperse from her natal
troop if it contained eighteen individuals, as this was the maximum troop size noted (Rudran and Fernandez-Duque, 2003). Adult females in established troops could disperse only if they had no infants and were a first or second year adult, as few older adult females have been noted to disperse (Rudran, 1979; Crockett, 1984; Crockett and Pope, 1993).

Dispersing females could not join established troops because this event rarely occurs in wild populations. Instead, they had to search for other dispersing individuals or extra-troop associations (Crockett, 1984). Female dispersers preferred associations with adult, subadult, or large juvenile males, and if this was not possible, they settled for any other type of association. Females could disperse a maximum of 2.8 km per time step (14 patches), which is estimated to be the twice the mean dispersal distance for females (Crockett and Pope, 1993).

Dispersing females had a 5% chance of dispersing from an extra-troop association, and a 95% chance of remaining in it until a new troop was formed. This assumption permitted extra-troop associations to be transient despite the lack of information on the actual rate at which extra-troop associations disbanded (Rudran, 1979; Crockett and Pope, 1993). Once these individuals dispersed, they followed the same rules of female dispersal outlined above.
Male dispersal

Dispersal of males in established troops was contingent upon the number of adult males in the troop or troop size. Juveniles and subadults would disperse if there were eighteen individuals in the troop and adults would disperse if there were six other adult males in the troop, as this is the maximum number of adult males recorded per troop (Rudran and Fernandez-Duque, 2003). Males would not disperse if there were no other adult males in their troop. If none of these conditions applied, males of different age classes had different probabilities of dispersing. Males sometimes dispersed in the company of other males (Agoramoorthy and Rudran, 1993; Crockett and Pope, 1993). Although males sometimes dispersed in groups of three, this appears to be uncommon and the model allowed males to disperse singly or with one partner. If other males of dispersal age were present in the troop, males had a 50% chance of dispersing with a partner.

In contrast to females, dispersing males could join either established troops or extra-troop associations (Crockett, 1984; Crockett and Pope, 1993). When males were dispersing, they searched preferentially for troops with adult or subadult females. If none were found, they settled for any other type of troop or extra-troop association. Adult and subadult males also attempted to take over established troops they encountered, and the only constraint they had in taking over a troop was that it should have at least one adult female. Males could disperse a maximum of .6 km per time step (three patches), which corresponded to slightly greater than the estimated mean dispersal distance for males (.55km) (Crockett and Pope, 1993).
Males in extra-troop associations had the same dispersal probability as extra-troop females. Once these males began dispersing, they followed the same rules for male dispersal as outlined above.

**Turnovers**

During male dispersal, if an adult or subadult encountered an established troop, he attempted to take it over. The likelihood of him successfully taking over the troop depended on whether or not he had a dispersal partner to help him overcome the resistance of the resident adult and subadult males, and the number of these resident males (Crockett, 1984; Crockett and Pope, 1993). If there were no resident adult males in the troop, invading males succeeded in taking over the troop. The probability of a turnover was determined with the equation below,

\[ P_{\text{turnover}} = (A \times ((M_m - M_r) / M_m)) + (A \times M_i) \]

where \( M_m \) = the larger of eight or number of resident adult and subadult males in the invaded troop, \( M_r \) = the number of resident adult and subadult males in the invaded troop, \( M_i \) = the number of male adult and subadults invading the troop, and \( A = .115 \). The value of \( A \) was set at this level as it produced a number of turnovers per year that was similar to values estimated in the literature (Crockett and Sekulic, 1984). A successful invasion could result in the resident male(s) being killed or evicted from the
troop, or coexisting with the invader(s) after the social change (Rudran, 1979; Crockett and Sekulic, 1984; Crockett and Pope, 1993). If the invading male had a dispersal partner, they would either kill or evict the resident male(s). However, if a male invaded alone, there was a 25% chance that he could evict or kill the resident male(s), and a 75% chance that he would enter the troop and coexist with the resident male(s) (Crockett and Sekulic, 1984). If the single male succeeded in killing or evicting the resident males or if a pair of males invaded, there was a .2% chance that the resident male(s) would be killed and a 99.8% chance that they would be evicted. Although resident males are killed and seriously injured during turnovers, the frequency of male deaths during these events is not well known (Rudran, 1979; Crockett and Pope, 1993). However, it appears that mortality during turnovers may be low (Crockett and Pope, 1988). Thus, I estimated that the resident males had only a .2% chance of being killed (as this did not produce an unreasonable number of male deaths per year). After a successful turnover of a troop, there was a 50% probability that infanticide occurred as an infant has an equal chance of surviving or being killed during a turnover event (Crockett and Sekulic, 1984).

Invading males, like resident males could be killed or injured during a social change. They could also be repulsed from entering the troop, or they could enter the troop and coexist with the resident male(s). The likelihood of invading males being killed was also .2%. If invading males were not killed, they had a 50% chance of succeeding or failing to enter the troop. Invading males were given an equal chance for either outcome because the frequency of successful male invasions was not well known.
**Hunting**

In hunted areas, hunting mortality was assumed to be additive to natural mortality. As noted previously, harvest rate varied with distance from the center of patch in order to correspond to indigenous hunting patterns (Hames, 1980a; Koster, 2007). Starting at the center of the patch and moving to the edge, harvest rates within the rings encompassing 1/5 of the patch radius were set at 35%, 100%, 84%, 93%, and 58% of the overall model’s hunting rate. I modeled harvest rates to reflect indigenous hunting patterns with the majority of hunting pressure falling on older individuals. I calculated hunting bias factors from the age distribution of an undisturbed population and the age distribution of indigenous harvests (Vickers, 1994; Alvard, 1995; Mena et al., 2000). There was a strong bias for hunting adults (1.861), subadults were hunted in nearly in proportion to their availability (.867), and juveniles were not preferred (0.141). An individual’s overall probability of being hunted is shown in the equation below,

\[ P_{\text{harvest}} = H_m \times H_r \times H_{\text{bias}} \]

where \( H_m \) = the overall hunting rate of the model, \( H_r \) = the hunting rate of the ring in which the individual is found, \( H_{\text{bias}} \) = the hunting bias for the particular age class. In addition, infants died if their mothers were hunted, but they did not contribute to the number of individuals hunted as infants are preferred by hunters. Biomass of the individuals hunted was estimated using mean weights for the various age classes (Rudran, 1979).
### Appendix B, Model input parameters

**Table 2-4. Survival and dispersal probabilities for the various red howler age/sex classes.**

<table>
<thead>
<tr>
<th></th>
<th>Minimum survival rates</th>
<th>Maximum survival rates</th>
<th>Male dispersal from established troops</th>
<th>Female dispersal from established troops</th>
<th>Dispersal from extra-troop associations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Women adults</td>
<td>0.90</td>
<td>0.93</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Women subadults</td>
<td>0.81</td>
<td>0.87</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Women large juveniles</td>
<td>0.87</td>
<td>0.92</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Women small juveniles</td>
<td>0.87</td>
<td>0.92</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Women infants</td>
<td>0.92</td>
<td>0.94</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Men adults</td>
<td>0.82</td>
<td>0.88</td>
<td>0.05</td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>Men subadults</td>
<td>0.95</td>
<td>0.97</td>
<td>0.05</td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>Men large juveniles</td>
<td>0.92</td>
<td>0.95</td>
<td>0.03</td>
<td></td>
<td>0.05</td>
</tr>
<tr>
<td>Men medium juveniles</td>
<td>0.85</td>
<td>0.90</td>
<td>0.00</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>Men small juveniles</td>
<td>0.85</td>
<td>0.90</td>
<td>0.00</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>Men infants</td>
<td>0.94</td>
<td>0.95</td>
<td>0.00</td>
<td></td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 2-5. Reproduction probabilities for adult females.

<table>
<thead>
<tr>
<th>Event</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Previous infant infanticide victim</td>
<td>0.42</td>
</tr>
<tr>
<td>Previous infant survived</td>
<td>0.35</td>
</tr>
<tr>
<td>Chance of having male infant</td>
<td>0.50</td>
</tr>
<tr>
<td>Chance of having female infant</td>
<td>0.50</td>
</tr>
</tbody>
</table>

Table 2-6. Probabilities during male takeovers of troops.

<table>
<thead>
<tr>
<th>Event</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turnover success (multiplied by number of invading and resident males)</td>
<td>0.12</td>
</tr>
<tr>
<td><strong>After successful turnovers</strong></td>
<td></td>
</tr>
<tr>
<td>Ability of invading males to either evict or kill resident males</td>
<td></td>
</tr>
<tr>
<td>If 1 invading male</td>
<td>0.25</td>
</tr>
<tr>
<td>If 2 invading males</td>
<td>1.00</td>
</tr>
<tr>
<td>Resident males remain in troop</td>
<td></td>
</tr>
<tr>
<td>If 1 invading male</td>
<td>0.75</td>
</tr>
<tr>
<td>If 2 invading males</td>
<td>0.00</td>
</tr>
<tr>
<td>Resident males killed</td>
<td></td>
</tr>
<tr>
<td>Resident males evicted</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Infanticide</td>
<td>0.50</td>
</tr>
<tr>
<td><strong>After unsuccessful turnovers</strong></td>
<td></td>
</tr>
<tr>
<td>Invading males die</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Invading males join troop as subdominants or are evicted</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>Invading males join troop as subdominant</td>
<td>0.50</td>
</tr>
<tr>
<td>Invading males evicted from troop</td>
<td>0.50</td>
</tr>
</tbody>
</table>
Table 2-7. Initial age distribution and hunting bias factors.

<table>
<thead>
<tr>
<th>Age distribution</th>
<th>Hunting bias factors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female adults</td>
<td>0.30</td>
</tr>
<tr>
<td>Female subadults</td>
<td>0.03</td>
</tr>
<tr>
<td>Female large juveniles</td>
<td>0.06</td>
</tr>
<tr>
<td>Female small juveniles</td>
<td>0.07</td>
</tr>
<tr>
<td>Female infants</td>
<td>0.08</td>
</tr>
<tr>
<td>Male adults</td>
<td>0.18</td>
</tr>
<tr>
<td>Male subadults</td>
<td>0.04</td>
</tr>
<tr>
<td>Male large juveniles</td>
<td>0.06</td>
</tr>
<tr>
<td>Male medium juveniles</td>
<td>0.06</td>
</tr>
<tr>
<td>Male small juveniles</td>
<td>0.06</td>
</tr>
<tr>
<td>Male infants</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Table 2-8. Initial troop composition.

<p>| Percent of multimale troops | 0.46 |
| Percent of unimale troops   | 0.54 |</p>
<table>
<thead>
<tr>
<th>Troop type</th>
<th>Multimale</th>
<th></th>
<th>Unimale</th>
<th></th>
<th>Extra-troop association</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Female adults</td>
<td>0.00</td>
<td>0.00</td>
<td>0.50</td>
<td>0.50</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Female subadults</td>
<td>0.80</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.80</td>
<td>0.20</td>
</tr>
<tr>
<td>Female large juveniles</td>
<td>0.52</td>
<td>0.48</td>
<td>0.00</td>
<td>0.00</td>
<td>0.52</td>
<td>0.48</td>
</tr>
<tr>
<td>Female small juveniles</td>
<td>0.32</td>
<td>0.68</td>
<td>0.00</td>
<td>0.00</td>
<td>0.52</td>
<td>0.48</td>
</tr>
<tr>
<td>Female infants</td>
<td>0.35</td>
<td>0.65</td>
<td>0.00</td>
<td>0.00</td>
<td>0.35</td>
<td>0.65</td>
</tr>
<tr>
<td>Male adults</td>
<td>0.00</td>
<td>0.00</td>
<td>0.80</td>
<td>0.20</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Male subadults</td>
<td>0.58</td>
<td>0.42</td>
<td>0.00</td>
<td>0.00</td>
<td>0.58</td>
<td>0.42</td>
</tr>
<tr>
<td>Male large juveniles</td>
<td>0.51</td>
<td>0.49</td>
<td>0.00</td>
<td>0.00</td>
<td>0.51</td>
<td>0.49</td>
</tr>
<tr>
<td>Male medium juveniles</td>
<td>0.38</td>
<td>0.62</td>
<td>0.00</td>
<td>0.00</td>
<td>0.58</td>
<td>0.42</td>
</tr>
<tr>
<td>Male small juveniles</td>
<td>0.45</td>
<td>0.55</td>
<td>0.00</td>
<td>0.00</td>
<td>0.65</td>
<td>0.35</td>
</tr>
<tr>
<td>Male infants</td>
<td>0.48</td>
<td>0.52</td>
<td>0.00</td>
<td>0.00</td>
<td>0.48</td>
<td>0.52</td>
</tr>
<tr>
<td>Mean # individuals in initial troop</td>
<td>9.31</td>
<td></td>
<td>7.51</td>
<td></td>
<td>4.5</td>
<td></td>
</tr>
</tbody>
</table>
Chapter 3

Tropical warming and the dynamics of endangered primates

Abstract

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, I document influences of the El Niño Southern Oscillation and Hemispheric climatic variability on population dynamics of four genera of ateline (neotropical, large-bodied) primates. All ateline genera experienced either an immediate or lagged negative effect of El Niño events. ENSO events were also found to influence primate resource levels through neotropical arboreal phenology; fruit and flower production was positively affected in El Niño years and negatively affected during La Niña years. Furthermore, frugivorous primates showed a high degree of interspecific population synchrony over large scales across Central and South America attributable to 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.
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 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 (Holmgren et al., 2001; Root et al., 2003; Walther et al., 2002); however very few studies have been conducted on primate species. Studies conducted on catarrhine (Old World) monkeys and lemurs found that global warming would result in a reduced and fragmented range for gelada baboons while ENSO events lead to declines in sifaka fecundity, both of which posed threats for continued population viability (Dunbar, 1998; Dunham et al., 2008). The only study conducted on New World primates found some evidence of negative effects of ENSO events for capuchin and howler monkeys populations (Milton et al., 2005). Furthermore, primates (generally restricted to tropical, less seasonal environments) are evidently sensitive to the climatic conditions of their ranges with present and past distributions of primates structured by physiological tolerances to temperature and rainfall (Baumgarten and Williamson, 2007; Brandon-Jones, 1996; Fernandez-Duque et al., 2001; Korstjens et al., 2006; Strier, 2003). In addition, a variety of extant populations have been negatively affected by climatic events such as droughts and fruit failures showing increased mortality rates and depressed birth rates during such
times of environmental stress (Gould et al., 2003, 1999; Hamilton, 1985; Jolly et al., 2002; Milton et al., 2005; Savage et al., 1996). Thus, in the face of global warming and climate change, knowledge of the implications of El Niño events for primate population dynamics is greatly needed.

Multiple changes in neotropical forest dynamics in response to global climate change have been documented which could have direct effects on the primate populations living there. For instance, in Amazonian and Atlantic tropical moist forests, El Niño induced drought and land use change have been linked to increased fire, leaf shedding, and tree mortality rates, while declines in fruiting basal area and above ground biomass have been noted (Barlow and Peres, 2004, 2006; Laurance and Williamson, 2001; Rolim et al., 2005). Furthermore, El Niño events have been observed to affect tree phenology and fruiting events, and when followed by a mild dry season in the succeeding year, have caused famines in frugivorous species (Wright et al., 1999).

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) are of particular conservation interest as the majority of ateline species for which there are data are listed as vulnerable, endangered, or critically endangered on the IUCN red list; ateline primates are the most sensitive of all platyrrhine (New World) monkeys to anthropogenic activities (Di Fiore and Campbell, 2007).

Population synchrony is important to assess for threatened species as synchronous population dynamics can exacerbate the global extinction risk of multiple populations (Heino et al., 1997). The general observable pattern is that population synchrony
declines with increasing distance between populations; closer populations should exhibit a higher degree of synchrony than more distant populations if the cause of synchrony is more likely to affect populations at shorter distances (Koenig, 1999). Population synchrony is hypothesized to be attributable to three different causes: nomadic predators switch between areas with high densities of prey, thereby increasing mortality rates and lessening heterogeneity in population densities, migration can equalize the growth rates between populations that are connected, or populations are exposed to similar environmental factors (e.g. climate) that affect their growth rates in the same way (Ydenberg, 1987; Ranta et al., 1998; Koenig, 1999). The latter hypothesis, the Moran effect, is of particular interest as the study populations investigated here are widely dispersed (all populations were >600 km apart) and unlikely to be synchronized by the first two causes. The Moran theorem predicts that the correlation between a pair of populations should scale linearly with the degree of correlation between the environmental factors that influence the dynamics of those populations (Moran, 1953). Therefore, I investigated whether there was a climate signal in the primate population dynamics to assess the potential for large-scale climate change to synchronize their fluctuations or population trends (Post and Forchhammer, 2002).

Here, I aim 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. I then examine the level of interspecific synchrony among these populations and quantify the role of large-scale climatic variability in synchrony.
Materials and Methods

Study species and areas

Data on primate annual abundances and resource phenology were taken from four neotropical sites. Population censuses were conducted regularly, and counts were available for most of the years. The muriqui (*Brachyteles arachnoides*), currently classified as endangered on the IUCN red list, was censused from 1982 to 2005. The study population was located at the Estação Biológica de Caratinga, Minas Gerais, Brazil (19° 44' S, 41° 49' W), a semideciduous montane forest (Strier, 2005). The Colombian red howler monkey (*Alouatta seniculus*) is classified as declining but of least concern on the IUCN red list due to its wide distribution. The study population was censused from 1970 to 1999 at Hato Masaguaral, Guárico State, Venezuela (8° 34' N, 67° 35' W), a habitat of gallery forest and forest patches (matas) among seasonally inundated grasslands (Rudran and Fernandez-Duque, 2003). The woolly monkey (*Lagothrix lagotricha*), currently appearing on the IUCN red list as vulnerable, was studied from 1987 to 1998. The study population was located at the Macarena Ecological Investigations Center, Parque Nacional Macarena – Tinigua, Meta, Colombia (2° 40' N, 74° 10' W), a tropical moist forest (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), a tropical moist forest, from 1964 to 2003 (Milton and Hopkins, 2006). Tree phenology data was also obtained from Barro Colorado Island, Panama. All population counts were log-transformed to stabilize variance.

**Phenology data**

Tree phenology data from Barro Colorado Island, Panama (a lowland, moist tropical forest) are available from 1987 – 2004 (Wright and Calderon, 2006). Inter-site variation is likely to exist, however, as lowland moist to wet tropical forests are the dominant vegetation form of Northern South America (Daly and Mitchell, 2000), BCI vegetation data represent an approximate index of resource availability. The rain of seeds and flowers were censused monthly using 200 .5m² traps from a 50-ha plot. Counts were available of numbers of species fruiting and flowering along with production levels for species captured in 10 or more traps in any given year. Seed production equaled the number of seeds captured plus mature fruit captured multiplied by a species-specific mean seed to fruit ratio, while flower production equaled the number of flower presences (the number of times flowers were present in a trap). I used the monthly maximum and minimum number of species fruiting and flowering for each year as an index of resource availability, along with annual values of flower and seed production for a subset of 44 mammalian-dispersed species. These values were log-transformed to normalize residuals.
Climate data

The Southern Oscillation Index (SOI), the ENSO3, 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). Extreme negative values of the SOI correspond to El Niño years and extreme positive values to La Niña years; the SOI and the ENSO indices are inversely related. Annual rainfall data were obtained from the San Fernando de Apure weather station, Venezuela (7º 54’ N, 67º 25’ W), while the Northeast Brazil Rainfall Anomaly index (http://jisao.washington.edu/data_sets/brazil) was used for the Brazilian site. Mean annual temperature, annual rainfall, dry and wet season length were obtained from Barro Colorado Island, Panama (http://striweb.si.edu/esp/physical_monitoring/summary_bci.htm). In order to compare local climatic conditions between sites, I used annual, wet season, dry season, and 3-month quartiles values for temperature and rainfall data interpolated to a 0.5 by 0.5 degree grid resolution for each site from 1960 to 1990 (http://climate.geog.udel.edu/~climate/html_pages/archive.html).
Population models

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

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

where \( X_t \) are logs of population densities in year \( t \), \( a_0 \) is a constant representing the intrinsic rate of population increase, \( a_i \) are the estimates of the strength of density-dependence at lags of \( i \) years, \( b_i \) quantifies the effects of climate or phenology on population density in year \( t \), \( \gamma_t \) is the SOI, ENSO3 index, rainfall, or phenology value in year \( t \), and \( \varepsilon_t \) is the random error component in year \( t \). 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. I then included the climate variables (SOI, ENSO3 Index, and rainfall) 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.

Although climatic events could affect primate population dynamics directly, it is likely that the influence of climate is mediated through their resource levels. Thus I
examined the potential effect of climate on primate resource levels. I first performed correlation analyses between the various phenology indices and climate variables (BCI rainfall, temperature, dry and wet season length, SOI, ENSO3, ENSO34, ENSO4, and ENSO12 indices) with lags up to 3 years. First-, second- and third-order models were examined to determine which best explained the various phenology indices, and then I incorporated the climate terms with the strongest correlation coefficients. Parameter coefficients were obtained by using ARIMA in SPSS (SPSS Inc., Chicago, IL) and model fit was assessed using a Bayesian Information Criterion score (Burnham and Anderson, 1998).

In order to assess patterns of population synchrony, I quantified all pairwise lag-0 correlations between the raw time series of yearly primate abundances, and repeated this using the detrended time series. Detrended time series make use of the residuals from linear regressions to remove long-term trends from the data. Such time series are used to examine regional processes of interest without interference from patterns caused by large-scale trends (Koenig, 1999).

According to the Moran theorem, the more similar the effects of climate or environmental perturbations on a pair of populations, the greater the degree of synchrony they should exhibit (Moran, 1953). Therefore I tested for correlations between density-independent factors that could be influencing these primate populations. First, I conducted correlation analyses between the local climatic conditions for each pair of sites (rainfall and temperature data from 1960 - 1990). I used annual, wet season, dry season, and 3-month quartiles values for each site in the correlation analyses. I then conducted correlation analyses between the ENSO3 index, SOI, and temperature anomaly.
coefficients with lags up to 3 years from the primate population models. These coefficients indicate the effects of ENSO events or temperature anomalies on the population densities of these species after accounting for density dependence. Then, to investigate whether primate population synchrony could be attributed to climatic factors, I 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 and Forchhammer, 2002). The degree of population synchrony between a pair of populations should be matched by correlations in the local climate conditions if these conditions were driving population synchrony, or by correlations between the climate index coefficients if large-scale climate was the agent synchronizing the populations.

Results

The results indicated that the howler population showed second-order density dependence while the other primate genera (spider, woolly, and muriqui) showed first-order density dependence. The SOI entered the best fit model for the howler monkey (SOI\(_t\)) and muriqui population (SOI\(_{t-1}\)), while the ENSO3\(_{t-1}\) index entered the best fit model for the spider and woolly monkey populations (Table 1). The standard errors associated with the climate coefficients for the howler and woolly monkey populations are fairly large; however, these data suggest that the more frugivorous ateline populations
(muriquis, spider, and woolly monkeys) declined one year following El Niño events (corresponding to positive values for the ENSO indices and negative values for the SOI), while howler monkeys declined in the same year that El Niño events occurred.

Resource availability (the phenology indices) was then included into the population models as a mechanism of explaining how climate may be affecting population densities (Table 1). For howler and spider monkeys, there was a 2 year lagged positive effect of resource availability; the best fit model included annual seed production and the monthly maximum number of species flowering for howler and spider monkeys respectively. For woolly monkeys and muriquis on the other hand, there was a negative effect of resource availability during the wet season. The best fit model for woolly monkeys included the monthly minimum number of species fruiting with a 2 year lag, while muriquis included the monthly minimum number of species flowering in the current year. These 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, two of the indices included a local weather effect in the best-fitting models of phenological dynamics (Table 2). These local weather factors are indicative of El Niño events on BCI as these years are associated with longer dry seasons (correlation with SOI, $r = -.286$, p-value = .04), higher temperatures, increased
irradiance, and lowered rainfall (while La Niña years generally experience the opposite conditions) (Wright and Calderon, 2006). Inter-annual variability in the remaining resource indices was best explained by one of the ENSO indices. Two of the phenology indices exhibited a positive effect of an El Niño event in the current year, while the rest exhibited a lagged negative effect of an El Niño event. The phenology indices that included a 2 year lagged ENSO index in their best fit models experienced negative effects for both years following an El Niño event.

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 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).
Discussion

This 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. Muriqui, spider, and woolly monkey populations appear to experience a one year lagged negative effect of an El Niño event. In contrast, howler monkeys appear to experience an immediate effect of an El Niño event. Furthermore, these results suggest that the more frugivorous and threatened genera (muriquis, woolly, and spider monkeys) experience the greatest declines following El Niño events, whereas howler monkeys, the most folivorous genus, experience the smallest declines.

I hypothesized that the effects of El Niño and seasonal weather on primate populations are likely mediated through food availability. These analyses indicated either an immediate or lagged effect of resource availability on primate populations. Howler and spider monkey populations experienced a positive effect of resource availability; however, more unusually, woolly monkeys and muriquis experienced a negative effect of increased resource availability during the wet season. This result could reflect increased competition over resources during a time of seasonal scarcity. Indeed woolly monkeys have been found to have a high dietary overlap with spider monkeys, and to a lesser extent with capuchins and howler monkeys (Dew, 2005; Stevenson et al., 2000).
However, little overlap of fruit diet was found between muriquis and howler monkeys (Martins, 2008).

Secondly, I found that potential primate resource levels are affected by climatic variability; neotropical fruit and flower production were strongly affected by El Niño events. These results are consistent with the findings of Wright & Calderon (2006) who showed that the number of species flowering and fruiting were positively correlated with temperature and peaked during El Niño events. The negative effect of an El Niño event in the previous year is also concurrent with Wright et al. (1999), who documented a two year cycle of high then low fruit production on BCI during El Niño and La Niña years respectively. They hypothesized that the increased insolation during El Niño events simulates high fruit production, which consequently consumes stored reserves and limits the next reproductive event. Additionally, the reduced incident radiation experienced in La Niña years could limit fruit production. Likewise, they found El Niño events, when followed by a mild dry season in the succeeding year, have caused famines in frugivorous mammals (Wright et al., 1999). Similarly, the more frugivorous primate genera experienced a one year lagged negative impact of El Niño years, which could reflect reduced resource availability during La Niña years.

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 compared with the other populations (Campbell et al., 2007). Furthermore, I documented that as the populations’ responses to ENSO events and temperature changes were more similar, they exhibited a higher degree of synchrony. The
degree of synchrony also did not decline with distance, which emphasizes the role of large-scale climate factors over regional process in population 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 risk of global extinction when exhibiting synchronous versus asynchronous population dynamics (Heino et al., 1997).

Furthermore, another risk posed by climate change is the potential for global warming to cause changes in the frequency of favorable and unfavorable conditions and the autocorrelation of environmental conditions (Wilmers et al., 2007). Modeling studies have indicated that a high positive correlation in environmental conditions can lead to large population fluctuations, whereas negative correlations in environmental conditions lead to low-amplitude dynamics. If a high positive correlation in environmental conditions exists, a string of favorable years potentially can occur, leading to high population densities. However, once a year with poor environmental conditions occurs, high levels of density dependence can occur in several vital rates (fecundity, juvenile, and adult survival rates), and a population crash may ensue. Therefore, if global warming leads to a positive correlation of environmental conditions (with poor years such as El Niño years still occurring occasionally), this could lead to large population fluctuations and an increased extinction risk for a species. However, this risk is dependent on the ability of climate change to increase the frequency of favorable conditions and alterations in the frequency of ENSO events under global warming. For instance, if an increased frequency of ENSO events leads to a negative correlation in environmental conditions, this could lead to lower population fluctuations and feasibly, a lowered extinction risk. In
addition, highly fecund species are more likely to have large population fluctuations and are consequently more vulnerable to temporal correlations in environmental correlations. As ateline primates have slow rates of reproduction, they appear less susceptible to this risk than more fecund species; nonetheless more studies are needed to assess this potential effect of climate change on primate populations.

In sum, these 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 quantity the effects of climate and environmental variability on primate species are needed.

Notes

This chapter is published in Biology Letters.
Table 3-1. Best-fit primate population models quantifying the effect of climate or phenology on log density.

<table>
<thead>
<tr>
<th>genera</th>
<th>model equations*</th>
<th>climate or phenology coefficient ± s.e.</th>
<th>BIC†</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alouatta</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + b_1(\text{SOI}_t) + \text{yr} + \epsilon)</td>
<td>0.013 ± 0.019</td>
<td>-3.059</td>
<td>0.823</td>
</tr>
<tr>
<td>Ateles</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + \text{yr} + \epsilon)</td>
<td>-0.052 ± 0.032</td>
<td>-3.176</td>
<td>0.857</td>
</tr>
<tr>
<td>Lagothrix</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_2(\text{ENSO3}_{t-1}) + \text{yr} + \epsilon)</td>
<td>-0.04 ± 0.051</td>
<td>-3.352</td>
<td>0.604</td>
</tr>
<tr>
<td>Brachyteles</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_2(\text{SOI}_{t-1}) + \text{yr} + \epsilon)</td>
<td>0.02 ± 0.011</td>
<td>-4.917</td>
<td>0.975</td>
</tr>
<tr>
<td>Alouatta</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + a_3(X_{t-2}) + b_3(\text{seed}_{t-2}) + \text{yr} + \epsilon)</td>
<td>0.302 ± 0.042</td>
<td>-3.642</td>
<td>0.984</td>
</tr>
<tr>
<td>Ateles</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_3(\text{mxflwr}_{t-2}) + \text{yr} + \epsilon)</td>
<td>0.009 ± 0.010</td>
<td>-4.327</td>
<td>0.946</td>
</tr>
<tr>
<td>Lagothrix</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_3(\text{minfrt}_{t-2}) + \text{yr} + \epsilon)</td>
<td>-0.009 ± 0.002</td>
<td>-4.339</td>
<td>0.681</td>
</tr>
<tr>
<td>Brachyteles</td>
<td>(X_t = a_0 + a_1(X_{t-1}) + b_1(\text{minflwr}) + \text{yr} + \epsilon)</td>
<td>-0.004 ± 0.001</td>
<td>-6.482</td>
<td>0.982</td>
</tr>
</tbody>
</table>

*seed = 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
† Bayesian Information Criterion
Table 3-2. Best-fit model coefficients quantifying the influence of climate on phenology.

<table>
<thead>
<tr>
<th>phenology indices*</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&lt;sub&gt;t&lt;/sub&gt;</td>
<td>9.057 ± 2.094</td>
<td>4.325</td>
<td>0.001</td>
</tr>
<tr>
<td>Monthly min. number of spp fruiting</td>
<td>ENSO3&lt;sub&gt;t+2&lt;/sub&gt;</td>
<td>-5.29 ± 2.009</td>
<td>-2.632</td>
<td>0.020</td>
</tr>
<tr>
<td>Monthly max. number of spp flowering</td>
<td>BCI temperature</td>
<td>6.608 ± 2.953</td>
<td>2.237</td>
<td>0.042</td>
</tr>
<tr>
<td>Monthly min. number of spp flowering</td>
<td>ENSO4&lt;sub&gt;t+2&lt;/sub&gt;</td>
<td>-3.974 ± 2.343</td>
<td>-1.696</td>
<td>0.112</td>
</tr>
<tr>
<td>Annual seed production</td>
<td>ENSO3&lt;sub&gt;t+2&lt;/sub&gt;</td>
<td>-0.248 ± .115</td>
<td>-2.158</td>
<td>0.050</td>
</tr>
<tr>
<td>Annual flower production</td>
<td>BCI dry season length&lt;sub&gt;t-1&lt;/sub&gt;</td>
<td>-0.003 ± .002</td>
<td>-2.163</td>
<td>0.051</td>
</tr>
</tbody>
</table>

*All the phenology indices were characterized by first-order density dependence with the exception of annual flower production which displayed second-order density dependence.
Figure 3-1. 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.
Figure 3-2. 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.

Barlow, J. and Peres, C., 2006. Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest. Biodiversity and Conservation, 15:985-1012.


Abstract

The effects of global warming and potential intensification of El Niño events on primate reproduction and population viability have been little studied; however, an understanding of the role of extrinsic, environmental factors on primate reproduction is critical to assessing the effects of global climate change on these species. Given the threatened status of many primate species, the impacts of global warming on primate reproduction and consequently population growth is of great concern. Here I tested the effects of climatic variability on the reproduction, birth seasonality, and infant sex ratios of two ateline primate genera, northern muriquis and woolly monkeys. In both species, the annual birth season was delayed by dry conditions, and during El Niño years, and delayed birth seasons were linked to lower birth rates. Additionally, increased annual mean temperatures were associated with lower birth rates for northern muriquis. Finally, El Niño years were characterized by male-biased offspring sex ratios, which may contribute to reduced population growth rates. These results illustrate that global warming, increased drought frequency, and changes in the frequency of El Niño events...
could limit primate reproductive output, threatening the persistence and recovery of ateline primate populations.

Introduction

One of the most clearly identifiable consequences of recent climate change has been an increase in global temperatures of 0.74º C over the last century, with an additional increase of 1.8º – 4º C expected over the next century (IPCC Climate Change 2007). Given that such a warming may have large effects on drought frequency and global net primary production, and is also cause for concern due to the potential to alter the amplitude, nature, and frequency of El Niño events (Guilyardi 2006; Latif & Keenlyside 2009; Timmermann et al. 1999; Yeh et al. 2009; Zhao & Running 2010), it is of critical importance to understand the effects of large-scale climate change on wildlife populations. In general, the role of climate change and El Niño events in primate population dynamics or their reproduction has been under-studied (Dunbar 1998; Dunham et al. 2008; Dunham et al. 2010; Milton et al. 2005; Wiederholt & Post 2009). Such a lack of knowledge of the implications of climate change for primate populations is problematic as, globally, up to one-third of primate species are threatened with extinction (Di Fiore & Campbell 2007). Furthermore, the subfamily Atelinae (large-bodied New World primates) is of particular conservation concern because it is a highly threatened group (Di Fiore & Campbell 2007). Thus, understanding the effects of global climatic
change on primate reproduction is vital due to the importance of population productivity for long-term population viability and persistence.

Climatic change could have direct as well as indirect effects on primate reproduction, potentially threatening the viability of primate populations and altering infant sex ratios. The capacity for climate to affect primate birth rates, and infant and adult female survival and physical condition has been well documented in widespread species (Hamilton, 1985; Crockett and Rudran, 1987a; b; Goldizen et al., 1988; Fedigan and Rose, 1995; Savage et al., 1996; Koenig et al., 1997; Gould et al., 1999; Strier, 1999; Jolly et al., 2002; Gould et al., 2003; Nishimura, 2003; Dunham et al., 2008). For instance, lowered primate fecundity and adult female and infant survival rates have been noted after climatic events such as droughts, ENSO events, and fruit failures (Gould et al., 2003, 1999; Hamilton, 1985; Jolly et al., 2002; Milton et al., 2005; Savage et al., 1996; Dunham et al. 2010).

A less studied possibility is that climate could indirectly affect reproduction and infant sex ratios by causing changes in birth seasonality. Seasonal and interannual variation in climate could feasibly affect the timing of births for large-bodied primates, as adult female condition and energy levels likely respond to changes in resource availability (Becovitch 1987; Di Fiore & Campbell 2007; Knott 2001; Strier et al. 2001; Ziegler et al. 2000). Primate reproductive seasonality may be correlated with female reproductive condition or male sperm quality, or modified so that conception, infant weaning, or energetically expensive phases correspond to the times of maximum food availability (Campbell et al. 2007; Hernández-López et al. 2002). It also may be timed to avoid weaning during periods of high temperatures, low moisture content of food, and
potential heat stress (Crockett and Rudran, 1987a). Thus, any shifts in the timing of reproduction have the potential to affect prenatal and infant survival.

Variation in infant sex ratios is another important factor for threatened populations as it can affect population growth rates (Strier 2000). Many hypotheses have been proposed to explain primate sex ratio variation (Chapman et al. 1989; Hiraiwa-Hasegawa 1993); however, the most common hypotheses (the Trivers-Willard hypothesis, the local resource competition hypothesis, and a modified version of the latter) generally invoke social influences as the principal explanatory factors (Clark 1978; Silk 1983; Trivers & Willard 1973). The Trivers-Willard hypothesis predicts that for polygynous species, adult females in good condition should produce sons while those in poor condition should produce daughters, presumably because sons are more expensive to produce than are daughters in such species (Trivers & Willard 1973). In contrast, the local resource competition hypothesis predicts that under resource competition, the birth sex ratio should be skewed towards the sex that disperses (Clark 1978); thus its predictions are at odds with those of the Trivers-Willard hypothesis for many polygynous, dimorphic species. Lastly, the modified version of the local resource competition hypothesis predicts that under resource competition and female philopatry, females should reduce recruitment of immature females into their group, resulting in low-ranking females producing more sons (Silk 1983). A closely related hypothesis, the advantaged daughter hypothesis, also predicts that under female philopatry and rank inheritance, low-ranking females should produce more sons and high-ranking females should produce more daughters. However, the latter hypothesis emphasizes the benefits daughters receive from inheriting their mother’s rank while the former emphasizes the
costs to low-ranking mothers of producing daughters (Simpson and Simpson, 1982). Thus, testing of these hypotheses requires knowledge of maternal condition, resource competition, and female ranking among primate populations. In studies of primate infant sex ratios, little support has been found for the Trivers-Willard hypothesis in studies of primate infant sex ratios (Hiraiwa-Hasegawa, 1993; Brown, 2001), while in contrast, evidence has been found for both the original and modified versions of local resource hypothesis (Van Schaik and Van Noordwijk, 1983; Altmann et al., 1988; Van Schaik and De Visser, 1990; Hiraiwa-Hasegawa, 1993; Debyser, 1995; Nevison et al., 1996; Watson et al., 1996; Nunes and Chapman, 1997; Perret and Colas, 1997; Maestripieri, 2002; Silk and Brown, 2008; Zhao et al., 2009).

Thus, social rank and resource competition may affect infant sex ratios, yet the influences of such factors can vary according to population density, food availability, and population growth rates, and ultimately be dependent on prevailing environmental conditions (Hiraiwa-Hasegawa 1993; Kruuk et al. 1999; Van Schaik & De Visser 1990). The potential role of external, environmental factors in sex ratio variation has been formalized as the extrinsic modification hypothesis (Post et al. 1999). This hypothesis states that offspring sex ratios in polygynous vertebrates may vary with changes in maternal condition during pregnancy due to extrinsic fluctuations in the abiotic environment. Such variation may be favored by natural selection, although it does not reflect an adaptive, maternal strategy of sex allocation as it is likely independent of maternal influence (Post et al. 1999). Support for the extrinsic modification hypothesis has been found among other mammalian species including red deer *Cervus elaphus*
(Forchhammer 2000; Kruuk et al. 1999; Post et al. 1999), springbok *Antidorcas marsupialis* (Krüger et al. 2005), white-tailed deer *Odocoileus virginianus* (Garroway & Broders 2007), and reindeer *Rangifer tarandus* (Weladji & Holand 2003) but, to my knowledge, has not been explicitly investigated in primates.

The objective of this study was to test the effects of global warming and climate change on the reproduction of ateline primates focusing on populations of two declining genera. I hypothesized that climatic variation could alter birth rates and offspring sex ratios either directly through changes in maternal condition, or indirectly via shifts in reproductive seasonality in these primates. First, I examined the effects of large-scale and local climate on birth seasonality, and then examined the combined effects of large-scale climate and birth seasonality on infant sex ratio variation and birth rates.

**Materials and Methods**

**Study species and areas**

Data on primate annual abundances were used from two neotropical sites. Population censuses were used to assess the effects of climate on overall infant production, while subsets of the data with more detailed records were used to examine sex ratio variation and birth seasonality. The northern muriqui, or woolly spider monkey (*Brachyteles hypoxanthus*), is currently listed as declining and endangered by the IUCN
red list (IUCN 2010). The population included here, a troop varying from 22 to 81 individuals (8 to 21 adult females), was censused from 1982 to 2005. The study site was the Estação Biológica de Caratinga, Minas Gerais, Brazil a low, semideciduous montane forest with mean annual rainfall 1,134 mm (s.d. = 266 mm) (19° 44' S, 41° 49' W) (Strier 1999; Strier 2005; Strier et al. 2001). The woolly monkey (*Lagothrix lagotricha*) currently appears on the IUCN red list as vulnerable and declining (IUCN 2010). The focal population, a troop varying from 14 to 24 individuals (5 to 9 adult females) and was censused from 1987 to 1998. The population was located at the Macarena Ecological Investigations Center, Meta, Colombia (2° 40' N, 74° 10' W), a tropical moist forest with a mean annual rainfall of 2600 mm (s.d. = 281 mm) (Nishimura 2003b). All population counts were log-transformed to stabilize variance.

**Climate data**

The Southern Oscillation Index (SOI) and the four sea surface temperature indices, ENSO3, ENSO34, ENSO4, and ENSO12 indices (National Oceanic and Atmospheric Administration, Climate Prediction Center, [http://www.cdc.noaa.gov/data/climateindices/list](http://www.cdc.noaa.gov/data/climateindices/list)) were used to represent large-scale ENSO conditions. El Niño years are marked by below average rainfall, above average temperatures, reduced cloudiness, and increased incident radiation for Central America, Northern South America, and the Amazon (Kiladis & Diaz 1989). Extreme negative values of the SOI correspond to El Niño years and extreme positive values to La Niña.
years; the SOI and sea surface temperature indices are inversely related. Finally, I used local climate data for a .5° by .5° grid (Climatic Research Unit, University of East Anglia, http://www.cru.uea.ac.uk/cru/data/hrg/) including total annual precipitation, mean annual, wet, and dry season temperatures.

**Birth seasonality**

Birth rates were recorded for both *Lagothrix* and *Brachyteles* as part of long-term monitoring efforts of these populations (Nishimura 2003; Strier 1999; Strier 2005; Strier et al. 2001). Records on births were available from 1983 to 1999 for *Brachyteles*, and from 1987 to 1998 for *Lagothrix*; birth data included the month of birth along with the sex of the infant produced. Numbers of monthly births were expressed as cumulative percent births per year (Caughley & Caughley 1974; Post et al. 2003). I used nonlinear regression analysis of cumulative percent births per month versus the mean Julian day per month to estimate the onset of the birth season (date of 10% births), the mean birth date, and the length of the birth season for each year. The length of the birth season was defined as the difference between the dates of 10% and 80% births (Post et al. 2003). The fitted function used in the regression analysis was $Y = 1/(1 + e^{-a - bX})$, where $Y$ is percent births, $X$ is the mean Julian date per month, and $a$ and $b$ are constants.
Birth rate, seasonality, and sex ratio analyses

The effects of climatic factors were assessed on ateline birth seasonality, birth rates, and infant sex ratio variation. I used linear regressions to examine the effects of large-scale and local climate on birth seasonality, and the influence of both climate and birth seasonality on birth rates. I used logistic regressions to assess the effects of climate and birth seasonality on sex ratio variation. The sex ratio was calculated as the annual percent of total births comprising male births; infants of unknown sex were excluded from the analysis. Annual 10% birth date (the onset of the birth season), mean birth date, and length of the birth season were used as measures of birth seasonality. The general form of the model employed for the analysis of birth seasonality was:

\[ P_t = a_0 + a_1(\gamma_t) + b_1(X_t) + b_2(X_{t-1}) + \varepsilon_t \]

in which, \( P_t \) = length of the birth season, or date of 10% births, or date of 50% births in year \( t \), \( \gamma_t \) is either the SOI, the ENSO3 index, or local climate value in year \( t \), \( a_t \) quantifies the effects of climate on birth seasonality year \( t \), \( X_t \) is log-transformed total population count from each field site, \( b_t \) are the estimates of the strength of density-dependence at lags of \( t \) years, and \( \varepsilon_t \) is the random error component in year \( t \).

The general form of the model employed for the birth rate analysis was:

\[ P_t = a_0 + a_1(T_t) + a_2(\gamma_t) + b_1(X_t) + b_2(X_{t-1}) + \varepsilon_t \]
in which, \( P_t \) = birth rate defined as total number of annual births per adult female or reproductive adult females in year \( t \), \( T_t \) = timing of births in year \( t \) (quantified as either the date of 10% or 50% births), \( \gamma_t \) is the SOI, the ENSO indices, or local climate value in year \( t \), \( a_t \) quantifies the effects of birth seasonality or climate on the birth rate in year \( t \), and \( X, b_t, \) and \( \epsilon_t \) are as defined above.

The general form of the model employed for the sex ratio analysis was:

\[
P_t = a_0 + a_1(T_t) + a_2(\gamma_t) + b_1(X_t) + b_2(X_{t-1}) + \epsilon_t
\]

in which, \( P_t \) = proportion of male births of total births in year \( t \), \( \gamma_t \) is the SOI, the ENSO3 index, or local climate value in year \( t \), and \( T, a_t, X, b_t, \) and \( \epsilon_t \) are as defined above.

First, models were run independently with the SOI or one of the ENSO indices to assess the effects of large-scale climate, and then with one of the local climate variables (total annual precipitation, mean annual, wet, or dry season temperatures) to assess the effects of local climate. Similarly, all birth rate and sex ratio models were run with either the onset of the birth season (date of 10% births) or mean birth date (date of 50% births) to assess the effects of birth seasonality on ateline reproduction. Birth rate models were first examined without climate terms, and then with the climate factors. For all analyses, first- and second-order models were examined to determine the most parsimonious model of density-dependent dynamics. The best overall model was then selected based on the corrected Akaike’s Information Criterion score (Burnham & Anderson 1998).

Regressions were run in R (R Foundation for Statistical Computing, Vienna, Austria).
Results

Birth seasonality

Models of annual birth seasons for both species, used subsequently to estimate dates of onset, termination, and mean length of the birth season, displayed goodness of fit values of $R^2 \geq 0.90$ for all years of birth data (Figure 1). The mean date of 50% births, which for *Lagothrix* occurred during the late wet/early dry season (October 1st, s.e. = 11.9), was significantly later than the mean date of 50% births (July 11th, s.e. = 7.6) for *Brachyteles*, which occurred during the dry season (*p*-value < 0.001). The mean length of *Lagothrix*’s birth season (52.1 days, s.e. = 18.8) did not vary (*p*-value = 0.214) from the mean length of *Brachyteles*’ birth season (82.3 days, s.e. = 14.4). These analyses were unable to detect significant predictors of the onset or the length of the birth season in *Lagothrix* (Table 1). However, the mid-point of the birth season in this species (date of 50% births) was significantly related to density, the ENSO 3 index, and rainfall: El Niño years and drier conditions (lack of rainfall) were associated with later mean birth dates, while increasing density was associated with earlier mean birth dates (Table 1). Notably, rainfall and the ENSO index were negatively correlated at *Lagothrix*’s site (ENSO 3 index and total annual precipitation, $r = -0.614$, *p*-value = 0.034), while annual temperatures and the ENSO index were positively correlated (ENSO 3 index and mean
annual temperature, $r = 0.689$, $p$-value = 0.013). For *Brachyteles*, I identified significant predictors in nearly all of the birth seasonality models. Density in the current and previous years was the primary predictor of timing of onset of the birth season (annual date of 10% births) and mid-point of the birth season (annual date of 50% births) in this species, while length of the birth season was additionally related to rainfall (Table 1). The overall best-fit model of the timing of the mid-point of the birth season in this species also included mean annual temperatures, higher temperatures were associated with earlier mean birth dates (Table 1). Similar to *Lagothrix’s* site, rainfall and El Niño events were negatively correlated at *Brachyteles’* site (monthly ENSO 3 index and total precipitation, $r = -0.172$, $p$-value = 0.014), while temperatures and El Niño events were positively correlated (monthly ENSO 3 index and temperature, $r = 0.153$, $p$-value = 0.029). Population densities in the current year were associated with an earlier onset of the birth season, and mean birth date, and longer birth seasons for *Brachyteles* (Table 1). The previous year’s population density had the opposite effect on *Brachyteles’* birth seasonality; it was associated with a later onset of the birth season and mean birth dates, and shorter birth seasons.

**Birth rates in relation to birth seasonality**

In *Lagothrix*, offspring production was best predicted by the date of onset of the birth season, the timing of the mid-point of the birth season, and dry season mean temperature (Table 2). For *Brachyteles*, annual birth rates was related to mean annual
temperature (Table 2). In both species, best fit models indicated a later onset of the birth season (for *Brachyteles*) or later mean birth date (for *Lagothrix*) was associated with lower birth rates (Table 2, Figure 2). Higher dry season temperatures were associated with higher birth rates for *Lagothrix* while increased annual temperatures were linked to lower birth rates for *Brachyteles*. Later onsets of the birth season and increased temperatures were associated with El Niño years for *Brachyteles*, while later mean birth dates were associated with El Niño years for *Lagothrix*. Dry season temperatures were not significantly correlated with El Niño years for *Lagothrix’s* site (ENSO 3 index and mean dry season temperature, $r = 0.407$, $p$-value = 0.19). For both *Brachyteles* and *Lagothrix*, the results of population densities on birth rates were conflicting.

**Sex ratio variation**

These results indicated that, for both genera, El Niño years had a direct positive effect on the sex ratio, quantified as the percent of males born in the population (Table 3, Figure 3a & 3b). Increased rainfall had slight positive effects on the percent of males born for *Brachyteles* and *Lagothrix*. A delayed onset of the birth season or mean birth date had weak positive effects on the percent of males born for *Brachyteles*, while results were conflicting for *Lagothrix*. Total population densities had negative effects on percent of male births for both *Lagothrix* and *Brachyteles*. 
Discussion

These analyses documented a clear role of large-scale and local climate in ateline primate reproduction: El Niño years and drier conditions were associated with shifts in the timing of birth seasons (delayed seasons for both genera and shortened seasons for Brachyteles), El Niño years and increased annual temperatures were linked to lowered birth rates, and sex ratios were altered by El Niño years (Table 1, 2, 3). Such effects are notable given the links between global climate change, warming trends, and increased frequencies of droughts and potentially El Nino events (IPCC Climate Change 2007; Zhao & Running 2010). The mean date of birth in *Lagothrix* corresponds to the late wet and early dry season, while that of *Brachyteles* corresponds to the mid dry season; both are times of low resource availability. However, conception occurs during the wet season, a period of high resource availability, and females may need to build up to a minimum level of energy and nutritional reserves before conceiving (Di Fiore & Campbell 2007; Nishimura 2003a; Strier 1996). Therefore, shifts in the onset and length of the wet season caused by dry conditions (or dry El Niño years) could alter the start of the mating season or compromise female condition. As for changes in birth season length, extended birth seasons have been reported to be associated with increased annual rainfall and food availability for *Brachyteles* (Strier 1996; Strier 1999). These results also indicated that rainfall lengthened birth seasons and it is plausible that the dry conditions of El Niño years precipitated shorter birth seasons. Finally, female reproductive history may have
played a role because multiparous *Brachyteles* females are known to give birth more consistently in the late dry season, while primiparous females give birth more frequently at the tail ends of the birth season (Strier 1996). If inexperienced mothers were less likely to mate or have successful pregnancies due to poor physical condition during El Niño years, this change could also cause the later, shortened birth seasons.

Alterations in birth seasonality driven by El Niño years and increased annual temperatures negatively affected ateline primate reproduction. A later onset of the birth season for *Brachyteles* and later mean birth dates for *Lagothrix* were associated with lower annual birth rates (Table 2; Figure 2), and these later birth seasons were promoted in El Niño years. Notably, *Lagothrix*, the more frugivorous genus was more negatively affected by the later birth seasons than *Brachyteles*, the more folivorous genus. Elevated temperatures have been linked to decreased primary productivity, and thus may negatively affect muriqui reproduction through lowered resource levels (Zhao & Running 2010), whereas ENSO conditions could affect ateline birth rates via shifts in reproductive seasonality in several ways. Alterations in climate and potentially resource levels caused by El Niño conditions could result in overall worsened female condition, lowering conception rates or fetal survival. Females in poor condition may breed later, possibly in the attempt to sequester greater nutritional reserves. El Niño conditions have been found to lower fecundity for Milne Edward’s sifakas (Dunham et al. 2010) whereas climatic factors associated with global warming and El Niño years (e.g. elevated temperatures, low rainfall) have been found to negatively affect female condition and reproduction in ateline primates. In addition to the negative effect of elevated temperatures on reproduction found in this study, annual rainfall in previous studies was positively
correlated with howler monkey birthrates and lower adult female mortality, and with food availability (new leaves) and conceptions for *Brachyteles* (Crockett & Rudran 1987b; Strier 1996). Moreover, El Niño events can have negative lagged effects on annual neotropical fruit and flower production (Wiederholt & Post 2009; Wright et al. 1999), and may affect the condition of male atelines and therefore sperm quality (Hernández-López et al. 2002). Alternatively, the change in birth seasonality may lead to conception and gestation in non-optimal times and, consequently, decreased fetal survival. Given that the timing of reproduction may be adjusted so that conception, weaning, or energetically expensive periods coincide with periods of resource availability, shifts in the timing of mating could cause a mismatch between these times, potentially reducing fetal and infant survival rates (Di Fiore & Campbell 2007).

There was also a large role of extrinsic climatic factors and El Niño events on ateline sex ratios at birth. While both genera experienced direct positive effects of El Niño years on the sex ratio at birth (percent of male births) (Table 3, Figure 3a & 3b), the effect was stronger for *Lagothrix*, the more sexually dimorphic genera (Di Fiore & Campbell 2007). These alterations in the sex ratio may be caused by changes in maternal condition during pregnancy due to El Niño conditions. El Niño conditions and altered seasonality could worsen female primate condition, leading to greater female mortality in utero (potentially via faster growth rates of females during certain periods of gestation) or male biases at the time of conception. In addition, the later birth seasons during El Niño years may affect sex ratios (Table 3). The increase in male births during El Niño years may reflect lower survival rates of female fetuses later in the year or could be the result of sex ratio variation due to changes in the timing of the mating (and consequently
insemination) relative to ovulation (Clutton-Brock & Iason 1986). This increase in male
births during El Niño years could be detrimental for declining populations, as it could
slow population growth and recovery (Strier 2000).

This study did not find strong support for the most common hypotheses
explaining primate sex ratio variation. First, these results did not support the Trivers-
Willard hypothesis (Trivers & Willard 1973). El Niño years are associated with a greater
percent of male births and an overall lower birth rate, suggesting females in poor
condition produce more sons. This lack of investment in males may be related to the
weak sexual dimorphism found in these species or potentially the use of the sperm
competition by males (Di Fiore & Campbell 2007). In regards to the local resource
competition hypothesis, this study had conflicting results (Clark 1978). As Brachyteles
and Lagothrix are marked by a high degree of female dispersal and greater male
philopatry, the local resource competition hypothesis predicts that sex ratios biased
towards females would occur under resource competition (Clark 1978; Di Fiore &
Campbell 2007). Assuming that higher population densities are an approximate
indication of resource competition, higher population densities were associated with
greater production of females. However, if El Niño years represent poor conditions (when
female condition or infant survival are lowered) and feasibly greater resource competition
occurs, greater production of males occurs during these times. Finally, for these genera,
the modified local resource competition hypothesis predicts that low ranking mothers
would produce more daughters while high ranking would produce more sons (Silk 1983).
Brachyteles societies are egalitarian, but hierarchical relationships may exist among
Lagothrix females (Di Fiore & Campbell 2007). I could not directly test this hypothesis
as female ranks were not available; however, one prediction from this hypothesis, that the philopatric sex will have higher juvenile mortality rates, was not supported by data from the study populations used here (Nishimura 2003a; Strier 1996; Strier 2005). Factors such as social hierarchies and resource competition do appear to affect sex ratios among other primate species but evidence for their influence among *Lagothrix* and *Brachyteles* in this study is equivocal. It is possible such factors are less important for ateline primates, or that their influence is dependent on conditions such as resource availability and competition, which are ultimately modified by environmental conditions (Hiraiwa-Hasegawa 1993; Kruuk et al. 1999; Van Schaik & De Visser 1990). Therefore, I conclude that these results do lend support for the extrinsic modification hypothesis, in that offspring sex ratios appear to vary with changes in maternal condition during pregnancy caused by extrinsic climatic factors that are not necessarily under adaptive control (Post et al. 1999). However, I cannot eliminate the possibility that alternative hypotheses I did not consider could be influencing sex ratios, for instance, the possibility that differential investment in female offspring during good conditions may lead to overall higher reproductive fitness.

In conclusion, global climatic change could have a significant negative impact on ateline primate reproduction, potentially threatening population viability. Dry conditions, elevated temperatures, and ENSO events negatively affected reproduction and indirectly lowered birth rates via shifts in birth seasonality. I found that climate had a large influence on infant sex ratios, and that El Niño events promoted male births. Given the threatened status of many ateline primate species, continued global warming, increased
drought frequencies, and El Niño events could pose a serious threat to their population recovery and persistence.

Notes

This chapter will be submitted for publication in the Proceedings of the Royal Academy, Series B with Eric Post as the co-author.
Table 4-1. Best-fit model coefficients quantifying the influence of large-scale and local climate on birth seasonality.

<table>
<thead>
<tr>
<th>genera</th>
<th>birth seasonality factor</th>
<th>independent variable*</th>
<th>coefficient ± s.e.</th>
<th>partial correlation coefficient</th>
<th>AICc</th>
<th>multiple $R^2$</th>
<th>adj $R^2$</th>
<th>model $p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>large-scale climate</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>10% birth date</td>
<td>ENSO3</td>
<td>24.750 ± 23.247</td>
<td>0.43</td>
<td>101.527</td>
<td>0.234</td>
<td>-0.072</td>
<td>0.514</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-138.817 ± 130.070</td>
<td></td>
<td>-0.431</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>50% birth date</td>
<td>ENSO3</td>
<td>13.501 ± 9.145</td>
<td>0.551</td>
<td>86.601</td>
<td>0.729</td>
<td>0.62</td>
<td>0.038</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-186.723 ± 51.171</td>
<td></td>
<td>-0.853</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>length of birth season</td>
<td>ENSO3</td>
<td>-18.350 ± 30.980</td>
<td>-0.256</td>
<td>106.123</td>
<td>0.176</td>
<td>-0.154</td>
<td>0.616</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-78.13 ± 173.35</td>
<td></td>
<td>-0.198</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>local climate</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>10% birth date</td>
<td>rain</td>
<td>-0.061 ± 0.067</td>
<td>-0.376</td>
<td>101.944</td>
<td>0.193</td>
<td>-0.13</td>
<td>0.585</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-52.494 ± 118.383</td>
<td></td>
<td>-0.195</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>50% birth date</td>
<td>rain</td>
<td>-0.054 ± 0.019</td>
<td>-0.783</td>
<td>81.897</td>
<td>0.849</td>
<td>0.789</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-133.216 ± 33.818</td>
<td></td>
<td>-0.87</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>length of birth season</td>
<td>drytemp</td>
<td>150.68 ± 91.87</td>
<td>0.591</td>
<td>103.221</td>
<td>0.427</td>
<td>0.197</td>
<td>0.249</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-127.49 ± 126.24</td>
<td></td>
<td>-0.412</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>10% birth date</td>
<td>ENSO3</td>
<td>9.482 ± 1.001</td>
<td>0.302</td>
<td>144.66</td>
<td>0.777</td>
<td>0.712</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-537.155 ± 95.755</td>
<td></td>
<td>-0.871</td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_{t-1}$</td>
<td>493.722 ± 91.363</td>
<td></td>
<td>0.863</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>50% birth date</td>
<td>ENSO3</td>
<td>2.129 ± 9.135</td>
<td>0.073</td>
<td>143.64</td>
<td>0.434</td>
<td>0.265</td>
<td>0.114</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-242.573 ± 92.331</td>
<td></td>
<td>-0.639</td>
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<tr>
<td></td>
<td></td>
<td>$X_{t-1}$</td>
<td>235.357 ± 88.097</td>
<td></td>
<td>0.645</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>length of birth season</td>
<td>ENSO3</td>
<td>-11.990 ± 14.24</td>
<td>-0.257</td>
<td>156.06</td>
<td>0.563</td>
<td>0.432</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>480.44 ± 143.88</td>
<td></td>
<td>0.726</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_{t-1}$</td>
<td>-421.37 ± 137.28</td>
<td></td>
<td>-0.697</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>10% birth date</td>
<td>rain</td>
<td>-0.054 ± 0.058</td>
<td>-0.28</td>
<td>144.8559</td>
<td>0.7742</td>
<td>0.7064</td>
<td>0.001</td>
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<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>-559.306 ± 96.062</td>
<td></td>
<td>-0.879</td>
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<tr>
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<td></td>
<td>$X_{t-1}$</td>
<td>525.240 ± 92.476</td>
<td></td>
<td>0.874</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>50% birth date</td>
<td>yrtemp</td>
<td>-25.02 ± 15.55</td>
<td>-0.454</td>
<td>140.493</td>
<td>0.548</td>
<td>0.413</td>
<td>0.04</td>
</tr>
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<td>$X_t$</td>
<td>-264.84 ± 82.64</td>
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<td>-0.712</td>
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<td>$X_{t-1}$</td>
<td>269.56 ± 79.97</td>
<td></td>
<td>0.729</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachyteles</td>
<td>length of birth season</td>
<td>rain</td>
<td>0.165 ± 0.074</td>
<td>0.577</td>
<td>151.354</td>
<td>0.688</td>
<td>0.594</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>524.946 ± 121.156</td>
<td></td>
<td>0.808</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>$X_{t-1}$</td>
<td>-490.681 ± 116.633</td>
<td></td>
<td>-0.799</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

*variables are listed by large-scale and local climate factors; rain = total annual precipitation, drytemp = mean dry season temperature, yrtemp = mean annual temperature, $X$ = log-transformed total population density

  partial correlation coefficient between the birth seasonality factor and the independent variable listed given the other independent variable(s)
Table 4-2. Best-fit primate coefficients quantifying the effect of climate, birth seasonality, and population density on birthrates.

<table>
<thead>
<tr>
<th>genera</th>
<th>dependent variable*</th>
<th>independent variable†</th>
<th>coefficient ± s.e.</th>
<th>partial correlation coefficient</th>
<th>AICc</th>
<th>multiple R²</th>
<th>adj R²</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lagothrix</td>
<td>Birth rate onset</td>
<td>large-scale climate</td>
<td>-0.002 ± 0.001</td>
<td>-0.793</td>
<td>1.363</td>
<td>0.659</td>
<td>0.522</td>
<td>0.068</td>
</tr>
<tr>
<td></td>
<td></td>
<td>local climate</td>
<td>0.079 ± 0.224</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagothrix</td>
<td>Birth rate meanbirth</td>
<td>large-scale climate</td>
<td>-0.006 ± 0.002</td>
<td>-0.889</td>
<td>13.969</td>
<td>0.84</td>
<td>0.7201</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td></td>
<td>local climate</td>
<td>0.002 ± 0.478</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.136 ± 0.286</td>
<td></td>
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</tr>
<tr>
<td>Brachyteles</td>
<td>Birth rate onset</td>
<td>large-scale climate</td>
<td>-0.0009 ± 0.0009</td>
<td>-0.31</td>
<td>-0.995</td>
<td>0.096</td>
<td>-0.084</td>
<td>0.603</td>
</tr>
<tr>
<td></td>
<td></td>
<td>local climate</td>
<td>-0.061 ± 0.208</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Brachyteles</td>
<td>Birth rate yrtemp</td>
<td>large-scale climate</td>
<td>-0.0006 ± 0.0007</td>
<td>-0.3</td>
<td>-5.398</td>
<td>0.581</td>
<td>0.441</td>
<td>0.042</td>
</tr>
<tr>
<td></td>
<td></td>
<td>local climate</td>
<td>-0.250 ± 0.078</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>0.101 ± 0.157</td>
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</tr>
</tbody>
</table>

*Birth rate is the total annual births per adult female or reproductive adult female
†variables are listed by large-scale and local climate factors; onset = 10% birth date, meanbirth = 50% birth date, drytemp = mean dry season temperature, yrtemp = mean annual temperature, X = log-transformed total population density
  partial correlation coefficient between the birth seasonality factor and the independent variable listed given the other independent variable(s)
Table 4-3. Best-fit primate coefficients quantifying the effect of climate, birth seasonality, and population density on infant sex ratios.

<table>
<thead>
<tr>
<th>genera</th>
<th>dependent variable*</th>
<th>independent variable†</th>
<th>coefficient odds ratio</th>
<th>partial correlation coefficient</th>
<th>AICc</th>
<th>pseudo $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lagothrix</strong></td>
<td>Birth sex ratio</td>
<td>onset</td>
<td>0.995</td>
<td>-0.096</td>
<td>46.927</td>
<td>0.229</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SOI</td>
<td>0.277</td>
<td>-0.531</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>0.001</td>
<td>-0.359</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Lagothrix</strong></td>
<td>Birth sex ratio</td>
<td>meanbirth</td>
<td>1.074</td>
<td>0.377</td>
<td>47.796</td>
<td>0.121</td>
</tr>
<tr>
<td></td>
<td></td>
<td>rain</td>
<td>1.005</td>
<td>0.375</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>12647.059</td>
<td>0.325</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Brachyteles</strong></td>
<td>Birth sex ratio</td>
<td>meanbirth</td>
<td>1.013</td>
<td>0.373</td>
<td>26.76</td>
<td>0.228</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ENSO3</td>
<td>1.327</td>
<td>0.232</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>0.226</td>
<td>-0.345</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Brachyteles</strong></td>
<td>Birth sex ratio</td>
<td>onset</td>
<td>1.008</td>
<td>0.39</td>
<td>26.607</td>
<td>0.314</td>
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<tr>
<td></td>
<td></td>
<td>rain</td>
<td>1.004</td>
<td>0.468</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$X_t$</td>
<td>0.207</td>
<td>-0.391</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Birth sex ratio is expressed as percent of male births of total annual births
†variables are listed by large-scale and local climate factors; onset = 10% birth date, meanbirth = 50% birth date, SOI = the Southern Oscillation Index, rain = total annual precipitation, $X = \log$-transformed total population density
partial correlation coefficient between the birth seasonality factor and the independent variable listed given the other independent variable(s)
Figure 4-1. R-squared values for the nonlinear regressions analyzing birth seasonality for both *Brachyteles* and *Lagothrix*. 
Figure 4-2. Annual birth rates (total annual births per adult female or reproductive adult female) plotted against the onset of the birth season (date of 10% births) for *Brachyteles* or mean birth date (date of 50% births) for *Lagothrix*. 
Figure 4-3. The primate sex ratio at birth (expressed as percent males births of total births) plotted against (a) the Southern Oscillation Index and (b) the ENSO 3 index.
References


Chapter 5

Conclusion

The second chapter examined the effects of anthropogenic disturbance through harvesting and reserve areas on red howler monkey populations and social dynamics via computer population model simulations. The results indicated that hunted populations could decline extensively under moderate to high harvest rates: *Alouatta*’s life history characteristics mean that spatially-uniform high harvest rates are unsustainable. However, if harvest rates were not spatially uniform, and the landscape contained undisturbed reserve areas, the populations persisted. Because ateline primate species of other genera have life history characteristics that make them more vulnerable to harvest than *Alouatta seniculus* (such as later ages of sexual maturation, longer interbirth intervals, and lower biomasses per unit area), these other species would most likely be less resilient to similar levels of harvest intensity (Di Fiore and Campbell, 2007). Empirical studies of hunting corroborate this idea, since populations of *Ateles* and *Lagothrix* were found to be extremely rare or extirpated at hunted sites where *Alouatta* populations persisted (Peres, 1990; Hill and Padwe, 2000; Mena et al., 2000; Thoisy et al., 2009). Also, modeling studies have estimated that maximum sustainable yields are lower while minimum amounts of reserve area necessary for population viability are higher for *Ateles* and
Lagothrix in comparison to Alouatta (Robinson and Redford, 1991; Novaro et al, 2000). Thus, it is likely that the species of the other ateline genera would exhibit greater declines under similar harvest intensity and would require large reserve areas for population persistence due to their larger home ranges and lower biomasses per area.

All red howler simulated populations persisted, even with high harvest rates, if any reserve area remained in the landscape, including small refugia (i.e. 17% of the landscape). This persistence may be attributable to Alouatta’s ability to occupy small home ranges due to their diet of primarily leaves, which are a ubiquitous resource (Di Fiore and Campbell, 2007). Finally, the simulations indicated that howler monkeys most likely had limited dispersal into areas with low population densities. The increase in the reserve population’s size under higher harvest rates was likely due to dispersing individuals moving into reserves, or remaining in un-hunted areas to improve their chances of joining a troop. Although this results could simply be a property of the model, it suggests that recolonization of extirpated areas will be slow.

The model also documented some changes in the social structure of howler monkey troops with hunting mortality such as increased rates of infanticide and decreased birth rates. Although these differences are moderate, they are suggestive of potential disruptions in social structures that may be occurring in hunted wild populations, which to my knowledge, has not been previously studied. The changes in birth rates also allow a comparison between the effects of environmental factors and anthropogenic disturbances on reproduction. Although these results present the birth rates for different ateline species, we can compare the change in Alouatta’s birth rates caused by hunting versus the differences in Lagothrix and Brachyteles’ birth rates due to climatic
variability (Figure 5-1 a, b). These results indicate that the effects of environmental factors and later starting birth season greatly exceed the effects of anthropogenic disturbances on birth rate variation. They also suggest that the role of environmental stochasticity on vital rates exceeds that of demographic stochasticity (as the individual-based model included only demographic stochasticity).

Red howler monkeys, and likely other ateline species, are vulnerable to high rates of mortality caused by humans, such as hunting, due to their long lifespan and slow reproductive rates. However, their ability to inhabit small areas allows for population persistence if a refuge from this source of mortality exists. Such refugia may subsequently act as a source of immigrants for recolonization of extirpated patches, although this may be a prolonged process.

The third chapter examined the effects of climatic variation and the El Niño Southern Oscillation on the dynamics of ateline primates. The results suggested that all the species were adversely affected by El Niño events; however, the nature of the response varied. *Alouatta* likely declined immediately during El Niño events while species of other genera likely declined the year after El Niño events. *Alouatta* may have declined during El Niño years due to shifts in seasonality and alterations in the availability of immature leaves, which are an important resource for howler monkeys (Di Fiore and Campbell, 2007). Also dry conditions during these years may have adversely affected howler monkey populations since rainfall has been found to have positive effects on birthrates and adult female survival (Crockett & Rudran 1987b). The other genera’s declines were likely due to low fruit production occurring one year after El Niño events.
In addition, it appears that *Ateles* and *Lagothrix* had the greatest population declines after El Niño events, *Brachyteles* exhibited intermediate declines, and *Alouatta* had the smallest declines. These variations in population declines may be due to intergeneric differences in diet; greater declines occurred in species with a greater degree of frugivory. Folivory has been posited to be an adaptation for more seasonal environments, and *Alouatta*’s and *Brachyteles*’ ability to utilize this resource during times of food scarcity (as can occur during La Niña events) may benefit these genera (Strier, 1992). Also, the folivorous species may benefit in comparison to the frugivorous species by a lack of pronounced birth seasonality. Howler monkey populations have been noted to have aseasonal reproduction, which is presumably due to their diet and ability to rely on foliage throughout the year (Crockett and Rudran, 1987; Strier et al., 2001). This capacity to breed throughout the year, and presumably better endure annual fluctuations in seasonal resource availability, may have contributed to their likely smaller declines during El Niño events.

In addition, species of frugivorous ateline genera exhibited population synchrony attributable to ENSO events or large-scale temperature anomalies, which poses an additional extinction threat for species of these genera. In contrast, *Alouatta* did not face this additional threat because their population dynamics were asynchronous. The synchrony of the frugivorous species may be linked to their closely related status and morphological and social similarities (Di Fiore and Campbell, 2007). Notably, the effects of El Niño events on climate and phenology are widespread, thus food shortages during these times are likely to occur over large areas. If local resource shortages occur, more frugivorous species may be less detrimentally affected due to their greater mobility.
and ability to forage over larger areas. Finally, the potential for global warming to cause a positive correlation of environmental conditions most likely poses a greater risk for species of *Alouatta* than species of the other ateline genera due to their higher rates of reproduction and the increased vulnerability of highly fecund species to this threat (Wilmers et al., 2007). In sum, the responses of the ateline species varied in both qualitative and quantitative manners to ENSO events and climatic change.

The fourth chapter examined the effects of climatic variation and the El Niño Southern Oscillation on ateline primate reproduction. Species of the two genera tested (*Brachyteles* and *Lagothrix*), both experienced indirect negative and direct positive effects of El Niño years on their reproduction and sex ratios, respectively. Nonetheless, *Brachyteles* appeared to be less sensitive to this disturbance than *Lagothrix*. For instance, the effect of El Niño years on the infant sex ratios of *Lagothrix* was likely much greater than on that of *Brachyteles*. Both genera are marked by a high degree of female dispersal and greater male philopatry; however, the potentially larger effect for *Lagothrix* may be due to other intergeneric differences. This discrepancy could be due to social factors, since *Lagothrix* is more sexually dimorphic than *Brachyteles* and their societies are hierarchical while *Brachyteles*’ are egalitarian, or due to dietary differences (Di Fiore and Campbell, 2007).

In addition, *Lagothrix’s* birth seasons appeared to be shifted more by El Niño years than those of with *Brachyteles*. Furthermore, a later onset of the birth season seems to have greater negative effects on *Lagothrix’s* birth rates and thus, such events would likely have larger impacts on their birth rates. This potentially stronger effect of climatic variability on birth rates and seasonality may be due to *Lagothrix’s* diet. *Lagothrix*, in
contrast to *Brachyteles*, exploits some animal prey, which may be affected during El Niño years, and they also rely heavily on fruit, which undergoes greater seasonal fluctuation in availability than do mature leaves (Di Fiore and Campbell, 2007). In contrast, for the predominantly folivorous howler monkeys, a lack of birth seasonality among some populations has been attributed to their diet, which is hypothesized to release them from the constraints of annual resource seasonality on reproduction (Strier et al., 2001). Strongly seasonal birth peaks may represent the constraints of resource seasonality on maternal condition and hence the timing of conceptions, or the benefits of weaning infants during times of high resource availability (Crockett and Rudran, 1987; Strier et al., 2001). Similarly, while *Brachyteles* does exhibit a birth season, its greater ability to rely on foliage than *Lagothrix* may allow it to endure fluctuations in resource availability. A more even temporal distribution of resources may permit *Brachyteles* females to maintain better physical condition and higher levels of nutritional reserves throughout the year, and provides a consistent resource base for energetically expensive phases of reproduction. Therefore the reproduction of *Brachyteles* may be less affected by shifts in seasonality and any consequent alterations in resource levels during El Niño years. In sum, these results are consistent with the findings of the second chapter, in that the more folivorous primates appeared better able to cope with environmental stress caused by climatic variation and El Niño events. Notably, the nature of their responses did not vary qualitatively but only in a quantitative manner.

In conclusion, the objective of this research was to address the question of which evolutionary strategy, folivory or frugivory, among ateline primates was more susceptible to environmental change and disturbances (including anthropogenic), and how their
responses to these events varied. In general, both strategies were quite sensitive to environmental variation and disturbance, most likely due to the overall slow life history characteristics of these genera. Nevertheless, I tentatively conclude that the folivorous strategy appears to be better adapted to environmental stress, although this finding may be dependent on the nature of the change. Under certain conditions, the frugivorous strategy may be better adapted to environmental variation (for instance, under small-scale perturbations). However, since a folivorous diet may have evolved as an adaptation to more seasonal and variable environments, such a strategy may serve these primates during times of stress (Strier, 1992). Also, the responses of the two strategies in some cases differed only quantitatively (e.g. declines in population size and reproduction), while in others, they varied in a qualitative manner (e.g. population synchrony and timing of population declines). Finally, as ateline species of both the folivorous and frugivorous genera have important roles in seed dispersal in neotropical forests, the extirpation of ateline populations of either evolutionary strategy could have negative consequences for these ecosystems.

Limitations of research

The individual-based population model developed in Chapter 2 uses multiple parameters. In such models, uncertainty in parameter estimation can be attributed to a complete lack of empirical data or small sample sizes. However, a sensitivity analysis
conducted to highlight the most influential parameters for the model output showed that overall, the model was robust to variation in the input parameters. Thus, uncertainty in parameter estimation may not have had a large effect on results. However, I did not conduct a sensitivity analysis assessing the structural components of the model, and whether a simplified version of the model (in terms of social dynamics such as dispersal and turnovers) would vary from the original, more complex model. Such an analysis would be useful as the results from this model were congruent with more general harvest models.

The individual-based model also had other limitations. I simulated a hunting strategy based on known neotropical indigenous harvest patterns to be as realistic as possible; nonetheless, other harvest strategies could be employed. Also, spatial variation in terms of harvesting pressure was incorporated into the model but habitat heterogeneity variation was not included, which could make the model more realistic. Also, as environmental variation was not included, the only form of stochasticity present in the model was demographic. The lack of environmental variation most likely contributed to the logistic growth and stability of the un-hunted subpopulation, and the high level of population persistence that occurred with small reserve areas. Thus, this model examined only the effects of anthropogenic disturbances; however as the other chapters indicated that the role of environmental variation on population dynamics is quite large, incorporating such variation would strengthen the model. In terms of social dynamics, I attempted to adequately simulate all important social interactions within troops. However, because howler monkeys are a social species with complex life histories, it is possible that the model did not capture all of the behavioral dynamics of this species or oversimplified
Some of the rules regarding processes such as dispersal and takeovers. Finally, the model did not include other threats besides harvesting which are likely to affect wild primate populations and could decrease population viability more than indicated by the model.

In the third chapter, the phenology analysis was limited by the availability of phenological data from only one neotropical site (Barro Colorado Island, Panama). Tree and liana phenology records from additional neotropical sites would allow an assessment of whether the cycle of fruit production noted in Panama during El Niño events is a widespread phenomenon, and permit a more precise investigation of the effects of resource availability on the ateline species. In addition, the phenology records documented only fruit, flower, and seed production. Data on leaf phenology would be useful because all of the ateline genera consume some leaves and two of the ateline genera are predominantly folivorous (Di Fiore and Campbell, 2007). Also, local climatic data (such as rainfall) were unavailable for some of the sites; such data would strengthen the analysis of the influences of climate on primate populations. Finally, the study analyzed only one population per ateline species and the measures of population synchrony were on an interspecific level. The analysis of additional populations for each of the four ateline species tested would be desirable to examine intraspecific population synchrony and intraspecific variation in response to climate change.

The fourth chapter also was limited by a lack of additional primate time series data, local climate data, and phenology records. In addition, the sex of some infants was unknown and these individuals were excluded from analyses. However, I have no reason to suspect that one sex was more likely to be identified and thus introduce a bias in the estimated sex ratios. Also, I was limited by the lack of independent measures of adult
female condition, which would be useful to clarify further how El Niño events affect reproduction. Furthermore, although I did not find strong support for the modified local resource competition hypothesis, information on the ranking of woolly monkey adult females would allow a useful assessment of whether the birth rates of high- or low-ranking mothers are differentially affected in El Niño years. Finally, data on sex-specific fetal mortality rates would improve the analyses. For instance, I could only speculate as to whether El Niño events affected the rate of conception or fetal survival and whether survival or conception rates varied between the sexes.

**Future research**

Additional population modeling could investigate the effects of harvesting and reserve areas on other genera of ateline primates. It remains unknown whether these populations would persist under hunting pressure with small reserve areas because they require larger foraging areas and have lower biomasses per unit area than howler monkeys (Rosenberger and Strier, 1989; Di Fiore and Campbell, 2007). Moreover, hunting may not disrupt their social structure to the same extent as observed in Alouatta because behaviors of other ateline genera are not known to include infanticide and male takeovers of troops.

My population model only simulated one hunting strategy that entailed high mortality for adult females. Other hunting strategies (e.g. strategies biased towards males
or juveniles) might result in smaller population declines and how other hunting strategies would disrupt social dynamics is unknown. Other landscape level factors also could be explored with a spatially explicit model. For instance, the spatial configuration, size, or shape of hunted areas could be altered to test their effect on hunting sustainability and population viability. In addition, one could incorporate environmental variation, habitat heterogeneity, and other environmental stressors in the model to represent a more realistic model of neotropical forest dynamics and better assess wild primate population persistence. It would also be useful to validate empirically the trends observed in this study. Hunted and un-hunted howler populations could be compared to observe if rates of infanticides, turnovers, and births varied between the populations. One could document the levels of immigration and emigration of these populations to investigate if decreased immigration and increased emigration of areas with suppressed population densities occurs.

Little research on climate change, primate population dynamics, and primate reproduction has been conducted and more research is needed (Dunbar, 1998; Milton et al., 2005; Dunham et al., 2008). For instance, the effects of climatic variation on the population dynamics and reproduction of other ateline, New, and Old World primate species should be assessed along with levels of population synchrony and potential drivers of synchrony to aid in potential management and conservation strategies. Among Old World primates, folivorous and frugivorous species could be contrasted to examine whether the frugivorous primates are also more strongly affected by climatic variation and assess if this difference in susceptibility is a broad-scale pattern. Also, it would be of interest to explore how primates of other dietary categories, such as omnivores or
frugivore/insectivores, respond to El Niño events and climate change to understand better how dietary factors may influence species’ capacities to respond to environmental change. Studies could be conducted on the effects of El Niño events and climatic variation on adult female condition, fetal, and infant survival, since such investigations would help clarify which juvenile stages are the most susceptible to climatic variability. Lastly, one could reanalyze existing datasets or studies of sex ratio variation that focused on factors such as maternal rank or local resource competition, and investigate if climatic factors had an influence. If so, it would be of interest to know how the influences of these social factors varied according to environmental conditions to gain a better understanding of the role of both these factors on sex ratio variation.

My research assessed the effect of single threats on primates; however, it would be important to examine the effects of multiple threats acting simultaneously on primate species. An investigation of this type would be pertinent because wildlife populations are often faced with several anthropogenic disturbances at the same time such as climate change, habitat destruction, fragmentation, and pollution (Peres, 2001; Di Fiore and Campbell, 2007; Brook et al., 2008). In this scenario, modeling a metapopulation could be a useful approach. For instance, modeling multiple populations would permit an investigation of levels of population synchrony under climate change or the effects of habitat fragmentation. By using this approach to examine habitat fragmentation, one could also assess the viability of the metapopulation depending on the size of the individual populations, degree of fragmentation, and level of dispersal between individual populations. Such a study would allow an assessment of the most pernicious individual threats and also potential synergistic effects.
In conclusion, the subject of environmental variation and primate population dynamics holds many avenues for future research, that is important for conservation decisions and our understanding of ecological systems. Such research is currently needed due to the threatened status of many primate species globally and the rapid change from anthropogenic disturbances occurring in much of their habitat (Di Fiore and Campbell, 2007). Therefore, to aid conservation related efforts, it is relevant to investigate how different life history strategies and primate taxa will be affected by such changes. In addition, more work on other primate species in this area would strengthen the findings of these studies, whereas comparisons of folivorous versus frugivorous diets in other primate and non-primate taxa would illustrate whether these results represent a broader pattern for dietary variation and its evolution. In sum, investigations of the response of various life history strategies and dietary preferences to environmental stress and variation are pertinent for ecological and evolutionary studies and the conservation of these species.
Figure 5-1. (a) Annual birth rates (total annual births per adult female or reproductive adult female) plotted against the onset of the birth season (date of 10% births) for *Brachyteles* or mean birth date (date of 50% births) for *Lagothrix* (b) Annual birth rates plotted against the various amounts of hunted area for *Alouatta*. 
References


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