Evaluating effects of deforestation, hunting, and El Niño events on a threatened lemur

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ARTICLE INFO

ABSTRACT

Madagascar ranks as one of the world's top extinction hotspots because of its high endemism and high rate of habitat degradation. Global climate phenomena such as El Niño Southern Oscillations may have confounding impacts on the island's threatened biota but these effects are less well known. We performed a demographic study of *Propithecus edwardsi*, a lemur inhabiting the eastern rainforest of Madagascar, to evaluate the impact of deforestation, hunting, and El Niño on its population and to re-evaluate present endangerment categorization under the IUCN. Over 18 years of demographic data, including survival and fecundity rates were used to parameterize a stochastic population model structured with three stage classes (yearlings, juveniles, and adults). Results demonstrate that hunting and deforestation are the most significant threats to the population. Analysis of several plausible scenarios and combinations of threat revealed that a 50% population decline within three generations was very likely, supporting current IUCN classification. However, the analysis also suggested that changing global cycles may pose further threat. The average fecundity of lemurs was over 65% lower during El Niño years. While not as severe as deforestation or hunting, if El Niño events remain at the current high frequency there may be negative consequences for the population. We suggest that it is most critical for this species continued survival to create more protected areas, not only to thwart hunting and deforestation, but also to give this endangered lemur a better chance to recover from and adapt to altered climate cycles in the future.

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1. Introduction

While many efforts have been made to elucidate the effects of deforestation and hunting pressures on the viability of wildlife populations, the confounding effects of global climate cycles such as El Niño Southern Oscillations (ENSO) have received relatively little attention. Given the potential role of human-induced climate change in altering the frequency of ENSO events (Fedorov and Philander, 2000; Timmermann et al., 1999), there is a critical need to asses the impact of such factors on the viability of wildlife populations. This requires detailed information on the population characteristics of

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the species concerned, which covers a time-series long enough to capture demographic rates (such as survival and fecundity) and their variability as well as patterns caused by global cycles.

The Milne Edward's Sifaka, (*Propithecus edwardsi*, formerly *P. d. edwardsi*; Mayor et al., 2004) of Madagascar, is an excellent candidate for such analysis because it has been the subject of two long-term studies (Erhart and Overdorff, 1998; Wright, 1995) which together encompass eight El Niño years. Data collected from these studies and recent field surveys (Irwin et al., 2005; Lehman et al., 2005a) provide detailed information on population vital rates and on the sizes and spatial structure of subpopulations. These data provide a suitable case study for evaluating the interacting effects of direct anthropogenic threats, such as deforestation and harvesting, as well as global climate cycles on the viability of small populations.

The high frequency of ENSO in the last few decades has raised questions about how human-induced climate change is affecting or will affect the frequency of ENSO (Fedorov and Philander, 2000; Timmermann et al., 1999). In Madagascar and southern Africa, ENSO events have been documented to cause drought (Thomson et al., 2003) and vegetational changes (Ingram and Dawson, 2005) which may negatively affect wildlife (Gould et al., 1999; Wright, 1999). The prospect of increased ENSO events in Madagascar is daunting given the severity of other anthropogenic threats to its biodiversity.

Madagascar is home to more endemic families and genera than any other conservation 'hotspot' in the world, and high rates of habitat loss and other anthropogenic disturbances severely threaten native species (Myers et al., 2000). Over 80% of the forest cover has already been lost and the populations of many remaining species are small and fragmented (Ganzhorn et al., 2001; Whitmore, 2000). Current deforestation mainly consists of slash-and-burn agriculture for rice cultivation. The government of Madagascar has recently committed to increasing its protected areas from 1.7 million hectares to 6 million hectares (Goodman and Benstead, 2005). With this new opportunity for designing and creating protected areas, knowledge about direct and indirect threats affecting species' viabilities in Madagascar is crucial.

Population viability analysis has become an important tool for assessing such threats. Even for populations with limited data it can be useful for evaluating the relative sensitivity of species to various anthropogenic pressures and for focusing conservation priorities and estimating efficacy of management efforts. However, few such studies have involved primates, a diverse order with over one third of its species threatened with extinction (Mittermeier et al., 2005). In Madagascar, the situation is especially dire, holding more threatened primates than in any other region (Mittermeier et al., 2005). *P. edwardsi* lemurs have been subject of long-term studies providing detailed demographic data useful for such analyses.

The long-term studies of *P. edwardsi* sifakas have shown that they are a long-lived and slowly reproducing lemur (Pochron et al., 2004) that is primarily folivorous (Hemingway, 1998). They live in groups of variable composition (Pochron and Wright, 2003) and are poor dispersers across matrix habitat (Lehman et al., 2006a). *P. edwardsi* are presently catego-

rized by IUCN as endangered based on a suspected past reduction in population size of 50% over the last three generations (39 years) due to decline of suitable habitat (IUCN, 2004). Recent studies have demonstrated that hunting is also a threat (Irwin et al., 2000; Lehman et al., 2006b).

We created population viability models with three stage classes (yearlings, juveniles, adults) with new estimates of demographic parameters of *P. edwardsi* sifakas, based on two long-term studies within Ranomafana National Park. With these models we quantitatively evaluated the effects of deforestation, hunting, and ENSO on their population dynamics to address the following questions. (1) How do direct anthropogenic threats including deforestation and hunting impact the dynamics of the sifaka population? (2) Does the global cycle, ENSO impact demographic rates including survival and fecundity? (3) If so, how does it affect the population trajectory and probability of decline? (4) What are the sensitivities of the population to uncertainty in or possible future changes in the three threats examined here? (5) Do results from these models based on long-term demographic studies, support the endangerment level categorization under IUCN criteria (IUCN, 2001)?

2. Methods

2.1. Species, study area, and population

P. edwardsi occur in the southeastern rainforests of Madagascar (Wright, 1995). They live in variable multimale–multifemale social groups ranging in size from 3 to 9 individuals (Pochron and Wright, 2003). Data for their population analysis came from individuals living within Ranomafana National Park (RNP; 21°15′S, 47°27′E), a 41,300 ha reserve located in south-eastern Madagascar. The park spans elevations of 600–1500 m and its vegetation consists primarily of submontane tropical rainforest (Wright and Andriamihaja, 2002).

Previous studies from RNP have reported age-specific demographic rates for *P. edwardsi* based on lemurs living in the Talatakely trail system (Pochron et al., 2004; Wright, 1995). This site was selectively logged for timber in 1986–1989. The present analysis combined data from the Talatakely study (by PCW) and from a study conducted at Vatoharanana, another site within RNP (by DJO and EME).

In both areas the sifakas were habituated to human observers and could be identified by color markings in the form of neck collars and tags (see Glander et al., 1991 for capture methods). The animals in both studies were routinely surveyed and followed by observers. During the studies all births, deaths and dispersal events were recorded. Deaths were recorded as deaths only when evidence warranted the classification. Wright (1995) and Erhart and Overdorff (1998) provide more complete details of their study methods.

From these long-term studies, demographic rates were estimated from a total of six groups of animals (two in Vatoharanana, and four in Talatakely) which varied in size over time. Both study sites are within the southern parcel of the park. Talatakely is located directly south of the Ranomafana Road (Route National 25), which bisects the park and Vatoharanana is 4 km south of Talatakely. For each area, detailed demographic data was obtained using all individuals

throughout the study periods with a sample size of 76 individuals (48 individuals from 1986–2003 in Talatakely; 28 individuals from 1992–2003 in Vatoharanana). As this was the only long-term data available for this species we applied it to all areas of their range in the model. However, because of the protected status of the lemurs within the two study areas it was assumed that if bias exists in predictions based on location of study subjects, they are most likely to be conservative (lower extinction risk prediction).

Sample sizes of individuals within age classes were small for individual study sites so statistical comparison of survival and fecundity rates was not meaningful (although 95% confidence intervals were overlapping for these vital rates). The average intrinsic rate of growth based on population time-series data (the total number of individuals surveyed in each area, each year), however, suggested very similar growth rates within the two areas (Talatakely, $\lambda = 0.9843$; Vatoharanana, $\lambda = 0.9844$). Data taken from the two sites were therefore combined to enhance sample size for the analysis.

The area of habitat occupied by sifakas was determined in ARC-GIS by overlaying vegetation maps (ANGAP, 2003; Du Puy and Moat, 1998) and previously reported range data taken from Irwin et al. (2005). For the purposes of this study, patches of forest <15 km^2 isolated by ⩾5 km of deforested matrix habitat, were not included in the model because we assumed they were unlikely to hold viable populations in the long term. These patches were also mostly found in areas where hunting is presumed common (Irwin et al., 2000; Lehman et al., 2006b) and the persistence of lemurs in these habitats is questionable. While this simplified our models, it does hold certain assumptions. However, we do not expect that the possible small additional numbers of animals in these patches would significantly influence results of this study given the current demographic characteristics of this population. All major roads bisecting the habitat were noted as they may severely limit dispersal and no observation has been made of this species crossing a road during the 18 years of study. Other work has suggested this species is very unlikely to cross deforested matrix habitat (Dehgan, 2003; Lehman et al., 2006a). Population size was estimated by multiplying our calculated area of occurrence by densities of *P. edwardsi* published by Irwin et al. (2005).

P. edwardsi was estimated to have approximately 4230.8 km^2 of habitat remaining (Table 1). The geographic range of this species is divided by roads or matrix habitat into five distinct areas that results in five separate subpopulations (see Fig. 1). Only 523.5 km^2 of their range consists of protected forest, found in Ranomafana National Park and Andringitra National Park. Although the core-protected area of Ranomafana National Park is 435 km^2 (Wright, 1997), image analysis of recent forest cover maps provided by ANGAP (2003) reveals that 373.67 km^2 is actually forested and available for lemur habitat. The park is divided north and south by a road and small villages, which separate subpopulations three and four. These parcels are each connected to unprotected habitat extending north and south of the park. Andringitra is located south of Ranomafana and occupies the northwestern region of subpopulation 5, containing 150 km^2 of protected forest. The total population of *P. edwardsi* in all areas is estimated to be approximately 28,600 (±4442) individuals. The number of females was calculated for the model assuming a 1:1 sex ratio.

2.2. Population models

Because of the long life span (up to 32 years, King et al., 2005) and limited numbers of marked lemurs, we could not justify using an age-structured model. Therefore, we constructed a female-only, stochastic, three stage population model in RA-MAS METAPOP (Akçakaya, 2002b). The model was based on a transition matrix, A, structured by stages of development. The transition matrix was made up of transition probabilities (vital rates), a_{ij}, representing the average number of individuals that an individual in stage i at time t would contribute to stage j at time $t + 1$. An individual could contribute to stage j through survival and growth to the next stage or through reproduction. For *P. edwardsi* lemurs, even fecundity may be interpreted as a probability since the maximum fecundity of a given female is one.

Transition probabilities were calculated for females of three stage classes (yearlings, juveniles, and adults) (Fig. 2). These life history stages were assigned to ages based on similarities in survival and fecundity values. Yearlings were defined as between 1 and <2 years of age, juveniles were 2–3 years and adults were >3 years. Determining gender of yearlings can be troublesome through observation alone. In cases when gender was unknown, birth and survival rates of female yearlings were estimated under the assumption of equivalent mortality levels among sexes and a 1:1 sex ratio. There was no significant difference in the ratio of males to females surviving to one year of age when offspring with known gender were compared (student's t-test, $t = 0.202$, DF = 17, $p = 0.842$).

| Table 1 – Estimated population sizes of *P. edwardsi* lemurs based on density estimates of Irwin et al. (2005)				
Subpopulation	Total forested area (km^2)	Protected area (km^2)	Estimated # of lemurs	Estimated # of lemurs in protected areas
1	340.85	0	2304 ± 358	0
2	1264.20	0	8546 ± 1327	0
3	573.11	246.25	3874 ± 601	1596 ± 248
4	849.31	127.22	5741 ± 891	860 ± 134
5	1203.30	150.00	8134 ± 1263	1014 ± 157
Total	4230.77	523.47	28,600 ± 4442	3540 ± 550
Numbers indicate the identification of the subpopulation (see Fig. 1).				
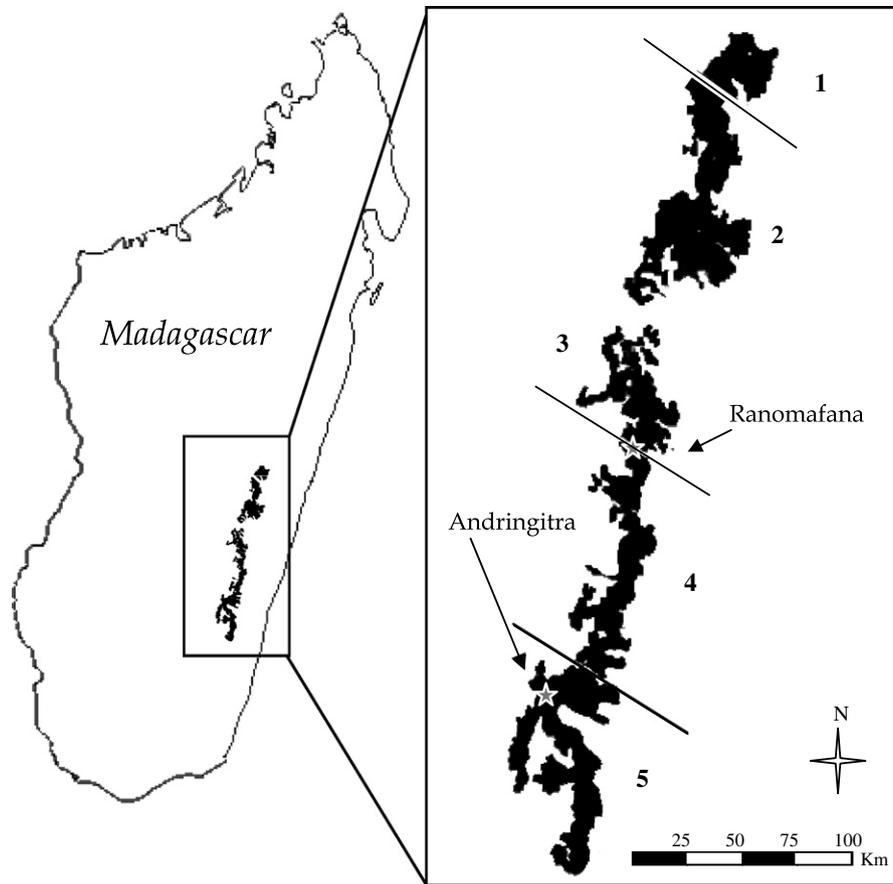
Fig. 1 – Map of the distributional range of the Milne Edwards sifaka. Lines represent roads or other barriers to dispersal. Subpopulations used for this study are numbered.

Fecundity was modeled here as the number of female offspring per adult female surviving to one year of age. This avoids correlational problems associated with using fertility (birth rate per female) and infant survival separately, since there is often a negative relationship between them. For *P. edwardsi*, the interbirth interval for mothers with offspring that survive their first year is greater than for females whose offspring do not survive (Pochron et al., 2004).

Despite the long duration of the study, estimating the average age of first reproduction is difficult as females often emigrate from natal groups before reproducing. Although in only one instance was a female observed from the time of birth to reproduction, the average age of first reproduction has been estimated to be about four years (Pochron et al., 2004). Most juvenile females transfer from their natal group between three and four years of age and are thought to begin breeding shortly after. Accurate age determination of immigrating females is presently not possible but may be achievable in the future with the refinement of techniques presently being developed using teeth casting (King et al., 2005). No three-year-old females were observed to reproduce during the years of 1989–2003 (N = 7).

Weighted measures of transition probabilities (Kendall, 1998) and environmental variance (Akçakaya, 2002a) were used because of the variation in sampling effort (some groups were not monitored all years). Weighted methods reduce bias when variation in sample size results from variation in sampling effort (Akçakaya, 2002a). The weighted transition probabilities were calculated as

$$a_{ij} = \frac{\sum_{t=1}^{Y} N_{it}}{\sum_{t=1}^{Y} X_{jt+1}} \tag{1}$$

where N_{it} is equal to the number of individuals of stage i at time t, and X_{jt+1} is equal to the number of individuals contributed by them to stage j at the next time step. This contribution can be through survival, survival and maturity, or fecundity depending on the transition described. Weighted measures of overall variance were calculated for each transition probability with the following equation as described in Kendall (1998)

$$\text{var}(p) = \frac{\sum_{t=1}^{Y} N_t (p_t - \bar{p})^2}{\sum_{t=1}^{Y} N_t} \tag{2}$$

where p_t is the observed transition rate (vital rate) at time step t, and N_t is the number of individuals at time step t in the stage for which the transition rate is calculated. We then calculated average demographic variance (from Akçakaya, 2002a) as

$$\text{demVar}(p) = \frac{\sum_{t=1}^{Y} p_t (1 - p_t)}{\sum_{t=1}^{Y} N_t} \tag{3}$$

This average demographic variance Eq. (3) was then subtracted from total observed variance Eq. (2) to obtain an estimate of environmental variance.
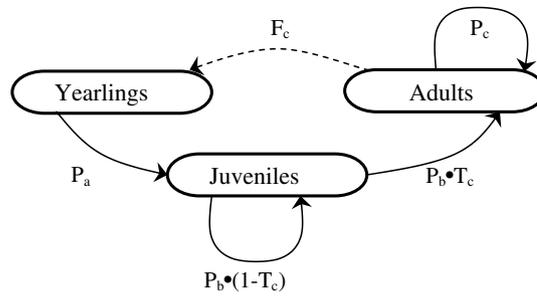
Transition Probabilities

Parameter	Weighted mean	Estimated Environmental Variation
P_a	0.862	0.293
$P_b \bullet (1-T_c)$	0.353	0.120
$P_b \bullet T_c$	0.294	0.100
P_c	0.946	0.032
Normal years		
F_c	0.250	0.028
ENSO years		
F_c	0.086	0.038

Fig. 2 – Schematic representation of life history stages of lemurs. Dashed line represents production of new individuals. Solid line represents movement of individuals within or between stages. P_x is the probability of survival of stage x to the next time step. T_x is the probability of moving to stage x. F_x is the fecundity of stage x.

The juvenile stage had a low sample size and data produced a variance that may have been overestimated (would have resulted in severe truncations). Thus, the environmental variance for juveniles was calculated with the coefficient of variation of the yearling stage, which was assumed to have a more similar response to environmental variability than the adult stage. However, until further data is available, this assumption is a possible source of error in the model. Environmental stochasticity was modeled with a lognormal distribution. RAMAS Metapop uses binomial distributions to model demographic stochasticity (Akçakaya, 2002b).

The following assumptions were implicit in the model. There was no significant correlation between fecundity and survival rates observed so they were modeled independently. Survival rates were modeled as correlated among themselves. Environmental stochasticity was correlated between patches. Because the probability of dispersal across major roads is so low, we assigned an annual probability of 0.001 between adjacent populations separated by roads. We assumed that dispersal between population 2 and 3 was 0 because of the extent of deforested habitat separating the two areas; *P. edwardsi* is very unlikely to cross deforested matrix habitat (Dehgan, 2003).

We performed a variance-stabilized sensitivity analysis (VSS) based on an arcsine square-root transformation (Link and Doherty, 2002) to determine which population parameters had the greatest impact on population growth. VSS works well for ranking the importance of probability based parameters because it does not scale prospective variance in the parameter to the size of mean as a standard elasticity analysis does (Link and Doherty, 2002) but instead uses an arcsine square-root scale, where the absolute magnitude of a change has meaning independent of the value of the parameter. This method has advantages over standard elasticity analysis (deKroon et al., 1986) because it does not rank complimentary rates unequally (i.e. survival and mortality) and is thus more appropriate for model parameters based on probabilities (Link and Doherty, 2002). We calculated VSS as

$$\text{VSS} = \frac{\partial \log \lambda}{\partial [2 \sin^{-1}(\sqrt{\theta})]} = \left(\frac{\sqrt{\theta(1-\theta)}}{\lambda} \right) \frac{\partial \lambda}{\partial \theta} \qquad (4)$$

where θ represents the demographic parameter being tested (Link and Doherty, 2002).

2.3. Population threats

2.3.1. El Niño Southern Oscillations
ENSO was defined as a year that falls during an El Niño event with an annual average standard deviation of Southern Oscillation Index $\leqslant -1.5$ and with at least three continuous months with monthly averages of the same. From 1986 to 2003, there were eight ENSO years (1987, 1991–1995, 1997, and 2002). To examine effects of ENSO, we compared vital rates with non-ENSO years. Fecundity was the only vital rate that demon-

strated an effect of ENSO based on comparisons with 95% confidence intervals (Table 2). Fecundity was found to be 65.6% lower in ENSO years.

This notable difference resulted in a bimodal distribution of fecundity values for the study species. To rectify this, we modeled ENSO separately as a stochastic event in which fecundity was decreased by 65.6% with a certain annual probability. If the parameter in question becomes unimodal when extreme events are excluded, the model can be improved by modeling the extreme events separately (Akçakaya, 2000). Thus, we were able to use a lognormal distribution for simulating stochasticity in fecundity by excluding the fecundity values for ENSO years and modeling them separately. The annual ENSO probability calculated over the time of the study period was 0.389. This may be unusually high so we examined effects of lower ENSO frequency as well (range, 0.14–0.389).

2.3.2. Habitat decline

Deforestation may be the largest threat to the sifaka population and has been estimated to occur in Madagascar rainforest at a rate of about 1.4–4.7% per year (Achard et al., 2002; FAO, 2003), predominantly due to slash-and-burn agricultural practices. In this study, the effects of deforestation (defined here as habitat loss) were modeled by imposing a carrying capacity that declined linearly with habitat area. A ceiling model of density dependence (manifested as a simple upper threshold) was employed for all models since these lemurs are known to have limited habitat, and it is unrealistic for this species to assume exponential growth. Previous work has suggested that ceiling models provide adequate predictions about the probabilities of population decline, and are less prone to underestimate risk than more complex non-linear forms of density dependence (Sabo et al., 2004). The population was assumed to be at carrying capacity at the start of each simulation.

2.3.3. Hunting

Hunting of lemurs in eastern Madagascar is generally for subsistence and for large leaping species such as *Propithecus* often involves hunting with blowguns, darts and slingshots (Lehman and Ratsimbazafy, 2001). Hunting is common in subpopulations north of Ranomafana National Park, (Irwin et al., 2000; Lehman et al., 2006c), but its severity has not yet been quantified. To examine what different hunting levels might have on the population we modeled several scenarios of hunting in these areas. Hunters are most likely to select large individuals (adults), therefore we altered adult mortality by varying degrees to understand the effects of different hunting pressures. Hunting was imposed only in areas north of Ranomafana in areas 1, 2 and 3, where hunting is known to occur (Fig. 1).

3. Results

3.1. Model results

The geometric mean of the finite growth rate of the population estimated from a time-series of numbers of P. edwardsi females of all stages surveyed in Ranomafana National Park between 1987 and 2003 was 0.993. The basic stage-based model which assumed density dependence, static habitat conditions, and ENSO frequency modeled as observed in the data, produced a similar estimate with an average growth rate of 0.997. This result suggests the sifaka population within the protected area is more stable than suggested by a previous demographic study which predicted a quickly declining population (Pochron et al., 2004).

We ranked population parameters in order of importance to population growth trajectories with a VSS sensitivity analysis. The results suggest that the growth rate is most sensitive to changes in adult survival (0.1824), closely followed by fecundity (0.1253). Growth was least sensitive to juvenile and yearling survival (0.0693, 0.0289, respectively) .

No model scenarios demonstrated a risk of extinction for P. edwardsi over the next 100 years but all models suggested the population is at risk of decline. Estimated probabilities of decline risk over the span of three generations (36 years) varied greatly depending on threat category and degree of threat applied to the model (Table 4).

3.2. Effects of ENSO

ENSO had strong effects on fecundity levels, reducing rates by 65.6% on average. All models included ENSO events occurring at various frequencies (Table 4), and when an event occurred in a simulation it reduced fecundity for all populations. Higher frequencies of ENSO events reduced average final population size (Fig. 3a), and increased risk of decline (Table 4). The sensitivity of outcomes to uncertainty in ENSO frequency was low, estimated to maximum of 3.2% difference in the risk of declining by 50% over three generations. When ENSO

Table 2 – Vital rates and 95% confidence intervals observed in data for ENSO and normal years (non-ENSO)

Vital rates	ENSO years (7 years)		Normal years (10 years)	
	Average	95% CI	Average	95% CI
Fecundity	0.086	0.070–0.124	0.250	0.238–0.290
Yearling survival	0.800	0.680–1.000	0.867	0.631–1.000
Juvenile survival	0.667	0.428–1.000	0.667	0.390–1.00
Adult survival	0.942	0.913–1.000	0.950	0.941–1.00

Effect of ENSO was only apparent for fecundity.

Table 3 – Levels of threat used in models to quantify impact on decline risk

Parameter	Level measure	Levels of threat examined		
		Low	Medium	High
ENSO	Annual probability	0.140	0.264	0.389[a]
Deforestation rate[b]	Annual proportion of habitat lost	0.014	0.029	0.047
Hunting rate[b]	Annual proportion of adults taken	0.02	0.06	0.10

a Rate observed in data.
b Only applied to areas outside of national parks.

Table 4 – Model results under various scenarios of declining carrying capacity (K), hunting pressures, and ENSO events				
Parameter	Low	Medium	High	Maximum difference
Probability of 50% decline in three generations (36 years)				
ENSO probability	0.036	0.049	0.068	0.032
Deforestation rate[a]	0.353	1.000	1.000	0.647
Hunting rate[a]	0.104	0.386	0.724	0.620
Combined parameters	0.365 (best case)	1.000	1.000 (worst case)	0.635
Probability of 80% decline in three generations (36 years)				
ENSO probability	0.000	0.000	0.000	0.000
Deforestation rate[a]	0.000	0.000	0.301	0.301
Hunting rate[a]	0.000	0.001	0.003	0.003
Combined parameters	0.000 (best case)	0.030	0.427 (worst case)	0.427

Maximum difference shows the sensitivity of results to uncertainty of each threat. See Table 3 for an explanation of parameter level.
a ENSO set at medium probability level (0.264).

events were modeled at their highest frequencies (equal to frequencies observed in the data), and other risks were held at zero, there was no estimated risk of declining by 80% over the next three generations. However, there was a slight risk of declining below 50% under all ENSO scenarios modeled (Table 4).

3.3. Effects of deforestation

In our models, realistic levels of deforestation of sifaka habitat had a strong effect on the population dynamics (Fig. 3b, Table 4). The recent, most conservative estimated rate of forest loss (1.4% per year, FAO, 2003) resulted in a 35.6% lower final average abundance than when modeled without deforestation (Fig. 3b). The highest estimate of deforestation rate used in the model (4.7% per year, Achard et al., 2002) resulted in 76.7% lower final average abundance than when habitat was modeled as static. Uncertainty in the rate of forest loss was shown to have a strong effect on the decline risk outcomes of the model. At intermediate and higher levels of deforestation the risk of decline by 50% in three generations was 100%. The model employing low values of forest loss resulted in a risk of 35% (Table 4). Under these scenarios the risk of *P. edwardsi* declining by 80% or more in just three generations (to qualify as critically endangered) was low or absent (Table 4). Only when high values were modeled was there any risk of such decline (30.1% chance).

3.4. Effects of hunting

In the models, hunting effects were applied only to *P. edwardsi* populations existing north of Ranomafana National Park because that is where hunting has been documented (Lehman et al., 2006b) and hunting of *P. edwardsi* in the southern areas is restricted due to local taboos (Wright et al., 2005). While all studies of hunting of this species have been qualitative, it is still useful to look at a range of potential hunting values to inform managers of how hunting rates may affect the viability of this species. The highest level of hunting used was 10% of adults harvested annually, which resulted in a 45% lower final average abundance than in models without hunting (Fig. 3c). The sensitivity of the outcome of the model to uncertainty in hunting is great. The difference in probability of a

50% decline over three generations between harvesting 2% versus 10% of adults was 62% (Table 4). High values predicted a 72% chance of 50% decline, while low values predicted 10% chance of decline. Chance of declining by 80% during the same time period was under 1% for all values of hunting intensity modeled.

3.5. Combined threats

The sifakas we studied are likely to be experiencing simultaneously all of the threats we examined separately here. We, therefore, created models with mixed threats to look at probabilities of decline for best and worst case scenarios (Table 4). Best case scenario for mixed-threat models was a 33.8% chance of declining by 50% over the next three generations. Under the worst case scenario, the model predicted a 100% chance of declining by half in three generations. Only the worst case scenario predicted any risk for an 80% decline, which was estimated as 33.1%. The models are most sensitive to uncertainty in hunting rates and deforestation (Table 4).

4. Discussions and conclusions

Although there were limitations to the data set and our model had several implicit assumptions, we were able to make some clear conclusions from this population viability analysis. While obvious anthropogenic disturbances such as deforestation and hunting pressures clearly threaten Madagascar's lemur populations, our analyses also suggest that changes in the frequency of the global cycle of ENSO through climate change could have confounding effects on populations by reducing fecundity. In this study the growth rate of the population of *P. edwardsi*, was found to be sensitive to changes in fecundity, second only to adult survival rates. With increasing global warming, changes in ENSO frequencies and intensities may become more frequent (Fedorov and Philander, 2000) and more of a problem for the population. In this study adult and juvenile mortality was not affected by the global cycles, however, if dry spells continue to increase in frequency and duration, it is possible that all stages will be affected; a scenario which was not modeled here, but which could have devastating impacts on the population.
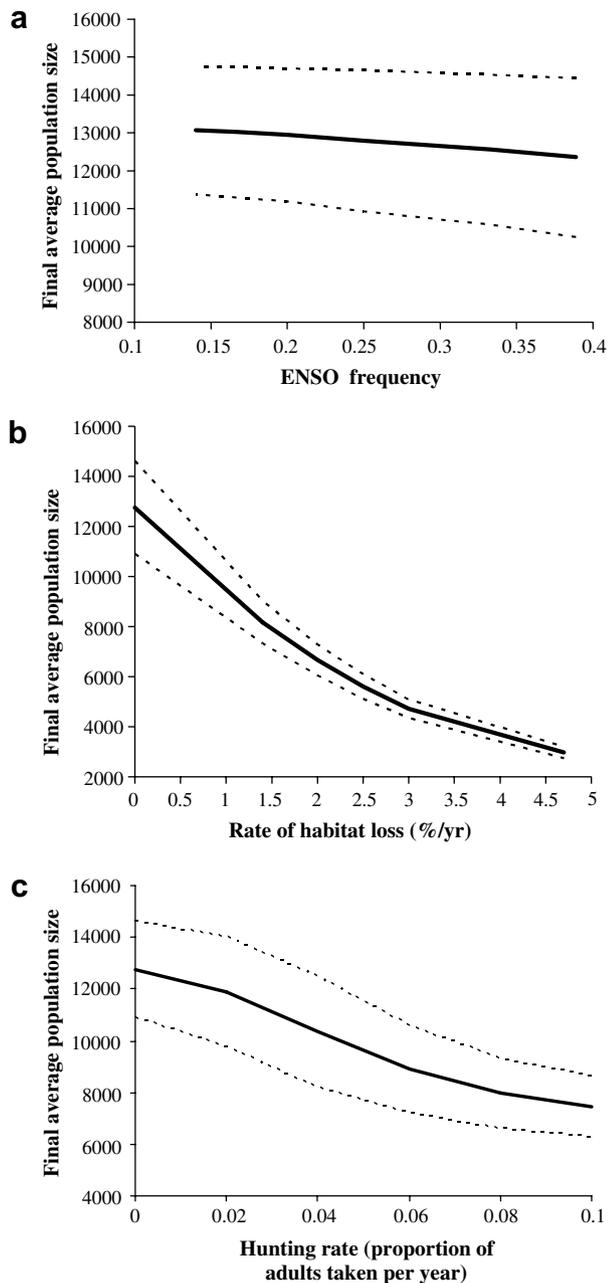
Fig. 3 – The effects of (a) ENSO, (b) deforestation, and (c) hunting on the final average population abundance of females after running models for three generations (36 years). Original population size was 14,000 females.

attributed to malnourishment during nursing and/or weaning stages, particularly for infants of older mothers (King et al., 2005). Malnourishment may also increase predation risks of older weaned infants because it may cause them to become weak and/or separated from the group and thus easy targets for predators (Gould et al., 1999). Drought conditions during ENSO years may also reduce fecundity by lowering fertility rates for *P. edwardsi*. A recent study of several sifaka species found that low body weights of adults were associated with prolonged drought seasons (Lehman et al., 2005b), which may cause reduced birth rates as in other primates (Bercovitch et al., 1999).

While ENSO cycles were shown to have important effects on *P. edwardsi*, the most pressing and obvious threat to the population of *P. edwardsi* sifakas is the present rate of deforestation. The models demonstrate that present rates of forest loss will seriously affect the long-term viability of this population and will likely result in a major decline in population size over just three generations (36 years). If deforestation is not halted, the eventual range of this species will become restricted to the protected areas of Ranomafana and Andringitra National Parks where the population size would be reduced to an estimated 3500 individuals and split among three isolated fragments including the north and south parcels of Ranomafana National Park, and the eastern half of Andringitra National Park. We suggest that under this scenario, the small subpopulation sizes and increased forest edge area, which facilitates further anthropogenic disturbance, would then severely threaten the viability of this species.

Although our model included several subpopulations, we were unable to assign habitat quality to a landscape model because of a lack of data. Habitat quality and elevational constraints are likely to affect survival and fecundities in the subpopulations and are an important area for future study and for refining population models. A closely related lemur species, *Propithecus diadema* has actually been shown to respond to degraded forest and edge with higher densities (Irwin, 2006) presumably because of increased available forage. The effects of this on vital rates of *P. edwardsi* are unclear. While we recognize that habitat quality may have important consequences for source/sink dynamics not examined here, we suspect that variability within the population, unless extreme, will have only a marginal effect on the results of this study. The geographic range maps of this species is also in need of revision and habitat area may already be smaller than presumed here because of habitat preferences and hunting pressures (Lehman et al., 2006c).

A run of the model in its present form does not show any negative effect of the habitat's present level of fragmentation when compared with a model of a similar but unfragmented population. Effects of fragmentation may become more of a problem in the future however, when subpopulations become smaller and/or habitat becomes more fragmented. Understanding how vital rates are linked with habitat quality and threats in the different areas would allow further exploration of this question and may provide different results depending on the source sink dynamics of the population.

Hunting, even at low intensity levels has a strong effect on decline risk of *P. edwardsi* sifakas. Our models demonstrate

ENSO events caused periods of reduced fecundity (averaging 65.6% lower) that may be linked to reduction in precipitation levels. While rainfall data for this species' range available to us was too patchy both temporally and spatially to compare differences between ENSO and non-ENSO years, ENSO is known to cause drought (Thomson et al., 2003) and changes in vegetational indices (Ingram and Dawson, 2005) in Madagascar's rainforests. Rainfall level during critical times of the year has already been shown to affect lemur vital rates (Gould et al., 1999; Jolly et al., 2002), including infant survival of *P. edwardsi* sifakas (King et al., 2005). This effect has been

that the life history characteristics of the sifakas make their population sensitive to perturbations in adult survival rates. Hunting, which is likely to target larger animals, has a strong potential to limit the viability of the population. This result underscores the critical need to quantify poaching of *P. edwardsi* so we can fully understand risks facing their population and implement effective management strategies for protecting their long-term viability.

A survey of lemurs by Lehman et al. (2005a, 2006b) conducted within the range of subpopulation one and two, suggests declines due to hunting may have already occurred in the northern areas. In seven of eight different sites they surveyed, no *P. edwardsi* individuals were sighted. *P. edwardsi* was only observed in the southern-most site. Although village informants explained that sifakas were common in the forests within the past one to ten years, it is possible that heavy hunting from blowguns, darts and slingshots have already dramatically reduced numbers in these areas (Lehman and Ratsimbazafy, 2001).

The presence of hunting in the southern region of the population (populations 4 and 5) has not been documented and was, therefore, not included in the models. In the southern region, hunting of sifakas is known to be taboo, and is not practiced (Wright et al., 2005). However, opportunistic hunting may occur in some areas. Also, attitudes about hunting in the south may change. With a growing economy in and around Ranomafana, immigrants are settling from other areas of Madagascar who may not share the same taboos. For these reasons it is critical to also monitor hunting pressures in this southern region. If hunting occurs in subpopulations 4 and 5 the rates of decline for the population are expected to be even greater than described by our results.

A recent demographic study by Pochron et al., 2004 used age-specific life tables to estimate that the population may be declining with a finite growth rate of 0.9371. If accurate, this level of decline suggests that the population may be facing >80% reduction over the next three generations, qualifying the population to be listed as critically endangered under IUCN criteria (IUCN, 2004). This is in contrast to our study which suggested that the population has nearly no chance of declining by 80% or more over three generations even under the worst case scenario. The demographic study of Pochron et al. (2004), however, was not meant as a population viability study, and the finite growth rate was based on a model with 22 separate age classes. Conclusions drawn from such detailed models with limited data (e.g. some age classes represented by one or a few individuals) are likely to lead to unreliable conclusions with a high level of uncertainty. In species such as *P. edwardsi* where long generation times preclude even long-term studies from supplying sufficient data for age-structured models, it may be appropriate to reduce model complexity to increase sample size for vital rate estimates as we did in our models.

Despite considerable uncertainty in the threat parameters used in our models, several scenarios supported the present IUCN listing of the sifakas as 'Endangered' (Table 4); results suggest a high likelihood of a reduction in population size by 50% or more over the next three generations (IUCN, 2004). Even the best case scenario suggested a probability of declining to this level, of nearly 40%. Given the present data available, we suggest that the listing of this species as 'Endangered' is appropriate for the present time.

Our sensitivity analysis suggested that changes in adult mortality and fecundity will have the largest effects on the population growth rate. We suggest, therefore, a focus on conservation strategies that include reduction of hunting pressures and maintaining intact habitat, which are both important to adult survival and fecundity. Future work leading to the understanding of specific adult mortality factors and their relationship to habitat quality is also important. For *P. edwardsi* it is particularly important to aim conservation strategies that protect adult breeders and quality habitat so they can successfully reproduce. We suggest a critical conservation effort for maintaining their population's continued survival is to increase protected area in the region, not only to thwart hunting and deforestation, but also to give this endangered lemur a better chance to recover from and adapt to altered climate cycles such as ENSO in the future.

Given our preliminary results, we suggest four types of data that would most improve the model and our understanding of the viability of this species. The first two data types needed include better estimates and spatial information about the deforestation rate and hunting rates faced by this species. These parameters resulted in the greatest amount of uncertainty in our model predictions. The third and fourth include dispersal information and data on the relation between habitat quality and its effect on vital rates for each subpopulation. The latter two would allow an exploration of the source/sink dynamics of the population and would provide information on the benefits of corridors or road bridges to link fragmented habitat.

Acknowledgements

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