

The Evolution of Extinction Risk: Past and Present Anthropogenic Impacts on the Primate Communities of Madagascar

Laurie R. Godfrey^a Mitchell T. Irwin^b

^aDepartment of Anthropology, University of Massachusetts, Amherst, Mass., USA;

^bDepartment of Biology, McGill University, Montreal, Que., Canada

Key Words

Lemurs · Extinction · Extirpation · Hunting · Forest fragmentation

Abstract

There are two possible approaches to understanding natural and human-induced changes in the primate communities of Madagascar. One is to begin with present-day and recent historic interactions and work backwards. A second is to begin with paleoecological records of Malagasy primate communities before and immediately following human arrival, and the associated evidence of human and nonhuman primate interactions, and work forwards. On the basis of biological and climatic studies, as well as historic and ethnohistoric records, we are beginning to understand the abiotic and biotic characteristics of Madagascar's habitats, the lemurs' ecological adaptations to these unique habitats, the extent of forest loss, fragmentation and hunting, and the differential vulnerability of extant lemur species to these pressures. On the basis of integrated paleoecological, archaeological and paleontological research, we have begun to construct a detailed chronology for late prehistoric Madagascar. We are beginning to understand the complex sequence of events that led to one of the most dramatic recent megafaunal extinction/extirpation events. Combining the perspectives of the past and the present, we see a complex set of interactions affecting an initially rich but vulnerable fauna. The total evidence refutes any simple, uncausal (e.g. hunting/habitat destruction/climate change) explanation of megafaunal extinctions, yet unequivocally supports a major role – both direct and indirect – for humans as the trigger of the extinction process. It also supports a change over time in the relative importance of hunting versus habitat loss, and in the trophic characteristics of the primate communities in Madagascar.

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Laurie R. Godfrey, Department of Anthropology
240 Hicks Way, University of Massachusetts
Amherst, MA 01003 (USA)
Tel. +1 413 545 2064, Fax +1 413 545 9494
E-Mail lgodfrey@anthro.umass.edu

Introduction

One of the most dramatic of late Pleistocene and Holocene extinction/extirpation events occurred on the island of Madagascar. At the time of human arrival, slightly prior to 2,000 years ago, the primate communities of Madagascar were ecologically and taxonomically diverse. There were 8 families of Malagasy lemurs; 3 (the Archaeolemuridae, Palaeopropithecidae and Megaladapidae) have disappeared completely, and an additional 2 (Daubentoniidae and Lemuridae) have lost their largest-bodied members. Three families – the Cheirogaleidae, Lepilemuridae and Indriidae – do not appear to have lost any species. That humans were the catalysts of extinction is incontrovertible, although debate continues over the specific nature of human impacts. Most, if not all, of the subfossil megafauna were present on the island when humans arrived [Burney et al., 2004]. Many (*Hadropithecus stenognathus*, *Pachylemur* spp., *Mesopropithecus* spp., *Daubentonia robusta*, *Aepyornis* spp., *Mullerornis* spp.) were still present near the end of the first millennium, and some (*Palaeopropithecus ingens*, *Megaladapis* sp., *Archaeolemur* sp. and the Malagasy pygmy hippopotamus) appear to have survived into the second half of the second millennium [Burney et al., 2004]. It is also clear that deforestation and forest fragmentation are proceeding at an exceedingly rapid pace today [Green and Sussman, 1990]. Geographic range reductions, even over the past century, have been documented for certain still extant taxa (especially *Hapalemur simus*) [Godfrey et al., 2004c].

This paper seeks to understand better the anthropogenic impacts on the primates of Madagascar, and how these impacts have changed through time. Were they primarily indirect, through impacts on the environment, or direct (i.e. hunting)? Was there a complex set of interactions? How might we know?

There is a rich literature on the Holocene extinctions in Madagascar (see review by Burney [1999]). Working from the past forwards, Burney et al. [2004] built a chronology of events describing changes in the environments and biota of prehistoric Madagascar. What we add here to previous analyses is a direct comparison of the patterns of species loss in the distant and the more recent past. Our goal is to ascertain whether the pressures on primate communities have remained stable over time. We also ask whether the extinctions resulted in any changes in the ecological characteristics of the primate communities of Madagascar, and if so, how? Do these changes carry implications for the processes of extinction? Do they carry implications for our interpretations of the convergence versus nonconvergence of primate communities of Madagascar with those of other continents?

We assume that (1) the process of extinction is comprised of multiple occurrences of local extirpation, and (2) we can assess processes in the past and in the present by comparing species lost to those that survive either in forest fragments or island-wide. For the past, this means comparing the characteristics (body mass, diet, life history) of extinct and extant taxa. For the present, it means examining species' 'resilience' within the context of habitat fragmentation and loss.

We test three hypotheses. The first two deal with the primary trigger of species loss in Madagascar, and the third deals with the cumulative ecological effect of species loss in Madagascar:

Hypothesis 1: habitat degradation, loss of key resources and fragmentation were the primary triggers of species extinctions or local extirpation. This is the 'indirect effects' hypothesis.

Hypothesis 2: hunting was the primary trigger of species extinctions or local extirpation. This is the 'direct effects' hypothesis.

Hypothesis 3: Madagascar's primate guild structure has remained unaffected by the extinctions. Alternatively, one might posit that Madagascar's primate guild structure has indeed been affected as expected under hypothesis 1, hypothesis 2 or some combination.

To test the first two hypotheses, we must consider the effects of species' characteristics on their vulnerability to different pressures. Which species should be most vulnerable to habitat disturbance and fragmentation? Which species characteristics might increase vulnerability to human hunting?

If species loss is triggered by reduced patch size or habitat degradation (indirect human effects), then we might expect a preferential loss of frugivores or mixed-diet generalists over strict folivores [Johns and Skorupa, 1987]. This is because species whose resources are sparsely or patchily distributed should require larger fragments, and thus display lower tolerance for habitat fragmentation, than those with densely distributed resources. Also, habitat disturbance tends to increase the density and quality of resources for folivores, but reduces it for frugivores. Body size may contribute to species vulnerability, in that larger-bodied species may require more area to maintain viable populations, but the influence of diet should be primary. Selection pressure may result in a diminution of body size of individuals living in fragments.

A primary role for hunting should result in a different pattern of species loss. Theoretically, larger body size and diurnality should increase vulnerability to human predation because these traits cause animals to be easier targets for a cunning, diurnal hunter. Life history characteristics may affect the vulnerability of populations to hunting pressure (though not the probability that they will be hunted in the first place), because species with slow life histories may have low reproductive resilience and therefore less ability to 'recover' from high hunting pressure. Such life history characteristics may covary with body size (but see below). Diet should not predict vulnerability, unless diet affects palatability or 'availability' for human exploitation (e.g. if, because of dietary requirements, individuals range nearer to the edges of forests, or spend more time on the ground or near water). Such variation is complex and no systematic bias is obvious. Under heavy human hunting pressure, selection may result in a diminution of body size and a shift to a faster life history schedule, but such shifts should be independent of habitat fragment size.

We can summarize our predictions by reformulating hypotheses 1 and 2 as follows:

Hypothesis 1 (indirect effects): there are relatively more primate folivores on Madagascar in the present than there were in the past. Diet predicts species loss.

Hypothesis 2 (direct effects): there are relatively more small-bodied, nocturnal species on Madagascar today than there were in the past. Body size and activity rhythm are the best predictors of species loss.

Methods

Analyzing Extant Lemur Vulnerabilities

In order to explore the patterns of vulnerability among extant lemur species, we used census data from a fragmented rainforest landscape [Irwin, unpubl. data]. Nine lemur species (*Propithecus diadema*, *Eulemur fulvus fulvus*, *Eulemur rubriventer*, *Haplemur griseus*, *Lepilemur microdon*, *Avahi laniger*, *Cheirogaleus major*, *Microcebus rufus* and *Daubentonia madagascariensis*) were censused in 27 forest fragments at Tsinjoarivo, eastern Madagascar (19°40.94' S, 47°45.46' E, 1,590 m elevation). The fragments covered an area of approximately 10 km², ranged in size from 0.46 to 228 ha, and the number of fragments occupied by each species ranged from 0 to 17 (0–63%). All fragments were previously part of a continuous forest block, approximately 50 years ago, and there is no evidence that significant heterogeneity in forest structure or composition existed prior to fragmentation [Irwin, unpubl. data]. Disturbance is predicted by fragment size; smaller fragments have significantly fewer large trees, less basal area and less canopy volume [Irwin, unpubl. data]. *Daubentonia* was excluded from analyses because its reclusive habits make it hard to census accurately; feeding traces indicated that this species was present in multiple fragments, yet it was never seen during censuses. Species richness increased with fragment area (SR = 0.852 + 2.048 · log area; adjusted R² = 0.629; p < 0.001). The 'temperature' of the species-fragment matrix as calculated using 'nestedness calculator' software [Atmar and Patterson, 1993] was significantly lower than expected due to chance for a matrix of its size (T = 12.92°, p < 0.001); this statistic varies from 0 (perfect nestedness) to 100 (complete disorder). The lemur communities of fragments are therefore highly 'nested'; as area decreases, fragments contain progressively smaller subsets of the species found in large fragments. This indicates that extirpation of species with decreasing fragment size is not random; rather, species' ecological characteristics render some more resilient to fragmentation than others. Because of this high degree of nestedness, it was possible to use minimum tolerable fragment size (MTFS), defined as the size of the smallest fragment in which a species was detected, as a measure of a species' 'resilience'. MTFS measures species' resilience without regard to the causes of extirpation. Hunting occurs in the study region but is not a major source of food for the region's inhabitants; therefore the causes of extirpation in fragments are likely to be a mixture of direct (e.g. hunting) and indirect (e.g. forest fragmentation and disturbance) anthropogenic impacts. We used individual and multiple regressions of log MTFS on diet composition (using percent feeding time) and log body mass (pooled sexes [Smith and Jungers, 1997; Irwin and Glander, unpubl. data]) to explain the variation in MTFS.

Analyzing the Characteristics of Extinct Species

Paleontologists use a wide variety of tools to reconstruct the characteristics of extinct species [Jungers et al., 2002; Godfrey et al., 2006a, b]. Most important for our purposes here are body mass, activity pattern and trophic characteristics; we also considered available data on life history characteristics. We used a combination of stepwise canonical discriminant function analysis, logistic regression analysis and simple crosstabulation (with a χ^2 test of significance) to analyze patterns in our data.

Our body mass estimates were derived from a study of humeral and femoral cortical cross-sectional areas [Jungers et al., 2005; in press]. Activity patterns (1 = nocturnal, 2 = cathemeral, 3 = diurnal) were reconstructed on the basis of optic foramen and orbit size [Jungers et al., 2002; Godfrey et al., 2006a]. Because such data are not available for the giant aye-aye, we conservatively reconstructed this species as nocturnal (like its congener, *D. madagascariensis*). Our data on giant lemur life histories (molar crown formation times and estimated ages at gingival eruption and weaning) are derived from recent studies of their dental microstructure [Schwartz et al., 2002, 2005; Godfrey et al., 2005, 2006a]. There is reason to believe that most, if not all, giant lemurs were ecologically limited to wooded landscapes and thus vulnerable to such landscape degradation; most were likely facile climbers, despite their large body size [Jungers et al., 2002; Godfrey et al., 2006a].

To reconstruct diet, we relied primarily on dental microwear analysis [Semprebon et al., 2004; Godfrey et al., 2004b]. Following Godfrey et al. [2004b], dietary guilds were identified

using a euclidean distance matrix that summarized the similarities and differences of microwear signatures of 38 species of extant primates and 16 species of extinct lemurs. This allowed us to identify those extant primates with microwear signatures most similar to each of the extinct lemurs; for example, for *Megaladapis edwardsi*, these include *Alouatta palliata*, *Avahi laniger*, *Lepilemur leucopus* and *Lepilemur mustelinus* – all folivores. Closest to *Archaeolemur majori* are *Cebus apella*, *Chiropotes satanas*, *Cacajao melanocephalus* and *D. madagascariensis* – all hard-object processors and seed predators. Omnivory in *Archaeolemur* is confirmed by coprolite analysis [Burney et al., 1997; Godfrey et al., 2005]. The palaeopropithecids show greater variability [Godfrey et al., 2004b], but most are best compared to colobines or, indeed, to extant Indriidae (their closest relatives). Like colobines, living indriids are physiological folivores many of which also consume significant quantities of fruit and seeds [Hemingway, 1996; Yamashita, 2002; Irwin, 2006]. It is likely that most palaeopropithecids were mixed foliage and fruit consumers that also relied on seed predation to varying degrees. *Pachylemur* spp. had diets very like those of extant lemurids. The dietary inferences drawn from low-magnification microwear analysis were largely consistent with those drawn by other investigators using other tools of analysis, such as shearing crest ratios [Jungers et al., 2002], dental microstructure [Godfrey et al., 2005], electron scanning microscopy [Rafferty et al., 2002] and stable isotope analysis [Burney et al., 2004; Godfrey et al., 2005].

To describe diet using a single variable, we selected the scores on the first principal component of a multivariate analysis of microwear signals (values published in Godfrey et al. [2004b]). This axis separates species with ‘coarse’ diets (and with wide scratches and many large pits on their teeth) from those with ‘fine’ diets (with fine scratches and relatively few pits). At the ‘coarse’ end of this spectrum (positive scores) are species processing hard objects (including the extant primates *C. apella*, *C. melanocephalus*, *D. madagascariensis*, *C. satanas* and *Pongo pygmaeus*). At the ‘fine’ end (negative scores) are folivores specializing either on tree foliage or bamboo (including the extant primates *L. mustelinus*, *A. laniger*, *H. griseus*, *Trachypithecus cristatus* and *Hylobates syndactylus*). Species with mixed diets of fruit and leaves fall in the middle of the spectrum, but seed predators tend to have higher scores on this axis than do species that spit seeds or swallow them whole.

Results

From the Present, Working Backwards

Of the variables describing diet composition, the contribution of fruits and seeds to the diet (expressed in terms of percent feeding time) explains more of the variation in MTFs than the contribution of plant vegetative tissues (foliage, shoots and stems). Thus, this measure was used in subsequent analyses.

In simple regressions, the contribution of fruit and seeds to the diet explains more of the variation in MTFs than does body mass (table 1). However, the inclusion of both variables explains the most variation (74.3%). These results suggest that diet is the most important factor governing extant species’ resilience to habitat fragmentation and disturbance; species that eat more fruits and seeds are more vulnerable. Body mass plays a secondary role; for a given diet composition, larger species tend to be more vulnerable. This is not unexpected, as several studies have shown that diet strongly influences species’ vulnerability to habitat disturbance (reviewed in Johns and Skorupa [1987]), but it is largely inconsistent with a scenario in which hunting is the primary cause of local extirpations.

To date, only one other study has examined the incidence patterns of lemur species in a fragmented landscape. Dehgan [2003] also found highly nested patterns of species incidence at Ranomafana but was unable to explain the observed variation

Table 1. Predicting species values for MTFs at Tsinjoarivo

Parameter	Adjusted R ²	Model p	Parameter p	Regression equation
<i>Simple regressions</i>				
log mass, kg	0.142	0.192	–	log MTFs = 0.919 + 0.860 · (log body mass)
Fruit + seeds, %	0.399	0.055	–	log MTFs = 0.057 + 0.020 · FRSD
<i>Multiple regression</i>				
log mass, kg	0.743	0.014	0.030	log MTFs = 0.063 + 0.022 ·
Fruit + seeds, %			0.012	FRSD + 0.966 · (log body mass)

FRSD = Percentage of feeding time devoted to fruit and seeds. Sources: Ganzhorn et al. [1985], Ganzhorn [1988], Harcourt [1991], Glander et al. [1992], Overdorff [1993], Wright and Martin [1995], Atsalis [1999], Tan [1999], Grassi [2001], Irwin [2006].

Table 2. Tolerance of extant species to habitat fragmentation and disturbance in eastern rainforests

Species	Body mass kg	Diet	Tolerance at		Overall resilience
			Tsinjoarivo (high altitude)	Ranomafana (mid altitude)	
<i>Lepilemur</i> spp.	0.97	FOL	high	high	high
<i>Avahi laniger</i>	1.18	FOL	high	high	high
<i>Hapalemur griseus</i>	0.71	FOL	high	high	high
<i>Microcebus rufus</i>	0.04	FR/IN	high	high	high
<i>Cheirogaleus major</i>	0.40	FR/IN	high	high	high
<i>Propithecus</i> spp.	5.05–5.74	mixed	moderate	moderate	moderate
<i>Daubentonia madagascariensis</i>	2.56	hard	moderate	moderate	moderate
<i>Eulemur fulvus</i> spp.	2.22	FR	low	high	variable
<i>Eulemur rubriventer</i>	1.96	FR	low	high	variable
<i>Varecia variegata</i>	3.58	FR	absent	low	poor
<i>Hapalemur aureus</i>	1.55	FOL	absent	low	poor
<i>Hapalemur simus</i>	2.45	FOL	absent	low	poor

FOL = Foliage; FR = fruit; IN = insects. Sources: Glander et al. [1992], Smith and Jungers [1997], Tan [1999], Irwin and Glander [unpubl.], Dehgan [2003].

in terms of fragment characteristics or simple species characteristics. He did, however, find a significant effect of a proxy variable representing behavioral flexibility.

Nevertheless, Dehgan's data on the vulnerability of individual species are largely consistent with the results presented here for the higher-altitude forests of Tsinjoarivo. Indeed, only 3 of the 12 species he studied at Ranomafana are not consistent (table 2). *Hapalemur aureus* and *H. simus* are two species that specialize on the veg-

Table 3. Predicting extinction (0 = extant, 1 = extinct) using logistic regression analysis, ignoring the effect of the best predictor (body size)

Predictor variable	Correct classification, %	p value	Regression coefficients	
			B	constant
Activity	87.5	<0.001	2.622	-7.211
Diet (PCA1)	71	0.06	0.991	0.322

etative parts of rare and patchily distributed bamboos; thus, despite their low reliance on fruits and seeds, their tolerance to fragmentation is quite low. This is likely due to resource patchiness on the regional scale, as these two species are patchily distributed even within large unbroken forest blocks. In contrast, *E. fulvus* devotes 80.6% of its feeding time to fruit [Overdorff, 1993] but is common in mid-altitude forest fragments. Dehgan [2003] attributes this to behavioral flexibility, but it is important to note that this species passes regularly among fragments and the local population's long-term viability has not been assessed. The stark contrast in response between Tsinjoarivo (where *E. fulvus* is extirpated from all but the largest forest fragments) and Ranomafana could be due to altitude-related differences in forest composition. Many frugivores have an altitudinal ceiling above which they cannot live (e.g. *Varecia variegata* [Irwin et al., 2005]). It is possible that Tsinjoarivo's higher altitude causes additional resource stress, which causes lower resilience in fragments. Hunting may also play a role, though there is no indication that *E. fulvus* faces higher hunting pressure at Tsinjoarivo.

From the Past, Working Forward

We began our comparison of extant and extinct species by running a canonical discriminant function analysis to distinguish the two on the basis of three traits: log body mass, first principal component (PCA1) scores for diet and activity rhythm. No cheirogaleids were included in this analysis. Unsurprisingly, when a stepwise procedure was used to enter predictor variables, only body size is entered (log body mass becomes the function). This is because body mass is a perfect discriminator of extinct versus extant species; post hoc classification success using body mass alone is 100% (Wilks' $\lambda = 2.5$; $\chi^2 = 38.2$, d.f. = 1, $p < 0.001$). Forcing additional variables into the function (i.e. entering all explanatory variables simultaneously) only confounds its discriminatory power and reduces classification success. It is noteworthy that scores on PCA1 are entirely uncorrelated with log body mass ($r = -0.056$, n.s.).

Logistic regression analysis was then used to test the ability of diet (as measured by PCA1 scores) and activity rhythm to independently predict extinction (0 = extant, 1 = extinct; table 3). Activity pattern does a better job of predicting species loss than diet, because the extinct lemur species were (apparently) largely diurnal [Jungers et al., 2002; Godfrey et al., 2006a], while only a small percentage of extant species are diurnal. Included in our analysis of activity rhythm were 64 lemur species. The classification success was 87.5% overall, with 85.1% success for extant and 94.1% success for extinct species ($p < 0.001$). If cheirogaleids are omitted from the analysis, clas-

Table 4. Crosstabulation analysis of dietary guilds, extant versus extinct lemurs

Species status		Diet					Total
		hard objects	mixed/ seeds	foliage	fruit/ no seeds	fruit/insects/ gums	
Extant	Observed count	1	4	14	11	17	47
	Expected count	4.4	7.3	13.2	9.5	12.5	47
The present: living species in each diet category, %		2.1	8.5	29.8	23.4	36.2	100.0
Extinct	Observed count	5	6	4	2	0	17
	Expected count	1.6	2.7	4.8	3.5	4.5	17
Extinct species in each diet category, %		29.4	35.3	23.5	11.8	0	100.0
The past: all species in each diet category, %		9.4	15.6	28.1	20.3	26.6	100.0

Analysis by χ^2 test: likelihood ratio = 25.0 (d.f. = 4), $p < 0.001$.

sification success drops marginally (83% overall, 76.7% success for extant species, with no change in the prediction success for extinct species). The p value for the regression changes to 0.002.

The results for the logistic regression of extinction on our proxy variable for diet (PCA1 scores) are less intuitive because extinct species lie at the high and low ends of the axis. We included in this analysis all 31 lemur species for which we have PCA1 scores. This analysis yielded a 71% success rate overall (64.3% for extant species and 76.5% for extinct species). Species with coarser microwear signatures were classified as ‘extinct’, and species with finer microwear signatures were classified as ‘extant’. The significance of PCA1 scores as a predictor of extinction is marginal ($p = 0.06$).

A crosstabulation analysis of diets in extinct versus extant species reveals significant differences (tables 4, 5; see also Godfrey et al. [2004b]). Changes in ecological guild structure from the past to the present reside largely in the loss of hard-object processors (from 9.4 to 2.1%) and mixed foliage, fruit and seed consumers (from 15.6 to 8.5%), along with a concomitant increase in the percentage of insect, gum and fruit consumers (i.e. the cheirogaleids, from 26.6 to 36.2% of the total lemur fauna). The percentage of strict folivores remained roughly constant (from 28.1% in the past to 29.8% today).

Using the set of regressions generated (largely based on anthropoid data) by Milton and May [1976] for predicting individual-based area requirements as a function of diet and body size, one might posit that the individual home ranges of archaeolemurids matched those of much larger-bodied *Megaladapis* (about 20–40 ha for both), because *Megaladapis* is reconstructed as a folivore, and archaeolemurids as reliant on fruit and seeds. Thus, any potential benefit of smaller body size, in terms of higher population density and resilience to hunting pressure, might have been negated by the archaeolemurids’ lower population density brought about by a reliance on rare and patchy food resources. In addition, the archaeolemurids’ increased terrestriality may have also increased their vulnerability to extinction via human hunting.

Some researchers have suggested that extinction risk is more a product of slow reproduction than body size, and that large-bodied species are vulnerable only to the extent they are also slow reproducers [Johnson, 2002]. This is difficult to evaluate for

Table 5. Inferred and observed diet and activity patterns in extinct and extant lemurs

Genus	Species	Diet	Activity rhythm
<i>Hadropithecus</i>	<i>stenognathus</i>	hard	diurnal
<i>Archaeolemur</i>	<i>majori</i>	hard	diurnal
<i>Archaeolemur</i>	<i>edwardsi</i>	hard	diurnal
<i>Archaeoindris</i>	<i>fontoyntii</i>	mixed/seeds	diurnal
<i>Palaeopropithecus</i>	<i>maximus</i>	mixed/seeds	diurnal
<i>Palaeopropithecus</i>	<i>ingens</i>	mixed/seeds	diurnal
<i>Palaeopropithecus</i>	sp. (Anjohibe)	mixed/seeds	diurnal
<i>Babakotia</i>	<i>radofilai</i>	hard	diurnal
<i>Mesopropithecus</i>	<i>dolichobrachion</i>	mixed/seeds	diurnal
<i>Mesopropithecus</i>	<i>pithecoides</i>	foliage	diurnal
<i>Mesopropithecus</i>	<i>globiceps</i>	mixed/seeds	diurnal
<i>Megaladapis</i>	<i>edwardsi</i>	foliage	diurnal
<i>Megaladapis</i>	<i>grandidieri</i>	foliage	diurnal
<i>Megaladapis</i>	<i>madagascariensis</i>	foliage	diurnal
<i>Lepilemur</i>	<i>mustelinus</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>microdon</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>septentrionalis</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>dorsalis</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>edwardsi</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>ruficaudatus</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>leucopus</i>	foliage	nocturnal
<i>Lepilemur</i>	<i>sealii</i>	foliage	nocturnal
<i>Indri</i>	<i>indri</i>	mixed/seeds	diurnal
<i>Propithecus</i>	<i>verreauxi</i>	mixed/seeds	diurnal
<i>Propithecus</i>	<i>diadema</i>	mixed/seeds	diurnal
<i>Propithecus</i>	<i>tattersalli</i>	mixed/seeds	diurnal
<i>Avahi</i>	<i>laniger</i>	foliage	nocturnal
<i>Avahi</i>	<i>occidentalis</i>	foliage	nocturnal
<i>Avahi</i>	<i>unicolor</i>	foliage	nocturnal
<i>Daubentonia</i>	<i>madagascariensis</i>	hard	nocturnal
<i>Daubentonia</i>	<i>robusta</i>	hard	nocturnal
<i>Pachylemur</i>	<i>insignis</i>	fruit/no seeds	diurnal
<i>Pachylemur</i>	<i>jullyi</i>	fruit/no seeds	diurnal
<i>Varecia</i>	<i>variegata</i>	fruit/no seeds	diurnal
<i>Varecia</i>	<i>rubra</i>	fruit/no seeds	diurnal
<i>Lemur</i>	<i>catta</i>	fruit/no seeds	diurnal
<i>Eulemur</i>	<i>mongoz</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>coronatus</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>rubriventer</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>fulvus</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>collaris</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>macaco</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>albocollaris</i>	fruit/no seeds	catheMERal
<i>Eulemur</i>	<i>sanfordi</i>	fruit/no seeds	catheMERal
<i>Hapalemur</i>	<i>simus</i>	foliage/bamboo	catheMERal
<i>Hapalemur</i>	<i>griseus</i>	foliage/bamboo	catheMERal/diurnal
<i>Hapalemur</i>	<i>aureus</i>	foliage/bamboo	catheMERal

Table 5 (continued)

Genus	Species	Diet	Activity rhythm
<i>Microcebus</i>	<i>murinus</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>rufus</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>myoxinus</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>ravelobensis</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>tavaratra</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>sambiranensis</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>griseorufus</i>	fruit/insects/gums	nocturnal
<i>Microcebus</i>	<i>berthae</i>	fruit/insects/gums	nocturnal
<i>Mirza</i>	<i>coquereli</i>	fruit/insects/gums	nocturnal
<i>Phaner</i>	<i>furcifer</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>major</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>medius</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>adipicaudatus</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>ravus</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>crossleyi</i>	fruit/insects/gums	nocturnal
<i>Cheirogaleus</i>	<i>sibreei</i>	fruit/insects/gums	nocturnal
<i>Allocebus</i>	<i>trichotis</i>	fruit/insects/gums	nocturnal

lemurs, because extant lemur life history characteristics do not correlate in a simple manner with body mass [Godfrey et al., 2004a], and available data for extinct lemurs show a similar lack of correlation (table 6) [Godfrey et al., 2006a]. Of giant lemurs, the Archaeolemuridae appear to have had the most prolonged life histories (at least with regard to dental development). The larger-bodied *M. edwardsi* and *P. ingens* show considerably more rapid dental development, contrasting sharply in this manner with like-sized anthropoids [Godfrey et al., 2006b]. It is noteworthy, also, that the frugivorous lemurids showing high vulnerability to habitat loss today reproduce more rapidly than do the more resilient and more folivorous indriids, again regardless of body size [Godfrey et al., 2004a].

Discussion

Patterns of local extirpation in extant lemur communities suggest that indirect human impacts pose the strongest threats. Diet composition explains more of the variation in species' tolerance of fragmentation and disturbance than does body mass. This suggests that the proximate causes of local extirpations lie in the ecological interactions between lemurs and anthropogenically altered habitats, rather than in direct human threats such as hunting (at least in some regions). Although hunting is common in Madagascar [García and Goodman, 2003], it seems possible that the pressures exerted may not be as strong as in the past. It is important to note, however, that hunting pressure varies geographically throughout Madagascar; in some regions it may indeed swamp the effects of habitat fragmentation and alteration.

Table 6. Life history characteristics of extinct lemurs

Species	Body mass (kg)	M1 CFT (days)	M2 CFT (days)	Age at M1 gingival eruption (months)
<i>Hadropithecus stenognathus</i>	35.4		945	
<i>Archaeolemur majori</i>	18.2	522	460	~15–19
<i>Archaeolemur edwardsi</i>	26.5			
<i>Archaeoindris fontoynontii</i>	161.2			
<i>Palaeopropithecus maximus</i>	45.8			
<i>Palaeopropithecus ingens</i>	41.5	221	246	~2–6
<i>Palaeopropithecus</i> sp. (Anjohibe)	25			
<i>Babakotia radofilai</i>	20.7			
<i>Mesopropithecus dolichobrachion</i>	13.7			
<i>Mesopropithecus pithecoides</i>	12			
<i>Mesopropithecus globiceps</i>	11.3			
<i>Megaladapis edwardsi</i>	85.1	380	517	~9–13
<i>Megaladapis grandidieri</i>	74.3			
<i>Megaladapis madagascariensis</i>	46.5			
<i>Pachylemur insignis</i>	11.5			
<i>Pachylemur jullyi</i>	13.4			
<i>Daubentonia robusta</i>	14.2			

CFT = Crown formation time. Sources: Schwartz et al. [2002, 2005], Godfrey et al. [2005, 2006b], Jungers et al. [2005; in press].

Diets rich in fruit and seeds pose a disadvantage for lemurs facing habitat fragmentation and disturbance in two distinct ways. Firstly, frugivorous and omnivorous primates tend to require more area per unit biomass than do folivores [Milton and May, 1976]. Although acceptable foliage is not uniformly distributed, it is *more* uniformly and densely distributed than fruits and seeds, which tend to be highly patchy in space and time; this difference has many effects on social structure and ecology [Janson, 1992]. This leads to lower beginning population densities for frugivores and omnivores, which makes their populations more susceptible to hunting and isolation in forest remnants (folivores are likely to persist longer in fragments due to larger local population size). Secondly, folivores' population density tends to increase following low- or medium-level disturbances such as logging, while frugivores and omnivores tend to undergo population declines [Johns and Skorupa, 1987]. This is likely a direct result of disturbance on the distribution of food resources; young foliage tends to increase in abundance as trees expand to fill light gaps, and pioneer species that invade gaps tend to offer higher-quality browse [Ganzhorn, 1995]. In contrast, fruits preferred by primates tend to be produced by the same large trees that are susceptible to human harvesting; thus, disturbance tends to reduce resource density for species that rely on fruit.

The only possible disadvantage for folivores is that as habitat fragmentation proceeds and forest edges are created, folivores will tend to be attracted to these edges,

as low-level disturbance increases food density there [Irwin, 2006]. Frugivores, in contrast, should tend to be repelled from edges. This may cause folivores to be more accessible to human hunters. However, this depends on the scale of fragmentation; when smaller patches are created, the frugivores' larger home range requirements will tend to increase their accessibility to humans as they will be required to cross between patches.

Our argument that hunting was more important in the past than in the present derives largely from two ecological characteristics (large body size, diurnality) of the extinct lemurs that suggest vulnerability to human hunting. The inference that diet also affected the probability of extinction is weak. Whereas it is true that lemur species with 'coarse' diets were more likely to suffer extinction than strict folivores, it is also true that the largest-bodied strict folivores disappeared alongside the largest-bodied hard-object processors and frugivores/folivores. The notion that diet's role was secondary is bolstered by the simultaneous disappearance of nonprimate, more open-habitat and entirely terrestrial grazers and browsers (pygmy hippopotamuses, elephant birds and giant tortoises), whose large body size and accessibility would have made them attractive as prey.

There is also indirect evidence that hunting provided the initial insult to the megafauna of Madagascar [Burney et al., 2003]. Burney and colleagues documented a sharp decline in the abundance of spores of the coprophilous (megadung) fungus *Sporormiella*, which occurred within several hundred years following human arrival, and which predated a dramatic rise in the abundance of charcoal microparticles in the sediment cores. An apparent crash in megafaunal biomass preceded the evidence of increased frequency or severity of fires. Burney et al. [2003] argue that it was indeed the decline in the biomass of those species responsible, effectively, for keeping the savannas 'mowed' (i.e. largely if not entirely the nonprimate megafauna) that precipitated a change in fire ecology that, in turn, slowly transformed the landscapes of Madagascar.

Paleoecological data also confirm that climate change (aridification at around the time of human arrival) may have contributed to the decline of the megafauna [Burney, 1999]. However, there were regular fluctuations in vegetation during the late Pleistocene prior to the arrival of humans, and none was accompanied by a major extinction event. The approximate time and place of initial successful human colonization is now known; multiple lines of evidence point to human presence as early as 2,350 years BP in the southwest, followed by a slow spread to the interior and the other coasts [Burney et al., 2004]. Humans did not occupy the whole island until around the beginning of the second millennium AD. Finally, there is direct evidence of butchery and other modification of bones and teeth of giant lemurs and other megafauna early in the human period [MacPhee and Raholimavo, 1988; MacPhee and Burney, 1991; Burney, 1999; Perez et al., 2005]. The extinction window was at least 1,500 years long [Burney et al., 2004]. There is no archaeological evidence that the livelihood of the Malagasy people ever depended solely on hunting and gathering [Dewar and Wright, 1993].

With regard to hypothesis 3, we can confirm that the trophic guild structure of Madagascar has changed from the past to the present. Folivores were well represented in the fauna in the past as in the present; the change in guild structure is largely a byproduct of the culling (probably via hunting) of the largest-bodied species (hypothesis 1), with a possible secondary effect of diet (probably related to differing area

requirements of species with different diets). It does not appear to be a simple or direct consequence, however, of the differential vulnerability to habitat loss of more frugivorous versus folivorous species.

Conclusions

Our data support a complex, multicausal explanation of population loss and species extinction, with a shift in the relative importance of hunting and habitat change. Body mass is overwhelmingly the strongest predictor of vulnerability to extinction in Madagascar's primate community. Among individual variables tested, activity pattern is the next-strongest predictor, and diet is the worst predictor. This, combined with the evidence of a precipitous early decline of spores of *Sporormiella*, strongly implicates human hunting as the primary trigger of Quaternary extinctions in Madagascar. Hunting pressure was not sufficiently strong to cause rapid extinction; nevertheless, it appears to have impacted lemurs and other endemic animals over an extended period of time – long after the paleoecological record indicates a change in fire ecology and increased levels of habitat disturbance. The result was a prolonged extinction window with continued loss, well into the second millennium, of large-bodied species, and a change in primate guild structure that is consistent with a primary role for human hunting and a secondary role for habitat loss and fragmentation in the extinction process.

In contrast, an extant lemur community occupying a fragmented landscape at Tsinjoarivo appears to suffer local extirpations determined primarily by dietary characteristics and only secondarily by body mass. It thus appears that contemporary hunting, though still a primary pressure in certain regions, might play a secondary role in present extirpations. Overall, the indirect anthropogenic effects of habitat alteration and fragmentation probably pose the primary threats to lemur survival today.

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