

Historical demography of a wild lemur population (*Propithecus verreauxi*) in southwest Madagascar

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Abstract The human colonization of Madagascar is associated with the extinction of numerous lemur species. However, the degree to which humans have negatively influenced the historical population dynamics of extant lemur species is not well understood. This study employs genetic and demographic analyses to estimate demographic parameters relating to the historical population dynamics of a wild lemur population, Verreaux's sifaka (*Propithecus verreauxi*). The genetic analyses are used to determine whether this population experienced a historically recent (i.e., within the last 2000 years) population bottleneck, as well as to estimate the historical population growth rate and the timing of any changes in population size in the past. In addition, a retrospective demographic analysis is used to determine sources of variation and covariation in the sifaka life cycle and how variation in life-cycle transitions contributes to variation in population growth rate. The genetic analyses indicate that the sifaka population did not experience a recent population bottleneck; however, the historical population growth rate was negative, indicating that the ancestral population size was much larger than the current size. The timing of the ancestral population decline has a point estimate of 2300 years ago, but with large credible intervals: 3611–1736 years ago. This point estimate corresponds with the first evidence for human arrival to Madagascar. Climatic variation has also likely influenced past (and current) population dynamics due to stochastic annual rainfall patterns and climatic desiccation, the latter of which began in southwestern Madagascar around 4000 years ago. Variation in the survival of 2-year-old

animals as well as large adult females makes the largest contribution to variation in population growth rate. In the absence of more explicit models pertaining to historical population dynamics, it is difficult to attribute the negative population growth rate of this species solely to a single factor (e.g., hunting, habitat destruction).

Keywords Habitat disturbance · Hunting · Life-table response experiment · Population growth rate · Sifaka

Introduction

Historically, when humans have colonized a previously unoccupied geographical region, they have often disrupted the endemic biodiversity of that region. Examples include the following: the arrival of humans to New Zealand and the subsequent extinction of the Moa bird and other bird species (Holdaway and Jacomb 2000; Duncan et al. 2002); the colonization of North America via Beringia and the extinction of many vertebrate fauna (Martin 1973; Alroy 2001; Guthrie 2006, but see Grayson and Meltzer 2003); and the colonization of Australia with the subsequent extinction of its megafauna (Miller et al. 1999; Roberts et al. 2001). In some of these cases, the degree to which humans directly caused extinctions is (vigorously) debated (cf. Grayson and Meltzer 2003, 2004; versus Fiedel and Haynes 2004; and Burney and Flannery 2006 versus Wroe et al. 2006). However, the global correlation of endemic population disruption and human colonization certainly suggests that humans often played some sort of negative role in influencing species diversity and population persistence of endemic fauna (Diamond 1989). This is particularly the case for islands. In terms of the recent

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history of human dispersal (i.e., within the last 5000 years), islands are generally the last regions to be colonized by humans. The arrival of humans to islands often results in a disruption of the resident ecosystem and fauna (Paulay 1994). This could be due to human hunting and human-induced habitat disturbance or to competition with introduced nonendemic species that subsequently outcompete or prey upon endemic species. In light of the potential for human disturbance, obtaining historical estimates of demographic statistics from endemic (and extinct) animal populations is useful for understanding whether humans have disrupted these populations.

Madagascar has long been viewed as a paradigmatic example of a location where human-induced extinction is historically evident (Goodman and Patterson 1997). Madagascar has been isolated from mainland Africa for about 150 million years and India for about 90 million years. Thus, many of its endemic mammalian fauna arrived via vicariant dispersal (Yoder and Nowak 2006). These included its carnivores at 24–18 million years and the strepsirhine primates around 66–62 million years (Yoder et al. 2003). The earliest evidence for human arrival to Madagascar is dated to 2300 BP. This evidence is found in the form of human-modified bones, human-introduced plants, a sharp increase in charcoal particles, and additional palynological evidence that indicates habitat disruption (Burney et al. 2004). As Burney et al. (2004) note, the evidence for human occupation was initially sparse but increases dramatically by 1000 AD. After the arrival of humans, numerous lemur species in addition to many nonprimate carnivores went extinct. Remnants of these extinct lemur species, as well as extant species recovered from geological deposits, are known as “subfossil lemurs” because insufficient time has elapsed since their deaths to promote fossilization. The subfossil record of lemur species (e.g., Godfrey and Jungers 2002; Godfrey et al. 2006) gives a picture of the scope of lemur extinctions on Madagascar. Depending on which taxonomy is followed, one third to one fifth of all lemur species went extinct, including all members of 3 speciose families. That said, the extinction of the subfossil lemurs was not so much “an event” as it was “a process.” This process spanned many centuries and was likely multifarious, with human hunting of lemurs, human subsistence practices, fire regimes, and climate change all contributing to the demise of subfossil forms (reviewed in Dewar 2003; Burney et al. 2004; Godfrey and Irwin 2007). Numerous researchers have hypothesized that the extant lemur species were also influenced by human activities. Such influences include hunting, habitat destruction, and the introduction of non-endemic species, which change community structure and thus (potentially) alter resource use, activity period, and social structure (Richard and Dewar 1990; van Schaik and

Kappeler 1996). Lemur habitat destruction continues today and is the major threat to almost all lemur species (Mittermeier et al. 2006).

It is unclear whether extant lemur populations have been impacted by past human activities such as hunting and habitat destruction. Have (some) extant lemur species rebounded from near-extinction due to hunting or habitat destruction in the past? Or were some of these extant species demographically and genetically unaffected by human activities while their extinct counterparts, the subfossil lemurs, were unduly affected? The answers to these questions will provide a historical perspective on lemur population dynamics and can also point to the degree to which extant lemur populations have recovered from genetic and demographic perturbations in the past. Ultimately, extinction is a demographic process in which individual patterns of survival, growth, and reproduction collectively contribute to a negative population growth rate. Thus, to answer these questions, it is necessary to estimate the historical population growth rate for a species as well as at any potential historical time point in which the population changed size. Further, it would be helpful to understand how variation in life-history traits (e.g., survival, growth, and reproduction) contributes to variation in population growth rate. Because demographic approaches focus on individuals, these approaches cannot determine historical patterns of population decline or growth unless historical records of individual life histories are available. Fortunately, genetic methods can recover demographic signatures of population dynamics. Hence, a combination of genetic-based estimation procedures and census-based demographic methods is useful for answering the questions posed above concerning extant lemur populations.

This study tests the hypothesis that historical human activities have negatively influenced the population growth rate of a wild population of lemur, Verreaux’s sifaka (“sifaka” hereafter) (*Propithecus verreauxi*; taxonomy follows Mittermeier et al. 2006) in southwest Madagascar. The study species resides at Beza Mahafaly Special Reserve (BMSR) in southwest Madagascar (ca. 23°30’S, 44°40’E). This study has two objectives: (1) to estimate the historical population growth rate as well as the timing and magnitude of a past population disturbance; and (2) to determine patterns of variation in life-history traits and how these traits contribute to variation in population growth rate. The general prediction to be tested is that the estimates of population parameters generated from genetic data should reflect a negative change within the last 2000 years. Specifically, the population growth rate as estimated from the genetic data should suggest that population sizes were larger in the past than in the present and the timing of the “downturn” in population size should occur during the period soon after humans arrived to

Madagascar. The analysis of life history traits provides contextual data (albeit from recent census data, see “Discussion”) with respect to how life history traits contribute to the population growth rate. This information is useful for determining how variation within and among life history stages contributes to the variation in population growth rate, and thus provides a demographic context for *how* the population grows or shrinks through time. The demographic analysis presented below is known as a retrospective perturbation analysis. It is appropriate in this context in that the results are specific to the observed (i.e., historical) pattern of covariation among life history traits and how this covariation contributes to variation in population growth rate (Caswell 2000).

Motivating these objectives is the fact that a paleontological site close to BMSR has yielded sifaka bones with evidence of butchering (and presumably hunting) (Perez et al. 2005) and that sifaka habitat in this region has been increasingly modified due to livestock introduction, likely introduced into the region in the last 800–900 years (Dewar and Wright 1993). A previous analysis of sifaka population dynamics used microsatellite loci as a means to detect a historical population bottleneck (Lawler 2008) using the program BOTTLENECK (Piry et al. 1999). This analysis found no evidence for a severe population bottleneck; however, the method uses summary statistics (e.g., average heterozygosity) and does not take advantage of the full distribution of allelic variation within a sampled population. Further, the method is unable to produce an estimate of either the historical population growth rate or the timing of a historical change in population size. In this study, three additional methods are used to analyze the historical demography of the lemur population. Used in combination, these methods estimate the historical population growth rate, timing of past changes in population size, and how variation in life history traits has contributed to population growth rate over time.

Methods

Verreaux’s sifaka are gregarious, diurnal, arboreal folivores. Social groups range in size from 2 to 13 animals and consist of relatively equal numbers of adult males and females plus juveniles and offspring. Females tend to be philopatric, whereas males disperse from their natal group upon reaching sexual maturity (Richard et al. 1993). They are characterized by a mating season that runs from mid-January through March. Mating is generally polygynandrous, and females will mate with males of their resident group and adjacent groups. Females give birth about 6 months later (July–August), and infants are weaned by December (Brockman 1999; Richard et al. 2000; Lawler

2007). Sifaka have been continuously studied at BMSR since 1985. Animals are censused periodically and every year (mostly in January or August); individual sifaka are captured using a blow-gun and tranquilizing dart. The anesthetized sifaka are measured, and a range of qualitative information (e.g., parasite load, tooth casts) is also collected on each animal. During the capture process, tissue samples (a 2×2 mm clipping of the top of the ear) and hair samples are taken from each sifaka for genetic analysis. Each animal is fitted with a nylon collar and numbered tag. Ages of yearling animals are known from census information, whereas adult animals are aged from tooth wear calibrated against known ages (see Richard et al. 2002). Captured and processed animals are released and rejoin their social group; they are routinely recensused to monitor their intergroup movements, reproduction, and survival (Lawler et al. 2009).

This study uses two genetic methods (the *M*-ratio test and a Bayesian analysis of historical population dynamics implemented in the program MS-VAR) and one demographic method (a life-table response experiment, or LTRE). These analyses are described below. Data collected on animals from 1985 to 2001 are used to estimate genetic and demographic parameters. Sixteen highly variable sifaka-specific microsatellites were isolated and characterized from this population. Six loci are used in this analysis, as these loci have been used to genotype 444 animals in the population (Lawler et al. 2001). Two genetic approaches are used to determine whether the sifaka population experienced some sort of population decline. The first approach is called the *M*-ratio approach, developed by Garza and Williamson (2001). This method focuses on two factors: allele number (*k*) and total size range of alleles (*r*) at a locus. The method compares the *k/r* ratio derived from empirical data to a ratio simulated to mimic mutation-drift equilibrium. The logic behind the comparison is that during a population bottleneck, *k* is expected to be reduced more quickly than *r* because an allele’s size range is independent of its probability of loss (e.g., 10 alleles spanning 100 base pairs might be reduced to 3 alleles during a bottleneck, but the remaining size range of the 3 alleles could still span 100 base pairs). *M*-ratio tests for the 6 loci were implemented using the software developed by Garza and Williamson (2001). The method estimates the *M*-ratio using 3 input parameters, $\theta (=4 \times N_e \times u)$ where N_e is the effective population size and *u* is the mutation rate, P_s (the average percentage of one-step mutations), and Δ_g (the average size of larger-sized mutations). Theta (θ) was estimated separately for each locus using the program BOTTLENECK (Piry et al. 1999). Following the recommendations of Garza and Williamson (2001) P_s and Δ_g were 0.88 and 2.8, respectively. This analysis was run on the software developed by Garza and Williams, available at

<http://swfsc.noaa.gov/textblock.aspx?Division=FED&id=3298>.

The second genetic approach uses coalescent simulations within a Bayesian framework (Beaumont 1999). This method estimates demographic parameters that indicate changes in population size over time. It assumes that at some point in the past (t_a), a stable population of size N_1 begins to grow or shrink up to its present size (N_0). The model uses a stepwise mutation model in which the rate of mutations (θ) is specified by $2N_0u$, where u is the mutation rate per locus. The method estimates three parameters: the population growth rate (λ), defined as N_0/N_1 , where $\lambda > 1$ indicates an expanding population and $\lambda < 1$ indicates a shrinking population (λ is denoted as r in Beaumont 1999); the time since the population started changing size, defined as t_f ($t_f = t_a/N_0$); and θ . The results below focus on the demographic parameters λ and t_f . Drawing from allele frequency data, estimates for the demographic and genetic parameters are sampled from the posterior distribution of each parameter using Markov Chain Monte Carlo approach (Beaumont 1999). Prior distributions of the parameters were uniformly distributed with a range of -5 to 5 . The population model of growth/decline was assumed to be exponential, as this “forces” much of the rate of population change to occur in more recent times (i.e., when the human impact on lemur habitats is likely to be more severe). Eight runs were analyzed with starting values for λ and t_f of 10, 100, and 1000. Starting values for θ were 1 or 5 for all runs; 50000 update steps were used with a thinning interval of 10000. Longer runs, with 100000 update steps, using similar combinations of starting parameters, produced similar results. The program MS-VAR was used to conduct these analyses (distributed by Mark Beaumont: <http://www.rubic.rdg.ac.uk/~mab>). The first 10% of recorded values from each run was discarded, and the remaining values were analyzed. All runs produced similar results, indicating convergence. Therefore, the results of all 8 runs were analyzed together; thus, the λ and t_f represent composite values from the eight runs (minus the first 10% of values from each run).

The genetic analyses used in this study are prone to some methodological assumptions. The M -ratio test assumes that the mutation model that follows a two-phase pattern, where mutations are mostly single-step mutations but there is some proportion of mutations that are multistep (Di Rienzo et al. 1994; Garza and Williamson 2001). If mutation rates are high and/or mutational steps are large, this can disrupt the signal of a recent bottleneck. Immigration of new alleles into the population can also remove the signature of a genetic bottleneck. This can be circumvented if immigration is sex-biased and the nonimmigrating sex is analyzed. At BMSR, much of the immigration into the reserve is from adult males, but a “female-only”

analysis of genotypes still failed to detect a population bottleneck (Lawler 2008). Busch et al. (2007) provide a general discussion of genetic tests for detecting recent population bottlenecks. Long generation times can also inhibit detection of recent genetic bottlenecks, as long generations times slow the rate of genetic drift and thereby preserves rare alleles across the duration of a bottleneck (Kuo and Janzen 2004; Hailer et al. 2006). The Bayesian analysis is particularly sensitive to the mutation model, and it assumes that microsatellite mutations are single steps. It is also sensitive to population structure if the sampled individuals come from different demes within a metapopulation (Nielsen and Beaumont 2009). The sifaka population is unstructured at the regional level (the animals are structured into social groups, however, but all animals in social groups were sampled in this analysis) (Lawler et al. 2003; Lawler 2008). Recent efforts at developing more explicit and complex models of demographic history are reviewed in Nielsen and Beaumont (2009) but are not examined here.

A demographic analysis is used to determine how variation in survival, growth, and reproduction contribute to variation in population growth rate. For this analysis, a five-stage life cycle for the sifaka was developed following a previous demographic analysis of females from this same population (Lawler et al. 2009). This female-only demographic analysis assumes that female life history schedules largely determine population dynamics. This is generally a safe assumption given that female reproductive success is not limited by adult males and the adult sex ratio just below 1 (Richard et al. 2002; also see Caswell 2001, pp. 570–571). The life cycle (Fig. 1) contains stages pertaining to 1-year-, 2-year, and 3-year-old animals and older who have not reproduced, mothers with yearling, and females who have reproduced in previous years but do not currently have an offspring (i.e., nonnulliparous females). The arrows on the life cycle graph show which transitions are possible from year to year. Coefficients on the arrows specify the average probability of moving within and between stages each year. Because the coefficients capture aspects of survival, growth, and reproduction within the sifaka life cycle, these coefficients constitute life history traits (also called vital rates, Caswell 2001). These coefficients enter into a 5×5 projection matrix (\mathbf{A}), with entries a_{ij} .

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & F_3 & F_4 & F_5 \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_3 & G_5 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \quad (1)$$

Estimates of life-cycle coefficients were calculated using the multistage mark-recapture methods as given in

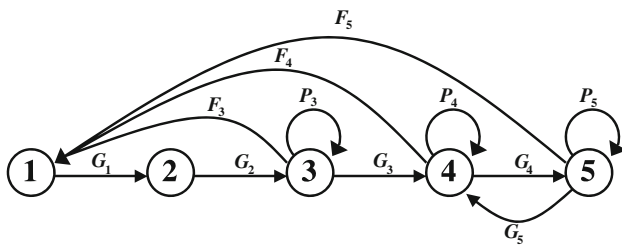


Fig. 1 Life-cycle graph for female sifaka. Arrows denote the biologically possible transitions that animals can make in this life cycle from year to year. Stage 1 corresponds to yearling females; stage 2 corresponds to 2-year-old females; stage 3 correspond to females ages 3 and older who have yet to reproduce; stage 4 corresponds to females with an offspring; stage 5 corresponds to females who have reproduced in the past but do not currently have an offspring

Fujiwara and Caswell (2002). The G_i , P_i coefficients in the projection matrix constitute a survival probability (σ_i) and a conditional transition probability (γ_i); that is, each life cycle transition from year to year requires the survival of the animal during the year and, conditional on surviving that year, making the transition to a subsequent stage. Because reproduction is incorporated as a stage in the life cycle, fertility (the F_i terms) can be calculated from the probabilities of moving into stage 4 from stages 3, 4, and 5. The nonzero fertilities for stages 3 and 5 represent contributions of offspring by individuals that are not reproductive in year t , but reproduce between t and $t + 1$ (Lawler et al. 2009). In the analysis of Lawler et al. (2009), the σ_i and γ_i coefficients were written as either time invariant, time dependent, or as a function of annual rainfall. An additional parameter, the recapture probability (p_i) was also estimated and was written as either time invariant or time dependent. Thirty-two different models were analyzed in which the survival, conditional transition, and/or recapture probability was written as either time invariant, time dependent, or rainfall dependent. Δ -AIC was used to rank-order the models, and five models, all of which had Δ -AIC scores <10 , were used to develop an average model. The average model was developed using Akaike weights (see Table 1 in Lawler et al. 2009). The best model was time invariant and the other four models had either σ_i and/or γ_i as dependent on rainfall. Because four of the five models showed rainfall dependence, the resulting average model also showed rainfall dependence. The average model was used to developed the LTRE (Caswell 1996).

The LTRE analysis is retrospective and determines how variation in life-cycle transitions (i.e., survival, growth, and reproduction) contributes to variation in population growth rate (Caswell 2000). Using 16 years of demographic data, this analysis develops a projection matrix for each year in the analysis. Population growth rate (λ) is calculated from

each of the yearly projection matrices, and the variation in these estimates across years can be broken down into components of (co)variation in the matrix entries using the following equation (this is a first-order approximation; Caswell 2001):

$$V(\lambda) \approx \sum_{ij} \sum_{kl} C(ij,kl) s_{ij} s_{kl} \tag{2}$$

where C represents the covariance between entries a_{ij} and a_{kl} among the projection matrices. The s_{ij} and s_{kl} represent the sensitivities of population growth rate to a matrix entry, holding all others constant (Caswell 2001). The sensitivities are evaluated at the mean projection matrix (\bar{A}), which is the average projection matrix calculated using each of the 16 separate yearly matrices. The covariance matrix is calculated by

$$C = E(\text{vec}(\mathbf{A})\text{vec}(\mathbf{A})^T) - \text{vec}(\bar{\mathbf{A}})\text{vec}(\bar{\mathbf{A}})^T \tag{3}$$

where vec is a function that stacks the columns of a matrix into a single vector, and the superscript T denotes the matrix transpose (note that if the projection matrix has the dimensions $n \times n$, the covariance matrix has the dimensions $n^2 \times n^2$). The matrix of contributions to variation in λ by the vital rates is given by (also $n^2 \times n^2$)

$$V = C \circ (\text{vec}(\mathbf{S})\text{vec}(\mathbf{S})^T) \tag{4}$$

where S is the sensitivity matrix calculated from the mean matrix and \circ denotes the Hadamard product. In short, this analysis provides a historical “glimpse” at the (co)variation in survival, growth, and reproduction as well as how variation in these factors contribute to variation in population growth rate using census data gathered over the last 16 years.

The Bayesian analysis requires an estimate of generation length. Generation length was calculated from a time-invariant matrix population model (and this value did not differ under the average model) given in Lawler et al. (2009). There are many ways to measure generation length (Coale 1972). One prevalent method is to measure the time it takes a population to grow by an amount R_0 , where R_0 is the expected number of female offspring left by a female. That is, for a population of females who start out at age 0, R_0 is the average number of female offspring expected to be born per female parent. The amount of time this process takes is a measure of generation length. When the population growth rate is at or near equilibrium, this measure of generation length is very similar to the average age of mothers of offspring produced by a cohort over their lifetime. It is also equivalent to the average age of mothers of offspring produced by a population of females at a stable age distribution (Charlesworth 1994; Caswell 2001). The sifaka population has a time-invariant and stochastic

growth rate of 0.98 (with confidence intervals encompassing 1), so this measure of generation time used here is similar to the more intuitive measure of using the average age of mothers of a cohort of offspring. Following Caswell (2001) and Charlesworth (1994), generation time (T) is calculated as

$$T = \frac{\log R_0}{\log \lambda_1} \quad (5)$$

Results

The results of the M -ratio analysis are presented in Table 1. The average M -ratio across all loci was 0.929 [standard deviation (SD) = 0.098]. The six loci employed did not reveal significantly low M -ratios. These results indicate that the sifaka population did not experience a historical reduction in population size. The estimates of t_f and λ (both

in Log10) are shown in a bivariate plot (Fig. 2). A non-parametric density fit to the data was fitted using the statistical program JMP 8.0 (SAS Institute, Cary, NC, USA). Ninety-five percent of data cut-mark points fall below the innermost ellipse (Fig. 2). Examination of a three-dimensional density plot (inset, Fig. 2) allowed visual determination of area of maximum density, the maximum values of λ and t_f , indicated by the crosshairs, are -2.156 and -0.128 , respectively (Fig. 2). The negative value of Log10 λ suggests that the past population size was larger than the current size. The antilog point estimates of λ and t_f were estimated to be 0.007 and 0.745, respectively. These point estimates have rather wide credible intervals, given here as antilog values. The 97.5% and 2.5% quantiles for λ were 0.021 and 0.0004, respectively; the same quantile values for t_f were 1.14 and 0.548. The value of t_f depends on population size (N_0) and generation time. The effective size of the sifaka population, taking into account reproductive skew and overlapping generations, is 91 (this is a harmonic mean estimate of four point estimates using the equation from Nunney 1993; Lawler 2010). Thus, $N_0 = 181$, which corresponds to the number of chromosomes. In the sifaka population, R_0 is 0.692 and, using Eq. 5, the generation time calculated from this is 17.5 years (Lawler et al. 2009). This estimate might seem counterintuitively lengthy for a cat-sized animal, but the estimate is very robust and based on 16 years of mark–recapture data from approximately 160 animals. Given a generation length of 17.5, the estimate for when the population first started to decline is $0.745 \times 181 \times 17.5 = 2359$ years ago. Converting the

Table 1 Results of the M -ratio test and significance levels (α is set at 0.05)

Locus	M -ratio	P value
Pvv 1.0	0.917	0.67
Pvv 6.0	0.909	0.28
Pvv 8.0	1.000	0.15
Pvv 14.0	1.000	0.24
Pvv 15.0	0.750	0.16
Pvv 16.0	1.000	0.53

Fig. 2 Bivariate density plot of $\log \lambda$ (population growth rate) and $\log t_f$ (time since population decline, measured in generations). Point estimates for λ and t_f (crosshairs) represent areas of maximum density, as visualized from the three-dimensional plot (inset)

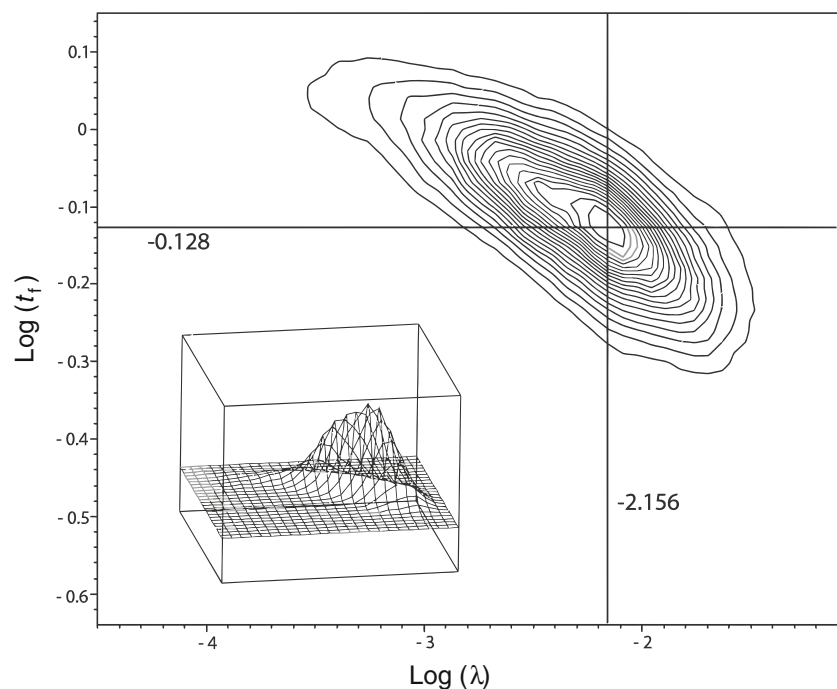
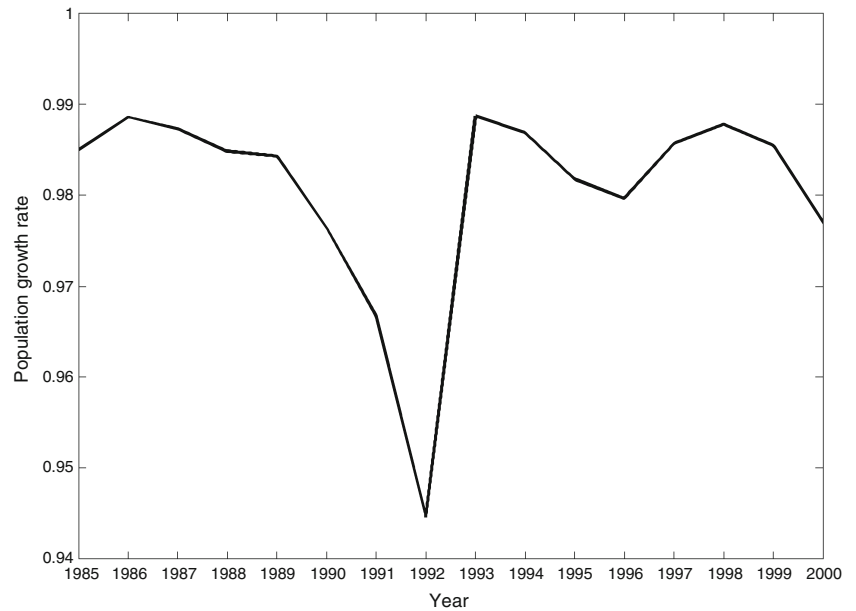


Fig. 3 Population growth rate (λ) calculated from the life-table response experiment (LTRE) plotted against year. The low value of λ for 1992 corresponds to a drought year



credible limit value for t_f to years, the credible limit around this estimate is 3611–1736 years BP.

LTRE results are presented in Figs. 3 and 4. The population growth rate calculated from each of the 16 projection matrices fluctuates between 0.99 and 0.95 across 16 years of census data, suggesting the population is shrinking by about 1–5% per year (Fig. 3), though many of the confidence intervals for these yearly estimates encompass 1. Results from the LTRE analysis are commonly represented as a surface plot (e.g., Brault and Caswell 1993). Figure 4 shows a surface plot of the variation and covariation in the a_{ij} entries (Fig. 4a) as well as surface plot of the contribution these entries make to variation in λ (Fig. 4b). Peaks in the surface plot correspond to entries in the projection matrix. It is possible to find peaks that correspond to entries in the projection matrix by counting inward on the surface plot from the top and left edge and noting this value (see Fig. 4). The recorded value corresponds to the value in the projection matrix (Eq. 1) when all columns are stacked on top of each other to form a 25×1 column (e.g., in the resized projection matrix, the G_2 entry is the 8th value from the top; the P_5 entry is the 25th value in this column). The largest variation among the a_{ij} entries is for transition P_5 , and the largest covariation among entries is for G_2/P_5 (see Fig. 1 for transitions in the life cycle). The contributions of covariances to variation in lambda are life cycle transitions G_2/P_5 , P_3/P_5 , and P_5 .

Discussion

Multiple data sources indicate that human colonization and subsequent population growth and migration in Madagascar

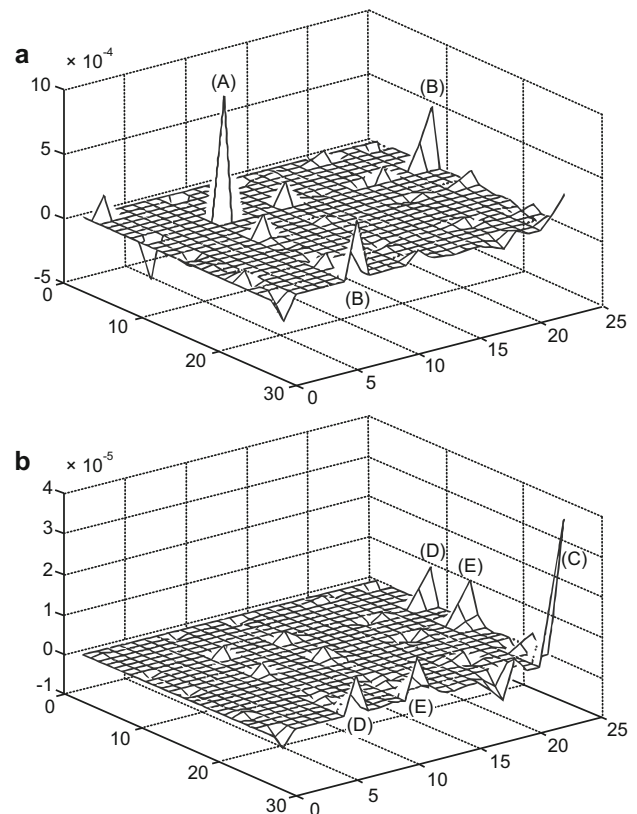


Fig. 4 Surface plots representing (co)variation in life cycle transitions (a) and the contributions these transitions make to variation in λ (b). Each plot is a 25×25 grid whose coordinates correspond to a matrix entry, as described in the text. The vertical axis is measured in units of variance (a) or units corresponding to the variance multiplied by the sensitivity (b). Transition G_2 (A) and transitions G_2/P_5 (B) show the most variation/covariation in the life cycle. The covariation between G_2/P_5 (D), G_3/P_5 (E) and variation in P_5 (C) make the largest contributions to variation in λ

have disrupted the endemic fauna and native ecosystems. This evidence comes from archaeological sites, historical records, paleoecological and paleontological evidence, and comparative socioecological studies of extant lemurs (Richard and Dewar 1990; van Schaik and Kappeler 1996; Goodman and Patterson 1997; Dewar 2003; Mittermeier et al. 2006; Godfrey and Irwin 2007). In addition to these sources, molecular data provide yet another window into historical population dynamics. In this study, two genetic analyses were used to test the prediction that the sifaka population experienced a historically recent population disruption due to human activities on Madagascar. In addition, the LTRE provides insight into how variation in life history transitions influence variation in population growth rate (i.e., fitness, Lande 1982). Although the genetic and demographic analyses operate on different time scales—genetic analysis spans multiple generations, whereas LTRE spans a single generation—they are complementary in their retrospective approach to analyzing past population dynamics (sensu Caswell 2000). In order to understand if and how sifaka population dynamics at BMSR have been historically influenced by humans, it is necessary to review the major sociocultural and economic factors that have potentially influenced sifaka livelihoods.

Several lines of evidence suggest that the sifaka population at BMSR has been historically affected by human hunting and habitat alteration. First, as noted in the “Introduction”, Perez et al. (2005) documented butchery on three lemur species at Toalambiby, a site <10 km from BMSR. Using microscopic analysis, they document cut-marks on bones of extinct species of lemur (*Palaeopropithecus*, *Pachylemur*) as well as one extant lemur, Verreaux’s sifaka (*Propithecus verreauxi*). Both the pattern of butchery and the chronology differ between the extinct and extant species. Radiocarbon dates indicate that the extinct lemur bones date to about 2300 BP, whereas the sifaka bones are much more recent (Burney et al. 2004). Extinct species have bones with more cut marks, whereas extant species have more chop marks—a pattern consistent with present-day preparation/cooking techniques, in which small mammals are basically de-furred, chopped up, and put into a cooking pot. The recovered sifaka bones fall outside the size range of extant sifaka and do not show any evidence of scavenging marks. These observations, as Perez et al. (2005) note, indicate that sifaka were likely targeted for hunting in this region, with a human preference for larger-sized animals. Unfortunately, the magnitude and duration of hunting pressure that this population of animals experienced is unknown.

Second, the sifaka population resides in the regional home of the Mahafaly people. Currently, the region is composed of predominantly Mahafaly people but also includes members from the Antandroy and Tanala cultural

groups. The predominant mode of subsistence in this area is livestock breeding and agriculture. Of relevance to the sifaka population, some subsistence patterns in this area have been associated with the destruction of forests that house sifaka. This is largely due to the use of fires. Fires are intentionally set for slash-and-burn agriculture (*teteke*), to renew grassland vegetation for livestock, and to rid a pasture of harmful livestock parasites (Kull 2003). The practice of *midada* (open roaming of cattle) only exacerbates the increase in grassland at the expense of forests because livestock distribute grass seeds via their dung and fur (Kaufmann and Tsirahamba 2006). Paleoecological and archaeological evidence shows that habitat modification—changes from woody vegetation to grasslands—and the introduction of cattle occurred around 1200 BP in southwest Madagascar (Burney et al. 2004). The evidence for this modification comes in the form of pollen analysis and an increase in the subfossilized spores of *Sporomiella*, a dung fungus that serves as a proxy for megafaunal biomass. Fires (caused by lightning) were a part of the Malagasy landscape prior to the arrival of humans; however, the frequency and pattern of landscape fires has certainly changed with the arrival of humans (Burney 1999; Dewar 2003).

Finally, deforestation and habitat destruction also occurs due to production of charcoal, which is used for cooking. Madagascar’s population has increased dramatically in the last 5 decades and continues to increase (Olson 1984; Cincotta et al. 2000). In turn, the demand for charcoal has also increased, largely due to an increase in urban centers. Cooking over gas fires is not the norm in many urban and rural areas. The increasing demand for charcoal is a major factor with respect to deforestation. As Dewar (2003) notes, the current demand for charcoal relates to cooking and subsistence, whereas charcoal production in the past also related to iron production (cf. Burney 1999). Either way, deforestation due to charcoal production is another factor that negatively influences sifaka livelihoods.

Overlaying these scenarios is a system of informal social institutions that acts to culturally ensure or prevent a particular behavior or activity. In particular, numerous cultural groups in Madagascar adhere to one or more *fady*, or taboos, that culturally protect certain fauna and flora (Jones et al. 2008). In and around BMSR, it is *fady* to kill or harm any ring-tailed lemur (*Lemur catta*) or sifaka. As documented in Loudon et al. (2006), Mahafaly lore states that a jealous dispute between two wives of a Mahafaly man led to their violent and instantaneous transformation into a ring-tail and sifaka, respectively. Thus, according to Mahafaly tradition, these species should be accorded protection and respect because they are derived from humans, and harming them will bring bad luck. A detailed study of *fady* with respect to conservation ethics showed that they can sometimes erode due to changing economic conditions

and the immigration/emigration of different cultural groups (Lingard et al. 2003; Jones et al. 2008). This is important because the local population at BMSR is a mixture of different cultural groups and thus the protective *fady* against diurnal lemurs might have eroded over the past few decades (Loudon et al. 2006); recently, lemur hunting has occurred just outside the protected reserve (A. Axel, personal communication).

In light of the factors that led to sifaka extirpation—hunting and habitat destruction—it is expected that the sifaka population will show a historical decline in numbers. Whereas *fady* may offer some protection against hunting, it is unclear when the *fady* originated and the degree to which it is completely obeyed around BMSR (currently, it should be noted that the sifaka population within the reserve is protected largely due to a combination of national law, *fady*, and the hard work of local scientists and conservationists; however, the reserve was only formally established in 1984). The goal of this study was to bring genetic analyses as another source of evidence in understanding the historical population dynamics of a lemur species in this region. The results of the *M*-ratio test indicate that there was no recent and severe population bottleneck in the sifaka population. This result is congruent with a previous study that found no evidence of a recent population bottleneck (Lawler 2008), using the program BOTTLENECK (Piry et al. 1999). The results of Bayesian analysis suggest that the sifaka population was larger in the past than in the present. Under an exponential model of population decline, where most change in size is forced to occur in recent times, the timing of the decline began just before 2300 BP. This value only slightly predates the earliest radiocarbon dates corresponding to a human presence at Toalambiby in southwest Madagascar (Burney et al. 2004). Also, as noted above, additional habitat modification occurred around 1200 BP, corresponding to the introduction of cattle to southwest Madagascar. That said, the credible intervals for t_f , pertaining to the timing of population decline range from 3611 BP to 1736 BP. Thus, the upper limit of this interval predates any evidence for human activities on Madagascar. The point estimate of λ suggests a considerable reduction in population size of almost two orders of magnitude; it is important to note, however, that the credible intervals around λ are large, although they never indicate positive growth rate. Results of the Bayesian analysis, when coupled with results of the *M*-ratio test and previous results (Lawler 2008), suggest the following: the sifaka population was larger in the past than today, but there was no recent drastic population bottleneck strong enough to be registered in the genotypes of extant sifaka; only a long-term population decline was detected. In essence, the *M*-ratio analysis, coupled with the previous analysis of a historical population bottleneck (Lawler 2008), rule out a severe

population bottleneck, but the Bayesian analysis suggests a population decline beginning around 2300 BP. It is likely that humans played at least some role in this decline due to the archaeological and historical evidence pertaining to hunting and habitat destruction in this region over the past centuries. The demographic pattern of a long-term population decline without strong evidence for a recent population bottleneck is fairly common among some vertebrate populations (cf. Storz et al. 2002; Lucchini et al. 2004; Aspi et al. 2006; Zhang et al. 2007), and the methodological implications of this pattern are explored by Busch et al. (2007).

It is also important to consider nonanthropogenic factors that can influence long-term population decline. Using archeological and palynological evidence, Burney (1993) documents a shift in the habitat and floristic composition of forests in southwest Madagascar. In particular, there is shift in habitat from a more humid, woodland mesic forest to a savanna-type habitat characterized by more arid conditions. This shift began around 3000–4000 years ago (Burney 1993; Burney et al. 2004; also see Virah-Swamy et al. 2009 for habitat changes in southeast Madagascar). The value for the upper credible limit for t_f is 3610 BP and thus falls within the estimated period of climatic change documented by Burney (1993). To the extent that sifaka population numbers are entrained to habitat size and habitat type, reduction and/or fluctuations in habitat can negatively influence sifaka population dynamics and ultimately reduce effective population size (Vucetich et al. 1997). Population dynamics of sifaka are also influenced by the hypervariable rainfall environment of southwest Madagascar (Dewar and Wallis 1999; Dewar and Richard 2007). Dewar and Richard (2007) document that Malagasy mammals are characterized by an extreme fastness or slowness of life history schedules, which they link to this pattern of stochastic rainfall. In this region, stochastically occurring droughts can drastically reduce sifaka population size, as documented for the drought in 1992 (Richard et al. 2002). The effects of the 1992 drought can be seen with respect to the very low value of λ for that year (Fig. 3). If these droughts are a regular but stochastic occurrence, they can lead to delayed life history schedules, whereby a population spends most of its time experiencing negative growth rates (punctuated by positive growth rates—see Fig. 1 in Caswell 1982). Due to this, individual animals are selected to live long lives and delay reproduction (Caswell 1982), a pattern empirically documented by Richard et al. (2002); the relatively long generation time of sifaka is also likely linked to the stochastic rainfall pattern (Lawler et al. 2009).

Population growth or decline is determined by individual schedules of survival, growth, and reproduction. Therefore, it pays to determine not only whether a population is growing or shrinking but also which life history

traits make the largest contribution to changes in population size or population growth rate. Similar to the Bayesian analysis, the LTRE is a retrospective analysis that looks at (co)variation in life-cycle transitions and how this variation contributes to variation in population growth rate. As noted by Caswell (2000, p. 621), a retrospective analysis, “...looks back at an observed pattern of vital rates and asks how that pattern has affected variation in λ . The factors causing the variation in vital rates can be thought of, in very general terms, as treatments in an experiment”. In this case, the experiment takes place at BMSR and the treatments correspond to annual rainfall levels. It should be obvious that the Bayesian analysis and the LTRE operate on different time scales. The Bayesian analysis analyzes data in a time frame of hundreds to thousands of years, whereas the LTRE looks at demographic variation over tens of years (16 years in the case presented here). However, the LTRE can provide insight into the factors that govern the population growth rate by assuming that the life history traits that contribute the most to variation in λ have not changed drastically over the last 2000 years (i.e., the time period corresponding to the initiation of population decline). Such uniformitarian assumptions are common in evolutionary ecology and include modeling microevolutionary phenotypic change across generations by assuming an unchanging **G**-matrix (Roff 1997) or the out-group assumption in systematics, in which a particular out-group is chosen as a stand-in for an ancestral taxa when polarizing characters (Sober 1988). The LTRE analysis shows that a lot of variation in the life cycle over the past 16 years is due to variation in the survival of females in stage 5 (i.e., experienced mothers), as well as covariation among transitions G_2/P_5 (Fig. 4a). Female sifaka reach sexual maturity at age 3 (the earliest age they can enter into stage 3 in the life cycle via transition G_2) but may not give birth for several years later—hence the self-loop in stage 3. The P_5 transition refers to the continued survival of females who are not reproductive in a given census year but have reproduced in past years. The covariation between G_2/P_5 suggests that the same biological mechanism operates similarly on these two transitions. Elucidation of this mechanism requires further investigation, but stages 2 and 5 in the sifaka life cycle have the lowest survival probabilities when annual rainfall decreases to drought levels (Lawler et al. 2009). As annual rainfall influences the primary productivity of the sifaka forest, a lack of sufficient food could account for the variation in survival of animals in these stages (Lawler et al. 2009), both in terms of reaching sexual maturity (stage 3) as well as keeping experienced mothers alive in the population (transition P_5) such that they can re-enter the maternity stage in subsequent years. Variation in transition P_5 , along with covariation between transitions G_2/P_5 , and P_3/P_5 contribute

the most to explaining variation in λ (Fig. 4b). Thus, much of the variation in λ over the past 16 years is due to covariation in the recruitment of animals into sexual maturity and their continued survival as nulliparous females (stage 3) and experienced mothers (stage 5). Thus, in order to understand how λ changes across time, either due to anthropogenic or environmental factors, it is necessary to identify factors that influence the survival of stage 3 and stage 5 animals. This issue warrants further investigation, but targeted hunting of large adult females in the past (many of which occupy stage 5), as well as environmental factors that influence female sifaka survival such as food availability (Richard et al. 2000) and predation (Brockman et al. 2008) are potential candidates for this population. It should also be noted that transitions G_3 , G_5 , P_5 , and P_3 have the highest sensitivity values; thus, in a prospective and predictive sense, changes to these transitions will have the greatest impact on population growth rate (Lawler et al. 2009).

Madagascar has a complex biogeographic and cultural history (reviewed in Goodman and Patterson 1997; Goodman and Benstead 2003), and the relationship between human colonization and lemur extirpation is complex. Numerous sources of evidence suggest that humans were primarily involved in the extinction of subfossil lemurs; however, the role of humans in shaping the historical population dynamics and behaviors of extant lemurs is less straightforward. The results presented here demonstrate that genetic and demographic analyses can shed light on historical population dynamics of extant species (also see Markolf et al. 2008; Olivieri et al. 2008; Razakamaharavo et al. 2009), and such analyses can be particularly useful when buttressed with additional data from archaeology, paleoecology, and historical records. In the absence of human disturbance, animal population sizes historically fluctuate due to climatic and socioecological factors. When humans have also played a role in shaping animal population dynamics, the central issue is to analyze these dynamics in order to separate out anthropogenic effects from natural ones. Future research concerning the population dynamics of Malagasy fauna should focus on separating these effects. Such efforts will have propitious implications for understanding both naturally and anthropogenically driven mechanisms that govern the population dynamics of endemic species on recently colonized islands.

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