AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 132:267–277 (2007)

Fitness and Extra-Group Reproduction in Male Verreaux's Sifaka: An Analysis of Reproductive Success From 1989–1999

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KEY WORDS lemur; *Propithecus*; mating systems; fitness components

ABSTRACT Adult males in social groups often compete with other male group members for access to adult females. In some primate species, males also seek mating opportunities in neighboring social groups. Such extra-group fertilizations (EGFs) provide an additional source of variation in male fitness. This additional component of fitness provided by EGFs must be incorporated into analyses that investigate sources of variation in male lifetime reproductive success. In this study, a model is analyzed in which male fitness over a 10-year sample period is decomposed into additive and multiplicative variance and covariance components. The data come from an ongoing study of a wild population of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) located at Beza Mahafaly Special Reserve, Southwest Madagascar. Paternity and demographic data for 134 males are used to decompose male fitness into the following three multiplicative components: reproductive lifespan during sample period, fertility, and offspring survival. These multiplicative components are estimated for males reproducing within their resident groups plus (i.e., the additive portion) for males reproducing in neighboring social groups. The analysis shows that variation in fertility makes the largest contribution to variation in total fitness, followed by variation in amount of time spent in sample period (which is a proxy of total reproductive lifespan) and variation in offspring survival. EGFs contribute an important source of variation to male fitness, and numerous factors enhance the opportunities for EGFs in male sifaka. These include female choice, a high degree of home range overlap, and a limited mating season. Am J Phys Anthropol 132:267–277, 2007.

Group-living is thought to evolve when the fitness of individual animals is enhanced by associating with other conspecifics. For most mammalian species, such associations may not be permanent or typical, but for the majority of primate species the stable (i.e., year-round) bisexual social group is a demographically important unit of social organization (Wrangham, 1987; Sterk et al., 1997; van Schaik, 2000). Gregariousness provides collective benefits in terms of safety from predators, resource monopolization, and associations with kin, "friends," and potential mates (Wrangham, 1980, 1987; van Schaik, 1983; Janson, 1992; Palombit et al., 1997; Silk, 2002). Nevertheless, despite the benefits to group living, members of social groups must compete with each other for access to mates, fertilizations, and food (Andelman, 1986; Smuts, 1987; Janson, 1988; Sterk et al., 1997). It is the distribution and abundance of these fitness critical resources—mates, fertilizations, food—that shape membership and mating patterns within groups. While the etiology of group formation is largely a function of female spatial dispersion, the mating system results from the interaction of male and female reproductive strategies (Clutton-Brock, 1989; Davies, 1991; Kommers and Brotherton, 1997). Both sexes are expected to behave in ways that maximize their fitness within a group, yet reproductive strategies differ fundamentally due to differential investment in resources allocated to reproduction (Trivers, 1972; Clutton-Brock, 1991).

Due to differences in parental investment and reproductive rates between the sexes, males in most primate species tend to engage in behaviors that maximize mate acquisition rather than offspring care (Altmann, 1990; Clutton-Brock, 1991; Clutton-Brock and Parker, 1992; Andersson, 1994). The lack of available females and surplus of reproductively active males can create potentially high variance in male reproductive success (e.g., elephant seals; Le Boeuf and Reiter, 1988; western gorillas; Bradley et al., 2004). Variance in lifetime reproductive success (LRS) is a function of a diverse array of selection pressures (and chance events) that act on different periods of the breeding careers of males (Sutherland, 1985; Clutton-Brock, 1988). Male mating strategies are thus likely to be adaptively diverse, and observations of males in many primate species indicate that males pursue various behavioral strategies to increase access to mates and to increase exclusivity (e.g., Alberts and Altmann, 1995; van Schaik, 1996; Kappeler, 1999; Periera et al., 2000; van Schaik and Janson, 2001). Because individual primate social groups do not exist in isolation, but are parts of a larger network of social groups (i.e., a population), individual males may also seek reproductive opportunities in adjacent groups—that is, males can seek extra-group fertilizations (EGFs). Thus, additional mating opportunities for adult males can

Grant sponsors: Yale University; The Peter and Marion Schwartz Foundation; Grant sponsor: National Science Foundation; Grant number: DEB 9902146.

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Received 6 September 2005; accepted 8 August 2006.

DOI 10.1002/ajpa.20507
Published online 28 November 2006 in Wiley InterScience (www.interscience.wiley.com).

be achieved during periods of intergroup contact and solitary visits to neighboring groups (Cords et al., 1986; Rowell and Chism, 1986; Cheney, 1987; Manson, 1992; Sprague, 1992; Palombit, 1994; Chism and Rogers, 1996; Launhardt et al., 2001; Lawler et al., 2003).

EGFs have been thoroughly documented for numerous bird species, especially in relation to monogamous social systems (called "extra-pair fertilizations") (e.g., Gowaty, 1985; Westneat et al., 1990; Webster et al., 1995; Jones et al., 2001; Freeman-Gallant et al., 2005). However, there has been comparatively little research on the opportunities and genetic consequences of extra-group reproduction in primate species. EGFs engender varying effects on population-wide variance in male reproductive success, but the overall effect for polygynous species is that variance in male reproductive success will be reduced when females mate with nonresident males (Webster et al., 1995; Jones et al., 2001). This occurs because males in multi-male groups can pursue copulations in neighboring groups. Variation in paternity is a key factor in creating opportunities for sexual selection and kin selection (by uniting offspring cohorts through paternal alleles), and influencing variance effective population size (N_{EV}) (Crow, 1958; Altmann, 1979; Arnold and Wade, 1984a,b; Nunney, 1993); therefore, determining how both within- and between-group reproduction influences variation in male fitness is important for understanding the proximate factors that govern evolutionary dynamics in primate populations. In turn, total male fitness can be decomposed into components of variation. Important components of fitness for primates include reproductive life span, fertility, and offspring survival (e.g., Altmann et al., 1988; Cheney et al., 1988).

The objective of this study is to determine the relative contributions of different fitness components to total fitness for males in a gregarious primate species. Because social groups often interact—providing an additional source of reproductive opportunities—male fitness is partitioned into within-group and extra-group components. The study species is a population of wild lemur, Verreaux's sifaka (*Propithecus verreauxi verreauxi*—"sifaka" hereafter) that inhabits the dry forests of Southwest Madagascar. The data used in this study come from an ongoing study of sifaka ecology and behavior at Beza Mahafaly Special Reserve. This is an ideal study species to investigate the effects of within- and extra-group reproductive success on male fitness. Sifaka at Beza Mahafaly are organized into about 50 social groups within the 80-ha Parcel 1 of the reserve. Sifaka form relatively stable year-round social groups of about six animals (range, 2–13 animals) that contain adult males, females, subadults, and dependent young. The socionomic sex ratio within groups is relatively equal. There is often substantial overlap among the home ranges of social groups (see Discussion), but each group makes use of a somewhat exclusive core area. Sifaka females are generally philopatric, while males leave their natal group around age 5 and often transfer into an adjacent group; some males may transfer several times over their lifetime (Richard et al., 1993; Lawler et al., 2003). There is high variability with respect to group membership and composition: some groups remain relatively stable for several years, while other groups show a high turnover of membership due to emigration and immigration. Sifaka have a brief, 6–8 week mating season beginning in mid-January in which some males make forays into adjacent social groups to seek mating opportunities (Richard, 1992; Richard et al., 1993; Brockman, 1999). Additionally, each year, a fraction of the offspring born into social groups are sired by nonresident males (Lawler et al., 2003). Drawing on previous studies of paternity, demography, and population structure (Richard et al., 1993, 2002; Lawler et al., 2003), this study investigates the sources of variation and covariation that contribute to male reproductive success over 11 breeding seasons.

METHODS

The population and paternity analysis

The population of Verreaux's sifaka has been studied continuously at Beza Mahafaly Special Reserve, Southwest Madagascar, since 1984. Information about the study site and regional habitat can be found in Richard et al. (1991, 2002). Each year, individual animals are captured, individually marked (with numbered tags and color-coded collars), measured, and released back into the wild. Yearly and monthly census data yield information on population size, numbers of social groups, group composition (sex and age), transfers of individuals, disappearances, deaths, and births.

Seven polymorphic microsatellite loci were isolated and screened in this population to determine paternity (Lawler et al., 2001). The probability that these seven loci exclude a random individual from parentage is 99% when one parent is known, and 96% when neither parent is known (Lawler et al., 2001). Parentage analysis was estimated using maximum likelihood as implemented in the program CERVUS 2.0 (Marshall et al., 1998), assuming a genotyping error rate of 0.01 and that the proportion of males sampled was 0.9. For a given offspring, CERVUS assigns a likelihood-based "LOD score" to each candidate sire, with the highest LOD score indicating the most likely sire. Confidence values for paternity assignments are calculated by taking the difference in LOD scores for the two most likely candidate sires and comparing the difference with a distribution of simulated values (Marshall et al., 1998). Following convention (e.g., Coltman et al., 1998), confidence levels for paternity assignment were set at the 80 and 95% levels. The sample size for paternity analysis consists of 134 reproductively mature males living in the population between the years 1989 and 1999. The distribution of paternity from the sample is compared with a Poisson distribution. Implicitly, in models of drift, reproduction is assumed to follow a Poisson distribution in which each individual has an average expectation of producing an offspring that is equal to the variance in offspring production. Deviations from the Poisson distribution reflect skew in reproduction (Wright, 1938).

After paternity was assigned, census data were used to identify the social group in which each sire resided during the time when his offspring was conceived. For the purposes of calculating variance components, sires were classified into three groups: *resident*—meaning that all the offspring sired by a male during 1989 and 1999 were members of the same social group as their father (i.e., the male resided in the same social group into which he sired offspring); *nonresident*—meaning that all the offspring sired by a male during 1989–1999 were born into social groups of which their father was not a member (i.e., the male sired offspring in adjacent social groups but did not sire offspring with females in his own resident group); and *both*—indicating that the sire-fathered offspring in both his resident social group and in neighboring groups during the period of 1989–1999.

Fitness estimation and components of fitness

In this study, a measure of partial LRS is used. It is the total number of offspring sired by males between 1989 and 1999; thus, what is referred to as "fitness" or "total fitness" below, is actually "a window" that portrays the reproductive success of males in the population over 11 annual breeding seasons. In the following discussion, the words "fitness" or "total fitness" (T) will always refer to male reproductive success during the sample period (1989–1999).

Following the conventions of Brown (1988; also see Cheney et al., 1988; Clutton-Brock et al., 1988), male fitness is decomposed into three multiplicative components: reproductive lifespan *during the sample period* (R), fertility (F), and offspring survival (S); that is, male fitness $= R \times F \times S$. Reproductive lifespan is defined as the number of years a reproductively mature male spent in the sample period. Males achieve sexual maturity around age 5 (Lawler, 2003), thus R was calculated from the census data as the total number of years a male spent in the sample period aged 5 or above. For example, an 11-year-old male who died 2 years in the sample period would have a reproductive lifespan of 2 years. Sample sizes for males who have spent 1, 2, 3, . . . , 11 years in the sample period are given in Table I. Fertility is defined as the rate of offspring production over the course of the sample period and is calculated as the number of offspring sired by each male divided by R—the number of years spent in the sample period (e.g., Clutton-Brock et al., 1988). Thus F is the rate of offspring production by males during the period of 1989–1999. These data were calculated using paternity analyses and census data. Offspring survival is the proportion of offspring surviving to age 4 for each male; thus, S is calculated for each male by determining the fraction of offspring he sired during the sample period that survived until age 4. This is an underestimate of offspring survival because offspring mortality is high in the first year of life. On average, 52% of infants survive the first year of life, but there is wide variation from year to year (Richard et al. 2002). Offspring are not captured and collared until after their first year of life. In this regard, "offspring survival" (S) actually represents the number of *yearlings* reaching age 4, minus the "invisible fraction" that have died prior to capturing (Grafen, 1988). To explore relationships between age (and not R, which is simply the number of years in the sample period) and other variables, six age classes were defined. These age classes are defined as the following: age class 1 (5–7 year olds); age class 2 (8–10 year olds); age class 3 (11–13 year olds); age class 4 (14–17 year olds); age class 5 (18–20 year olds); and age class 6 (21 years and above). These age classes are calculated by taking either the final age of the male at the end of the sample period or the age of the male at death if the male died during the sample period. The age classes do not represent age-specific fertilities or any measure of age-associated fitness; they simply reflect the final age of the male during the sample period.

Using the above definitions of R, F, and S, total male fitness (T) in a nonsubdivided population can be described by the equation,

$$T = RFS \tag{1}$$

and variation in total fitness can be expressed as the product of its variance components,

$$\mathrm{Var}(T) = \mathrm{Var}(RFS) \tag{2}$$

Because the sifaka population is divided into social groups, population subdivision adds opportunities for male fitness to be enhanced by mating outside the social group. Males can pursue within-group fertilizations and EGFs. Therefore, total fitness (T) must first be partitioned into two additive components that correspond to reproductive success *within* a group (W) plus reproductive success *outside* the group (O) (i.e., the EGF component) (Webster et al., 1995). Given that males can sire offspring within and outside their resident group, fitness is expressed additively as

$$T = W + O \tag{3}$$

and, as in Eq. (2), variance in total fitness can be expressed as

$$\mathrm{Var}(T) = \mathrm{Var}(W) + \mathrm{Var}(O) + 2\mathrm{Cov}(W, O) \tag{4}$$

The variance components of within and outside sources of fitness are determined by the variation in male propensities to survive and sire viable offspring within and outside their own social group, that is, by R, F, and S. Recalling Eq. (2), we can then write (fitness components are subscripted by "w"—*within* or "o"—*outside*)

$$\mathrm{Var}(W) = \mathrm{Var}(R_\mathrm{w}F_\mathrm{w}S_\mathrm{w}) \tag{5}$$

and

$$\mathrm{Var}(O) = \mathrm{Var}(R_\mathrm{o}F_\mathrm{o}S_\mathrm{o}) \tag{6}$$

By substituting Eqs. (5) and (6) into (4), we get

$$\mathrm{Var}(T) = \mathrm{Var}(R_\mathrm{w}F_\mathrm{w}S_\mathrm{w}) + \mathrm{Var}(R_\mathrm{o}F_\mathrm{o}S_\mathrm{o}) + 2\mathrm{Cov}(R_\mathrm{w}F_\mathrm{w}S_\mathrm{w}, R_\mathrm{o}F_\mathrm{o}S_\mathrm{o}) + D_\mathrm{T} \tag{7}$$

Equation (7) represents the total decomposition of fitness based on contributions of R, F, and S derived from reproduction within and outside the social group. This approach to fitness decomposition follows that of Webster et al. (1995), who drew from the statistical work of Bohrnstedt and Goldberger (1969). For males siring all offspring within their social group, variation in R, F, and S contributes only to the Var(W) and Cov(W, W) terms. For males siring all offspring outside their social group, variation in R, F, and S contributes only to the Var(O) and Cov(O, O) terms. For males that sired offspring both within and outside their social group, variation in R, F, and S contributes to both the Var(W) and Var(O) terms, as well as Cov(W, O) terms. The term D_T is a remainder term. It captures multivariate skewness and the fact that total variance is not a straightforward sum of the component variances and covariances (Bohrnstedt and Goldberger, 1969). It is difficult to interpret the biological significance of "D" without understanding how higher order moments of the distribution of fitness components influence total fitness; therefore, the possible biological significance of D_T

TABLE 1. Sample size of males spending 1, 2, 3, . . . , 11 years in the sample period

Number of males	Number of years spent in sample period
15	1
11	2
13	3
11	4
17	5
9	6
5	7
10	8
18	9
6	10
19	11

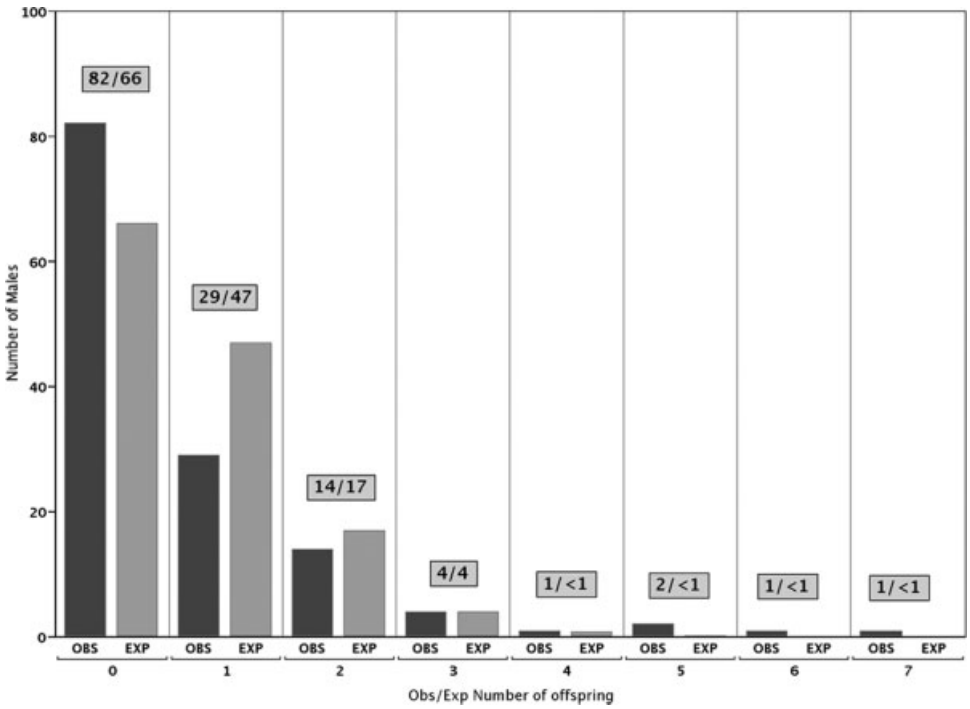

Fig. 1. Distribution of paternity for males used in this study. Shown in this chart is the actual number of males (dark bars) versus Poisson-expected (light bars) number of males who have sired zero, one, two, three . . . up to nine offspring. The numbers in the boxes show the observed versus expected (OBS/EXP) number of males siring a particular quantity of offspring. For example, 29 males sired one offspring in this study but the expected number of males is 47.

will not be discussed below. However, a straightforward interpretation of D_T is that there is some amount of "real" unexplained biological variation in male fitness that is not captured by this decomposition method. Results calculated from Eq. (7) are presented in terms of standardized values, percentage contribution to total fitness, and a qualitative measure of each term's "importance." Standardized values are the absolute values weighted by specified coefficients (Bohrnstedt and Goldberger, 1969) and then divided by the squared mean of total fitness. The percentage contribution represents the proportionate amount that the standardized value contributes to total fitness. The qualitative measure uses a cut-off of 15% to determine whether a component is a "major" (above 15%) or "minor" (below 15%) contributor to variation in total fitness. Naturally, other cut-off points will produce different measures of impact; therefore, the qualitative measure is used here only to guide which components will be discussed later.

The sample period used above, spanning 11 breeding seasons, can be viewed as a window into the reproductive behaviors of males. A male sifaka can live to about 25 years of age (though many die prior to reaching 25) (Richard et al., 2002; R. Lawler, unpublished data). This means that a male's reproductive lifespan is potentially about 20 years long. If complete data on reproductive success were available for every male for his entire reproductive career, this would constitute data on LRS and one could decompose this variation into R, F, S, as earlier. In the present study, the sample period encompasses about half (or more) of a male's reproductive lifespan, providing a reasonable approximation of LRS. It should be obvious that taking a different window of time (and a different sample size) will likely give a different picture of male reproductive success because males in the population enter into reproductive maturity, reproduce, and die in different years. There are techniques to account for time-dependent differences in survival and reproduction among males as well as censored data (e.g., Caswell, 2001; Williams et al., 2001), but these issues are not addressed in this study. In this study, R, F, and S are biased estimators, but they are assumed to have some connection to *actual* lifetime reproductive lifespan, lifetime fertility, and lifetime offspring survival and will be interpreted as such.

RESULTS

Parentage analysis

The distribution of paternity in the population is given in Figure 1. As is evident, the majority of adult males in the sample did not sire offspring (82 out of 134 sired no offspring). Mean number of offspring per male was 0.71 with a variance of 1.52. Figure 1 also shows expected number of males who should sire 0, 1, 2, 3, . . . up to 9 offspring; this distribution was generated by parameterizing a Poisson distribution using 0.71—the observed average reproductive success in this sample. A total of 96 offspring were sired by 52 males in the population during the sample period (i.e., 1989–1999). Twenty three males sired one or more offspring solely within their resident group (i.e., "resident"), 14 males sired one or more offspring outside of their resident group (i.e., "nonresident"), and 15 males sired one or more offspring both within and outside their resident group (i.e., "both"). Figure 2 shows the distribution of siring patterns for males classified as "resident," "nonresident," and "both."

Confidence in paternity assignments ranged from 83 to 99% with a mean of 89.2%. A t-test on the mean confidence value indicated that it was significantly different from

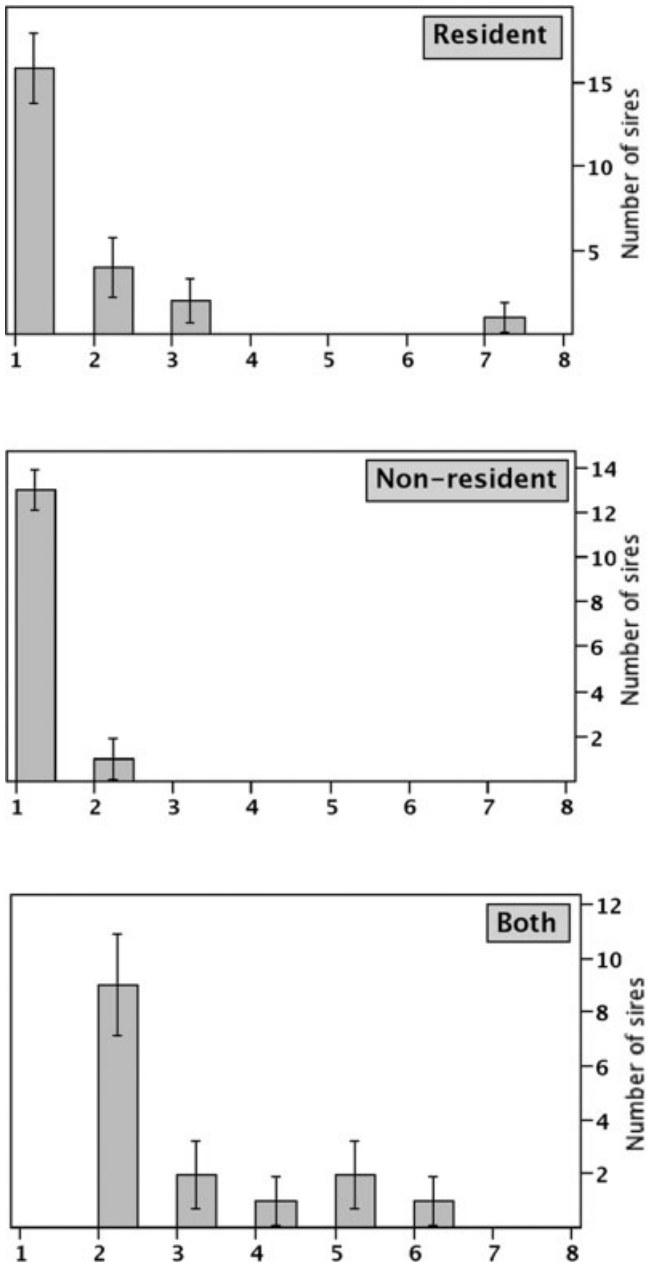

Fig. 2. Distribution of paternity for males classified as "resident," "non-resident," and "both." The horizontal axis is the number of offspring sired. For example, for resident sires, 16 males sired one offspring and 4 males sired two offspring. Numbers of offspring for "both" are split between two groups (resident and non-resident).

80%—the lowest conventionally accepted value used in the literature (e.g., Coltman et al., 1999) ($t = 22.24$, $df = 95$, $P = 0.001$). Paternity was checked against census and location data to provide a post hoc check of sire–offspring relationships. Sires were located within or adjacent to the social group into which they sired offspring, and no sire was geographically distant from the group at the time of conception. This finding matches behavioral observations of mating behavior and movements of adult males in the population: males tend to mate within their own group and/or in an adjacent group (Richard, 1992; Brockman, 1999).

TABLE 2. Average values of the within-group and outside-group fitness components

Component	Term	Average value
Within-group reproductive lifespan	R_w	5.79
Within-group fertility	F_w	0.20
Within-group offspring survival	S_w	0.88
Outside-group reproductive lifespan	R_o	5.70
Outside-group fertility	F_o	0.17
Outside-group offspring survival	S_o	0.93

TABLE 3. Decomposition of total fitness into its various components [see Eq. (7)]

Term	Standardized value	Percentage of total variance	Relative impact
Total variance			
Var (T)	2.95	100.00	
Within-group components			
Var(R_w)	0.64	21.70	Major
Var(F_w)	0.84	28.55	Major
Var(S_w)	0.24	8.28	Minor
Cov(R_w, F_w)	−0.58	−19.77	Major
Cov(F_w, S_w)	0.00	0.09	Minor
Cov(R_w, S_w)	−0.03	−1.12	Minor
Outside-group components			
Var(R_o)	0.52	17.53	Major
Var(F_o)	0.61	20.63	Major
Var(S_o)	0.11	3.68	Minor
Cov(R_o, F_o)	−0.29	−9.75	Minor
Cov(F_o, S_o)	0.08	2.55	Minor
Cov(R_o, S_o)	−0.02	−0.79	Minor
Within/outside components			
Cov(R_w, F_o)	−0.13	−4.55	Minor
Cov(R_w, R_o)	0.16	5.48	Minor
Cov(R_w, S_o)	−0.05	−1.81	Minor
Cov(F_w, R_o)	0.01	0.49	Minor
Cov(F_w, F_o)	0.25	8.50	Minor
Cov(F_w, S_o)	−0.06	−1.88	Minor
Cov(S_w, R_o)	0.12	3.90	Minor
Cov(S_w, F_o)	0.06	1.97	Minor
Cov(S_w, S_o)	−0.05	−1.61	Minor
Remainder			
D	0.53	17.91	

Components of fitness are expressed as a standardized value and as percentage contribution to total fitness as well as a qualitative expression of each component's impact on total fitness.

Components of fitness

Average values of the fitness components are listed in Table 2. The average number of years a male spent in the sample period is around 6 years ($R_w = 5.79$; $R_o = 5.70$). On average, resident sires produced the equivalent of 0.20 offspring per year (F_w), whereas nonresident sires produced 0.17 offspring per year (F_o). Offspring survival was 0.88 for resident sires (S_w) and 0.93 for nonresident sires (S_o). Using both parametric and nonparametric tests, there were no statistical difference in mean values between R_w versus R_o, F_w versus F_o, and S_w versus S_o. For males who sired offspring outside their resident group (i.e., *nonresident* or *both*), there was no clear pattern of subsequent group transfers in which fathers and offspring would later come to reside in the same social group. Of the 40 cases of extra-group paternity, eight cases resulted in the father and offspring residing in the same group at a later date (either the father subsequently joined the offspring's group or the offspring subsequently transferred into father's group), and in 32 cases, the

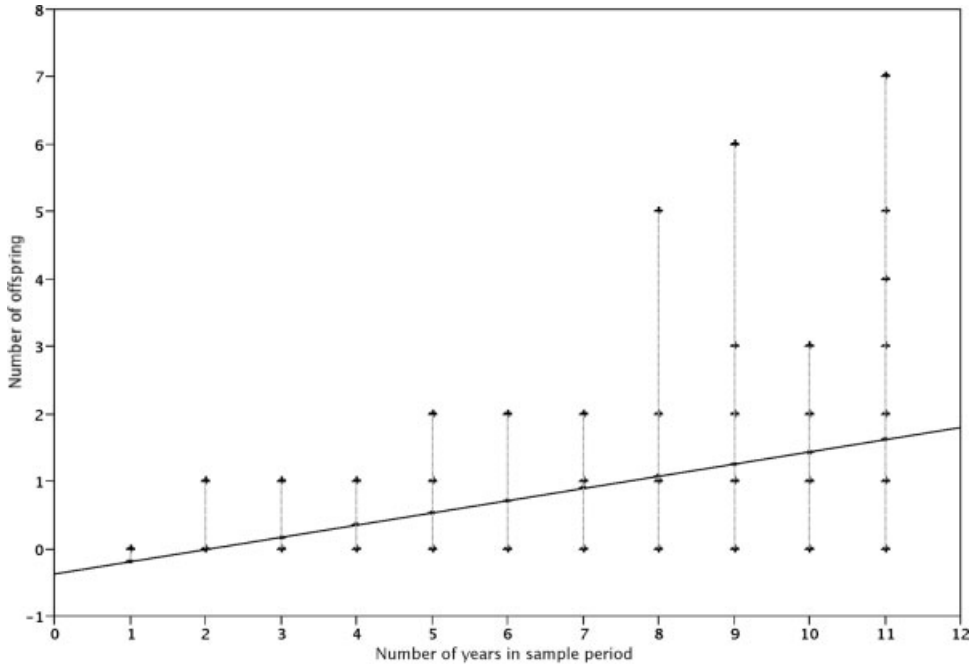

Fig. 3. Plot of number of offspring against number of years spent in sample period (R). Shown are the ranges (dotted lines) of offspring production for males who spent one or more years in the sample period. The black line reflects the predicted number of offspring a male should sire given the amount of time he spends in the sample period.

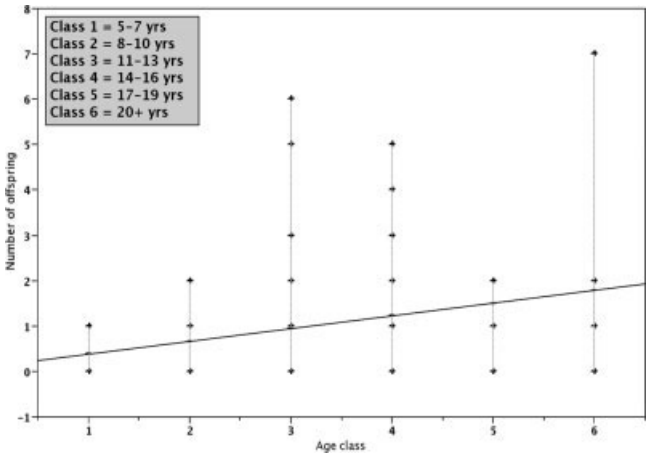

Fig. 4. Plot of number of offspring against age class for all males in the study. Shown are the ranges (dotted lines) in offspring production for males of a given age class. The black line reflects the predicted number of offspring for a male of a given age class.

father and offspring never became reunited in the same group.

Variance components of fitness are listed in Table 3. Table 3 is broken down into "within-group" sources of (co) variation, "outside-group" sources of (co)variation, and "within/outside-group" sources of covariation. Fitness components for both within and outside the group are broken down into variation in R, F, and S. Among these three multiplicative components, variation in fertility contributes the most to total fitness for both within and outside sources of variation ($F_w = 28.55\%$, $F_o = 20.63\%$), followed by reproductive lifespan ($R_w = 21.70\%$, $R_o = 17.53\%$) and offspring survival ($S_w = 8.28\%$, $S_o = 3.68\%$). Recall that total fitness is not a straightforward sum of the variances and covariances, thus the sum of the percentage contributions of each component will not total 100%.

Figure 3 shows the relationship between reproductive lifespan in the sample period and number of offspring sired for all males (sires and nonsires) used in this study. The vertical dotted lines represent the range in the different numbers of offspring sired by males during the sample period. The black line reflects the predicted number of offspring a male should sire for each year he spends in the sample period. There is a significant and positive relationship between reproductive lifespan and total number of offspring produced by males as indicated by the positive slope of the black line (F ratio = 49.20, df = 133, P = 0.0001). Figure 4 shows the relationship between age class and number of offspring sired for all males (sires and nonsires) used in this study. The vertical dotted lines represent the range of offspring production (same as Fig. 3), and the black line gives the predicted number of offspring a male should sire by age class (F ratio = 18.75, df = 133, $P = 0.0001$).

DISCUSSION

Interpreting *R, F,* and *S*

Within a single episode of selection, those fitness components showing the highest variation provide the greatest opportunity for selection to modify them (Crow, 1958). However, when components of fitness are values taken over a portion of a lifetime, they only provide a rough approximation to the total opportunity for selection (Brown, 1988; Grafen, 1988). This is because chance events (i.e., nonselective forces) also contribute to the variation in fitness components; therefore, the variation exhibited by each component is not directly proportional to the oppor-

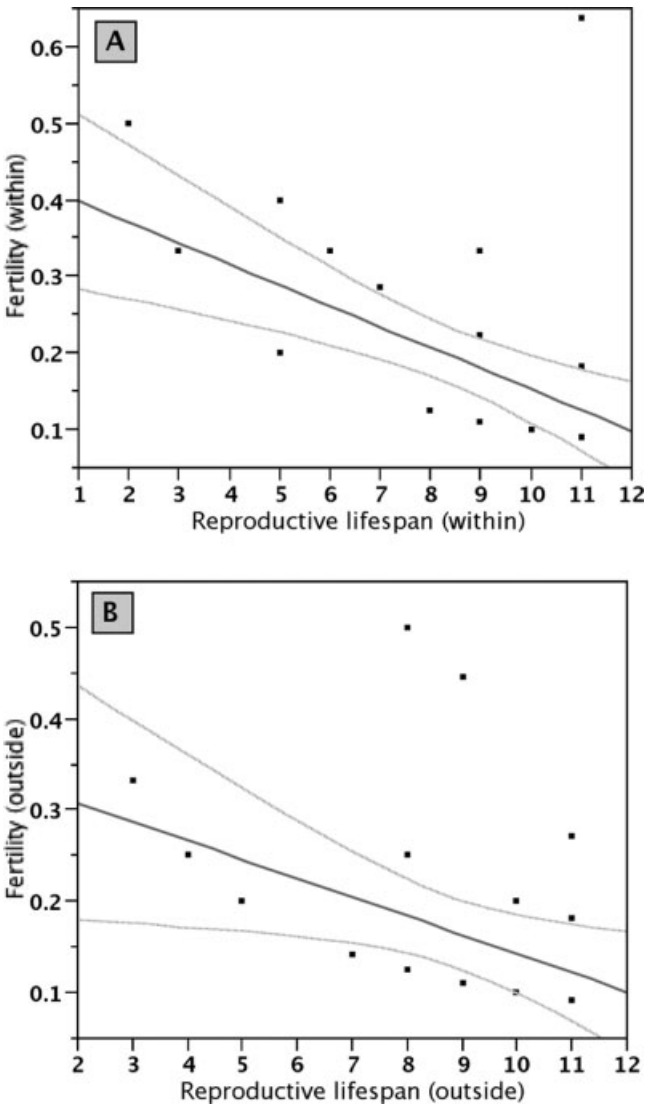

Fig. 5. The relationship between fertility and reproductive lifespan (i.e., time spent in sample period) for males reproducing within groups (A) and males reproducing outside of groups (B). The slope in A becomes more steeply negative if the outlier in the upper right corner is removed. Lines of 95% confidence are shown.

tunity for selection. Nevertheless, partitioning fitness remains helpful for identifying the *relative* variation among fitness components and how much each component contributes to total fitness. It also sets up the possibility for future studies to examine the ecological factors contributing to the variation in each component (assuming that past conditions are an accurate portrayal of current and future conditions). Comparing the relative amount of variation in fitness components helps prioritize hypotheses that can be studied in the field. For example, in male sifaka, the largest source of variation in fitness is due to variation in fertility during the sample period. Given these results, field studies should focus on what factors—both selective and accidental—covary with variation in male mating success in each breeding season, and perhaps deemphasize what factors covary with offspring survival, since this component is the smallest contributor to variation in male fitness. In this sense, decomposing variation in total fitness into components of fitness represents the first step—not last—in understanding the factors contributing to variation in LRS in males (Webster et al., 1995).

Figures 3 and 4 suggest that male fitness increases with age (as proxied by age-class and reproductive lifespan in sample period). Each figure shows a positive relationship between total offspring production and either years spent in the sample period, or the age of the male at the end of the sample period (or the age at death, if the male died during the sample period). Reproductive lifespan (R) contributes a significant proportion of variation to total fitness among male sifaka at Beza Mahafaly. This is the case for males who reproduce within-groups and for males who reproduce outside their resident group. Reproductive lifespan can be viewed as the "per-year opportunity" that a male has to increase his reproductive success. On average, those males who survive across many years are also expected to sire more offspring. The variation in reproductive lifespan during the sample period and its effect on opportunities for reproduction is captured by the large contributions of R_w and R_o to total fitness. If R is a reasonable approximation of actual reproductive lifespan, this suggests that simply by extending their reproductive lifespan, males can increase their fitness independent of the group (resident or neighboring) into which they may eventually sire an offspring. However, reproductive lifespan, as noted earlier, is a summary statement of males born at different times and under different climatic conditions. Because of this, reproductive lifespan does not take into account random factors that affect different age cohorts. Cohorts of males born in different years may be subject to differing food availability, predator susceptibility, etc. These factors likely influence the total variance in reproductive lifespan in the sample. Therefore, cohort models are needed to tease apart the effects of survivorship and reproduction with respect to temporal variation (e.g., Williams et al., 2001).

Figures 3 and 4 also show that there is much variation in offspring production across different age classes and years spent in the sample period, indicating that the rate of offspring production—male fertility—is also a contributor to fitness. Table 3 shows that variation in male fertility makes the largest contribution to variation in male fitness. In this sense, male fitness is not only a matter of surviving another breeding season, but also depends on turning each breeding season into one or more reproductive events. Behavioral observations during the mating season have shown that there is much variability from group to group in terms of inter- and intrasexual interactions (Richard, 1992; Brockman et al., 1998; Brockman, 1999). Female sifaka mate preferentially with older, resident males, but will also mate with nonresident males. Males also aggressively compete for access to sexually receptive females (Richard, 1992; Brockman, 1999). Male mating competition in sifaka involves physical combat, as well as extended arboreal episodes of chasing and lunging (Richard, 1992). Variation in fertility specifies the rate of offspring production over a given period. However, selection acts on phenotypes, and thus it is necessary to identify the traits that covary with male fertility in order to understand how fertility influences phenotypic evolution in this population. Traits that have been found to covary with male fertility are body mass and leg shape. An analysis of selection pressures revealed that body mass experiences stabilizing selection, while leg shape (a trait related to locomotor performance) experiences directional selection. Selection on these traits is functionally related to locomotor perform-

ance (i.e., chases) and not physical aggression (Lawler et al., 2005). Thus the relatively large F_w and F_o terms influence intrasexual evolutionary dynamics in this population because these terms covary with traits that enhance arboreal mating competition in some males.

Figure 5 examines in more detail two of the covariance relationships shown in Table 3. This figure depicts reproductive lifespan plotted against fertility for resident sires (Fig. 5A, R_w vs. F_w) and nonresident sires (Fig. 5B, R_o vs. F_o). The negative slope in each graph captures the negative covariation among the Cov(R_w, F_w) and Cov(R_o, F_o) terms given in Table 3. The slope is significantly negative in both graphs (in A: F ratio = 14.33, df = 37, P = 0.0006; in B: F ratio = 5.64, df = 28, P = 0.023). It is tempting to interpret this negative relationship as a trade-off between fertility and reproductive lifespan, since reproductive rate (i.e., fertility) decreases as males survive longer into the sample period. Because reproduction is assumed to be a costly endeavor, fertility at every age-class cannot be simultaneously maximized. This is because energy that is devoted to immediate reproduction will not be available for future reproduction or survival (Stearns, 1992; Roff, 2001). However, this decrease in reproductive rate across years is likely a consequence of the fact that a male who spends only 2 years in the sample period but sires one offspring will have a fertility of 0.5—a value much higher than males who have spent 6 or more years in the sample period. To get a better picture of the trade-off between fertility and reproductive lifespan, it is necessary to eliminate males who have spent relatively less time in the sample period. By recalculating the slopes in Fig. 5A,B, but eliminating all males who have spent 5 years or less in the sample period, the significantly negative relationship between fertility and reproductive lifespan disappears (although the relationship is still negative). Theory suggests that there should be a trade-off between fertility and reproductive lifespan (e.g., Partridge and Harvey, 1985; Roff, 2001), but this relationship cannot be *significantly* demonstrated using the "sample period" approach in this study.

Of the three multiplicative variance components, offspring survival makes the lowest percentage contribution to total male fitness. Offspring mortality is most likely caused by random climatic factors, differences in maternal experience and condition, and predation (Richard, 2003). Longitudinal records indicate that females who gave birth to surviving offspring in previous birth seasons were likely to continue to have viable offspring in subsequent birth seasons (Richard et al., 2002). The conditions contributing to successful maternity have been linked to differences in female body mass (Richard et al., 2000). Male sifaka contribute negligible amounts of paternal care (Richard, 1976). The comparatively small contribution of offspring survival to total male fitness is probably due to the fact that—relative to climactic factors and maternal condition—males play a minimal role in influencing the viability of the offspring they sire.

Extra-group fertilizations

The distribution of male reproductive output in primate populations is contingent on numerous factors. From the male's perspective, reproductive opportunities are influenced by the number of other adult males and females within the social group, mechanisms maintaining priority-of-access to mates, and the opportunity for alternative reproductive strategies, including EGFs. Genetic studies documenting the impact of EGFs on variance in male reproductive success are scarce for wild primate populations (Ohsawa et al., 1993; Keane et al., 1997; Feitz et al., 2000; Launhardt et al., 2001; Vigilant and Boesch, 2001; Nievergelt et al., 2002). In a study of wild toque macaques (*Macaca sinica*), Keane et al. (1997) found that 11% of the infants born into social groups were sired by nonresident males. Oshawa et al. (1993) examined paternity in the seasonally breeding patas monkeys (*Erythrocebus patas*) over a 2-year period. Although their sample size is limited, Oshawa et al. (1993) determined that during periods of male influxes, 50% of the offspring in some groups were sired by nonresident males. Launhardt et al. (2001) assessed paternity in a wild population of langurs (*Semnopithecus entellus*) in southern Nepal. They found that resident males sired all the offspring within uni-male groups, but that in multi-male groups, 21% of all offspring were sired by nonresident males. These studies attest to the idea that there is not always a direct correspondence between the social unit and the reproductive unit (Richard, 1985).

What is perhaps most interesting about the data presented in Tables 2 and 3 is the fact that there is an equal fitness payoff for males reproducing within their resident social group and males who sire offspring in an adjacent social group. That is, the average (i.e., expected) values for reproductive lifespan, fertility, and offspring survival are very similar. Nevertheless, the *variance* in fitness components differs between the two types of males, suggesting different behavioral and ecological factors impact on resident and nonresident sires (see Table 3). Several important factors likely facilitate the opportunity for EGFs in sifaka. One factor is female mate choice and mate availability. During the mating season, some sifaka groups remain stable with no incursions of nonresident males; other social groups are characterized by frequent aggression and are unstable, often receiving visits from nonresident males (Richard, 1992; Brockman, 1999). The basis for group stability during the mating season is not known, but may relate to females in stable groups directing mating opportunities solely to one or a few "chosen" resident males (Richard, 1992). Determining which aspects of male behavior females use as cues for mate choice is important for understanding why certain males may obtain EGFs and others do not. Females may seek nonresident males to conceal paternity. Such a strategy may preempt nonresident males from entering the female's group and committing infanticide (Brockman and Whitten, 1996); this possibility has also been suggested for langurs (Launhardt et al., 2001; also see Pereira and Weiss, 1991). In addition, the socionomic sex ratio of males to females in groups may facilitate the degree to which nonresident males obtain mating opportunities. When the adult socionomic sex ratio in the population is biased toward females (e.g., on average each group contains more females than males), a significant fraction of the offspring born into social groups are sired by nonresident males (Lawler et al., 2003).

A second factor that may facilitate EGFs is the large degree of home range-overlap among social groups. Extra-group reproduction can be viewed as a very brief, nonpermanent dispersal event, and many studies have documented the costs a resident animal incurs by leaving its resident social unit (e.g., Pusey and Packer, 1987; Alberts and Altmann, 1995; Belichon et al., 1996). Individual dispersers, when away from familiar conspecifics or habitat, suffer from reduced foraging efficiency and increased vulnerability to predation. Additionally, these animals may also sustain injuries when trying to gain residence in a

new social group (Dunbar, 1987; Pusey and Packer, 1987). Isbell and van Vuren (1996) divided dispersal costs into "locational" and "social" components. Locational costs result from leaving a familiar habitat, while social costs are incurred by leaving a familiar social unit and entering a new one. Isbell and van Vuren (1996) examined data on dispersal in primates and found that when home-range boundaries overlap, animals are more likely to incur social costs as opposed to locational costs. In the sifaka population, group density is quite high, home range overlap is considerable, and the habitat is relatively homogenous (Richard et al., 1993). The reserve is organized into a trail system that follows an orthogonal grid pattern. Trails are cut $\sim$100 m apart from each other such that the reserve is divided into 1-ha quadrats. The average number of social groups inhabiting each quadrat is $\sim$2.7 (using data from 2000; range, 1–5 groups per quadrat), indicating that, on average, up to three social groups utilize the same area. Because of this, males in different social groups range over similar habitat and suffer few locational costs by leaving their current home range. In the sifaka population, data indicate that the costs males incur by attempting to reproduce outside their resident groups are social, reflected in injuries sustained while trying to enter neighboring groups (Richard, 1992; Brockman et al., 1998).

A third component that facilitates EGFs is a restricted mating season. In baboons and macaques, visits by nonresident males are associated with the rapid availability of receptive females (e.g., Berenstain and Wade, 1983). In hanuman langurs and patas monkey, seasonal influxes of nonresident males occur only during the mating season (Ohsawa et al., 1993; Chism and Rogers, 1996; Borries, 2000). The relationship between female reproductive status and male visits is variable in sifaka (Brockman et al., 1998; Brockman, 1999). However, for male sifaka, seasonality of mating restricts the time-window that males have to increase their fitness. From the perspective of a male, females coming into estrus within this limited time-window can be thought of as an expanding population of reproductive opportunities. Given the very brief period of female receptivity (Brockman and Whitten, 1996), males who exploit these expanding opportunities earlier (i.e., males who are the first ones to fertilize females) are likely to leave more offspring than males who do not quickly exploit these opportunities; this explains the positive covariance term, $\mathrm{Cov}(F_w, F_o)$. It is easy to see how this strategy of visitation could get started. If the initial population consisted of nonvisiting males, any male who visited a neighboring group could obtain a fitness advantage over nonvisiting males (assuming that the male sired offspring in both the resident and neighboring groups). If this strategy were heritable (or even imitated), it would quickly spread due to the high fitness it confers. Eventually, an equilibrium would be reached because males engaging in too many visits might have their resident reproductive opportunities coopted by other visiting males. This does not indicate that there are two fixed strategies in the population. The "decision" to engage in EGFs is likely frequency-dependent and will also depend on, among other things, male condition, age, social status, as well as mate availability. Estrus asynchrony within and between groups will not necessarily disrupt this scenario, but will only add a variable encounter-rate to those males who opt to visit neighboring groups during this period of increasing mate availability.

In this regard, male influxes may not be entirely predicted by female receptivity or immediate sociosexual cues. Given the large degree of home range overlap and variation in female mating preferences, males may have little to lose in monitoring the reproductive status of females in adjacent groups during the mating season. Males who are unable to mate in their resident group can pursue fertilizations in neighboring groups. Given the large contribution to total fitness made by EGFs, the results presented earlier suggest that EGFs are worth pursuing.

CONCLUSIONS

This study decomposed variation in male reproductive success into components of variation corresponding to reproductive lifespan, fertility, and offspring survival. Both variation in reproductive lifespan and fertility are key determinants of variation in male fitness, whereas variation in offspring survival is not a major contributor to variation in male fitness. These results suggest that field studies should pay particular attention to the ecological and behavioral sources of mortality and mating success among males. Such studies will help separate out random from nonrandom causes of death, as well as illuminate the behavioral contexts of male mating success. The results also show that pursuing reproductive opportunities in neighboring groups is a major component of fitness in male sifaka. There is a relatively equal fitness payoff (in terms of the average reproductive lifespan and fertility) for males mating within their resident group and males mating outside their resident group. Factors likely facilitating extra-group reproduction in sifaka males are female choice, home range overlap, and a restricted mating season. Field studies focusing on the proximate ecological and sociosexual circumstances leading to extra-group reproduction would go a long way toward explaining a major source of variation in fitness among male sifaka. Such studies would be particularly important for determining the behavioral mechanisms that underlie the large amount of variation in patterns of group membership and sociosexual interactions observed in this population.

ACKNOWLEDGMENTS

I thank David Watts, Margaret Riley, and Alison Richard for reading and criticizing an earlier version of this manuscript. Michael Webster kindly answered questions about fitness and provided me with a copy of the program used to calculate fitness components. Jennifer Wernegreen also offered feedback and comments on this manuscript. Three anonymous reviewers and *AJPA* editor Clark Spencer Larsen provided very helpful feedback that made the present study much stronger. I thank the government of Madagascar for permission to conduct this research. The Beza Mahafaly Monitoring Team collected a lot of the primary data used in this study, and I am very grateful to the team's coordinator Dr. Joelisoa Ratsirarson and to the team members Enafa, Elahavelo, Emady Rigobert, and Ellis Edidy. Diane Brockman and Kashka Kubzdela also collected census data and I thank them for their efforts. I thank Marion Schwartz for managing the sifaka database and providing me with copies of the relevant data. Support for the Beza Mahafaly Monitoring Team is kindly provided by the Liz Claiborne and Art Ortenberg Foundation.

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