Variability in Reproductive Success Viewed From a Life-History Perspective in Baboons

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ABSTRACT   Nonhuman primates, like humans, mature slowly and have low fertility during a relatively long life. As data have accumulated on life-history patterns of nonhuman primates, comparative studies have yielded important insights into the evolution of this slow life-history style of primates. However, in order to understand selection pressures and evolutionary potential within species, it is important to complement comparative studies with detailed studies of life-history variability within species and to identify sources of this variability. Here we present a summary of how foraging environment, social status, and group size (a measure of population density) contribute to within-population variance in reproductive success for savannah baboons. We also discuss the extent to which savannah baboons, with their highly flexible and adaptable behavior, change their foraging environments by shifting home ranges and seeking rich food sources and how low-ranking females, which disproportionately bear the costs of social life, may mitigate those costs. Am. J. Hum. Biol. 15:401–409, 2003.   © 2003 Wiley-Liss, Inc.

Reproduction is a long-awaited event within the lives of anthropoid primates (monkeys and apes) and once reproduction begins, primates accrue offspring very gradually. In life-history terms, anthropoid primates, human and nonhuman, exhibit slow life histories compared to mammals of similar size in most other orders. Maturation is relatively late, litter size is small (usually only one except for some of the smallest monkeys), interbirth intervals are long, offspring tend to grow slowly, and adult lifespan is long.

Successful reproduction involves much more than zygote production, of course, although mating or zygote production remains the main focus of evolutionary research on reproductive success. For all mammals, the presence and behavior of mothers and sometimes of fathers has a major role in determining postnatal as well as prenatal survival and quality of offspring. In the case of anthropoid primates, a slow life history and extensive parental care, primarily from the mother, are combined with almost ubiquitous sociality and a high degree of social complexity. The result is a potentially high degree of social impact on an individual's reproductive success.

The past four or five decades have witnessed the accumulation of basic descriptions of behavioral ecology and life history for an increasingly large number and diversity of primate species, often in their natural habitat. This accumulation has fueled a rich body of research in which evolutionary hypotheses are examined through the comparative approach (e.g., Harvey and Clutton-Brock, 1985; Smuts et al., 1987; Lee, 1999; chapters in Kappeler, 2000; Kappeler and Pereira, 2003). In this approach, a single point represents each species or some higher taxonomic units of analysis. Data derive either from single studies for lesser-known species or from some form of average for the better-known ones. These comparative studies have yielded much insight into the evolution of primate behavior and life history. However, key questions remain unanswered with this approach. In particular, we cannot understand how selection might be acting within a species without an analysis of the magnitude and sources of variance in fitness within that species. The comparative

approach cannot undertake such an analysis, and hence it must be complemented with detailed, within-species analyses of variance in lifetime reproductive success.

Detailed within-species analyses require data from a range of sites or social groups or from the several-decade period required for the accumulation of substantial life-history data. Such data are available for very few species, even the better-known ones. Baboons (*Papio* spp) provide one of the first and most extensive such datasets (see, e.g., on *cynocephalus* baboons in Amboseli, Kenya: Altmann et al., 1988; Alberts and Altmann, 2003; on *cynocephalus* in Mikumi, Tanzania: Wasser et al., 1998, Rhine et al., 2000; on *anubis* baboons in Gombe, Tanzania: Packer et al., 1998, 2000; on *anubis* in Gilgil, Kenya: Strum and Western, 1982; Bercovitch and Strum, 1993; on *ursinus* baboons in Okavango, Botswana: Bulger and Hamilton, 1987). Found throughout sub-Saharan Africa, baboons are among the most geographically and ecologically diverse of nonhuman primates; they are found from forests to arid regions, from coastal ones to mountains, and are particularly abundant in the great expanses of semiarid savannahs.

In the present article we focus on variability in components of reproductive success for female and male baboons, based on three decades of continuous observations on the baboon population in the Amboseli basin, to the north and west of Mt. Kilimanjaro. We bring together some of the findings of those studies and indicate the future investigations to which they point. In particular, we review the impact of three sources of variability in reproductive parameters: foraging environment, group size (density), and social dominance status. Each of these has been documented as a source of variance in at least one and often several populations of baboons. Here we focus on their effects in the Amboseli population but cite effects in other populations where appropriate.

BABOONS: THE BASIC LIFE-HISTORY THEME

Baboon taxonomy remains in dispute (see, e.g., Hayes et al., 1990; Jolly, 1993; Altmann SA, 1998, pp. 14–15), and baboons are variously classified as a superspecies with five species (*Papio anubis, P. ursinus, P. cynocephalus, P. hamadryas, P. papio*), as two species (*P. hamadryas* and *P. cynocephalus*, the latter containing all the other species as subspecies), or a single species with several subspecies. The savannah baboons (*Papio* species or subspecies other than hamadryas baboons of the horn of Africa) live in groups with multiple adult females and almost always multiple males. They are matrilocal; females remain in their group of birth, while males disperse around attainment of adulthood. If they survive dispersal, males typically experience several bouts of secondary dispersal, based to a considerable extent on mating opportunities (Packer, 1979; Alberts and Altmann, 1995a). Hamadryas baboons, confined to more arid regions, exhibit a different social organization; the basic social unit is a one-male, multifemale group, and females as well as males disperse from their natal unit (Kummer, 1968; Stammbach, 1987).

Various components of baboon life histories have been described from a number of sites and are broadly similar (see, e.g., Altmann et al., 1988; Packer et al., 1995, 2000; Alberts and Altmann, 1995a,b, 2003, and references therein). Born after a 6-month gestation, baboon infants grow at about 5 g/day from a birthweight of a little under 1 kg until they are approximately 5 years old. At approximately 5 years, males begin an adolescent growth spurt, more than doubling their growth rate for a period of several years. Females reach menarche between 4 and 5 years of age, experience a period of adolescent subfertility, and then conceive their first infant when around 5½ years old. At the age at which females conceive their first infant, their male peers experience rapid testicular enlargement, onset of sperm production, and the beginning of a protracted period of subadulthood. By the time males attain adult dominance status, at about 8 years of age, they have achieved a body mass of approximately 25 kg. Sexual dimorphism is great among baboon adults: females are about 50% the body mass and 80% the skeletal dimensions of adult males. Although male mating success declines precipitously throughout adulthood, for surviving females reproduction remains fairly stable throughout 10–12 years, into the third decade of life. The oldest reported females are 26–27 years (e.g., Bronikowski et al., 2002); adult male mortality is higher than that of females and males in their late teens appear much older than their female age peers. This basic picture of

baboon life histories is, as far as we know, characteristic of all the baboon (sub)species. We now make a departure and focus only on the baboons that live in multimale groups, that is, excluding the hamadryas.

Like many other matrilocal cercopithecine primates, baboon females form dominance hierarchies that are predominantly stable within and between generations as older juvenile daughters usually assume a rank immediately below that of their mothers (Melnick and Pearl, 1987; Walters and Seyfarth, 1987). As in many other multimale primate societies, males also form dominance hierarchies, but these are highly unstable and age-graded; males usually achieve their highest rank very soon after defeating any adult male and rank declines throughout adulthood (Hamilton and Bulger, 1990; Packer et al., 2000). Baboons exhibit external signs of menstruation, highly regular sexual skin swellings that closely reflect a female's hormonal state and her likelihood of fertility, and an area of paracallosal skin that turns pink during pregnancy (see review in Hrdy and Whitten, 1987; also Smuts, 1985; Altmann et al., 1988).

Amboseli study groups and data collection

In Amboseli, we undertake near-daily plotting of these female reproductive signs for all adult females in our study groups. We also collect near-daily records of ecological, demographic, and behavioral data, including affiliative, agonistic, and mating behavior. This allows a detailed reconstruction of all pregnancies and their outcomes, which yields measures of reproductive success for females (Altmann et al., 1988; Alberts and Altmann, 2003). For males, behavioral records of mate guarding and mating yield relative measures of mating success, which our genetic analyses indicate are good assays of actual reproductive success (Altmann et al., 1988, 1996; Alberts and Altmann, 2003). The study groups in the population (Fig. 1) include five completely wild-foraging groups that arose from two
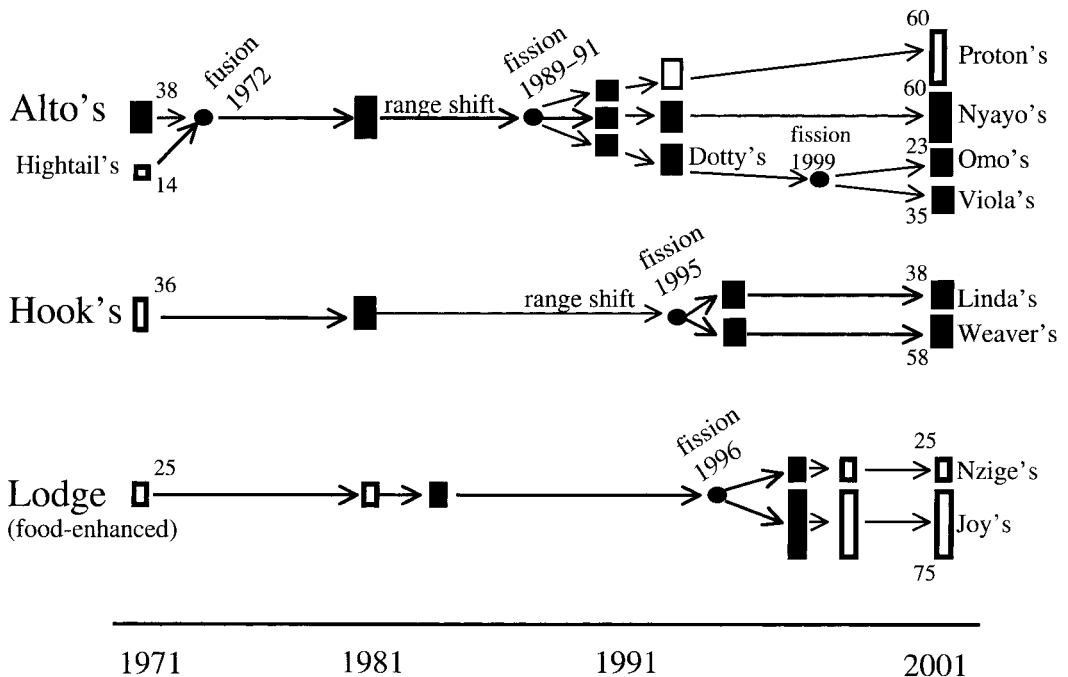

Fig. 1. Amboseli study groups through time. Solid rectangles represent study groups, open rectangles represent nonstudy groups that were monitored opportunistically. Each of the original study groups, Alto's, Hook's, and Lodge Groups, underwent permanent fissions and Alto's and Hook's each underwent a home-range shift prior to fission (see text for details). Lodge Group is food-enhanced and forages part of the time at a refuse pit near a tourist lodge. Group sizes for original groups and groups in 2001 are indicated next to the group symbols.

original study groups through permanent group fissions. An additional study group (Lodge Group) lives in an enhanced foraging environment, feeding partially at a refuse pit associated with a tourist lodge (Muruthi et al., 1991; Altmann et al., 1993).

FORAGING ENVIRONMENT AS A SOURCE OF VARIABILITY IN REPRODUCTIVE SUCCESS

Foraging environment has a large, pervasive impact on components of reproductive success in baboons (Fig. 2a; see also Strum and Western, 1982; Strum, 1991; Packer et al., 1995; Altmann and Alberts, 2003). However, far from merely experiencing the

foraging environment as a fixed, exogenous circumstance, Amboseli baboons actively improved their foraging environments. They did this in two ways. One group, as noted above, moved into the vicinity of a tourist lodge and made regular visits to its refuse pit. This provided access to a concentrated, abundant, and easily processed and digested food resource. As a consequence, the Lodge Group baboons take in almost the same calories and protein as the wild-foraging baboons but spend much less time and travel less to do so (Muruthi et al., 1991). The results are manifold. Offspring growth rates in Lodge Group are almost double those of wild-foraging animals (9 vs. 5 g/day). Maturation occurs a year earlier; infant
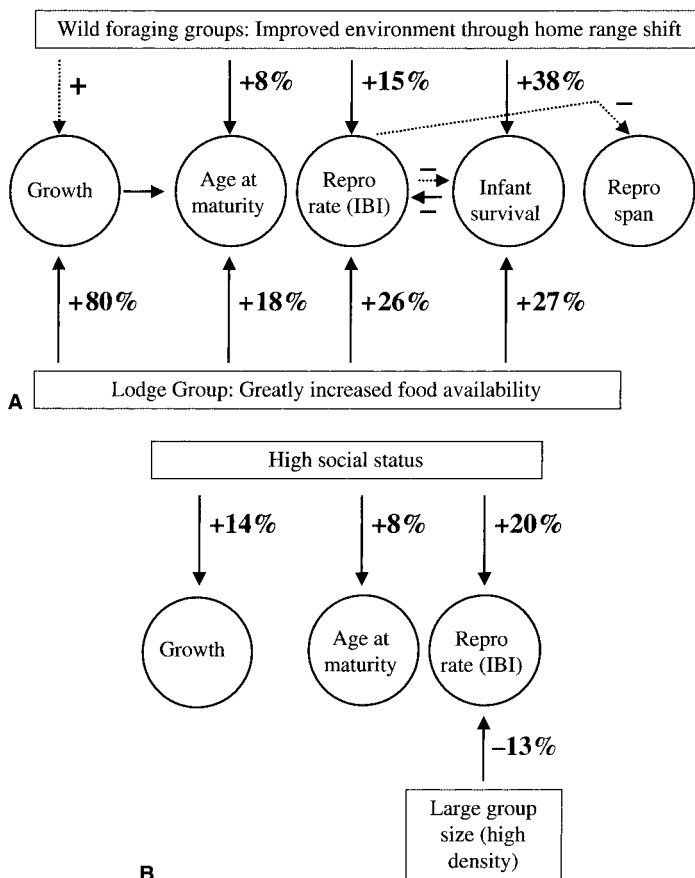

Fig. 2. Effects of (**A**) foraging environment, and (**B**) social status and group size (density) on components of reproductive success. Components of the life history are enclosed in circles; "Repro span" indicates reproductive lifespan; "Repro rate" (IBI) indicates reproductive rate as measured by interbirth interval after surviving offspring. Environmental effects are enclosed in boxes. "+" indicates a positive effect, "−" a negative effect. Solid lines indicate demonstrated effects, dashed lines indicate probable effects. See text for details of measures and magnitude of effects.

survival reaches 90% (approximately 27% higher than in wild-foraging groups); and interbirth intervals are reduced almost 6 months for females whose most recent offspring is still alive, from about 22 months in the wild-feeding groups to 16 months in Lodge Group (if infants die, the female always conceives again within a 2–3 months of the death; hence, we included in our analysis only interbirth intervals after surviving infants; Fig. 2a; see also Altmann and Alberts, 2003).

The wild-foraging groups also actively improved their foraging environments, through marked home-range shifts. Both of the original study groups, Alto's and Hook's Groups, abandoned the home range they had occupied in the central Amboseli basin during the 1970s and 1980s. These original home ranges experienced extensive die-off of fever trees, *Acacia xanthophloea*, during the 1960s, 1970s, and 1980s (Western and van Praet, 1973; Young and Lindsay, 1988; Altmann SA, 1998, pp. 15–19). In each case, the groups moved 5–6 km west (Alto's in 1987–88, Hook's in 1991–92), to a home range still within the Amboseli basin, but that showed little or no overlap with their previous home range (Bronikowski and Altmann, 1996; Alberts and Altmann, 2001; Altmann and Alberts, 2003). The new home ranges contained a relatively high density of *A. xanthophloea* trees, which are important food and refuge species for baboons. These home-range shifts resulted in life-history changes that were similar to those experienced by Lodge Group (Fig. 2a), although more modest in magnitude. Infant survival increased nearly 40%, from 51% to 70%. Age at maturity for females occurred 5 months earlier, and interbirth intervals for females with surviving offspring was reduced from 1.8 to 1.6 years (Fig. 2a; see also Altmann and Alberts, 2003).

These changes within a single population, even for completely wild-foraging animals, may explain observed differences in parameters from other sites (e.g., differences in age at maturity, interbirth interval, and infant survival in Gombe, Gilgil, Mikumi, and Amboseli; compare e.g., Strum and Western, 1982; Altmann et al., 1988; Bercovitch and Strum, 1993; Wasser et al., 1998; Rhine et al., 2000; Packer et al., 2000; Altmann and Alberts, 2003). That is, as foraging conditions change within and between populations, life-history parameters change.

Because high rates of reproduction incur a survival cost to females or to their semi-independent previous infant under some conditions (Altmann et al., 1988; Altmann and Alberts, unpubl. data), female reproductive output may be under stabilizing selection in a balance between survival and additional offspring production (see Fig. 2a).

SOCIAL LIFE AS A SOURCE OF VARIABILITY IN REPRODUCTIVE SUCCESS

Not only is variability in reproductive success induced by variability in the foraging environment, it is also affected by the social environment. The impact of social environment generates more intragroup variability than the foraging environment does, and differs considerably between the sexes. Here we consider group size (a measure of immediate density) and dominance status, first for females and then for males.

Females

The number of females in Amboseli groups varied from about 5–25 and total group size from 15–60. When group size is small, and especially when the number of adult females in a group is few, interbirth interval (for females whose most recent offspring survived infancy) is approximately 13% shorter (Fig. 2b; see also Bulger and Hamilton, 1987; Rhine et al., 1988; Wasser and Starling, 1988; for density effects in other populations). Viewed alternatively, an increase of 10 adult females in a group was associated with a 2.5-month increase in interbirth interval for females whose most recent offspring survived infancy (again, interbirth intervals after the death of an infant were excluded from the analysis).

These costs of living in larger groups are borne disproportionately by females who are of lower dominance rank (Fig. 2b). A 10-rank difference in dominance status was associated with a 2.5-month difference in age of menarche and a 1.5-month difference in interbirth interval (Altmann et al., 1988; Altmann and Alberts, 2003; see also Bulger and Hamilton, 1987; Bercovitch and Strum, 1993; Packer et al., 1995). Thus, low-ranking females in larger groups incur a considerable cost to their reproductive success — they will produce, on average, one offspring fewer than high-ranking females over the course

of a 12-year reproductive career, if they live that long. What is a female in a matrilocal species to do in order to mitigate these costs? Fissioning of groups is common in the rapidly expanding cercopithecine groups that are "food-enhanced," such as the Lodge Group in Amboseli, but is only very rarely seen otherwise. Three such fissions have occurred in Amboseli wild-foraging groups (Fig. 1). By fissioning, low-ranking females escape the reproductive costs of living in a group with many other females (see review in Bercovitch, 1991). However, this does not mean that fission is always the best option for low-ranking females. If large groups provide greater protection against predators or in competition with other groups for scarce resources, then fission itself imposes a cost. The balance between the costs and benefits of large group size will differ among females and will be habitat-dependent; a great deal of flexibility in behavior will be required to achieve an optimal balance.

Males

How is male reproductive success affected by group size and by the male's dominance status? A group that has many females in it would at first consideration seem to be one in which a male would have more mating opportunities, and hence a good one for a male to join. In other words, whereas a group with many females may not always be a good thing for a female, particularly a low-ranking female, it should be so for a male. Males do join groups that have more females, so groups with more females end up with more males; males go where the females are, although they also experience constraints that prevent them from distributing themselves perfectly across available females (Alberts and Altmann, 1995; Altmann, 2000; see reviews in Mitani, 1996; Nunn, 1999).

Male dominance rank accounts for approximately 50% of the variance in mating success — this is true across cercopithecine species, among populations of baboons, and within the Amboseli population across years and groups (Fig. 3; Hausfater, 1975; Cowlishaw and Dunbar, 1991; Bulger, 1993; Alberts et al., 2003). In a small group, the top-ranking male may be able to monopolize all the matings, but much of the time no females may be in estrus. In a group with many females, estrus females will be available on more days of the year. However, a number of variables — group dispersion, visibility, the greater opportunity for other males to form coalitions that challenge the top-ranking male — may limit the top-ranking male's ability to completely monopolize matings, even when only a single female is in estrus (Cowlishaw and Dunbar, 1991; Bulger, 1993; Alberts et al., 2003). In Amboseli, we found that both the number of other males and the length of tenure of the top-ranking male (the stability of the hierarchy at the top) predicted the relationship between male rank and mating success.
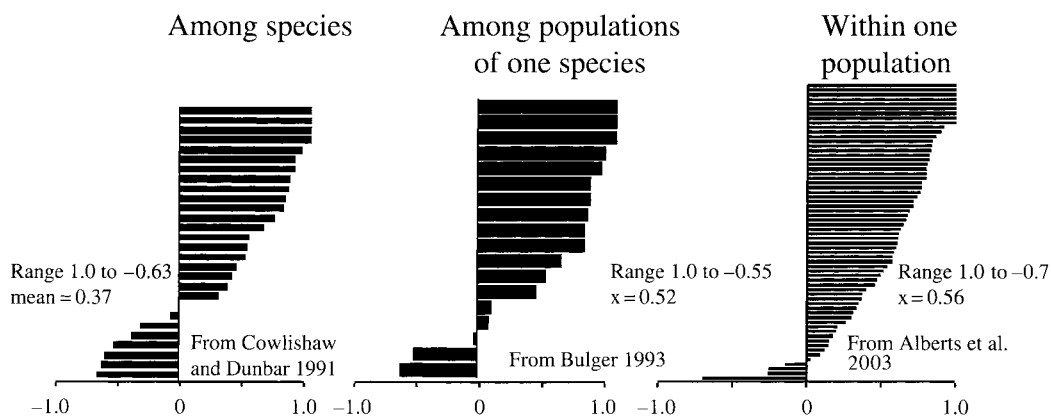

Fig. 3. Variance in the relationship between male rank and mating success. Each graph shows the distribution of Spearman correlation coefficients for the relationship between male rank and mating success. Similar variance occurs at all levels of analysis; among species, among populations of a single species, and within a single population.

When the top-ranking male had been in the highest-ranking position for a long time, and when few other males were in the group, rank was a good predictor of a male's mating success (Alberts et al., 2003).

Thus, the effects of group size and dominance status on male mating success will be a complex function of these variables and others, including number of cycling females, and perhaps individual social skills that lead to matings through means other than dominance, such as coalitions or female choice (literature reviewed in Alberts et al., 2003). Males can certainly leave a group and search for one with a more advantageous mating situation. However, such emigration comes with a number of costs: dispersal entails higher predation risks, opportunity costs while searching for another group to enter, the risk of suboptimal choice of group due to imperfect knowledge of available groups, and resistance by group males to entry of new males (Alberts and Altmann, 1995a; Altmann, 2000). These are to be "weighed against" the potential of obtaining additional mating opportunities. In addition, even though baboons are not characterized by a high degree of paternal care, males perform behavior that may enhance the survival of their offspring (Altmann, 1980; Stein, 1984; Noë and Sluijter, 1990; Bercovitch, 1995; Palombit et al., 1997). A male that has previously had mating success in a group can protect his offspring in intragroup aggression (including, at the extreme, infanticide; see chapters in van Schaik and Janson, 2000), may facilitate food acquisition by the infant (reviewed in Altmann SA, 1998), and may sometimes carry the infant or protect it against predators. How important paternal behavior is in offspring survival and what mechanisms males use to identify their offspring is a major unanswered question for any nonhuman primate. An integration of genetic, behavioral, and perhaps endocrine studies are needed.

CONCLUSIONS

Baboons exhibit a high degree of plasticity in components of reproductive success. This feature enables them to adjust to changing conditions, to capitalize on transient good conditions, to slow down and "wait out" poor conditions, to make major shifts in home range that provide enhanced conditions, and to respond to the social environment in ways that mitigate negative effects of density and social status. This plasticity is facilitated by a number of characteristics: a high degree of selective omnivory (see review in Altmann SA, 1998), relatively large social groups, particularly imposing adult males that provide defense against predators, and nonseasonal reproduction, an unusual trait among primates that is restricted primarily to humans, chimpanzees, and gorillas. The neuroendocrine and other physiological mechanisms of this plasticity remain an important topic of investigation, one that parallels a major area of human research in several disciplines (see synthetic reviews in Dixson, 1998; Hrdy, 1999; Ellison, 2001; other articles in this volume).

In this article, we have tried to give a sense of the great variance in reproductive parameters that is seen within this single species. We have also highlighted some of the sources of the variance that parallel sources known in humans, as well as the significant role of behavior in creating this variance. Major gaps in our knowledge remain, particularly of the mechanisms mediating both the variance and the behavioral responses that enable individuals to respond to conditions and to change them (see also Altmann and Alberts, 2003). When comparable analyses become available for other species, including ones with different social systems, comparative studies may ultimately be able to examine interspecific differences in variability in reproductive success and in plasticity of responses (Lee and Kappeler, 2003; Pereira and Leigh, 2003). Relatively large species with slow life histories experience considerable variability in environment from season to season and year to year, as well as smaller directional changes in habitat and climate (e.g., Altmann et al., 2002, for Amboseli). Physiological and behavioral plasticity may have been significant in primate evolution and in current environments as a mechanism of adapting life-history components to variable conditions.

ACKNOWLEDGMENTS

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