

Life History of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya

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Abstract Comparative data from wild populations are necessary to understand the evolution of primate life history strategies. We present demographic data from a 29-yr longitudinal study of 8 groups of individually recognized wild blue monkeys (*Cercopithecus mitis stuhlmanni*). We provide estimates of life history variables and a life table for females. Most females had their first infant at 7 yr. The mean interbirth interval was 28 mo, and decreased from 31 to 18 mo if the first infant died within a year. Interbirth intervals did not differ according to infant sex, but females had longer intervals after their first vs. subsequent births. Infant mortality was 23% and did not differ strongly by sex or mother's parity. Maximal female lifespan was 32.5–34.5 yr. Across the lifespan, both survivorship and fecundity showed typical primate patterns. Survivorship was lowest in infants, leveled off among juveniles, and then decreased gradually with increasing age in later life. Fecundity was highest among young females and decreased among older females. Births were seasonal, with 64% occurring within 3 mo at the end of the dry season and beginning of the wet season. Survival to 12 mo was higher for infants born during drier months. Birth season timing is plausibly related to thermoregulation of infants, weanling foods, or maternal energy demand. Blue monkeys are a forest-dependent species with a very slow life history and relatively low immature and adult mortality rates compared to closely related guenons living in open habitats. Even among cercopithecines as a whole, they appear to have an exceptionally slow life history relative to body size. Differences in life history “speed” between blue monkeys and their close relatives

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seem to be related to lower juvenile and adult mortality in forests relative to more open habitats.

Keywords age at first birth · birth seasonality · fast-slow continuum · infant mortality · interbirth interval · life table · survivorship

Introduction

The study of animal life histories is important for understanding the behavioral strategies of individuals and the dynamics of populations. Life history traits both influence and are influenced by behavioral and ecological variables (Altmann and Alberts 2003; Kappeler *et al.* 2003). In gregarious animals, for example, life history and demographic processes affect the size and composition of social groups, which influence in turn the behavior of individuals whose choice of mates or social partners, and whose competitors, are constrained by their availability (Dunbar 1987). Studies of life history and demography are also important for conservation purposes, for which an understanding of population trends over time is essential (Alberts and Altmann 2003; Dunbar 1987).

Primate life histories are slow relative to those of other mammals, and several evolutionary explanations have been advanced to explain this difference, including the high energetic cost of large primate brains, high juvenile mortality risk, and the typically arboreal lifestyle (Kappeler *et al.* 2003). Among primate taxa, there is also considerable variation in life history characteristics. As in other mammals (Millar and Zammuto 1983), many life history variables correlate strongly with body size (Ross 1998) and brain size (Deaner *et al.* 2003), which in turn may be associated with differences in behavior and ecology (Ross 1998). However, increasing knowledge of primate life histories has revealed that observed variation is not easily explained by body size alone, or by any other isolated factor.

Environmental variability and the effects of ecologically determined variation in mortality are now known to be major selective forces on life history evolution generally (Reznick *et al.* 2002). Variable life history traits in natural populations are viewed as adaptations to extrinsic mortality rates (Charnov 1993). Thus high juvenile mortality or high adult mortality, or both, should lead to the evolution of faster life histories (faster growth, early maturation, higher fertility, shorter lifespan), whereas the converse would be expected for low mortality rates (Promislow and Harvey 1990). Considering 72 primate species and controlling for body size, Ross (1992a) found that faster life histories were associated with life in more open habitats, whereas slower life histories characterized species living in tropical rain forest. She attributed these differences to higher mortality rates in the more seasonal, less predictable open environments (Ross 1998). However, because habitat preferences correlate with phylogeny, she called for further comparative study of closely related taxa (Ross 1992b) to control for a potential phylogenetic confound. In addition, she noted that data on mortality would be essential to interpret any habitat-related patterns.

The guenons provide a promising opportunity to examine habitat effects on primate life histories, as this species-rich tribe of similar-sized Old World monkeys includes

species that live in disparate habitats, from dry and highly seasonal savanna-woodland to rain forest (Butynski 2002a). Isbell *et al.* (2009) recently compared the 2 open-country forms, vervet (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*), and related differences in their life histories to differences in mortality patterns. Here, we present the first extensive life history data set from a highly arboreal, forest-dependent guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*). Based on a 29-yr field study of identified individuals, we describe life history parameters of female blue monkeys, including age at first birth, interbirth interval, infant survival, offspring sex ratio, and longevity. Based on age-specific birth and death rates, we provide a life table for female blue monkeys. Lastly, we describe timing of births and consider adaptive explanations for observed breeding seasonality.

These data allow us to extend the comparison of Isbell *et al.* (2009) within the cercopithecine tribe (the guenons) to a markedly different habitat, and thus to evaluate further the importance of mortality patterns in predicting fast vs. slow life histories. In addition, and from a broader perspective, whereas most life history studies of natural populations in the cercopithecine subfamily have focused on terrestrial or semiterrestrial species living in relatively seasonal and unpredictable savanna-woodland habitats (Table 1), our report contributes data from an arboreal forest-dwelling species, most of which remain poorly known, especially in nature (Ross 1998).

Methods

Study Site and Population

The focal population inhabits the Isecheno site of the Kakamega Forest, Kenya (0° 19' N, 34° 52' E, 1650 m), an 85-km² rain forest fragment that was once part of a more extensive central African forest belt (Mitchell *et al.* 2009). Annual rainfall averages about 2000 mm. Rain falls seasonally, although the exact timing of wet and dry seasons varies interannually. Temperatures are fairly stable throughout the year, averaging 18.7°C (Mitchell *et al.* 2009).

Blue monkeys at Isecheno occur at a relatively high density of 170–220 individuals/km² (Fashing and Cords 2000). We collected demographic and reproductive data from 418 individuals in 8 habituated groups for varying periods. We monitored T group from 1979 to 1984, when it fissioned into Tw and Te. We monitored Te until 1989, and Tw until 2005, when it fissioned into Twn and Tws, each of which we monitored through December 2008, the end of the study period. We observed G group from 1993 to 1999, when it fissioned into Gn and Gs, for which data also extend through 2008. Except for group fissions, demographic changes within groups were caused only by births, deaths, and the emigration of natal males. Females are strictly philopatric (Cords 2002b). Although some males entered the focal population as adults, we were unable to estimate their ages, and did not include them in our data set.

We recognized subjects individually via natural characteristics. Although we distinguished all adults from the first months of study of their groups, juvenile identification was not fully accurate until about 1997.

Table 1 Comparative reproductive parameters for cercopithecine monkeys, including only wild, nonprovisioned and non-heavily-hunted populations

Species	Location	Habitat	Study length (yr)	Female body mass (kg)	Age at first birth (yr)	Interbirth interval (mo)		Infant mortality (≤ 12 mo)	Reference
						Population-wide	First infant lived 1 year		
<i>Cercopithecus mitis</i>	Kakamega, Kenya	Rain forest	29	4.2	7.2 (66)	27.9 \pm 11 (256)	30.7 \pm 9.3 (193)	23% (341)	This study
<i>Chlorocebus aethiops</i>	Amboseli, Kenya	Savanna woodland	7	2.98 ^b	4.4–5.7	13.8 \pm 3.5–21.3 \pm 5.0 ^a		57%	Cheney <i>et al.</i> 1988
	Laikipia, Kenya	Savanna woodland	10		5.1 \pm 0.8 (3)	13.3 \pm SE 0.6 (31)		48% (10)	Isbell <i>et al.</i> 2009
<i>Erythrocebus patas</i>	Kala Maloue, Cameroon	Savanna woodland	14	6.3	3.1 (9)	14.4 MD=12.4 (33)	14.5 MD=12.4 (28)	43% (117)	Nakagawa <i>et al.</i> 2003
	Laikipia, Kenya	Savanna woodland	2+10		3 (24)	12.9 \pm SE 0.8 (29)		22%; 26% (85)	Chism <i>et al.</i> 1984; Isbell <i>et al.</i> 2009
<i>Macaca fascicularis</i>	Ketambe, Sumatra, Indonesia	Rain forest	12	3.6 ^b	5.2 (22)	22.6 ^c	29.3 ^c		van Noordwijk & van Schaik 1999
<i>Macaca sinica</i>	Polonnaruwa, Sri Lanka	Dry ever-green forest	6.5	3.6 (24)	~4.5–5 ^d	~17.4 ^c		53% (38)	Dittus 1975, 2004
<i>Macaca cyclopis</i>	Mt. Longevity, Taiwan	Rain forest	5	~5	5 (79)	13.4 \pm 4.2 (288)		16% to ~6 mos	Hsu <i>et al.</i> 2001, 2006
<i>Macaca maurus</i>	Karenta, Sulawesi, Indonesia	Rain forest	10	6.1 ^b	6.5 (6)	22.4 \pm 6.4 (33)	24.1 \pm 5.7 (27)	17.1% (35)	Okamoto <i>et al.</i> 2000
<i>Macaca fuscata</i>	Yakushima, Japan	Broadleaf evergreen forest	19	8.03 ^b	6.1 \pm 0.9 (17)		26.9 \pm 10.2 (42)	25% (76)	Takahata <i>et al.</i> 1998
	Kinkazan, Japan	Broadleaf deciduous/ coniferous forest	9		7.1 \pm 0.9 (20)		28.4 \pm 6.8 (49)	23% (97)	Takahata <i>et al.</i> 1998
<i>Macaca sylvanus</i>	Algeria (2 sites)	Cedar/oak + deciduous/ oak forest	8	11 ^b	5.3 (10)–5.5 (17)				Menard and Vallet 1993
<i>Papio hamadryas cynocephalus</i>	Tana River Primate Reserve, Kenya	Riverine forest + savanna ^e	4.7	9.0 \pm 0.5 (14)		27.9 \pm 6.0 (13)		12% (35)	Bentley-Condit and Smith 1997; Bentley-Condit 2009

	Mikumi, Tanzania	Savanna woodland	20		6.5 CI=6.1–6.9 (27)	21.3			Rhine <i>et al.</i> 2000
	Amboseli, Kenya	Savanna woodland	13	11.9	6.5 MD=5.8 (97)		21 (9)	45% (30)	Altmann <i>et al.</i> 1977, 1993; Charpentier <i>et al.</i> 2008
<i>Papio hamadryas anubis</i>	Gashaka-Gumti National Park, Nigeria	Forest + savanna woodland ^f	5	13.3 ^b			29.9 ^g (2)	47%(19)	Higham <i>et al.</i> 2009
	Gilgil, Kenya	Savanna woodland	10		5.8–7.7		25.0±SE 1.1 (23) ^h	28% (39)	Smuts and Nicolson 1989; Strum and Western 1982
<i>Papio hamadryas hamadryas</i>	Erer Gota, Ethiopia	Semi-arid bushland	5.5	11.5	6.1 R=5.5–7 R (8)		22 R=18–28 (12) ⁱ	18% (40)	Sigg <i>et al.</i> 1982; Swedell 2010
<i>Theropithecus gelada</i>	Simien Mountains, Ethiopia	Mountain grassland	~2	14	4–4.5	28.7 ^g			Dunbar 1980; Swedell 2010
<i>Papio hamadryas ursinus</i>	Moremi, Botswana	Savanna woodland	10	15 ⁱ	6.8 R=5.8–7.9 (28)		23.6±2.8 –24.9±2.7	38% (42)	Cheney <i>et al.</i> 2004
	Drakensberg, South Africa	Mountain Grassland	1.5	15		38 ^c		7% by 2 yr (16)	Lycett <i>et al.</i> 1998

Tribe cercopithecini listed first, papionini second, ordered by habitat (forest, nonforest) and then by female body mass. Mean ± SD and sample sizes (in parentheses) given when available; other summary statistics, from original reports, include *MD* median, *R* range, *SE* standard error of the mean, *CI* 95% confidence interval

^a Range of means ± SD for 3 groups

^b Smith and Jungers (1997)

^c Interbirth interval calculated as inverse of fertility rate, i.e. (X infants/adult female/year)^{−1}

^d Estimated age at first pregnancy

^e Riverine forest accounts for 9% of area, but used 42% of time by baboons; savanna accounts for remainder

^f Rain forest accounts for 65% of area and savanna bushland for 35%

^g We calculated the second value for Gashaka-Gumti and the sole value for Simien Mountains by adding mean post-partum amenorrhea, cycling duration, and gestation length

^h The first infant survived until the mother conceived again

ⁱ Stillbirths and neonatal deaths excluded, the first infant survived 24 mo

The Isecheno monkeys were never provisioned, but beginning in 1997, the Tw group (and its progeny, Twn and Tws) included in their home ranges a forest station with indigenous and exotic plants, as well as some intermittently available human-associated food (refuse, drying maize). We are unable to provide quantitative estimates of the amount of food enhancement that resulted from this change in home range. However, comparisons of groups with vs. without access to the station, as well as the T group before vs. after they used the station, revealed no changes in life history parameters (data not shown), suggesting that access to these food sources had negligible effects.

Sources of mortality in the focal population are poorly known. Crowned eagles (*Stephanoetus coronatus*) prey on blue monkeys (Struhsaker and Leakey 1990), and are regularly seen in the forest. Monkeys respond behaviorally as if eagles are dangerous (Cords 2002a). However, the only confirmed case of predation on blue monkeys at Kakamega, was 1 case of fatal snakebite (Förster 2008). Disease has never been diagnosed, but a few individuals became weak and lost weight precipitously, or showed subcutaneous lumps or lesions before they disappeared or died. A few individuals were likely to have died of injuries. Although most local people have cultural taboos against eating monkeys, we occasionally discovered monkey traps and witnessed hunting dogs in action, and we know that local people tried to kill crop-raiding monkeys. Although the females and juveniles in our focal groups did not raid crops, it is likely that some traps we found were set for unselective retribution.

Collection of Demographic Data

During the 29-yr study period (1979–2008), observations occurred on a variable schedule. From June 1997 to December 2008, observers made near-daily contact with each group, whereas contact was more intermittent in earlier years, averaging 12 d/mo throughout the year (1979–1981), or 2–5 mo of near-daily records per year, with intervening gaps averaging $5.5 \pm \text{SD } 3.1$ months (maximum 11, $N=22$, 1982–1997). We recorded all births, deaths, disappearances, and emigrations. In years with intermittent observation, it is possible that females gave birth and lost neonates without our noticing. We have therefore reported summary statistics (mean \pm standard deviation) for the entire study period, and also separately for the post-1997 period, when monitoring was essentially continuous.

There were very few cases of confirmed death when a carcass was actually found or an individual was seen weak or emaciated immediately before disappearing. Therefore, we inferred most deaths based on our knowledge of the species' behavior. Given strict female philopatry, most females that disappeared from their groups were presumed dead. Males were generally presumed dead if they disappeared at an age <7 yr, the mean age of confirmed natal emigration (Ekernas and Cords 2007). Most infants that disappeared in the first year of life were presumed to have died: these individuals were often not identifiable without reference to their mothers, so we interpreted an absence of maternal nursing over a 2-mo period as indicating infant death. Exceptions to the aforementioned "rules" involved some infants and juveniles that disappeared early in the study: our limited ability to track immature individuals continuously at that time, along with significant gaps in population monitoring,

meant that these individuals may simply have become unrecognizable as they became independent of their mothers or grew. Such individuals were right-censored, classified as having unknown fates after their last confirmed sighting. We distinguished male emigrations from disappearance by resighting the individual in a new location.

We knew the birthdates of infants born into the focal groups ($N=359$) to the day (58%), a few days (12%), a month (21%), a few (1–4) months (6%), or a year (3%). When we did not know birth dates to the day, we assigned them to the midpoint of a range of possible values.

We either knew the birthdates of mothers ($N=43$) or estimated them ($N=23$). Known maternal birthdates characterized individuals born during the study. Estimated birthdates characterized mothers that we first identified as older juveniles, mainly in early years of the study. We estimated their birthdates based on body size categories (small, medium, large) assigned at first sighting and subsequent changes therein. Once we were able to identify juveniles continuously from birth (*ca.* 1997), it became possible to calibrate size classes to known ages, enabling retrospective age estimation. Because each size class spanned ages that varied by 2–3 yr, our estimated ages had an error of 1–2 yr. There were 36 additional females, identified as adults of unknown age early in the study. Thirty-four of them gave birth during the study period. They were included in only some of our analyses because of the great uncertainty concerning their ages.

Life History Variables and Life Table Analysis

We used age-specific survivorship and fecundity rates to calculate survival and fertility rates, and from these we constructed a life table based on a yearly interval scale. We included the births and deaths of individuals present at the start of the study as well as those born into the population. Thus, although we did not follow a cohort, we combined information from individuals born at different times as if they were a cohort. For males, survivorship data generally extended only through the time of emigration when we usually lost track of them, with the exception of a few males that we subsequently resighted in other groups. We did not analyze male fertility because males did not copulate in their natal groups, and paternity was unknown.

Survivorship analyses included all individuals known or presumed to have died, those still alive at the end of the study period, and right-censored individuals that dropped out of the observational records but could not necessarily be assumed dead. We knew or estimated birth dates based on body size changes as described above. For 36 adult females with no known history when identified early in the study, we roughly estimated a birth date by subtracting 5 yr (the minimum known age at first birth) from the date of the first recorded birth ($N=34$) or first sighting when they did not give birth during the study period ($N=2$). These estimates represent the latest possible birth date, which means that estimates of the age at death are minimum estimates. We knew death dates either to the day or estimated them to a period of a few days to several months.

Specifying an individual's age at death to the day was possible only when both birth and death dates were precisely known ($N=6$). In addition, there were 7 perinatal deaths, in which an apparently full-term infant was dead the first time we

saw it carried by its mother. In all other cases, we did not precisely know birth or death date, or both, so we calculated a range for the age at death using estimated birth or death dates, or both, and then used the minimum of this range to estimate the individual's minimum survival. We assigned confirmed or assumed deaths to specific age classes and calculated the exact time spent in that age class until death. We similarly calculated the amount of time spent within the last age class until disappearance by individuals whose fates were unknown or until the end of the study for individuals still alive then.

With these data, we calculated age-specific hazard rates, H_i , as N_i/T_i , where N_i is the number of individuals that died in the i th age class and T_i is the total amount of time spent in the i th age class by all individuals that entered that age class, whether they died, survived, or were right censored in it (Alberts and Altmann 2003). Finally we calculated age-specific survivorship, $l(i)$, as $l(i) = (1 - H_i)l(i - 1)$, starting with $l(0) = 1$, which is the survivorship of all newborns (Alberts and Altmann 2003).

Survival, P_i , is defined as the probability that an individual in age class i will survive from one time step to the next. It is calculated directly from survivorship rates (Alberts and Altmann 2003; Caswell 2001) as $P_i = (l(i) + l(i + 1))/(l(i - 1) + l(i))$ where $l(i)$ = survival from birth to age class i . We used hazard rate survivorship to calculate survival rates for the life table.

For comparison with other studies, we also calculated annual mortality rates for each year of the study. Annual mortality was the number of individuals that died during each year as a proportion of the number of individuals alive at the beginning of the year.

We calculated fecundity as the average number of male and female offspring born in each maternal age class (Alberts and Altmann 2003; Caswell 2001). We included only 65 adult females with known birth dates or those estimated from changes in body size. We did not include the 34 mothers whose birthdates we roughly estimated by counting back 5 yr from first observed birth because of the great uncertainty in their ages.

A female's age at each of her births could be influenced both by uncertainty in her age if her own birthdate was estimated (with an error of 2 mo–2 yr) and by uncertainty in the birthdates of her offspring (with an error of 1 d–4 mo). We knew birthdates of many offspring (225/239) to the day or to the month. However, we often did not know mothers' dates of birth exactly, which affected how precisely we could specify the mothers' age at reproduction. We estimated mothers' age at birth to the day in 32% of 239 births, to ± 1 d for 13%, 2–30 d for 5%, 1–12 mo for 32%, to 1–2 yr for 14%, and to 2.2 yr for 3% of births.

Because we calculated the life table based on a yearly interval, we had to assign each birth to an age class that spanned 12 mo. In a few cases, the mother's age range at her offspring's birth spanned an interval >12 mo. Here we prorated the birth to different intervals based on the amount of their overlap with the range of possible birthdates. As a result, the number of births assigned to a particular age class was not necessarily an integer. In cases of substantial uncertainty about the age of a female, coupled with >1 birth in quick succession, an age class may contain the chances of birth from 2 consecutive births, which we summed to get the total number of births at that age.

To calculate age-specific fecundity, we divided the number of births in each age class by the number of females in that class. However, some uncertainty was

introduced in summing the number of reproductive females in each age class, because some females died during a 12-mo interval. If we knew age at death exactly, we could simply prorate the female's presence in her final annual period. When the age at death was a range, we apportioned a female's presence in multiple age classes according to the overlap between them and the date range of her death. As a result, the number of females present in a given age class was not always an integer value.

The fertility rate, F_i , for an age class i is the expected number of female offspring born to a female entering the i th age class. It can be calculated from fecundity rates, m_i (Alberts and Altmann 2003; Caswell 2001) as $F_i = l(0.5)[(m_i + P_i * m_{i+1})/2]$, where $l(0.5) = l(0)\sqrt{l(1)}$. Because we based fecundity rates, m_i , on both male and female births, and because the birth sex ratio did not deviate from 1:1, we calculated fertility rates for female offspring, F_i , by dividing fecundity rates, m_i , by 2.

Analysis of Birth Seasonality

We investigated the distribution of births by month. We included only births assigned to a period of ≤ 3 mo ($N=347$). Where the birth date range spanned >1 calendar month, we assigned the probability of birth to each month in proportion to the number of days in the birthdate range included in that month. To explore the adaptive value of birth seasonality, we compared survivorship of infants born in wet vs. dry seasons, and in peak vs. nonpeak months. We classified a month as wet if its average rainfall exceeded the mean monthly rainfall, and dry otherwise. We also compared the subsequent interbirth interval for mothers whose first infant was born in peak vs. nonpeak months.

Results

In the 29-yr study period, we registered 359 births (132 male, 136 female, 91 undetermined) to 100 females. The overall sex ratio of 49% males was not significantly different from a null expectation of 50% (binomial test, 2-tailed $p=0.86$).

Age at First Reproduction

Most first births (94%) occurred between the ages of 5 and 8 yr inclusive, with 6- and 7-yr-old females accounting for two thirds of all births (Fig. 1). The mean age at first birth for 43 females with birthdates known at least to the month was 6.9 ± 1.0 yr (range 4.6–9.1, median 7.0). If we included 23 females with birthdates estimated based on descriptions of changing body size, mean age at first reproduction for all 66 females was 7.2 ± 1.1 yr (range 4.6–10.8, median 7.2, Fig. 1). For these 23 females considered separately, the age at first birth was 7.8 ± 1.1 yr (range 5.8–10.8, median 7.9) when we used midpoints of the range of estimated age at first birth. For the period 1998–2008, when we monitored the groups more intensively, the mean age at first reproduction of females with both known and estimated ages was 7.1 ± 1.1 yr (range 4.6–9.7, median 7.2, $N=41$).

The mean ages at first reproduction of the females with known vs. estimated birth dates differed significantly (unequal variance t -test: $t'=-3.2$, $df=44$, $p=0.002$;

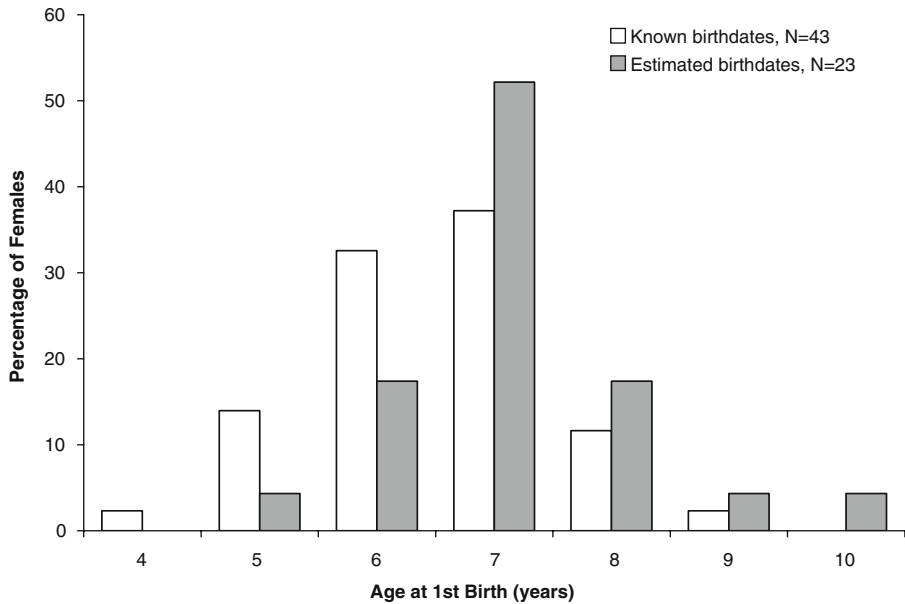


Fig. 1 Distribution of age at first reproduction for 66 females whose own birthdates were known (*white bars*, $N=43$) or estimated based on body size changes (*gray bars*, $N=23$).

Ruxton 2006). Exclusion of two outliers in the estimated set, each >2 standard deviations above the mean, did not change the significance of this difference.

Interbirth Intervals

Most (40%, $N=256$) interbirth intervals (IBIs) were 2–3 yr. Intervals slightly shorter than the mode (1–2 years, 34%) were more common than those slightly longer (3–4 yr, 15%). Intervals <1 yr (6%) or >4 yr (5%) were rare. Mean IBI was 27.9 ± 11.0 mo (range 7.2–81.9, median 25.3, $N=256$ intervals). If we averaged mean values per female, the mean IBI was 29.2 ± 8.6 mo (range 8.4–59.4, median 28.2, $N=74$ females). When we limited analysis to the period of more intensive population monitoring (1998–2008), interbirth intervals averaged 25.3 ± 9.7 mo (range 7.2–59.8, median 24.1, $N=141$ intervals).

IBIs were significantly shorter if the infant died within the first year of life (17.6 ± 8.8 months, range 7.2–46.9, $N=53$) than when it survived to ≥ 1 yr (30.7 ± 9.3 mo, range 10.5–62, $N=193$; $t'=-9.4$, $df=86$, $p < 0.001$; 10 infants with unknown fate within the first year excluded). The same difference occurred when we analyzed data from 1998 onward only (when monitoring was most continuous): intervals after infant death within 1 yr (16 ± 8 mo, range = 7.2–46.4, $N=39$) were shorter than those after infant survival to ≥ 1 yr (28.8 ± 7.7 mo, range = 10.5–59.8, $N=102$; $t'=-8.6$, $df=66$, $p < 0.001$).

Infant sex did not affect subsequent IBIs: intervals after the birth of males that survived 12 mo averaged 30.9 ± 8.8 mo (range = 10.5–62, $N=88$) whereas females averaged 29.6 ± 9.2 mo (range = 13.5–59.8, $N=90$; $t'=0.96$, $df=176$, $p=0.33$). Again, the result held when we restricted analysis to intervals after births from 1998

onward (IBI after male births: 29.4 ± 6.8 mo, range = 10.5–43.1, $N=49$; IBI after female births: 28.4 ± 8.5 mo, range = 13.6–59.8, $N=52$; $t'=0.64$, $df=96$, $p=0.53$).

Over the entire study period, the IBI after a female's first birth was longer than after subsequent births. For 47 females that gave birth to ≥ 3 infants, the interval after the first birth (29.9 ± 9.4 months, range = 10.7–52.9) was significantly longer than the mean of that female's IBIs after the second and subsequent births (25.8 ± 7.8 mo, range = 11.5–46.9; paired $t=3.1$, $p=0.004$). Only 21 females had their first ≥ 3 births in or after 1998, but in this sample, there was no significant difference between the IBI after primiparous births (26.3 ± 8.9 mo, range = 10.7–43.1) vs. the mean of that female's IBIs after later births (22.6 ± 7.1 mo, range = 11.5–38; paired $t=1.7$, $p=0.10$).

Infant Survival

We were able to evaluate survival to 1 yr for 341 infants, 72% of which (246 of 341) survived ≥ 1 yr while 23% (79 infants) presumably died within 12 mo and 5% (16 infants) had unknown fates. Of infants with known fates, the mortality rate was 24% (79/325). The causes of infant death are not well known. There were six cases of confirmed infant death, after an infant had been seen alive at least once. In addition, there were seven perinatal deaths, in which the mother carried her infant's body for ≤ 2 d: these infants all appeared full term but were never seen alive. We attributed nine deaths to infanticidal attacks by males (Cords and Fuller 2010). Five infant deaths may have been human induced, whether directly or indirectly, including 1 case wherein the mother was found alive with a snare. One death occurred after a hawk disturbed the group repeatedly. Two infants went missing with their mothers, 1 of which was emaciated. The remaining 49 of the 79 infants that died early simply disappeared.

Female infants tended to show a slightly higher survival rate than males (females: 90%, 118 survived, 7 died, 6 right-censored; males: 82%, 101 survived, 17 died, 5 right-censored; Fisher Exact Test, 2-tailed $p=0.071$). Our chances of sexing an infant increased with its age, so data on sex differences in infant survival are likely to be biased toward mortality that occurred later in the first year of life, and 83 infants of unknown sex are excluded from this comparison (of which 53 died, 25 survived, and 5 were right-censored).

Infant survival was indistinguishable for primiparous vs. multiparous mothers. Survival to 1 yr was 74% for primipares (51 survived, 13 died, 5 right-censored) and 72% for multipares (177 survived, 59 died, 10 right-censored; Fisher Exact Test, 2-tailed $p=0.88$). Considering only females with known age, we compared infant mortality for 6 primiparous females whose first birth occurred unusually early (≥ 1 standard deviation younger than the population mean) vs. all other primiparous females. The early-breeding females suffered 50% mortality (3/6), while those breeding at more typical ages lost only 28% of their infants (9/32) in the first year of life. However, this was not a significant difference (Fisher Exact Test, 2-tailed $p=0.357$).

Longevity

Many adult females that died early in the study could not be aged and many that could be aged, accurately or by estimation, are still alive; thus we cannot report a reliable average lifespan. However, we can estimate how long blue monkey females

at Kakamega have lived from a few individual records. The longest-lived female had a lifespan of 32.5–34.5 yr. Two other females lived to 27.9–28.9 yr and 26.7–28.7 yr, respectively. Other estimated lifespans for females whose deaths were likely due to natural causes are 27.4 yr, 23 yr, and 20.8 yr. The female with the longest known lifespan did not give birth during the last 11 yr of her life. Observations were not intermittent, so the long nonreproductive period cannot be attributed to undetected births followed by neonatal death. Two other females lived to ≥ 27 yr; however, each gave birth within 2 yr before her death.

Survivorship, Fecundity, and Life Table

The survivorship curve (Fig. 2) follows the pattern typical of most primate species (Dunbar 1984). Survivorship is lowest in the earliest stage of life, i.e., among infants. Survivorship plateaus during the juvenile period (*ca.* 2–5 yr) and decreases gradually with age in later life. Survivorship declines at a slow pace in younger adult females and after *ca.* 16 yr of age declines more quickly. Survivorship values in the very old age classes (≥ 28 yr) are based on only 1 female.

Annual mortality rates for 1979–2008 for juveniles (yr 2–4 inclusive) averaged 0.05 ± 0.08 (range: 0–0.375). For adult females (≥ 5 yr) they were very similar (0.05 ± 0.05 , range: 0–0.158).

The youngest female to give birth was 4.6 yr old (age class 5, Fig. 3; this was a known age) and the oldest had an estimated age of 26 yr. Blue monkey females appear to maintain fecundity rates > 0.3 for most ages throughout their reproductive

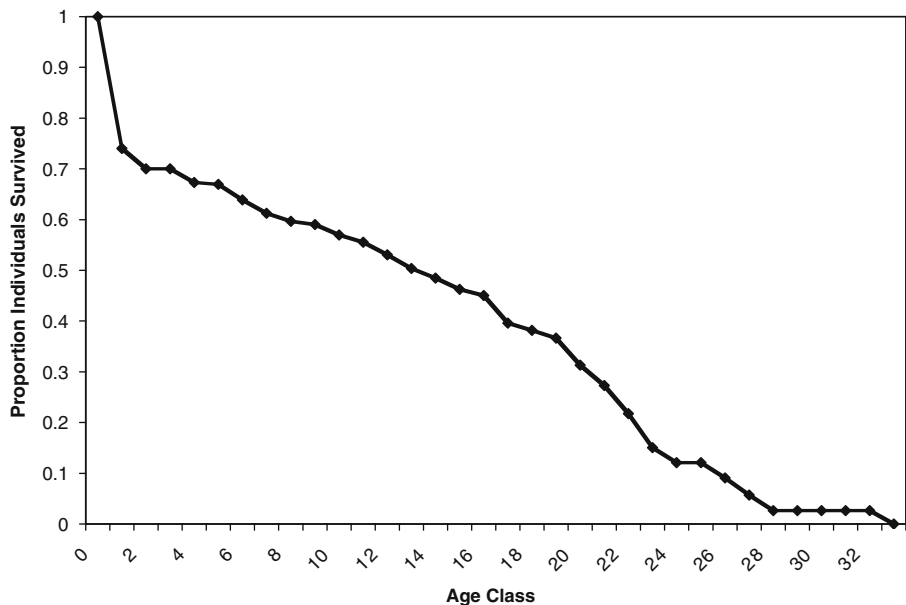


Fig. 2 Age-specific survivorship based on hazard rates calculated from minimum survival ($N=418$ individuals). Age class 0 refers to all newborns, 1 to 0–1 yr old, 2 to 1–2 yr old, and so on.

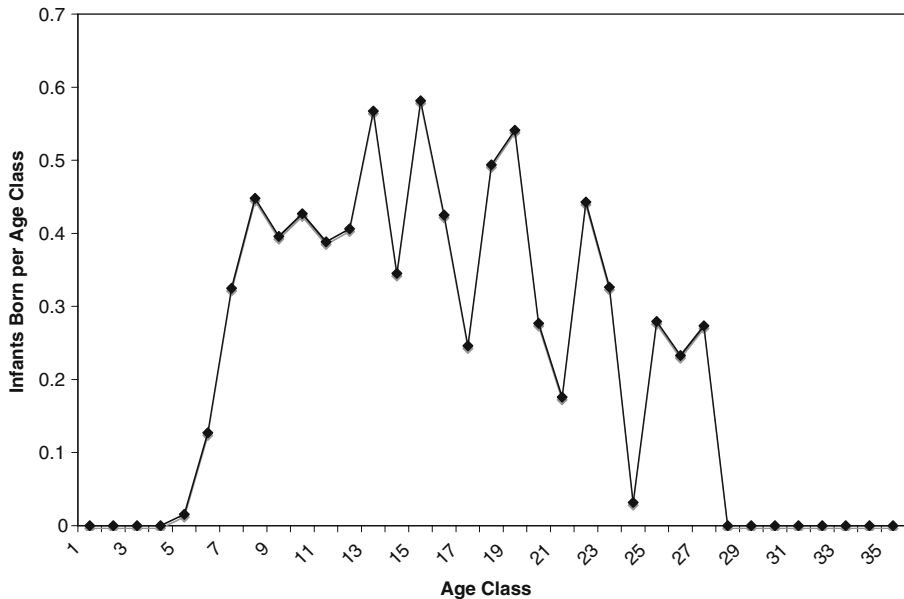


Fig. 3 Age-specific fecundity (includes both male and female offspring; $N=65$ adult females). Age class 1 refers to 0–1 yr old, 2 to 1–2 yr old, and so on.

life. Nevertheless, fecundity does seem to be higher at younger ages and begins to decrease in the late teens.

From survivorship and fecundity rates we calculated survival and fertility rates for female blue monkeys at Kakamega, and present these in a complete life table for all study groups combined (Table II).

Birth Seasonality

Our investigation of birth seasonality included 347 births from 1979 to 2008. We knew or estimated 318 births to the month, and estimated 29 births to 2–3 mo. Births occurred in all months of the year, but were not evenly distributed (Fig. 4). Ninety-one percent of births occurred in the 7-mo period between November and May, and they were particularly concentrated in the 3-mo period of January–March (64% of births). Only 9% of births occurred in the 5-mo period between June and October. Birth frequency showed a clear negative relationship with rainfall (Fig. 4). Most births occurred during the driest season of the year and the subsequent transition to the wettest season of the year; births were generally rare when rainfall was high (May–October). Conception dates are offset from births by 6 mo (gestation length = 176 d; Pazol *et al.* 2002); conceptions peaked during the short rains (July–October).

Survivorship to 12 mo was generally higher for infants born in dry months (November–February, July) than for those born in wet months (March–June, August–October), with the greatest difference at the end of the first year (Fig. 5). However, the proportion of infants, including right-censored individuals, that survived to 12 mo was not significantly different for wet vs. dry months (146/198

Table II Life table for female blue monkeys at Kakamega Forest, Kenya

Age class	Age (yr)	Survivorship, $l(i)$	Fecundity, m_i^a	Survival, P_i	Fertility, $F_i^{b,c}$
0	Newborn	1.0000			
1	0–1	0.7405	0.0000	0.8276	0.0000
2	1–2	0.7000	0.0000	0.9719	0.0000
3	2–3	0.7000	0.0000	0.9809	0.0000
4	3–4	0.6732	0.0000	0.9780	0.0000
5	4–5	0.6697	0.0155	0.9746	0.0300
6	5–6	0.6391	0.1270	0.9562	0.0941
7	6–7	0.6125	0.3247	0.9659	0.1629
8	7–8	0.5965	0.4478	0.9817	0.1799
9	8–9	0.5903	0.3960	0.9776	0.1750
10	9–10	0.5699	0.4270	0.9701	0.1729
11	10–11	0.5556	0.3883	0.9651	0.1678
12	11–12	0.5306	0.4060	0.9523	0.2036
13	12–13	0.5039	0.5672	0.9556	0.1930
14	13–14	0.4846	0.3451	0.9580	0.1941
15	14–15	0.4623	0.5815	0.9639	0.2133
16	15–16	0.4505	0.4252	0.9272	0.1406
17	16–17	0.3959	0.2461	0.9188	0.1505
18	17–18	0.3818	0.4937	0.9624	0.2182
19	18–19	0.3666	0.5412	0.9083	0.1705
20	19–20	0.3131	0.2768	0.8621	0.0922
21	20–21	0.2729	0.1760	0.8365	0.1176
22	21–22	0.2173	0.4428	0.7504	0.1480
23	22–23	0.1505	0.3264	0.7380	0.0753
24	23–24	0.1210	0.0319	0.8911	0.0604
25	24–25	0.1210	0.2795	0.8750	0.1039
26	25–26	0.0907	0.2328	0.6985	0.0912
27	26–27	0.0571	0.2736	0.5651	0.0589
28	27–28	0.0264	0.0000	0.6324	0.0000
29	28–29	0.0264	0.0000	1.0000	0.0000
30	29–30	0.0264	0.0000	1.0000	0.0000
31	30–31	0.0264	0.0000	1.0000	0.0000
32	31–32	0.0264	0.0000	0.5000	0.0000
33	32–33	0.0000	0.0000		

^a Fecundity, m_i , includes both male and female offspring

^b Fertility, F_i , includes only female offspring. Fecundity rates divided by 2 were used to calculate fertility rates (see [Methods](#))

^c $l(0.5) = 0.860501$ was used to calculate fertilities

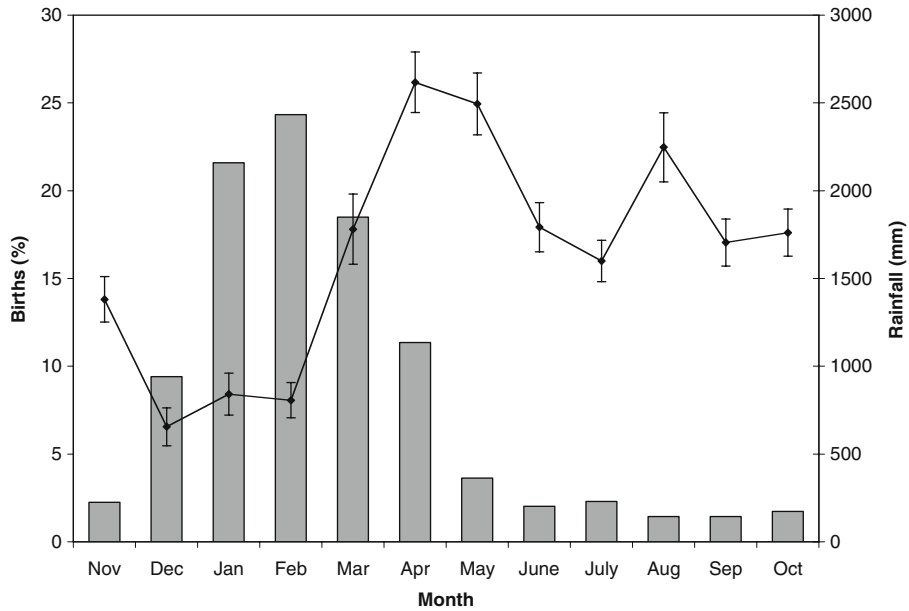


Fig. 4 Monthly distribution of births (bars, $N=347$) and rainfall (solid line, mean \pm SE) from 1979 to 2008.

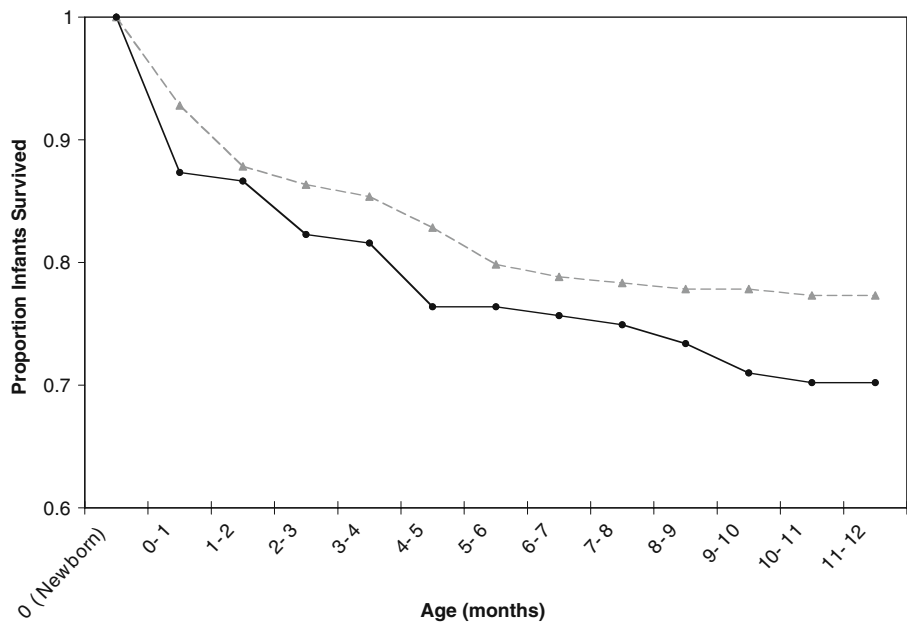


Fig. 5 Survivorship of infants born in the dry season (gray triangles with dotted line, $N=207$) and in the wet season (black circles with solid line, $N=139$).

dry, 89/130 wet; Fisher Exact Test, 2-tailed $p=0.32$). We also examined 12-mo survivorship for infants born in the peak (January–March, 158 survived, 46 died, 8 right-censored) vs. nonpeak birth months (April–December, 77 survived, 35 died, 4 right-censored), but again, the difference was not significant (Fisher Exact Test, 2-tailed $p=0.13$). The subsequent interbirth interval of females that gave birth during the peak months (27.6 ± 10.4 mo, $N=154$) vs. other months of the year (28.1 ± 12.1 mo, $N=94$) also did not differ significantly ($t'=-0.28$, $df=175$, $p=0.78$).

Discussion

Life History of Blue Monkeys Compared to Other Cercopithecines

In comparing our results to other cercopithecine species, we emphasize wild populations. Studies of captive or provisioned cercopithecines have served as important reminders of how differential food availability, predation pressure and disease—which differ for wild vs. human-influenced populations—can affect life history variables within species (Cheney *et al.* 2004; Fa and Southwick 1988). Although some have tried to control for such effects by comparing *only* captive populations (Anderson *et al.* 2008; Ross 1992b; Rowell and Richards 1979), we compare our results from a wild population with other species also studied under natural conditions.

Blue monkeys appear to have a very slow life history in the context of cercopithecine monkeys, all the more remarkable given that they are not among the largest species (Table 1). The average age at first birth of females in our study population was *ca.* 7 yr, and the mean interbirth interval was 29–31 mo when the first infant survived ≥ 12 mo. These values are at the high end of the reported range for all cercopithecines, in which age at first birth ranges from 3 to 7 yr, and comparable interbirth intervals (when the first of two infants survives) range from 13 to 31 mo (excluding the outlying value of 38.5 mo for Drakensberg *Papio hamadryas ursinus*; Table 1). Blue monkey age at first birth and interbirth interval are roughly on par with most baboons, which are 2–3 times heavier, but higher than most macaques of comparable or larger body size, and substantially higher than the most closely related guenons, *Erythrocebus patas* (patas monkeys) and *Chlorocebus aethiops* (vervet; Table 1). Mumby and Vinicius (2008) similarly found that *Chlorocebus mitis* had the lowest growth constant (an estimate of growth rate) of 36 species examined, which included 10 other cercopithecines.

It is not possible to compare these life history variables to assessments of adult mortality across cercopithecines because mortality data are not available for most species. However, a more limited comparison among guenons is possible, building on the examination of Isbell *et al.* (2009) of sympatric vervet and patas monkeys. Their study emphasized the importance of mortality schedules in driving the very fast life history of patas, whose high adult female mortality is similar to that of infants, in contrast to the typical mammalian pattern. The fast life history of patas monkeys relative to vervets does not relate to relative body size, as patas are considerably larger-bodied (Table 1); indeed, patas apparently have an intrinsic rate of increase that is among the fastest of any anthropoid primate when body mass is taken into account (Isbell *et al.* 2009; T. Young, unpublished data).

Blue monkeys extend the comparison of Isbell *et al.* (2009) of cercopithecines to the forest environment, and support the importance of adult mortality rates in influencing the fast vs. slow distinction. Infant mortality in blue monkeys, at 23%, is quite similar to values reported for patas in Laikipia, Kenya (26%, Isbell *et al.* 2009) and in Cameroon (20–40%, Nakagawa *et al.* 2003), and considerably lower than for vervets in their natural range (57%, Amboseli, Cheney *et al.* 1988; 48%, Laikipia, Isbell *et al.* 2009). However, mortality of juveniles and adults is much lower in blue monkeys. For juveniles, annual average mortality was very low ($5 \pm 8\%$) relative to patas ($32.5 \pm 7.3\%$) or vervets ($18.9 \pm 9.2\%$). Annual average adult female mortality in blue monkeys, at $5 \pm 5\%$, was also much lower than for adult female vervets ($14.7 \pm 4.0\%$, Isbell *et al.* 2009) or patas monkeys ($33 \pm 6\%$, Isbell *et al.* 2009; 22%, Nakagawa *et al.* 2003).

As expected from relative adult mortality rates, the blue monkey lifespan is longer than that of vervets, which lived maximally into the teens (≥ 12 yr) in Laikipia, Kenya (Isbell *et al.* 2009), and of patas monkeys, which can live 17 yr in Cameroon (Nakagawa *et al.* 2003), but less long in Laikipia (≥ 9 yr; Isbell *et al.* 2009). Thus, among these 3 guenon species, **lifespan follows the same pattern as age at first birth and interbirth interval**, with blue monkeys clearly showing a slower life history than their open-country relatives. Overall, this 3-way comparison agrees with theory that postulates a critical role for mortality in adults and juveniles in driving a species' position on the fast-slow continuum of life history (Promislow and Harvey 1990).

Rowell and Richards' (1979) study of these same species in a single captive location demonstrates that species differences persist even when environments are similar, and thus argues for evolved strategies rather than phenotypic plasticity. Captive *Cercopithecus mitis* (a combination of 2 subspecies) had a later age at first birth, longer interbirth intervals, and an older maximum lifespan than vervets and patas. Rowell and Richards (1979) emphasized the habitat correlations of life history variables across their sample of seven African cercopithecids, which included another slow forest guenon (*Cercopithecus neglectus*), although data were not available to relate such differences to natural mortality.

It seems likely, however, that habitat contrasts, to the extent they exist, coincide with (and are caused by) contrasting mortality rates, with the rain forest environment associated with lower levels of extrinsic mortality, especially among adults. As Table I shows, infant mortality does not appear to be consistently lower in forest-dwelling cercopithecine species (macaques, blue monkeys) than in species that routinely inhabit more open country (all others), although the highest values for infant mortality do occur among open-country populations. A good understanding of adult mortality differences will require more information on causes of death.

Meanwhile, one might consider whether lower predation or disease risk or less extreme shortages of food in forests are potential explanations for lower mortality there (Ross 1998). Hill and Lee (1999) categorized predation risk in 64 cercopithecine populations on a 3-point scale (high, medium, low), based on reported observations of predator presence, predator evasion behavior, and predation attempts. Habitats with high predation risk were more common for open-country taxa (vervet, patas, baboons), where they characterized 40% of study populations, than for forest taxa (macaques, mangabeys, *Cercopithecus* and *Miopithecus* guenons), where they accounted for only 8% of study populations; conversely,

low-risk habitats characterized 18% of open-country sites, but 38% of forest sites. Predation risk may index past selective pressure (Young 1994), in this case on life history traits. However, the idea that life is more dangerous for terrestrial open-country primates has not gone unchallenged (Isbell 1994), and ultimately empirical study must resolve the issue. While studies of vervets and baboons have implicated predation as a major source of mortality (Cheney *et al.* 1988, 2004; Isbell *et al.* 2009), comparable data from forest-dwelling taxa do not exist.

We are unaware of similar comparative datasets on nutritional constraints that would allow an interhabitat comparison, but the evergreen, highly 3-dimensional and floristically diverse nature of wet forests suggests more diverse opportunities for coping with periods when high-quality foods are rare. In addition, forests persist in regions of the world where rainfall is high and relatively invariant (Rubenstein and Lovette 2007), so water stress is less likely to be a problem there. The relationship of habitat to disease-based adult mortality in primates is also poorly known; even the relationship between terrestriality—which is associated with open habitats in cercopithecines—and disease burden is as yet unresolved (Nunn and Altizer 2006). Taken together, these observations suggest some ways in which extrinsic mortality may be lower for forest-dwelling adults, but also highlight the need for more data.

Comparisons of other cercopithecine taxa allow further but limited examination of habitat-related differences in fast vs. slow life histories. Ross (1992b), using data from captive populations only, showed that age at first birth and interbirth intervals were greater and intrinsic rate of increase lower for macaque species living naturally in broadleaf-evergreen forest compared to those inhabiting more variable (including more open) habitats. Singh and Sinha (2004) replicated this finding. Among *Papio* baboons (Table I), 2 study populations are largely forest dwelling. The Tana River forest baboons, *Papio hamadryas cynocephalus*, appear to have longer interbirth intervals (28 mo) than 2 savanna-dwelling counterparts (Amboseli, Mikumi: 21 mo), but the Gashaka-Gumti (forest) and Gilgil (savanna) *P. h. anubis* baboon—whose habitats are even more extremely divergent—have essentially identical intervals averaging 25 mo (Table I). However, baboons, are primarily savanna-dwelling monkeys, even if some forms (*Papio hamadryas anubis* and *P. h. cynocephalus*) occasionally inhabit forest; they evolved from savanna-dwelling ancestors and only recently differentiated (*ca.* 0.5–2 mya; Newman *et al.* 2004). By contrast, the guenons discussed above diverged much earlier (4.8 ± 1.2 mya; Tosi *et al.* 2005). Thus a relative lack of life history divergence among baboons is not unexpected, and the apparent habitat-correlated difference among yellow baboons probably reflects phenotypic plasticity in response to local environmental conditions.

Low adult mortality may favor late age at first reproduction because delaying reproduction allows animals to achieve a larger body size at the time of first reproduction. We considered the possibility that the relatively late age at first birth of female blue monkeys (7 yr) may be an adaptive response to minimize infant mortality. Because blue monkey females continue to grow until the age of 9–10 yr (Leigh 1996), a female that delays her first birth will be larger. In addition, she may gain valuable experience through allomothering (Förster and Cords 2005). Delaying reproduction in primiparous females may confer an advantage in terms of higher



infant survivorship to 12 mo, but a small sample for females giving birth at exceptionally early ages likely prevented the observed (1.8-fold) difference from reaching significance.

Birth Seasonality

Births should occur at the optimal time for the survival of the mother and offspring, and many primates appear to time births according to the availability of food (Janson and Verdolin 2005). Capital and income breeding strategies differ according to whether females store energy during periods of food abundance to be used later for reproduction or whether they more immediately channel energy consumed to underwrite the most costly stages of the reproductive cycle; these different strategies lead to distinct predictions about which part of the breeding cycle—conception vs. mid-late-lactation—corresponds most closely to peak food abundance (Brockman and van Schaik 2005; Janson and Verdolin 2005). For some guenons, Butynski (1988) and Nakagawa (2000) concluded that birth peaks were timed to ensure high food availability around the time of late gestation and early lactation, and as such these species would likely be considered income breeders (Janson and Verdolin 2005).

Blue monkeys at Kakamega have a distinct birth season, with a peak in the driest months. Similar birth periodicity coinciding with the dry season (December–May) characterizes blue monkeys and other guenons at other sites (Butynski 1988). In Kakamega, the peak occurs when more trees are fruiting (N. Fahrwig, unpublished data) and when the major fruits consumed by the monkeys are relatively abundant (fruit availability indices, Förster, Pazol, *pers. comm.*). Births also occur just before an annual trough (April–July) in fruit abundance. Thus, whereas late gestation and early lactation correspond to a relative abundance of fruit, later lactation, which is likely most energetically demanding for the mother (Hinde *et al.* 2009), occurs when fruit availability is at an annual low. This finding is inconsistent with the idea that birth peaks ensure an abundance of high-energy food when maternal energetic demand is highest, and suggests instead that late gestation and early lactation may be more critical periods in which adequate maternal nutrition can promote reproductive success.

Another possibility is that the birth peak is timed so that infants are weaned when appropriate foods are available to them, as has been proposed for open-country guenons (vervets and patas; Butynski 1988). Infant blue monkeys are quite independent by 6 mo: at this age, they spend very little time (<5%) on the nipple during the day, and have high rates of independent feeding and foraging (Förster and Cords 2002). Although independent feeding in the first year has not been studied, 2- to 3-year-old juveniles feed more on fruits than on leaves (Cords 1986), and it is likely that infants do the same. Infants born during the birth peak (January–March) will reach their sixth month in July–September, when there are secondary peaks in fruit availability (N. Fahrwig, S. Förster, unpublished data), thus perhaps facilitating their growing independence.

The timing of births might also minimize infant mortality from exposure to rain (Dunbar 1980). At Kakamega, infants born during the birth peak will face the 2 rainiest months (April–May) at the age of 1–4 mo. Rain at this time often falls in the

afternoons, and monkeys may settle for the night while they are still damp. Temperatures often drop to 11°C at night. Young infants that still spend most of their time in contact with their mothers may have a thermoregulatory advantage during this wet period. Consistent with this suggestion, infants born during dry months had higher survivorship than those born during wet months.

A more proximate explanation for reproductive seasonality would focus on the timing of conceptions. The peak conception months of July–September are relatively rainy months in which fruit production has typically increased from the April–July trough (Fahrwig, Förster, *pers. comm.*). Glucocorticoid hormone levels in the focal population are responsive to nutritional factors, particularly a lack of fruits, and a reduction in metabolic stress may trigger conceptions at this time (Förster *et al.*, in prep.) More detailed study of year-to-year variation in rainfall patterns, food abundance, and scheduling of conceptions could help to clarify whether conceptions (and hence births) relate to improved female condition at this time of year (Brockman and van Schaik 2005).

Conclusion

Blue monkeys appear to have a notably slow life history, even in a primate context. Among cercopithecines, they have the latest age at first birth, the longest interbirth intervals and exceptional longevity, and yet they are among the smaller-bodied species. While the general shapes of their mortality and fecundity schedules resemble those of other primates, their late age at first birth, long interbirth intervals, and long lifespan together with a low adult mortality rate as compared to other cercopithecines, support both general life history theory (Charnov 1993) and the role of the environment in influencing life history variation (Ross 1992a). As the most complete data from this subfamily come from species inhabiting more seasonal and unpredictable habitats, these data on a forest-dwelling species provide an important contrasting point of reference. If the patterns they reveal can be generalized to other tropical forest-dwelling cercopithecines, they further suggest that populations of these monkeys may be particularly vulnerable to population decline. Many forest guenons, for example, are subject to human hunting (Butynski 2002b) and would be unlikely to recover quickly.

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