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## Growth rates in a wild primate population: ecological influences and maternal effects

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**Abstract** Growth rate is a life-history trait often linked to various fitness components, including survival, age of first reproduction, and fecundity. Here we present an analysis of growth-rate variability in a wild population of savannah baboons (*Papio cynocephalus*). We found that relative juvenile size was a stable individual trait during the juvenile period: individuals generally remained consistently large-for-age or small-for-age throughout development. Resource availability, which varied greatly in the study population (between completely wild-foraging and partially food-enhanced social groups), had major effects on growth. Sexual maturity was accelerated for animals in the food-enhanced foraging condition, and the extent and ontogeny of sexual dimorphism differed with resource availability. Maternal characteristics also had significant effects on growth. Under both foraging conditions, females of high dominance rank and multiparous females had relatively large-for-age juveniles. Large relative juvenile size predicted earlier age of sexual maturation for both males and females in the wild-feeding

condition. This confirmed that maternal effects were pervasive and contributed to differences among individuals in fitness components.

**Keywords** Growth · Primates · Sexual dimorphism · Maternal effects · Food availability

### Introduction

Growth rates are of interest because they shed light on between-species life-history differences (Case 1978; Harvey et al. 1987; Read and Harvey 1989; Charnov 1991; Kozłowski and Weiner 1997; Harvey and Purvis 1999), and because they represent a potential source of fitness variance within a species (Hofer and East 1993; McAdam and Millar 1999; Lochmiller et al. 2000; Dobson and Oli 2001; Johnson 2003). Growth rates are also important because they are susceptible to maternal effects in a wide range of species (Bernardo 1996; Mousseau and Fox 1998). Maternal effects occur whenever maternal phenotype affects offspring phenotype, independent of offspring genotype. For instance, larger mothers may produce larger offspring simply because they have sequestered more resources at the time that offspring are conceived, an effect independent of offspring genotype. Maternal effects have been the subject of much recent attention in the evolutionary literature, and the range of documented maternal effects is large (reviewed in Bernardo 1996). Maternal effects are increasingly viewed as adaptations that may mitigate the effects of selection by modifying offspring phenotypes solely through the behavior or physiology of the mother (reviewed in Mousseau and Fox 1998). Thus, they represent a non-genetic transmission of traits from one generation to the next.

For understanding between-species life-history differences, species-typical patterns of growth are required, and such data are available for many species of mammals, at least in captive settings and sometimes in the wild. However, for examining sources of fitness variance

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among individuals within a species and for documenting maternal effects, data on differential growth trajectories among individuals within populations are required. Mammalian data of this sort, particularly for wild populations, are rare in the literature.

Here we present a large and detailed data set on individual growth trajectories in a wild, unmanipulated population of primates. We used this data set to evaluate the magnitude, sources, and consequences of intraspecific variability in offspring growth rates. We focused particularly on differences in foraging ecology and on maternal effects in our study population, testing predictions that are based on what is already known about primate growth. Primates are characterized both by slow average growth relative to other mammals (Charnov and Berrigan 1993; Janson and van Schaik 1993; Pereira 1993; Rubenstein 1993) and by considerable plasticity of growth rates (see e.g., Coelho 1985; Altmann and Alberts 1987; Strum 1991; Pereira and Leigh 2003). Differences among individuals in the ability to enhance their offspring's growth rates will have major fitness consequences if survival, age at reproductive maturity, or adult fertility are directly or indirectly size-limited. However, the advantages of rapid infant growth may be countered by increased costs of maternal investment, such as higher maternal mortality rates, which increase the risk that a dependent infant will be orphaned (Altmann 1980, 1983; Altmann and Samuels 1992). Similarly, rapid juvenile growth may be countered by higher juvenile mortality due to increased foraging-related predation risk (Janson and van Schaik 1993).

#### Population and predictions

The research was conducted in the semi-arid and highly seasonal, short-grass savannah habitat of Amboseli, Kenya, and its environs. The subjects were the members of three baboon groups that have been part of longitudinal, observational research projects. The groups had relatively exclusive, though adjacent, home ranges, and adult males dispersed among these and other groups in the population (Samuels and Altmann 1991; Alberts and Altmann 1995a; Altmann 2000). The two fully wild-foraging groups, Alto's and Hook's, traversed 8–10 km during their daily foraging, and travel-plus-feeding time occupied three-quarters of the daylight hours (Altmann 1980; Bronikowski and Altmann 1996). The third group, Lodge group, chose sleeping sites near a tourist lodge within their range, and supplemented their diet of wild foods with discarded human foodstuffs that were easy to obtain and process (Altmann and Muruthi 1988; Muruthi et al. 1991). Hence, they traveled less than 4 km per day and spent less than half the daytime in feeding-plus-traveling, but achieved the same energy intake and nearly the same protein intake as the wild-feeding animals (Muruthi et al. 1991). As a consequence of these differences in activity and energetic balance, Lodge group animals were substantially larger as adults, and most of

the difference in body mass was due to fat accumulation in food-enhanced animals (Altmann et al. 1993).

Differences among the study groups in adult body size and fatness and in rates of birth, death, and maturation (Altmann and Alberts 2003) suggest that these groups span most of the range of resource conditions that have been reported for active, healthy members of this genus, including both wild and captive populations (Hamilton et al. 1978; Sigg et al. 1982; Coelho 1985; Whiten et al. 1987; Eley et al. 1989; Smuts and Nicolson 1989; Dunbar 1990; Strum 1991; Henzi et al. 1992; Henzi and Lycett 1995; Packer et al. 2000; Johnson 2003).

#### *Predicted effects of resource availability on growth*

Enhanced growth or development with increased food availability has been demonstrated in a variety of animal species (examples from birds: Quinney et al. 1986; Smith and Arcese 1988; Simons and Martin 1990; Keller and van Noordwijk 1994; Lepage et al. 1998; examples from mammals: Mori 1979; Strum and Western 1982; Lyles and Dobson 1988; Strum 1991; Hofer and East 1993; McAdam and Millar 1999; Lochmiller et al. 2000; Dobson and Oli 2001; LeBlanc et al. 2001). The high overall energetic balance experienced by the Amboseli food-enhanced study group presumably increased maternal condition and milk production, which would have enabled the infants themselves to obtain nutrients on their own at a younger age compared to the completely wild-foraging groups (Altmann 1980; Muruthi 1997; S.A. Altmann 1998). Those differences, in turn, were predicted to result in higher infant and juvenile growth rates for the food-enhanced group.

#### *Predicted effects of maternal dominance rank on growth*

Within baboon groups, mothers of high agonistic dominance status experience lower rates of interruption during feeding bouts (Post et al. 1980; Samuels and Altmann 1984; Muruthi 1989; Smuts and Nicolson 1989). In addition, high-ranking females are generally thought to have access to higher-quality foods that are obtained with less expenditure in "local" travel among food patches. Even more significant may be that infants of high-ranking mothers experience a greater freedom of uninterrupted movement as they begin to explore and obtain their own food (Altmann 1980). These advantages accrued by high-ranking females, for both nutritional intake and expenditure, were predicted to result in greater relative body size for their offspring (see Johnson 2003 for size advantage conferred on daughters but not sons of high-ranking female wild chacma baboons).

*Predicted effects of maternal parity and maternal investment period on growth*

Primate females often reproduce before achieving full body size and full development of the skills required for simultaneously providing infant care and foraging efficiently. Probably as a consequence, firstborn infants experience higher mortality rates (e.g., Altmann et al. 1988; Smuts and Nicolson 1989). These firstborn infants may be small or weak at birth, and they seem to interfere more with their mothers' foraging activities, either because of maternal or infant deficiencies [personal observation; also Whitten 1982 for grivet (vervet) monkeys, *Cercopithecus aethiops*]. Firstborn offspring were, therefore, predicted to be small-for-age as juveniles.

If all other things are equal, infants are predicted to benefit from a longer period of maternal investment (Trivers 1972, but see, e.g., Altmann 1980) and to be relatively large as juveniles. However, longer periods of maternal investment also entail a delay in a mother's subsequent reproduction. Johnson (2003) reported that low-ranking female chacma baboons tended to have longer investment periods, as well as smaller offspring, so that the longer investment periods essentially functioned as compensatory investment, and offspring of low-ranking mothers tended to be weaned at the same weight as offspring of high-ranking mothers. We have also reported longer investment periods for lower-ranking females in Amboseli (Altmann and Alberts 2003), raising the possibility that longer investment will not result in larger infants but will be essentially compensatory. Hence, we also examined investment period as a function of rank for the subset of animals in this study.

*Predicted effects of growth differences on survival and age at maturity*

Relatively large juveniles were predicted to experience higher survival and earlier age of sexual maturation—menarche for females and testes enlargement for males—than their smaller age peers (e.g., Hofer and East 1993; McAdam and Millar 1999; Dobson and Oli 2001).

## Methods

### Subjects and data collection

All subjects were identified visually by individual physical characteristics, and the histories of the animals were known since birth from near-daily records of demographic events, of reproductive cycles, of social interactions (agonistic, grooming, and sexual), and from monthly evaluations of physical maturation. These life-history records provided dates of conception, birth, death, and maturation, as well as data on maternal parity and social dominance status (see, e.g., Altmann et al. 1981, 1988; Alberts and Altmann 1995b for details). Subjects of the current analysis included those animals for which we obtained longitudinal body-size measurements over a 5-year period beginning in 1985 (see below). Hence, they represent a subset of our study population, and so values for life-history events

reported here may differ slightly from those reported elsewhere for this population (e.g., compare age at maturation values reported below with those in Altmann et al. 1988; Alberts and Altmann 1995b).

Growth rates were monitored by periodically placing an unbaited scale near a frequented site and then recording body mass when animals voluntarily climbed onto the scale (details in Altmann and Alberts 1987; see also Altmann and Samuels 1989). This data set was later supplemented for some juveniles during a short period of immobilization achieved through use of an anesthetic-bearing dart propelled from a blowpipe (detailed in Sapolsky and Altmann 1991; Altmann et al. 1993).

We distinguished several life-history stages before full maturity. Infancy was considered to end when the infant's mother conceived again, which is approximately 16–18 months in the wild-feeding baboon groups (see discussions for primates in Lee 1996; see also S.A. Altmann 1998, Figs. 6.6, 6.7, 6.8). Thereafter, the offspring was considered to be a juvenile until it reached sexual maturity—menarche (for females) or testicular enlargement (for males)—after which it was considered adolescent (or subadult). Adolescence ends and adulthood begins with the onset of offspring production. First offspring production occurs at approximately 6 years of age for females and 8 years of age for males (Altmann et al. 1977; Alberts and Altmann 1995b; Packer et al. 1998, 2000).

### Data measures and analysis

#### *Maternal characteristics*

A mother's parity, and thus the infant's birth order, was taken as equivalent to the mother's pregnancy number, regardless of outcome (Altmann et al. 1977) and including the current infant.

All females that have reached menarche are ranked each month in a dominance hierarchy of adult females based on wins and losses in pairwise agonistic encounters (Hausfater 1975). A female's rank in this hierarchy the month that her infant was conceived was considered the maternal dominance rank for that infant (see, e.g., Altmann 1980; Altmann et al. 1988; Alberts and Altmann 1995a, 1995b). Considerable stability of dominance ranks throughout adulthood and even across generations has been documented for baboon and macaque females (see reviews in Melnick and Pearl 1987; Walters and Seyfarth 1987; Pereira 1995).

The duration of maternal investment was estimated as the number of days in the interval from the date that the infant was conceived until the onset of its mother's next pregnancy.

#### *Body mass*

If multiple measurements were available for an individual in a month, we used the mean of those values for analysis. The result was 1,012 values representing mean monthly body-mass measures of 113 individuals, with a range of 1–23 months of data per individual. The individuals included 34 wild-feeding males, 44 wild-feeding females, 20 food-enhanced males, and 15 food-enhanced females. Although some measurements were obtained during infancy, most data are from post-weaning ages. Our analysis strategy, described below, involved three steps. First, we characterized the overall pattern of growth for the whole period up to adulthood for each sex and each foraging condition; second, we sought to demonstrate individual differences within sex and foraging condition, and finally, we identified sources and consequences of individual differences in deviation from the average pattern, i.e., in being a relatively large or small juvenile.

*Overall pattern of growth from infancy to adulthood.* To characterize the overall pattern of growth, we used the full set of 1,012 values. In doing so, we included values for the same individual during different months, resulting in some pseudo-replication. When doing so, therefore, we used the conservative jackknife sample re-use procedure (Mosteller and Tukey 1977; Sokal and

Rohlf 1995), with individuals as the sampling unit. Statistical values subject to pseudo-replication are also indicated as “nominal” when presented in the results below.

Our first analysis examined sex differences and effects of food availability using the small data set for infants pooled across gender and foraging conditions. In characterizing the overall pattern of growth during the post-weaning years, however, we separated four classes based on gender and on food availability (high vs low).

To determine growth rate for each class and to evaluate quantitatively whether each class of baboons experienced an adolescent “growth spurt”, we modeled growth for each class using the piecewise linear regression procedure in SYSTAT™. This procedure iteratively finds both the best-fit pair of straight lines for each curve (class) and the breakpoint between the two lines. The slopes of the lines can then be used as estimates of the growth rates, and the breakpoints as the age of onset of an adolescent growth spurt if the slopes are significantly different before and after the breakpoint (see also description in Leigh 1994 where piecewise regression with quadratic fit is used).

*Individual differences and their sources.* Piecewise linear regression provided a sufficiently good fit for each class (see Results) that evaluation of individual differences might have proceeded by using variability around these regression lines. However, scatter around the regression was greater at some ages than others. In particular, variance around the line was greater near the breakpoint, the transition from juvenile to adolescent growth rates. Because individuals differed considerably in the ages at which they were weighed, and such differences would confound analyses of individual differences in growth, we used a more “locally sensitive” age-specific deviation from the average pattern, the LOWESS (with a window 0.5). All subsequent analyses, therefore, use deviations, or residuals, from the LOWESS-determined class average at each age. Each individual’s relative size at each month of measurement was measured by its deviation from the class average for that month of measurement. We calculated this deviation as the natural log of the ratio of the individual’s size to the average for that month of age. An individual that is small for its age will have deviations (residual values) that are negative; one that is large for its age will have positive values (Moses et al. 1992; see also Setchell et al. 2001; Johnson 2003).

For 71 individuals, we had measurements from at least 3 months during the juvenile period. We used data from this subset of subjects to evaluate individual differences within age classes in three steps as follows. First, for each class, we compared the within-individual variance in residuals to that among individuals. If within-individual variance is less than that between individuals, no more than a 12% reduction in efficiency results, on average, from collapsing an animal’s data, regardless of number of data points, to a single, summary value (see Bloch and Moses 1988; Moses et al. 1992). Second, to determine whether results using a single value would be robust, i.e. not sensitive to the particular choice among alternative values, we examined the correlation between three relative growth measures for each individual during the juvenile period: its first residual value (usually obtained within the first 6 months post-weaning), its median value, and its mean value. Finally, to explore the stability of individual differences, we applied linear regression analysis to each animal’s residual scores across ages. We did this to determine whether any departure from stability was systematic and might, therefore, affect subsequent tests for sources of individual differences. The results of these three analyses enabled us to use a single value for each individual, and regression and general linear models procedures (SAS Institute 1988) could confidently be applied to evaluate predictors and sequelae of a youngster’s relative size.

Hypotheses regarding differences between sets of individuals were tested using a two-tailed *t*-test (with Cochran’s correction when needed). To examine the effects of maternal dominance rank on relative juvenile size, we performed simple linear regressions on each of the four data sets (wild-foraging and food-enhanced males and females). To examine the independent effects of maternal rank and relative juvenile size on age at maturity, we performed stepwise

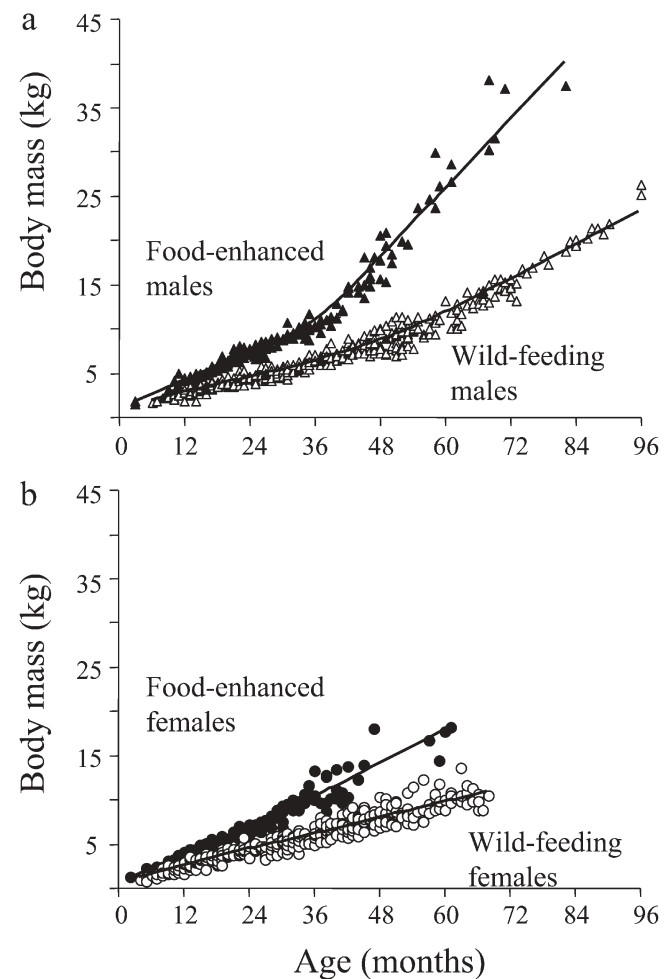
multiple regressions in which we forced maternal dominance rank to be the first of the two predictor variables. This allowed us to estimate the independent effects of relative juvenile size controlling for maternal rank.

## Results

### Effects of food availability and gender on growth rates

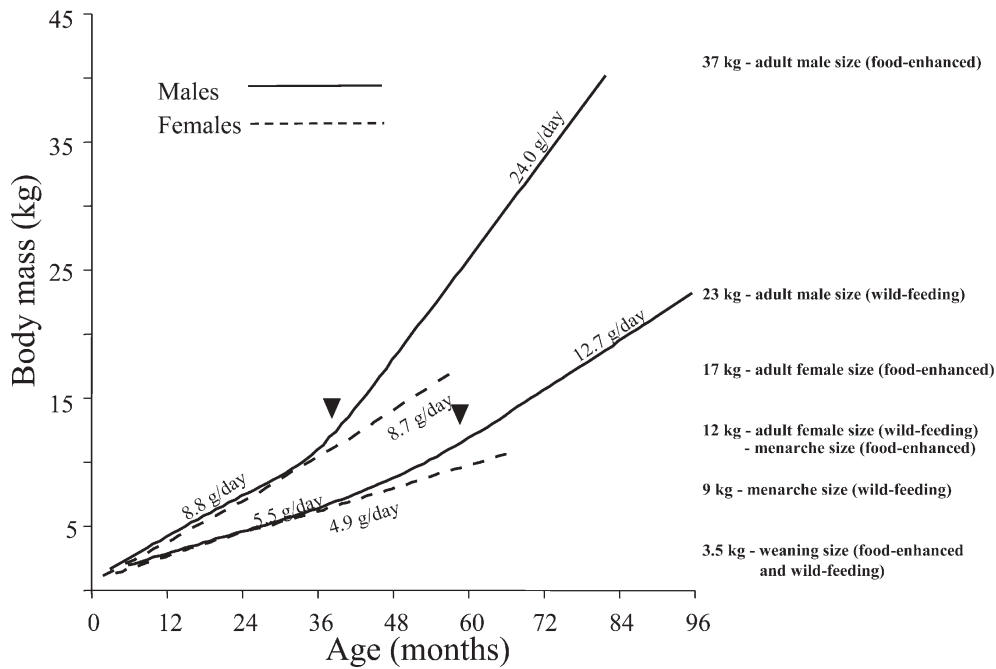
Greater food availability resulted in more rapid body growth for both males (Fig. 1a) and females (Fig. 1b). Even during the 1st year of life, youngsters in the food-enhanced group were larger than those in the completely wild-feeding groups ( $t=6.9$ ,  $df=38$ ,  $P<0.001$ ), and the growth difference resulted in ever-increasing body size difference with age.

Male infants were, on average, slightly heavier than females within both foraging conditions, but this differ-



**Fig. 1** Body size as a function of age **a** for males and **b** for females under two foraging conditions. Each point represents an individual’s mean value for that month of age. Lines are the LOWESS-smoothed curve for body mass as a function of age for each of the four subsets of animals defined by foraging condition and sex (see text for details).





**Fig. 2** Growth rates for males and females within each foraging condition. Superimposed on the LOWESS curves (see text and Fig. 1) are the values for growth rates (in g/day) that were obtained by applying a piecewise linear regression analysis to the data rather than the LOWESS (see text). The statistically identified breakpoints in the piecewise regressions for the males are indicated with arrowheads and the numerical values indicate the growth rates

before and after the breakpoint in each case. For females, growth was not significantly different during adolescence than before; consequently, for each feeding condition only a single numerical value is given for females (see text for details). In the column along the right side of the figure, approximate body sizes at major life-stages for each foraging condition are indicated.

ence was not statistically significant (for the food-enhanced group  $t=1.9$ ,  $df=16$ ,  $P<0.09$ , vs  $t=0.1$ ,  $df=20$ ,  $P=0.91$  for the wild-feeding). Linear regression analysis on each subset through 3 years of age indicated that the young food-enhanced animals grew at a rate of 8.8 g/day for males and 8.7 g/day for females. For wild-feeding animals, growth rate was 5.5 g/day for the young males, 4.9 g/day for the young females (nominal  $P>0.05$  for sex-difference comparison of slopes in each foraging condition; see Fig. 2).

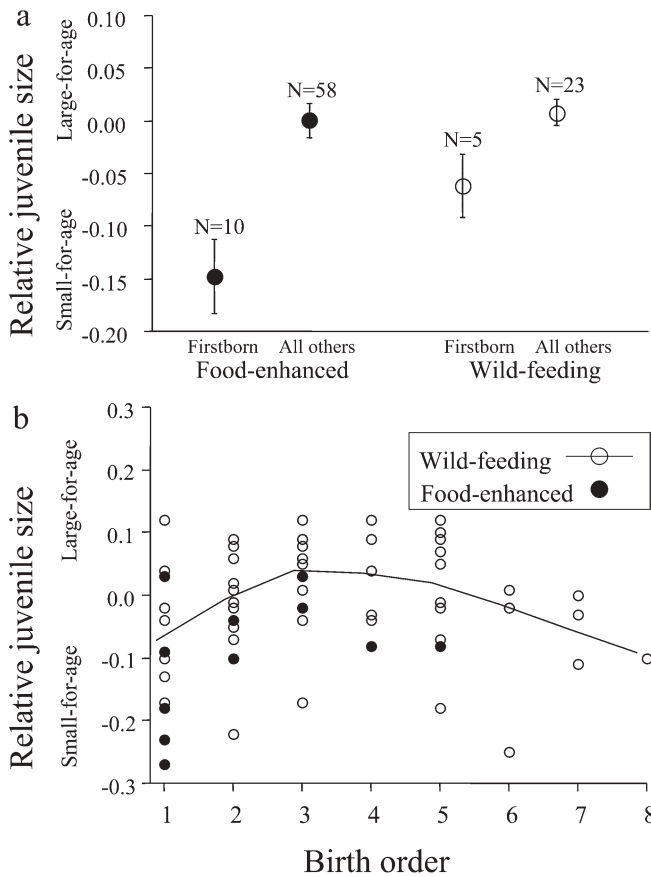
For males, an adolescent growth spurt in both foraging conditions was confirmed by a significant difference in slope in the piecewise linear regression analysis between the best-fit lines before and after the indicated regression "breakpoint" (arrowheads in Fig. 2; adjusted nominal  $R^2>0.97$ ,  $P<0.001$  for the piecewise regression in each food-availability condition). In the food-enhanced condition, males experienced almost a 200% increase in growth rate during the growth spurt. Identifying the onset of this growth spurt as the age at the breakpoint gives an onset at 38.6 months for the food-enhanced animals and 58.7 months for the wild-feeding ones. Among adolescent males, growth rate of food-enhanced individuals was almost double that of wild-feeding ones: 24.0 g/day for the food-enhanced animals, and 12.7 g/day for their completely wild-feeding counterparts (Fig. 2).

For females in contrast to males, growth was essentially constant up to menarche in both foraging conditions (adjusted nominal  $R^2>0.94$  and 0.91 for the food-en-

hanced and wild-feeding conditions, respectively,  $P<0.001$  in each case). Although a slight pubertal growth spurt was suggested in both cases by an estimated regression slope that was greater after a breakpoint in the 3rd year of life than before, in neither condition was the increase statistically different from zero.

Growth as an individual life-history trait:  
within-individual consistency within classes

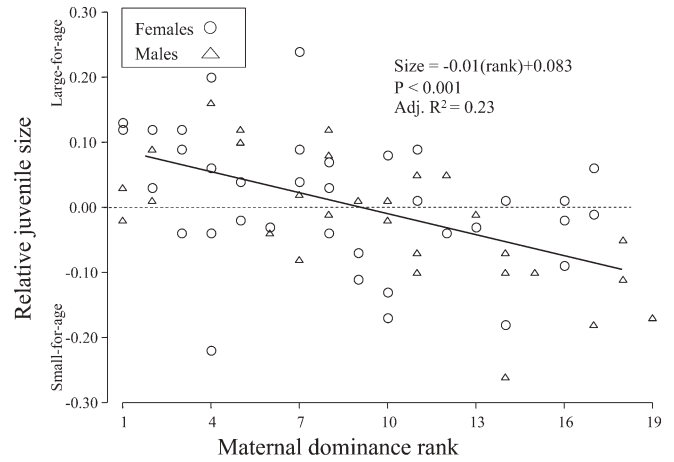
That relative size was usually a stable individual trait was strongly supported by all three statistical approaches (see Methods). Within each class, variance in relative size within individuals was less than that among individuals. Second, for most of the individuals, their first, mean, and median juvenile residual values were highly consistent as evaluated by Pearson correlation; that is, for the mean and median values:  $R>0.95$ ,  $P<0.0001$  for each of the four classes (wild-feeding males  $N=23$ , wild-feeding females,  $N=25$ , food-enhanced males  $N=12$ , food-enhanced females  $N=11$ ) and in the pooled data ( $N=71$ ); for the juvenile's first post-weaning residual value with its respective mean and median  $R>0.85$ ,  $P<0.0001$  for both wild-feeding males ( $N=23$ ) and females ( $N=25$ );  $R>0.79$  with the mean and  $R>0.71$  with the median,  $P<0.002$  and  $P<0.010$ , respectively, for food-enhanced males ( $N=12$ ); and  $R=0.50$  with the mean and 0.37 with the median,  $P<0.12$  and  $P<0.27$ , respectively, for food-enhanced fe-



**Fig. 3** Effect of birth order on individuals' juvenile size relative to others in their class (same foraging condition and gender). **a** Firstborn offspring are compared (mean and standard error) to all others of higher birth order, presented separately for each foraging condition. Numbers indicate the sample size (number of juveniles). **b** Each point represents a single individual for which measurements were available for at least 3 months during the juvenile years (see Methods for details). The LOWESS curve is calculated only for the wild-feeding condition (*unfilled symbols*).

males. No relationship was found between the number of months in which an animal was weighed, i.e. the number of data points included for that individual in these analyses, and the concordance among the measures ( $-0.45 < R < 0.15$ ,  $P > 0.05$  for each class,  $N$  as given above). Finally, 80% of the 71 individuals with data for at least 3 months showed no significant trend in residuals over time at a fiducial limit of 0.05; over 90% did not at a 0.01 level, and we could discern no characteristic shared by those few individuals that did change.

In light of these findings of stable individual differences, we use here each individual's mean residual score for the analyses of sources and consequences of variance among individuals.



**Fig. 4** Effect of maternal dominance rank on an individual's size as a juvenile; only wild-feeding males and females are plotted. The equation and  $R^2$  value are reported for males and females pooled; see Table 1 for separate analyses for males and females.

**Table 1** Effects of maternal dominance rank on relative juvenile size for each subset of data; results of linear regressions showing that offspring of high-ranking females are relatively large, those of low-ranking females are relatively small

	Slope	Adj. $R^2$	$P$	$N$
Wild-feeding females	-0.007	0.087	0.041	38
Wild-feeding males	-0.012	0.433	0.001	29
Food-enhanced females	-0.016	0.061	0.189	14
Food-enhanced males	-0.006	0.017	0.259	19

#### Maternal characteristics as sources of individual size differences

##### Maternal parity

Under both foraging conditions, 80% of the offspring from mothers' first pregnancy were relatively small as juveniles. The magnitude of the difference (Fig. 3a) was at least as great in the food-enhanced condition ( $t=2.8$ ,  $P=0.047$  with Cochran correction for unequal variances,  $N=10,58$ ) as in the fully wild-feeding one ( $t=2.2$ ,  $P=0.03$ ,  $N=5,23$ ). Maternal parity and relative size are not monotonically related for higher parities. The data suggest that offspring of the highest parity (oldest) mothers may also be at a slight disadvantage, but the available sample sizes provide inadequate power to detect effects of small magnitude (Fig. 3b).

##### Maternal dominance rank

Wild-feeding offspring of high-ranking mothers were relatively large as juveniles, and ones whose mothers were low-ranking were relatively small as juveniles (Fig. 4, Table 1). Rank was not a significant predictor of relative size for food-enhanced animals, although the slight trend was in the same direction (Table 1). The lack

**Table 2** Effects of relative juvenile size on age at maturity; results of linear regressions for each subset of data showing that large juveniles reach maturity earlier in wild-feeding (but not food-enhanced) groups<sup>a</sup>

	Slope	Adj. $R^2$	$P$	$N$
Wild-feeding females	-0.40	0.20	0.004	36
Wild-feeding males	-0.39	0.14	0.04	23
Food-enhanced females	-0.22	0.04	0.48	14
Food-enhanced males	-0.16	0.00	0.74	19

<sup>a</sup>The samples for each subset include only animals for which we have both longitudinal growth data and maturation age.

of a significant effect in the food-enhanced condition may be due to the relaxed environmental conditions or to the smaller samples size for that group, or both. The relationship between rank and juvenile size remained the same when first-parity offspring were excluded, as expected from the absence of a correlation between rank and parity in the data set.

### Maternal investment

A long period of maternal investment was not associated with relatively large juvenile size. Within each class of juveniles, the relationship between the duration of maternal investment and juvenile size was negative in direction, accounted for only approximately 4% of the variance in each case, and was not statistically significant ( $P > 0.05$ ). However, as we have reported elsewhere (Altmann and Alberts 2003), the length of the maternal investment period in Amboseli is predicted by mother's dominance rank at the infant's conception; higher-ranking females invest for shorter and lower-ranking females for longer periods.

### Effects of growth on age at maturity and survival

Food-enhanced animals experienced significantly earlier maturation than the fully wild-feeding ones (also see Altmann et al. 1993). Food-enhanced females reached menarche at a mean age of  $41.2 \pm 1.1$  months compared to  $56.0 \pm 0.7$  months for wild-feeding females ( $t = -10.16$ ,  $P < 0.0001$ ,  $N = 14$  and  $56$ , respectively). Food-enhanced males reached testicular enlargement at a mean age of  $52.5 \pm 1.7$  months compared to  $68.9 \pm 0.8$  months for wild-

feeding males ( $t = -9.8$ ,  $P < 0.0001$ ,  $N = 19$  and  $34$ , respectively).

Similarly, relatively large juvenile size within class predicted early maturity for all classes pooled. However, the predictability of maturation from juvenile size differed for the two foraging conditions. Among the wild-feeding animals, relatively large juveniles, both males and females, matured significantly earlier than their smaller peers (Table 2). In contrast, for neither males nor females in the food-enhanced group did relative juvenile size predict age of maturation (Table 2). As with the findings for effects of maternal rank, this may have been due to the relaxed environmental conditions experienced by the food-enhanced group, by the smaller sample size for that group, or both.

The relationship between juvenile size and age of maturation in the wild-feeding groups was not entirely a result of the association between high dominance status and high growth rates. For wild-feeding females, dominance status accounted for approximately 25% of the variance and large juvenile size independently accounted for an additional 10% of the variance in maturational acceleration (Table 3).

In contrast to the high rates of mortality during infancy, mortality is very low during the juvenile years (Alberts and Altmann 2003). For the juveniles with at least 3 months of growth data, none of the food-enhanced juveniles ( $N = 23$ ) and only 3 of the wild-feeding juveniles ( $N = 48$ ) died before maturity; all 3 had been large-for-age as juveniles. That is, within the limited power of this small mortality set, size and mortality were not related (see Discussion).

## Discussion

### Growth as a resource-limited trait

Large differences in growth and maturation have often been associated with major, persistent differences in food availability, both for cercopithecine primates and for other mammals (e.g., primates: Mori 1979; Sugiyama and Ohsawa 1982; Strum 1991; Bercovitch and Strum 1993; also reviewed in Fa and Southwick 1988; Asquith 1989; Lee 1999; Johnson 2003; e.g., other mammals: Hofer and East 1993; McAdam and Millar 1999; Lochmiller et al. 2000; Dobson and Oli 2001; LeBlanc et al. 2001). For the baboons in this study, differences in food availability provided the primary source of within-age variability in

**Table 3** Effects of maternal dominance rank and relative juvenile size on age at maturity: results of a stepwise multiple regression showing that maternal dominance rank and relative juvenile size

	Maternal dominance rank			Relative juvenile size, controlling for rank			
	Partial $R^2$	Coefficient	$P$	Partial $R^2$	Coefficient	$P$	$N$
Wild-feeding females	0.25	-0.007	0.01	0.10	-0.29	0.03	36
Wild-feeding males	0.34	-0.007	0.04	0.006	-0.09	0.68	23

contribute independently to age at maturation for wild-feeding females; for males, the effect of juvenile size on age at maturity can be attributed to the effects of maternal rank

body size for immature baboons. These results add support for the thesis that growth rates in wild primates are largely food-limited.

The extremes of resource availability represented by the food-enhanced and fully wild-feeding, semi-arid environmental conditions in Amboseli provide a model for much of the range of the genus *Papio* (see also comparisons in Strum 1991 and see Johnson 2003 for a comparison of growth in captive vs wild-feeding baboons). In Amboseli, these ecological extremes are associated with comparably large differences in infant survival, smaller differences in juvenile survival, and large differences in growth and in maturation (Altmann et al. 1993; Altmann and Alberts 2003; and herein).

## Maternal effects

### *Maternal dominance rank and parity as sources of differences in fitness components*

Although resource availability had the largest impact on growth rate, differences in relative size were also predicted by maternal characteristics, and these effects were similar in male and female offspring. Firstborn offspring and possibly offspring of the oldest females were relatively small-for-age. Offspring of high-ranking females were large-for-age, and those of low-ranking females were small-for-age. These maternal effects are typical of maternal effects seen in a wide range of species—they are dependent on characteristics of the mother, are unrelated to offspring genotype, and apparently have important fitness consequences for the offspring (Bernardo 1996).

In some baboon populations, a major fitness consequence of maternal rank lies in its impact on age at maturity (e.g. Altmann et al. 1988; Wasser et al. 2004). Maternal dominance rank here contributed to age at maturity both directly and indirectly through juvenile growth rates. The fitness consequences of early maturation for high-ranking females are substantial; we have estimated elsewhere that high ranking females in Amboseli have a half-offspring advantage relative to the mean reproductive output of Amboseli females (Altmann et al. 1988; see also Johnson 2003 for effects on reproductive rate and span in chacma baboons).

If high maternal dominance rank enhances offspring growth, accelerates first reproduction in offspring or positively impacts other fitness components (Bulger and Hamilton 1987; Bercovitch and Strum 1993; Cheney et al. 2004; Wasser et al. 2004 for various baboon populations), and also confers high rank on daughters (the non-dispersing sex in baboons and other cercopithecines), then we might expect that high-ranking females in a social group will outproduce and ultimately replace the lineages of lower-ranking females. Under such a system, all females in a social group will be related, and will have a single common female ancestor in the not-too-distant past. Our earlier models of status-correlated bias in offspring sex ratio (Altmann and Altmann 1991) demon-

strate that this effect occurs if high-ranking females systematically produce more daughters than low-ranking females do. The results presented here on growth and maturation suggest that this replacement of low-ranking female lineages by high-ranking lineages may occur even in the absence of sex-ratio biases, solely through maternal effects on growth and first reproduction. Thus, heritable traits carried by high-ranking females may rapidly reach high frequency as a result of maternal effects.

Maternal parity, in contrast, had no direct effect on age at maturity, but mortality rates for firstborn offspring are high, at least in the wild-foraging groups where mortality during the first 2 years of life is much greater for firstborn offspring than for those of higher birth order (Altmann et al. 1988). This means that because of selection at an earlier life-stage, the most vulnerable of firstborn infants never lived to contribute to our juvenile sample and we cannot know whether they were particularly small and were more at risk partly for that reason.

Whereas infancy is a very vulnerable life-stage, the juvenile period is much less so. Annual survival rates for juveniles are over 90% in both of the very different foraging conditions (Alberts and Altmann 2003; Altmann and Alberts 2003). We could detect no effects of growth rates on survival during these post-weaning juvenile years; growth impacted life-history solely through age at maturation.

### *Duration of maternal investment*

In contrast to our prediction, juveniles that experienced longer maternal investment periods were not large-for-age, and the slight trend was in the opposite direction. Further, high-ranking females tended to invest for shorter periods of time than low-ranking females (see also Bulger and Hamilton 1987; Altmann and Alberts 2003; Johnson 2003). This suggests that mothers determine duration of investment neither independently of neonatal size nor by biasing investment in favor of large neonates. In fact, it seems that females adjust the duration of investment such that small or weak neonates are cared for longer. The consequence will be that variance among offspring in body mass at birth is reduced by the time infants achieve independence (Wasser and Wasser 1995; Johnson 2003).

### *Pervasiveness of maternal effects and lack of compensatory growth among independent juveniles*

All other things being equal, the effects of maternal characteristics should decline after weaning, because once an infant is weaned, its ability to sequester resources should depend increasingly on its individual characteristics. Hence, compensatory or catch-up growth should occur in some cases. Compensatory growth is well-documented in laboratory and farm animals but poorly studied in wild mammals (see discussion in Lochmiller et al. 2000).



The juvenile baboons in our study were consistently small-for-age or large-for-age, indicating that animals that had a slow start did not experience compensatory growth, at least not before reproduction. Thus, the effects of maternal dominance rank and parity were pervasive, persisting well beyond the period of infant independence. This offers important evidence that compensatory growth may not always be an option for juveniles in natural populations or may not be uniformly advantageous (see also data on bighorn sheep, *Ovis canadensis*, in Festa-Bianchet et al. 2000; LeBlanc et al. 2001).

The pervasiveness of maternal effects on females is not surprising. Maternal dominance rank is transmitted to daughters, and maternal support is a critical component of adult-rank acquisition for females. Further, female baboons form strong, lifelong, mutually dependent bonds with their mothers and other female relatives (see reviews in Melnick and Pearl 1987; Walters and Seyfarth 1987; Chapais and Berman 2004). Hence, for females, maternal dominance rank is a characteristic with lifelong effects, consistent with the pervasiveness of the effects of maternal dominance rank throughout the growth period.

However, this is not true of male baboons. Maternal rank has no effect on adult-rank acquisition for males (Packer et al. 2000), and among juvenile males, dominance rank is determined by relative age rather than maternal rank (Pereira 1988, 1995). Hence, the effects of maternal rank should decrease after weaning for juvenile males.

We would also not expect maternal parity to impose limits on compensatory growth, for either sex. Unlike maternal rank, parity is a transient maternal characteristic. Therefore, we might expect that the effects of parity are easier for a juvenile to escape than the effects of rank, but this is not the case. Why, then, is compensatory growth so limited among small-for-age juveniles?

The absence of compensatory growth in small-for-age juveniles may simply reflect persistent ecological constraints. That is, compensatory growth may be strongly food-limited, and wild juvenile baboons simply cannot acquire enough food to compensate for a slow start. This idea is supported by our finding that within-individual consistency is substantially weaker in the food-enhanced than in the wild-foraging groups. An alternative explanation from this ecological perspective is that compensatory growth may entail costs that baboons cannot bear. For instance, it may increase predation risk (Lima and Dill 1990; Janson and van Schaik 1993; Lima and Zollner 1996; Metcalfe and Monaghan 2001), or it may make the organism more vulnerable to starvation during sudden periods of food shortage (see discussion in Metcalfe and Monaghan 2001).

A different level of explanation, an ontogenetic mechanistic one, is provided by the literature on metabolic “programming”; “It is as though the baby receives from its mother a forecast of the nutritional environment it will encounter after birth and changes its physiology and metabolism accordingly.” (Barker 2001, p. 1). Health risks associated with catch-up growth and obesity in hu-

mans are well documented for infants who initially had poor nutrition and subsequently abundant food. Recent experiments with mice demonstrate the health and survival costs of catch-up growth in response to newly abundant food resources (Ozanne and Hales 2004). In our study, even the food-enhanced group showed significant within-individual consistency in relative size-for-age, and males were more consistent than females (see also data on persistence of maternal effects in semi-free-ranging provisioned mandrills, *Mandrillus sphinx*, Setchell et al. 2001). Integrating these physiological and ecological perspectives, an absence of catch-up growth may suggest a history in which ontogenetic metabolic “inertia” based on neonatal programming may have evolved through natural selection. Barker and colleagues (e.g. Hales and Barker 2001) proposed a scenario of intergenerational transmission of such programming that would occur at least partially through maternal effects.

### Sexual dimorphism

Within each of the two foraging conditions, which supported very different overall growth rates, sexual dimorphism in body mass emerged in somewhat parallel ways. During the period of maternal investment (approximately 12 months for the food-enhanced animals and 18 for the wild-foraging ones) and for several years after, males and females were similar in relative size within either foraging condition, although infant males were slightly, but insignificantly, heavier than infant females, particularly in the food-enhanced group (but see Gomendio 1990; Pereira 1995).

At approximately 5 years of age for wild-foraging animals and 3 for food-enhanced ones, females attained menarche (Altmann et al. 1993), and gender differences in growth became apparent. Females then maintained their previous growth rates until completion of growth a year or two later, whereas males under both nutritional conditions began greatly accelerated rates of growth, which persisted for several years. Males not only grew faster than did adolescent females, they also continued to grow after females of the same age reached full size (for data on many primate species in captivity see Shea 1990; Leigh 1992, 1995; Leigh and Shea 1996).

Foraging condition affected the magnitude as well as the timing of the growth spurt. As males made the transition to adolescence, their growth rate (slope) increased by approximately 130% of the juvenile value for the wild-foraging animals and 180% for food-enhanced animals. Consequently, the initial difference in growth rates between conditions was magnified during adolescence, so that sexual dimorphism emerged at a younger age and then increased more rapidly among animals in the food-enhanced group than among those in the completely wild-foraging groups. Males achieved a body mass almost double that of adult females (Fig. 2; also Altmann et al. 1993) before 7 years of age among food-enhanced ani-

imals and not until at least 8 among wild-foraging ones (Figs. 1, 2).

Age at various life-history markers, such as the onset of sexual dimorphism or age at menarche, may not tell the whole story, however. Size may be a more important predictor and even pacer of other life-history components than is age (see, e.g., Lee 1996 for weaning age, Pereira 1995 for behavioral correlates). If so, then life-stages may in some cases be more comparable than ages across a wide range of conditions within a species, and a life-stage, rather than an age-based approach (Sauer and Slade 1988; McNamara and Houston 1996; Caswell 2001), may sometimes provide valuable insights as well.

The evolution of sexual dimorphism, its ontogeny, ecological basis and relationship to mating systems, has been the subject of several reviews (e.g. Jarman 1983 for large mammalian herbivores; Hedrick and Temeles 1989; Shine 1989; Bjorklund 1990 for birds; Leigh 1992, 1995; Leigh and Shea 1996 for captive primates). These focus on interspecific differences. The present study highlights the importance of also evaluating the extent and sources of intraspecific variability in the evolution of growth trajectories, sexual dimorphism, and reproductive maturation when considering the life-history consequences and evolution of these characteristics (e.g. Kirkpatrick and Heckman 1989; Kirkpatrick et al. 1990; Arnold 1992; Pereira 1995; Cornillon et al. 2000; Badyaev 2002; Pereira and Leigh 2003).

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## References

- Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, Mass
- Altmann J (1983) Costs of reproduction in baboons (*Papio cynocephalus*). In: Aspey WP, Lustick SI (eds) Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus, Ohio, pp 67–88
- Altmann J (2000) Models of outcome and process: predicting the number of males in primate groups. In: Kappeler P (ed) Primate males. Cambridge University Press, Cambridge, pp 236–247
- Altmann J, Alberts SC (1987) Body mass and growth rates in a wild primate population. *Oecologia* 72:15–20
- Altmann J, Alberts SC (2003) Intraspecific variability in fertility and offspring survival in a non-human primate: behavioral control of ecological and social sources. In: Wachter KW, Bulatao RA (eds) Offspring: human fertility behavior in a biodemographic perspective. National Academy Press, Washington, DC, pp 140–169
- Altmann J, Muruthi P (1988) Differences in daily life between semi-provisioned and wild-feeding baboons. *Am J Primatol* 15:213–221
- Altmann J, Samuels A (1989) Upscale baboons. *Nat Hist* 5:60–63
- Altmann J, Samuels A (1992) Costs of maternal care: infant carrying in baboons. *Behav Ecol Sociobiol* 29:391–398
- Altmann J, Altmann SA, Hausfater G, McCuskey SA (1977) Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates* 18:315–330
- Altmann J, Altmann S, Hausfater G (1981) Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. *Am J Primatol* 1:389–399
- Altmann J, Altmann S, Hausfater G (1988) Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 403–418
- Altmann J, Schoeller D, Altmann SA, Muruthi P, Sapolsky R (1993) Body size and fatness of free-living baboons reflect food availability and activity levels. *Am J Primatol* 30:149–161
- Altmann M, Altmann J (1991) Models of status-correlated bias in offspring sex-ratio. *Am Nat* 137:542–555
- Altmann SA (1998) Foraging for survival. University of Chicago Press, Chicago
- Arnold SJ (1992) Constraints on phenotypic evolution. *Am Nat* 140:S85–S107
- Asquith PJ (1989) Provisioning and the study of free ranging primates—history, effects, and prospects. *Yearb Phys Anthropol* 32:129–158
- Badyaev AV (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol Evol* 17:369–378
- Barker DJP (2001) Preface: type 2 diabetes: the thrifty phenotype. *Br Med Bull* 60:1–3
- Bercovitch FB, Strum SC (1993) Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behav Ecol Sociobiol* 33:313–318
- Bernardo J (1996) Maternal effects in animal ecology. *Am Zool* 36:83–110
- Bjorklund M (1990) A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating system in birds. *J Evol Biol* 3:171–183
- Bloch DA, Moses LE (1988) Non-optimally weighted least squares. *Am Stat* 42:50–53
- Bronikowski A, Altmann J (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav Ecol Sociobiol* 39:11–25
- Bulger J, Hamilton WJ III (1987) Rank and density correlates of inclusive fitness measures in a natural chacma baboon (*Papio ursinus*) troop. *Int J Primatol* 8:635–650
- Case TJ (1978) On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q Rev Biol* 53:243–282
- Caswell H (2001) Matrix population models: construction, analysis and interpretation, 2nd edn. Sinauer, Sunderland, Mass
- Chapais B, Berman CM (eds) (2004) Kinship and behavior in primates. Oxford University Press, Oxford

- Charnov E (1991) Evolution of life history variation among female mammals. *Proc Natl Acad Sci USA* 88:1134–1137
- Charnov EL, Berrigan D (1993) Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evol Anthropol* 1:191–194
- Cheney DL, Seyfarth RM, Fischer J, Beehner J, Bergman T, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25:401–428
- Coelho AM (1985) Baboon dimorphism: growth in weight, length and adiposity from birth to 8 years of age. In: Watts ES (ed) *Nonhuman primate models for human growth and development*. Liss, New York, pp 125–159
- Cornillon PA, Pontier D, Rochets MJ (2000) Autoregressive models for estimating phylogenetic and environmental effects: accounting for within species variation. *J Theor Biol* 202:247–256
- Dobson FS, Oli MK (2001) The demographic basis of population regulation in Columbian ground squirrels. *Am Nat* 158:236–247
- Dunbar RIM (1990) Environmental determinants of intraspecific variation in body weight in baboons (*Papio* spp.). *J Zool* 220:157–169
- Eley RM, Strum SC, Muchemi G, Reid GDF (1989) Body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *Am J Primatol* 18:209–219
- Fa JE, Southwick CH (1988) Ecology and behavior of food-enhanced primate groups. Liss, New York
- Festa-Bianchet M, Jorgenson JT, Reale D (2000) Early development, adult mass, and reproductive success in bighorn sheep. *Behav Ecol* 11:633–639
- Gomendio M (1990) The influence of maternal rank and infant sex on maternal investment trends in rhesus macaques: birth sex ratios, interbirth intervals and suckling patterns. *Behav Ecol Sociobiol* 27:365–375
- Hales CN, Barker DJP (2001) The thrifty phenotype hypothesis. *Br Med Bull* 60:5–20
- Hamilton WJ III, Buskirk RE, Buskirk WH (1978) Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *Am Nat* 112:911–924
- Harvey PH, Purvis A (1999) Understanding the ecological and evolutionary reasons for life history variation: mammals as a case study. In: McGlade J (ed) *Advanced ecological theory: principles and applications*. Blackwell Science, Oxford, pp 232–247
- Harvey PH, Martin RD, Clutton-Brock TH (1987) Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth R, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago
- Hausfater G (1975) Dominance and reproduction in baboons (*Papio cynocephalus*). Karger, Basel
- Hedrick AV, Temeles EJ (1989) The evolution of sexual dimorphism in animals—hypotheses and tests. *Trends Ecol Evol* 4:136–138
- Henzi SP, Lycett JE (1995) Population structure, demography, and dynamics of mountain baboons: an interim report. *Am J Primatol* 35:155–163
- Henzi SP, Byrne RW, Whiten A (1992) Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. *Int J Primatol* 13:601–629
- Hofer H, East ML (1993) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. *Anim Behav* 46:575–589
- Janson CH, van Schaik CP (1993) Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA (eds) *Juvenile primates: life history, development, and behavior*. Oxford University Press, Oxford, pp 57–74
- Jarman P (1983) Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biol Rev* 58:485–520
- Johnson SE (2003) Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. *Am J Phys Anthropol* 120:83–98
- Keller LF, Van Noordwijk AJ (1994) Effects of local environmental conditions on nestling growth in the great tit *Parus major*. *Ardea* 82:349–362
- Kirkpatrick M, Heckman N (1989) A quantitative genetic model for growth, shape, reaction norms and other infinite-dimensional characters. *J Math Biol* 27:429–450
- Kirkpatrick M, Lofsvold D, Bulmer M (1990) Analysis of the inheritance, selection and evolution of growth trajectories. *Genetics* 124:979–993
- Kozłowski J, Weiner J (1997) Interspecific allometries are by-products of body size optimization. *Am Nat* 149:352–380
- LeBlanc M, Festa-Bianchet M, Jorgenson JT (2001) Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Can J Zool* 79:1661–1670
- Lee PC (1996) The meanings of weaning: growth, lactation and life history. *Evol Anthropol* 5:87–96
- Lee PC (1999) Comparative ecology of postnatal growth and weaning among haplorhine primates. In: Lee PC (ed) *Comparative primate socioecology*. Cambridge University Press, Cambridge, pp 111–139
- Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *J Hum Evol* 23:27–50
- Leigh SR (1994) Ontogenetic correlates of diet in anthropoid primates. *Am J Phys Anthropol* 94:499–522
- Leigh SR (1995) Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *Am J Phys Anthropol* 97:339–356
- Leigh SR, Shea BT (1996) Ontogeny of body size variation in African apes. *Am J Phys Anthropol* 99:43–65
- Lepage D, Gauthier G, Reed A (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia* 114:226–235
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation—a review and prospectus. *Can J Zool* 68:619–640
- Lima SL, Zollner PA (1996) Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers. *Behav Ecol Sociobiol* 38:355–363
- Lochmiller RL, Ditchkoff SS, Sinclair JA (2000) Developmental plasticity of postweanling cotton rats (*Sigmodon hispidus*) as an adaptation to nutritionally stochastic environments. *Evol Ecol* 14:127–142
- Lyles AM, Dobson AP (1988) Dynamics of provisioned and unprovisioned primate populations. In: Fa JE, Southwick CH (eds) *Ecology and behavior of food-enhanced primate groups*. Liss, New York, pp 167–198
- McAdam AG, Millar JS (1999) Dietary protein constraint on age at maturity: an experimental test with wild deer mice. *J Anim Ecol* 68:733–740
- McNamara JM, Houston AI (1996) State-dependent life history. *Nature* 380:215–221
- Melnick DJ, Pearl MC (1987) Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts BB, Cheney DL, Seyfarth R, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 121–134
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Mori A (1979) Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. *Primates* 20:371–397
- Moses LE, Gale LC, Altmann J (1992) Methods for analysis of unbalanced, longitudinal, growth data. *Am J Primatol* 28:49–59
- Mosteller F, Tukey JW (1977) A method of direct assessment. In: Mosteller F, Tukey JW (eds) *Data analysis and regression*. Addison-Wesley, Reading, Mass, pp 133–163
- Mousseau TA, Fox CW (1998) The adaptive significance of maternal effects. *Trends Ecol Evol* 13:403–407
- Muruthi P (1989) Food intake and energy expenditure in savannah baboons. MSc Thesis, University of Nairobi, Kenya



- Muruthi P (1997) Socioecological correlates of parental care and demography in savannah baboons. PhD Thesis, Princeton University, Princeton, NJ
- Muruthi P, Altmann J, Altmann S (1991) Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* 87:467–472
- Ozanne SE, Hales CN (2004) Catch-up growth and obesity in male mice. *Nature* 427:411–412
- Packer CP, Tatar M, Collins A (1998) Reproductive cessation in female mammals. *Nature* 392:807–811
- Packer CP, Collins DA, Eberly LE (2000) Problems with primate sex ratios. *Philos Trans R Soc Lond B Biol Sci* 355:1627–1635
- Pereira ME (1988) Agonistic interactions of juvenile savanna baboons. I. Fundamental features. *Ethology* 79:195–217
- Pereira ME (1993) Juvenility in animals. In: Pereira ME, Fairbanks LA (eds) *Juvenile primates: life history, development, and behavior*. Oxford University Press, Oxford, pp 17–27
- Pereira ME (1995) Development and social dominance among group-living primates. *Am J Primatol* 37:143–175
- Pereira ME, Leigh SR (2003) Modes and phases of primate juvenility. In: Kappeler PM, Pereira ME (eds) *Primate life histories and socioecology*. University of Chicago Press, Chicago, pp 149–176
- Post DG, Hausfater G, McCuskey SA (1980) Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatol* 34:170–195
- Quinney TE, Hussell DJT, Ankney CD (1986) Sources of variation in growth of tree swallows. *Auk* 103:389–400
- Read AF, Harvey PH (1989) Life history differences among the eutherian radiations. *J Zool Lond* 219:329–353
- Rubenstein DI (1993) On the evolution of juvenile life-styles in mammals. In: Pereira ME, Fairbanks LA (eds) *Juvenile primates: life history, development, and behavior*. Oxford University Press, Oxford, pp 38–56
- Samuels A, Altmann J (1984) Feeding patterns of baboon mothers (*Papio cynocephalus*) in Amboseli National Park, Kenya. *Int J Primatol* 5:376
- Samuels A, Altmann J (1991) Baboons of the Amboseli basin: demographic stability and change. *Int J Primatol* 12:1–19
- Sapolsky RM, Altmann J (1991) Incidences of hypercortisolism and dexamethasone resistance increase with age among wild baboons. *Biol Psychiatr* 30:1008–1016
- SAS Institute (1988) *SAS/STAT User's Guide*. Release 6.03 edn. SAS Institute, Cary, N.C.
- Sauer JR, Slade NA (1988) Body size as a demographic categorical variable: ramifications for life history analysis of mammals. In: Boyce MS (ed) *Life histories of mammals: theory and patterns*. Yale University Press, New Haven, pp 107–122
- Setchell JM, Lee PC, Wickings EJ, Dixson AF (2001) Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *Am J Phys Anthropol* 115:349–360
- Shea BT (1990) Dynamic morphology: growth, life history, and ecology in primate evolution. In: DeRousseau CJ (ed) *Primate life history and evolution*. Wiley, New York, pp 325–352
- Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q Rev Biol* 64:419–461
- Sigg H, Stolba A, Abegglen A-A, Dasser V (1982) Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates* 23:473–487
- Simons LS, Martin TE (1990) The hunting behaviour of individual great tits in relation to spatial variations in their food densities. *Anim Behav* 19:695–706
- Smith JNM, Arcese P (1988) Effects of supplemental food on growth and adult size in the song sparrow. *Proc XIX Int Ornithol Congr* 2:1416–1423
- Smuts BB, Nicolson N (1989) Reproduction in wild female olive baboons. *Am J Primatol* 19:229–246
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. Freeman, New York
- Strum SC (1991) Weight and age in wild olive baboons. *Am J Primatol* 25:219–237
- Strum SC, Western JD (1982) Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *Am J Primatol* 3:61–76
- Sugiyama Y, Ohsawa H (1982) Population dynamics of Japanese monkeys with special reference to the effects of artificial feeding. *Folia Primatol* 39:238–263
- Trivers R (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man*. Aldine, Chicago, pp 136–179
- Walters JR, Seyfarth RM (1987) Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth R, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 121–134
- Wasser LM, Wasser SK (1995) Environmental variation and developmental rate among free ranging yellow baboons (*Papio cynocephalus*). *Am J Primatol* 35:15–30
- Wasser SK, Norton GW, Kleindorfer S, Rhine RJ (2004) Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons (*Papio cynocephalus*). *Behav Ecol Sociobiol* 56:338–345
- Whiten AR, Byrne RW, Henzi SP (1987) The behavioral ecology of mountain baboons. *Int J Primatol* 8:367–388
- Whitten PL (1982) Female reproductive strategies among vervet monkeys. PhD Thesis, Harvard University