Body mass and growth rates in a wild primate population

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Summary. We obtained data on body mass and growth rates for the immature members of two groups of wild baboons in Amboseli National Park, Kenya. Data were collected without feeding, trapping, or handling. The data were separated into cross-sectional and longitudinal components, allowing both the examination of body mass-age relationships and the calculation of growth rates for individuals. For animals less than three years old, body mass was well-predicted from age by a linear model. Differences based on social group membership were small but consistent, and their origins are discussed. We detected no differences in body mass based on sex or on maternal dominance rank. For older juveniles, those three to seven years of age, a better fit was obtained from log of mass than by mass in a linear model. This was also true for the cross-sectional data set over the whole age range (*zero to seven* years). For older juveniles, samples were too small for quantitative analysis of differences based on sex, rank, or group membership, but trends in the data are indicated. Growth rates derived from repeat measures of body mass for 38 animals are presented and discussed.

The growth rate values obtained in this study are consistent with data from cross-sectional studies of other wild baboon populations; these values for wild baboons are consistently one-half to one-third lower than growth rate values for well-provisioned captive baboons and equivalent to captive baboons fed a low-protein diet. Comparisons between primates and other mammals in the primate size range raise questions concerning ecological and behavioral constraints on primate growth rates; some possible mechanisms of constraint are suggested.

Key words: Baboons – *Papio cynocephalus* – Body mass – Post-natal growth rates – Developmental constraints

Recent evidence suggests that many primate populations are food-limited, as evidenced by the fact that if the animals receive better nutrition, either through natural increases in food supply or through human-supplied nutritional enrichment, age of first reproduction declines and fertility rates and population size increase (Sade et al. 1977; Mori 1979;

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Southwick et al. 1980; Strum and Western 1982; Sugiyama and Oshawa 1982). The effects on reproductive rates probably are mediated at least partially through changes in rates of body growth and in the ratio of body mass to skeletal measures (Mori 1979; Sugiyama and Oshawa 1982). This suggests that measurement of developmental changes in body mass and assessment of factors that are related to differences in growth rates will ultimately be essential for understanding the dynamics of these populations and differential reproductive success within them.

In previous studies of individually identified yellow baboons, (*Papio cynocephalus*) of known age in Amboseli National Park, Kenya, we obtained maturational data over a number of years entirely through regular assessment of developmental markers that are visible in the field: animals were never fed, trapped or otherwise handled. Age at attainment of developmental milestones, such as menarche for females or first visible rounding of the testes for males, was found to be much greater than had been reported previously based on data from captive animals: the ratio of age at attainment of developmental milestones for animals in captivity to that for unprovisioned wild animals was approximately 3.5 to 5 (Altmann et al. 1977, 1981). These results are consistent with field data for olive baboons (*P. anubis*) in Tanzania (Packer 1979).

Amboseli data on these developmental milestones and on the time course of infant behavioral development, combined with reports on growth rates of captive baboons (Snow 1967; Buss and Reed 1970), led us to hypothesize that young baboons in Amboseli grow at rates between five and six grams per day during the first few years of life (Altmann 1980, 1983). In the present paper we report recent data on body mass and growth rates that we obtained as part of a series of investigations into aspects of development, parental investment and reproduction.

Material and methods

The subjects of the study were the immature members of two social groups of yellow baboons, Alto's and Hook's, whose home ranges include Amboseli National Park, Kenya. The individually identified members of these groups have been observed almost daily, Alto's group since mid-1971, Hook's Group since late 1980. The groups have been relatively stable in age-sex composition and stable or slightly increasing in size for a number of years (Altmann et al. 1985). Starting in mid-August, 1984, we repeatedly

placed a dial-type platform scale (Avery model 3305) on the ground near the sleeping trees that were currently being used by one of the baboon groups. This was done either late in the afternoon, just before the baboons' ascent into a sleeping grove, or before descent from the trees in the morning. The scale was never baited. Our hope was that the youngsters would accomodate to this new object and climb on it as they do with most objects in their environment that are suitable for climbing or play. In Hook's Group, a few animals began to do so on the first day that the scale was presented; in Alto's Group, we still had only a few measurements by the end of the second month. By presenting the scale two or three times a week, however, we had obtained body-mass data on 56 (approximately 85%) of the immature animals by the end of July, 1985; for a few individuals, we gathered near-weekly measurements. Only one female who had attained menarche (approximately five years of age) got on the scale, only a few males who had reached subadulthood (about six years of age) did so, and only rarely did infants less than six months old do so: use of the scale was almost exclusively by older infants and by juveniles. Data for the other age ranges will probably be obtained, but slowly and for only a fraction of the individuals. For most animals, once they first used the scale, repeated measures were obtained.

Two observers were used to facilitate identification, check that all parts of a subject's body were on the scale, read the scale, and record data. They stood a few meters from the scale and read it with binoculars to the nearest 0.1 kg. The tare was checked before and after each weighing. When part of a subject's tail hung off the edge of the scale, we recorded the body mass along with an estimate of the proportion of tail that was on the scale. For all but the oldest animals the difference between full tail and no tail was 0.1 kg or less. Usually we were able to obtain measurements that included all or the major proportion of the tail. In addition to the date, time, subject, tare, tail portion, and body-mass measurement, we made a note if there were any potential sources of error, such as urine or feces on the scale, poor damping of the scale, etc. Measurement sessions usually lasted approximately 15 minutes, from the first to last values obtained, as the animals progressed past the scale and continued their ongoing activities. Between measurement sessions, we periodically checked the readings with known masses and performed routine adjustments and maintenance as needed.

Before the original data were entered into a computer file for analysis, we deleted a few values that were totally anomalous, were noted as being very poor, or were otherwise uncodable. These constituted less than a dozen values out of more than 500 and were primarily obtained during the first few days of weighing or were instances of several animals simultaneously on the scale. When multiple weights were obtained for the same animal during the same weighing session, these were reduced to a single record by using the record with the greatest part of tail and no problems indicated by notes. If more than one record met the criteria, then the mean of the several weighings was used. These several values for an individual during the same session differed only rarely and then almost always did so by no more than 0.1 kg. The result was a data set consisting of more than 250 usable body-mass values.

The data were then separated into cross-sectional and longitudinal components. The first measurement for each

animal for which all or most of the animal's tail was on the scale and for which there were no potential problems was used for cross-sectional analyses to compare the body mass values of known-age individuals. In the longitudinal analyses, repeated measurements of the same individual were used to calculate the growth rate for each animal for which data were available. The growth rate of an individual was calculated just from its morning weighings (see discussion of diurnal effects, below) as the slope of their linear regression, but only if we obtained at least two morning values for that individual that were at least one month apart. Analyses used GLM (general linear models) procedures in SAS (SAS Institute, Inc. 1985). Group membership, sex, maternal dominance rank (Hausfater 1975; Altmann 1980; Hausfater et al. 1982), season, and age were considered as independent variables predicting body mass.

Results

Values obtained for body mass were approximately six percent greater in the evening, at the end of a day of feeding, than those obtained upon descent from the sleeping trees in the morning before feeding commenced. The exceptions to this were the values for infants that were still suckling and were also sleeping huddled with their mothers; as a result of these behaviors, the infants obtained nutrition overnight and reduced heat loss, and thus experienced less weight loss overnight. Because of the night/morning difference in body mass and because the values from repeated weighings were not well distributed by time of day across individuals and subclasses, we restricted our growth rate analyses to the morning values, as indicated above. On the other hand, cross-sectional data were well-distributed by subclass across morning and evening weights, and so in order to reduce seasonal effects on the analyses we used the first good value for an individual, regardless of time of day.

In Fig. 1, cross-sectional body-mass values are presented for the 56 immature animals. For animals in the first three years of life, approximately encompassing the infant and young juvenile stages, body mass is well-pre-
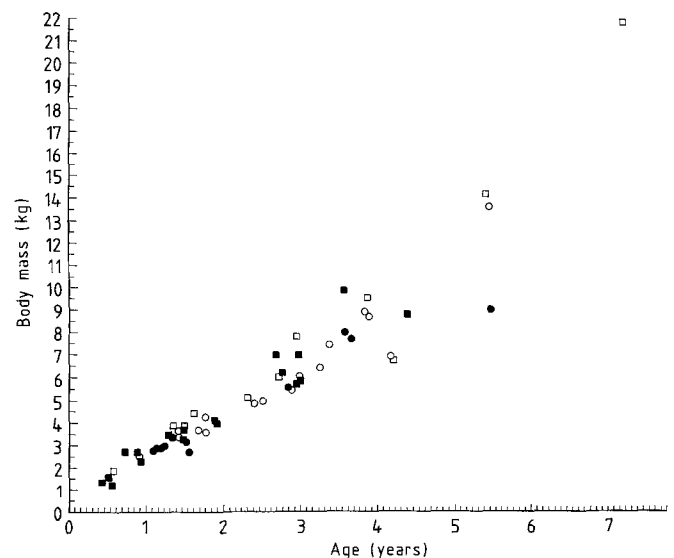

Fig. 1. Body mass as a function of age for 56 immature baboons. ● Alto's ♀; ○ Alto's ♂; ■ Hook's ♀; □ Hook's ♂
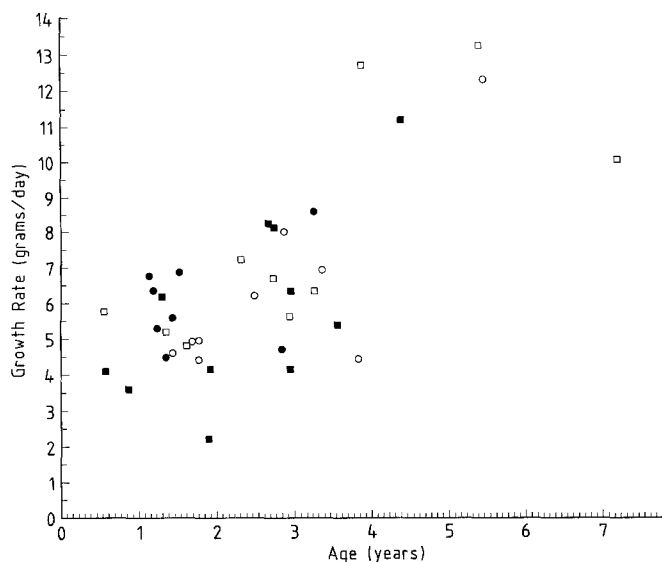
Fig. 2. Estimates of growth rates for 38 immature baboons based on at least two morning weighings over a span of at least one month. Growth rates are plotted against age at which the first weight was obtained for each animal, see text for details; symbols see Fig. 1

dicted ($r^2 = 0.89$) from age by a linear model with intercept of 710 g (body mass at birth) and slope of 5.1 grams per day; the fit is not improved by use of the logarithm of body mass.

For these young animals, only group membership was significantly related to body mass after age was taken into account: values for Hook's Group animals were higher than those for members of Alto's Group. Although adding group membership added only two percent to the explained variance, the effect was quite consistent: almost all members of Hook's Group had weights that fell above the regression line for Alto's Group. Moreover, the difference was one equivalent to almost a gram per day (approximately 4.5 vs. 5.5) difference in weight gain and is probably of considerable biological importance. No significant sex difference in body mass was detected in these young animals nor was there a difference based on dominance rank of mother. However, because dominance rank of mother is correlated with birth sex-ratio of offspring in this population (Altmann 1980; Altmann et al. 1987), we were not able to evaluate these parameters adequately at this time (see Discussion).

For animals between three and six or seven years of age, body mass was much greater than would be predicted from the body mass regression equation for younger animals. For these older animals and for the cross-sectional data set as a whole, an appreciably better fit was obtained from a linear model based on the logarithm of body mass rather than on body mass itself ($r^2 = 0.89$ vs. 0.50). For the cross-sectional data as a whole, log of body mass, in grams, was predicted from age, in days, by a linear equation with an intercept of 3.28 and slope of 0.00045. Although we do not yet have an adequate sample to examine sex differences quantitatively for the older immature animals, or effects of dominance rank or group membership on their growth, it appears that the group differences are maintained (i.e., individuals in Hook's Group are larger at a given age than are those in Alto's Group) and that during this

period there is a major growth spurt for the males but perhaps not for the females.

Estimates of growth rates were obtained for 38 animals over varying lengths of time during the year. The results for each immature animal of any age are plotted in Fig. 2 against that animal's age at the time that its value was obtained for the cross-sectional data set. The age changes in growth rate that were suggested by the cross-sectional data are confirmed by the actual data on growth rates of individuals. Over the entire age range, no statistically significant effects on growth rate were detected based on season, group membership, or gender. Sample sizes and distributions across subclasses were not adequate for separate analyses of the data exclusively for the young animals.

Discussion

Growth rates in captive and wild baboons and macaques. The growth rate values of approximately five grams per day for very young baboons in Amboseli were consistent with predictions (Altmann 1980, 1983) based on field-visible markers throughout development, data on behavioral development of infants, and reported growth rates for body mass in captivity. Recent cross-sectional data for a small set of immature wild baboons in two other populations indicate growth rates the same or somewhat lower than those we report here (Nicolson 1982 for anubis, Sigg et al. 1982 for hamadryas baboons). Nicolson (1982) obtained body mass data through a single trapping of 23 wild anubis baboons under two years of age, all members of a single social group that was part of a population near Gilgil in the Rift Valley area of Kenya. Based on these data she suggested that infants in that group gained body mass at a rate of approximately four or five grams per day. Sigg et al. (1982) also found that a cross-sectional data set from a single trapping of hamadryas baboons (*P. hamadryas*) in Ethiopia produced body mass results that were considerably below those that had been estimated for immature animals of the same age in captivity, and that developmental milestones were reached later than had previously been assumed based on captive animals. Estimation from a reading of the points on their graph gives a value of approximately three grams per day for young animals.

The growth rates for this diverse range of wild-foraging baboons are consistently one-half to two-thirds those of captive animals (see Snow 1967 for mixed *Papio* species, Glassman et al. 1984 and Coelho 1985 for anubis, Altmann et al. unpublished work for guinea baboons). Moreover, Buss and Reed (1970) found that breast-fed baboon infants grow at rates of approximately 8 to 10 grams per day in the first few months of life if mothers were fed their usual ration of chow, but if mothers were fed low-protein diets, infants growth rates were half those values, that is, about the same as those of wild foraging baboons. At that time the studies were discontinued after several months as a result of concern for the animals' health.

It is not surprising to us that in the present study we detected no consistent or statistically significant sex differences in body mass for infant and young juvenile Amboseli males and females, despite the two-fold difference in body mass of adults of this species. In our prior field estimates of relative size (Altmann et al. 1981; Altmann and Samuels unpublished work), we could first detect a sex difference

at between three and four years of age. The few data now available from Amboseli and from Sigg et al.'s study of hamadryas do not support a sex difference in body mass until at least the fourth birthday. On the other hand, data from several studies of baboons and macaques in captivity have demonstrated consistent sex differences in body mass, albeit of small magnitude and with considerable overlap in the size distributions for the two classes, during the first two years of life (Van Wagenen and Catchpole 1956; Snow 1967; Glassman et al. 1984; Coelho 1985). Consequently, sex differences in body mass for baboons have been statistically significant at these ages only in the captive studies with large sample sizes. In captivity, the differences that are present from the first year are magnified by increasing differences in growth rates by the end of the second year of life and result in major sex differences in body mass in the third year of life (refs as above).

Immature males in Amboseli were observed to be about the same size as adult females during their sixth year (Altmann et al. 1981). The few values we now have for body mass of older juveniles in Amboseli suggest that the males surpass adult female body mass (approximately 11 kg) early in the sixth year (Fig. 1). (The estimate for body mass of adult females is based on baboons captured in this geographical area [Bramblett 1969, Maples unpublished work; see estimates in Altmann 1980]). Sigg et al.'s (1982) extrapolation from their data is consistent with these results.

The present data set for Amboseli suggests an increase in growth rate beginning between ages three and four. This increase may represent the onset of an adolescent growth spurt that is of greater magnitude and duration in males than in females (see e.g. Coelho 1985 for captive baboons; Van Wagenen and Catchpole 1956; Watts and Gavan 1982; Watts 1985 and references therein for captive chimpanzees and rhesus monkeys). We cannot yet analyze in detail the late juvenile and adolescent growth period for wild baboons. However, the few measurements we have of older juveniles, sub-adult males, and a single adult male, suggest, as proposed by Nicolson (1982), that the wild animals continue to gain body mass until a later age than do captive animals. As a consequence, the difference in body mass of wild and captive adults is less than would be predicted from the differences in growth rates of the youngsters. This possibility and its implications warrant further attention.

The difference in body mass between the two social groups in Amboseli is a small but potentially important one and consistent with our expectations based on related unpublished data. Hook's Group, the one with slightly higher growth rates, spends somewhat less time feeding than does Alto's Group during the dry season (Altmann and Mututua unpublished work) and, unlike Alto's (Post 1982), members of Hook's Group retain a varied diet during the dry season (Altmann and Muruthi unpublished work). Overall Hook's Group appears less energetically stressed than Alto's Group, although recent evidence indicates that in some circumstances there may be no significant differences in energy intake between the groups (Stacey 1986).

No seasonal effects are yet detectable in our data on growth rates. This is probably because measurements were started in the last few months of a drought year and most of the longitudinal data that resulted in the estimates of growth rates come from the nine months following the drought, months of good rains and good food supply. The good conditions for the year are probably also responsible

for growth rates in general being slightly higher (Fig. 2) than would have been predicted from the cross-sectional data (Fig. 1). Good conditions may also partially account for the absence of a group difference in growth rates: only during times of reduced food availability, such as in the dry season, do we detect a difference in the two groups in time spent feeding (but see Stacey 1986). Baboon youngsters may be capable of considerable "catch up" growth when times are good (see Riopelle and Shell 1978 and Kerr et al. 1970 for experimental data on *Macaca mulatta*).

Among young animals we did not detect an effect of mother's rank on body mass, despite the fact that we might expect high-ranking females to garner more resources than low-ranking ones and thus have larger infants that grow faster. Our negative result may be merely a consequence of the fact that only fairly large or very consistent differences could have been confirmed with our present sample sizes. An alternative explanation may lie in our analyses of rank differences in behavior and rank-dependent offspring sex-ratios. Among Amboseli baboons, agonistic dominance rank of females is correlated with the birth sex-ratio of the offspring those females produce: high-ranking females produce primarily female infants and low-ranking females produce a preponderance of male infants (Altmann 1980; Altmann et al. 1987). Any small tendency for greater body mass and greater gain in body mass for young male infants might therefore be counteracted in this population by a tendency for low-ranking females, those primarily being the mothers of male infants, to be able to garner fewer resources for themselves and their infants. If that is the case, then even with large samples we would not find a sex difference in body mass of young animals.

Whether sex-by-rank effects exist would also depend on any sex-by-rank patterns of parental investment (Altmann et al. 1987; Altmann and Samuels unpublished work). For example, we have found a difference in maternal care that is correlated with dominance rank. High-ranking females tend to be less restrictive and protective of their infants than are low-ranking ones, and the infants of high-ranking females, on average, develop independence of their mothers at an earlier age (Altmann 1980). The consequence of this may be the absence of rank-related effects on body mass: high-ranking infants may obtain no more nutrition or may expend more energy than low-ranking ones. In addition, studies of Japanese macaques, *Macaca fuscata*, under differing food conditions (Mori 1979; Sugiyama and Oshawa 1982) suggest that effects of social status on growth, reproduction, and offspring survival are less pronounced in animals that are not food provisioned than among those that have their natural food supplemented by concentrated provisions.

Primate growth rates: flexibility and constraints. The twofold differences in growth rates between provisioned and wild-foraging primates is a considerable one. Food is implicated as the limiting factor. It seems reasonable to expect that intermediate rates will be found (as our group differences suggest) as an appropriate spectrum of environmental conditions are examined. However, data and analyses will have to be fine-grained because of the ability of these animals to respond to short-term fluctuations through catch-up growth and the ability of a flexible omnivore such as a baboon to alter its diet and damp the detrimental effects of specific shortages.

Despite considerable ontogenetic flexibility and a doubling of growth rates under conditions of unlimited food supplies, the post-natal growth rates of anthropoids are strikingly low (e.g. Case 1978; Eisenberg 1981). Pre-natal growth is also slow in primates. Evolutionary and developmental explanations for constraints on pre-natal growth remain a matter of debate (Sacher and Staffeldt 1974; Case 1978; Western 1979; Eisenberg 1981), and correlations between rates of pre-natal and post-natal growth show much scatter (Case 1978; Eisenberg 1981). Most orders of mammals, diverse in their diets, in their gestation lengths, in pre-natal growth rates, and in their litter sizes, have developed mechanisms that enable their young to grow much more rapidly post-natally than do primate infants. With few exceptions such as elephants and the extremely low-metabolic rate sloths, only marsupials, which also have slightly lower metabolic rates, as a group grow about as slowly as anthropoids (Case 1978). What may have selected for limited post-natal growth rates in primates?

Among orders of eutherian mammals, only carnivores and artiodactyls include species throughout most of the body size range of primates. Only Artiodactyls have gestations as long as those of primates and, like primates, produce only a single young in each litter. Even this group has young that are much more precocial and that locomote independently and rapidly within the first day of life. In addition, the lactation interval for these ungulates is about a fifth that of a primate in the size range of a baboon (Hayssen 1985). Moreover, the infant growth rates are an order of magnitude greater than that of baboons (Case 1978).

Carnivores, the only other order of eutherian mammals that extends throughout the size range of primates and that has species of baboon size, produce litters of about four, weighing in total what a single primate or artiodactyl infant does (Case 1978; Hayssen 1985). However, these litters are produced after a much shorter gestation, only 60 days or one-third the gestation time of baboon-sized primates (Hayssen 1985). Birth is followed by a lactation period that is, like ungulates, only about a fifth the length of primate lactation for a baboon-sized animal (Hayssen 1985). Growth rates are, per offspring, about five times that for a primate infant (Eisenberg 1981; Case 1978); per litter this is at least an order of magnitude greater than primate growth rates.

In a thorough review and analysis of the empirical and theoretical literature on growth rates, Case (1978), building on the work of Lack (1968), incorporates growth-dependent mortality in Ricklefs' (1969) model of optimal growth rates. This results in a more realistic model that under some conditions predicts optimal growth rates that are less than maximal ones. Primates, among mammals, would seem to exemplify a group in which there are potential costs, to both parent and offspring, entailed by very rapid growth.

Both learned behavior and fine motor skill probably are necessary for successful independent foraging in many primates (see, e.g. Gibson 1983; Hamilton et al. 1978), and development of these capabilities probably is age-rather than size-dependent. A large but immature primate young might, therefore, put itself or its parent at greater risk because of the increased foraging demands on the parent (Altmann 1983), almost always exclusively the mother.

In addition, for most anthropoid primates (and for marsupials), transport is provided by the mother for a considerable period. If a larger infant is not necessarily capable of greater locomotor independence, then a mother will be under greater energetic constraints as a result of costs of locomotion and interference with feeding while carrying a large infant (Altmann 1983; Altmann and Samuels unpublished work). Therefore, the absence of higher post-natal growth rates in primates probably results from a selective disadvantage to very rapid growth because other maturational rates are not growth-linked but time-linked: they are age- or experience limited, and rapid growth would therefore result in higher mortality. If rapid growth rates are still within the physiological capabilities of any anthropoid taxa, we would expect to find them in those small New World primates in which fathers and siblings carry the infants and sometimes share food with them.

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