

Physical Maturation and Age Estimates of Yellow Baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya

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In a longitudinal study of individually identified wild baboons in Amboseli National Park, Kenya, we collected data on physical development and reproductive maturation. Confirming and extending our earlier results, we demonstrated that the ratio of ages at which developmental milestones occur in the field as compared to those under extensive provisioning or in captivity were approximately 5:3. The age range for some developmental milestones was quite narrow and discrete, while for others there was considerable between-individual variability and more gradual changes. For infants, only the change from pink to gray of the paracallosal skin occurred within a brief age span. For older animals two important developmental events are readily identified and occur within a fairly narrow age range: Rapid enlargement of testes at 5 to 6 years for males and onset of menarche at 4 to 5½ years for females. In the present report, we considered some consequences of accelerated or delayed maturation. We further explored the need to employ different age-class criteria for different research problems.

Key words: age estimation, physical maturation, Amboseli baboons, growth rates, nutrition

INTRODUCTION

The relationship between age and physical development has important consequences for the study of several aspects of primate behavioral biology. First, variability in development among populations of the same species or of closely related species will be an important source of differences between the populations not only in the life histories of the individuals but also in the demographic conditions of the populations themselves. We may be able to detect relationships between advantageous environmental conditions and precocity on the one hand and environmental stress and illness or retardation on the other. Second, through an understanding of the within-population variability in physical maturation and the causes of this variability, we hope to obtain clues to factors affecting natural selection in the population. Deviations in development may be consistent within

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families and may correlate with dominance rank or with some characteristics of parental care. Developmental variance may have a heritable component.

Knowledge of age-development relationships also enables researchers to initiate study of animals of unknown birthdate and to conduct short-term research for comparison with data from more intensive longitudinal studies — data on physical maturation of known-age animals can be used to estimate the age of animals of unknown history. The need for age estimates continues even in long-term studies each time an animal of unknown age migrates into a study group, when research is started on a new group, or when brief or intermittent work is conducted on other groups in the same population as the primary study animals. Likewise, in laboratory investigations, similar needs arise whenever new animals are brought into a laboratory from the wild. In the past, laboratory researchers have probably estimated age by comparing stages of development with those of animals raised in the laboratory. However, such age estimates will usually be at least 1 or 2 years low due to the acceleration of growth and maturation that occurs in laboratories, from which most growth data come, and in the field under conditions of extensive provisioning. This difference in rates of maturation has now been documented by the few longitudinal field studies of wild primates [eg, Altmann et al, 1977; Dittus, 1975, 1977; Packer, 1979; Pusey, 1978] as well as by the recent work comparing various provisioning regimes for Japanese macaques on Koshima Island [Mori, 1979].

Finally, knowledge of the relationship between physical development and age also enables us to divide the continuum of development into biologically meaningful age classes. It is often convenient or necessary to group individuals by age classes that span several years. In much of behavioral and biological research there is a search for age classes within which variability is low relative to that between classes.

Data on physical change during a lifetime, like other life history data, accumulate slowly in studies of late-maturing, long-lived species, especially in natural populations without artificial feeding and with appreciable mortality. In the present report we examine the results obtained thus far in our studies of yellow baboons in Amboseli National Park, Kenya, and compare these results to the growing body of data becoming available for other baboons and macaques.

SUBJECTS AND METHODS

The subjects of the developmental study reported here are all members of a single primary study group, Alto's Group, that has consisted of approximately 45 animals. The individually recognized members of this group have been observed since 1971 [see Altmann et al, 1977 for observation periods prior to 1974; since May 1974 observation has been almost daily].

Methods of Assessing Physical Development in Primary Study Groups

During our first study, in 1963–1964, and at the onset of the longitudinal project in 1971, we were unaware that the course of development might be other than that assumed in the literature on the basis of laboratory data [see also Kummer, 1968]. In 1971 we initiated a longitudinal study of a primary study group, Alto's Group. The first several years of the longitudinal project included several appreciable breaks in the field work. During these first few years written observations of physical maturation were made sporadically, but it has been possible in some cases to provide supplementary data based on observations made from our annual photographic records. The frequency and level of detail of records each year depended on the interests of the particular researchers in residence. During the summer of 1974 systematic physical descriptions were made of all immature animals, because by then it was clear that maturation proceeded at a slower rate than we had thought. During 1975–1976 these physical descriptions were collected at frequent intervals during a study of mothers and infants. The Amboseli

data through 1975 [Altmann et al, 1977] enabled us to extend the previous descriptions of physical maturation to animals of older ages. We documented slower rates of maturation under field conditions, and provided sufficient evidence for variability in development that more systematic investigation seemed warranted. Starting in 1978 we initiated a regular schedule (weekly, fortnightly, or monthly, depending on age) and a coding sheet for observations on physical development for all immature animals as part of the monitoring to be conducted regardless of a researcher's specific primary study topic. Each new observer is trained by his or her predecessor, and informal checks on interobserver agreement are conducted during at least 1 month of overlap between observers, as well as during overlap periods between one of the authors and any current observer on site.

Because baboon infants are born with natal coloration of both skin and hair, the progress of color changes for various body parts constitutes some of the major records we keep for infants. We also follow infants' locomotor development by recording ages at which they ride dorsally and at which they climb on their own into and out of umbrella trees (*Acacia tortilis*) and the smoother-trunked fever trees (*Acacia xanthophloea*) with their higher, more vertical branching. The maturational records also include suckling, whether a youngster still sleeps with its mother, circumstances under which an older infant is carried, and both standing height and head to tail base length relative to mother. Juveniles are checked for development of canine ridge and of the canine teeth, testes enlargement, and onset of menarche. The complete developmental sheets are available from the authors.

RESULTS

First Year

The general pattern of change from the black coat and pink skin of early infancy to the golden-brown pelage and grey skin of older infants and juveniles has been well described in studies of anubis baboons (*Papio anubis*) by DeVore [1963] and by Ransom and Rowell [1972]. In contrast to these early reports that described the transition as complete at 6 months, more recent studies of two populations of yellow baboons [Altmann et al, 1977; for Amboseli, Kenya; Rasmussen, 1979, for Mikumi, Tanzania] have documented extensive individual variability in the loss of natal physical characteristics, a variability that probably exists within anubis baboon populations as well. Although an infant with totally natal coloration is almost surely less than 2 months of age and one with no natal coloration is more than 12 months old, infants retain considerable natal coloration into the second half-year of life in both Mikumi and Amboseli. Sufficient natal pelage is retained by most infants in both Amboseli and Mikumi that infants would be classed as "black" or "transitional" until about 8 months of age (see Fig. 1). In both Amboseli and Mikumi the only pelage or skin color transition that occurs within narrow age ranges is the change of the paracallosal skin from predominantly pink to predominantly grey at about 5 months of age (Fig. 1). This provides a useful age criterion, but only if animals of unknown birthdate can be observed at close range. For known-age animals, records of paracallosal skin color have one additional use, however. In Amboseli, delay in completion of changes in paracallosal skin color has been one of the first signs of abnormality in several infants who later exhibited delayed maturation, whitening of pelage, locomotor disability and finally, death [see also Klein, 1978 for evidence of morbidity in Amboseli vervet monkeys, *Cercopithecus aethiops*].

The order in which areas of skin change color is fairly consistent across individuals even within a given body part, so that, for example, the upper half of the paracallosal skin usually turned grey before the lower half. With the exception of the male's scrotum, which does not assume its grey coloration until 2 to 3 years of age (Fig. 2), the last por-

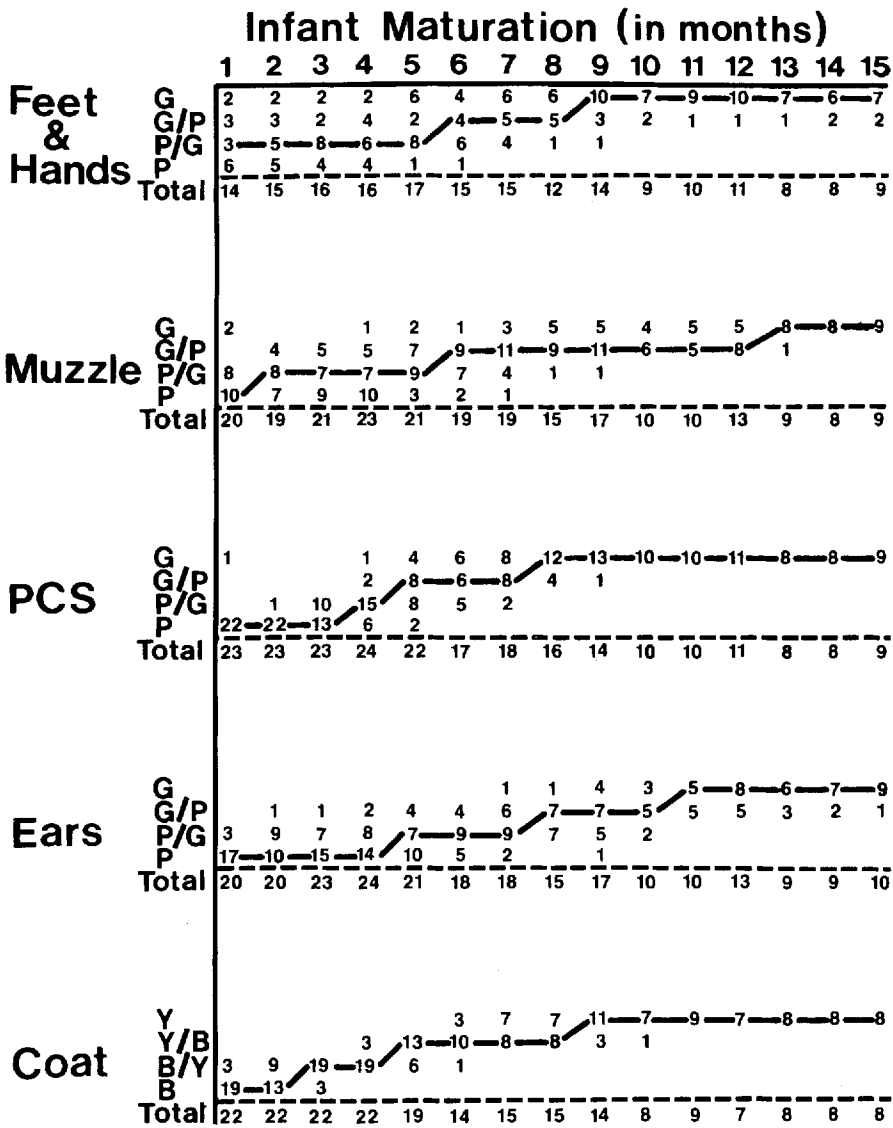


Fig. 1. Developmental changes in color of various body parts – the appearance of the skin, changing from all pink (P) to predominantly pink with some grey (P/G) to predominantly grey with some pink (G/P) and finally to all grey (G). This is plotted for feet and hands, muzzle, paracallosal skin (PCS), and ears. Coat color change is from black (B) to yellow (Y). The numbers plotted within each graph indicate the number of infants at each developmental stage. The line connects the median values.

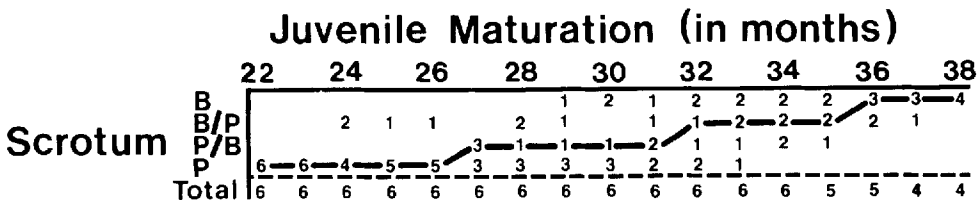


Fig. 2. Developmental change in scrotum skin color appearance. Conventions as in Figure 1.

tions of natal pink skin coloring remain on the infant's nose, on the skin immediately below the eyes, and on the ears.

In the loss of the black natal coat (Fig. 1), the transition stage, starting in the second or third month of life, is one of a blotchy coat, the first gold hairs usually appearing on the brow, wrist, and ankles. However, some infants attain a general overall sparse gold hue that signals the onset of a coat change that then proceeds with a much more even pattern. During the period from 8 to 15 months (usually by 12 months) the infant loses the last traces of natal coloration (Fig. 1).

A transition from ventral to dorsal riding, described by DeVore as a maturational change occurring at 4–6 months of age [DeVore, 1963], is much too variable in Amboseli to be of any use in determining infant age. Most infants began riding dorsally in the second month of life. For 17 infants the age of first dorsal riding was known to the nearest week. The mean, median, and modal age of first dorsal riding for these infants was 8 weeks of age, but some infants first rode dorsally when only 3 weeks old, and 3 of 27 infants for which data are complete throughout infancy never rode dorsally. We have no clear explanation for the variability in this trait, but there does seem to be some consistency within families, perhaps due to two maternal characteristics. First, infants seem to have more trouble climbing on and clinging dorsally on fat mothers than on thin ones, and some mothers discourage infants' early attempts to ride dorsally by not slowing down while the infant climbs or by pulling the infant onto a ventral position when it tries to climb dorsally. Even once they begin riding dorsally, infants are quite variable in the frequency with which they use this position relative to riding ventrally.

At 7 or 8 months the mother leaves her infant to climb out of the sleeping trees by itself in the morning (mean 7–8, range 6–9 months, $N=20$), but she still usually carries it when escaping during group alarms to external dangers. At this age, the infant still nurses occasionally during the day and sleeps, often on the nipple, with its mother in the trees at night. A mother's postpartum amenorrhea ends when her infant is about 8 to 16 months old (mean 12–13 months), and she becomes pregnant again by the time the present offspring is a year and a half old (mean 15–16 months): see Altmann et al [1977, 1978].

Second Year and Beyond

No dramatic physical changes mark the infant's second year of life, but a youngster is probably less than 18 months old if it is still seen to suckle occasionally during the day, if it is still short enough to be able to stand under its mother when she is in a standing position, and if its mother is not yet pregnant with her next offspring. All sampled infants in Amboseli still suckled during the day at 60–70 weeks of age; mean age at which suckling stops completely has been estimated at 85 weeks [S. Altmann, unpublished data]. Individual variability in this cut-off is primarily due to the fact that all youngsters have been allowed to suckle until approximately two-thirds through their mother's next pregnancy. Conversely, a youngster who cannot be associated with any adult female, even in the sleeping trees, is almost surely over a year and a half in age, with the possible rare exceptions of yearling orphans.

Although overall size seems to change quite gradually, with no highly visible developmental markers or size comparisons until about 4½ or 5 years of age, a few physical changes that require a close view of the animal are useful for determining age of 2- to 5-year-olds. For males the scrotum changes from pink to grey between about the second and third birthday (Fig. 2). Within this year the change is gradual and individually variable.

The skin of an infant's muzzle is very wrinkled; that of an adult, quite smooth. Facial wrinkling decreases as the youngster's muzzle elongates and as the adult canine ridge develops. Facial wrinkling essentially disappears at about 3 to 4 years of age, and during the fifth year of life a canine ridge can be detected, particularly in males, where it

becomes a very prominent feature of adults. The tail, which is held almost horizontally in infants, gradually moves to the more vertical carriage of adults [Hausfater, 1977]. Because the final tail position is individually variable, the angle is not useful for age estimation. Sexual dimorphism in size, which occurs in the second year of life in captivity [Snow, 1967] is not detectable in Amboseli until 3½ to 4 years of age.

At approximately 4½ or 5 years of age both males and females attain the height of average adult females at mid-back, although they are not usually as long as adult females from head to tail base: that takes about another 6 months to a year (N=16). The following year and a half is one of dramatic changes toward adulthood. Males' canines extend beyond the tooth row, the males become larger than all the adult females, develop considerable shoulder musculature, and undergo rapid enlargement of the testes, which create a very visible scrotal bulge (N=5 for animals of known birthdate; consistent with data for those of estimated age as infants or young juveniles) [Altmann et al, 1977]. Initially both the canine development and the scrotal enlargement are often visibly asymmetric.

Females in Amboseli reach menarche and have their first sex skin swellings at 4½ to 5 years of age (mean=4.8 years, range 4-5¾, N=10). A month or two prior to this we occasionally see a very small sex skin swelling for only about a day. This tiny, brief swelling is not followed by menstruation and is not readily confused with what we call the first cycle, nor are there any intermediate swellings between the two types. For only one female was vaginal bleeding observed before the first cycle of sex skin swelling. In her case, the bleeding occurred over an unusually long period of at least 8 days, about 2 months before her first cycle, and she was not observed to have any small sex skin swellings in those months before that first cycle. Usually (11 of 13 cases) the first cycle is characterized by a tumescent phase that is longer than the average for adults and a swelling that reaches a maximum volume only half that of most normal cycles. These young females experience a period of so-called adolescent sterility, not becoming pregnant for about a year after menarche (mean=13 months, range 7-18, N=14). In some cases fully adult males do not consort with adolescent females during the first several cycles.

For males, 2 years elapse between the time when they become subadults at age 6 and when it seems appropriate to classify them as adults. Although they do not complete their growth during those years, by about 8 years of age they have achieved sufficient size and strength to challenge fully adult males, to rise (often rapidly) in the adult male dominance hierarchy, and to mate with females at times of likely conception. The late subadult and young adult period is one of frequent migration out of and back into the natal group, followed by semipermanent residence in another group or sometimes (3 out of 6 males) back in the natal group.

Both males and females continue to grow for at least a year after entering full adulthood. In addition, the nipples of adult females elongate and turn from pink to grey, usually in the first several months of nursing the first infant. Very old animals seem to be identifiable by loose appearance of skin, very worn, broken or missing teeth, and very sloped backs resulting in part from incomplete leg extension. Although the youngest adults can be distinguished from the oldest ones, we know little of reliable age characteristics during adulthood, and we have found that observers can easily mistake infirmity for old age. A résumé of age-class criteria, including the 1974 version (Altmann et al. 1977), which was based on a smaller sample, is given in Table I.

DISCUSSION

Age Classes and Age Estimation

The physical characteristics that provide the best estimates of the age of a young animal under close observation are not necessarily those that can be used for estimating

TABLE I. Age Estimates of Amboseli Baboons

Class	Description	1974 age estimates	1980 age estimates
Infant-1	Hair completely or partially black (natal coat). Black spots in tail and shoulders remain longest. Skin pink or red from skin vascularity—ears and nose retain pink longest.	0 to $\frac{2}{3}$	0 to $\frac{2}{3}$
Infant-2	Hair brown to cream-colored, often lighter (in Amboseli) than that of adults. Skin pigmented black, as in adults (except for male scrotum, see below).	$\frac{2}{3}$ to 2	$\frac{2}{3}$ to 1½
Juvenile-1	Not sharply demarcated from previous class. Light hair retained. Face wrinkles disappear end of this period. Scrotum changes from pink to gray near end of this period.	2 to 4	1½ to 3 or 3½
Juvenile-2	Not sharply demarcated from previous class. Hair often darker, as in adult. Male's testes undergo rapid enlargement resulting in rounding of scrotum at end of this period. Male's canines extend beyond tooth row at end of this period.	Females: 4 to 5	Females: 3 or 3½ to 5 ^a
Adult female	Sexually mature, sexual skin swells periodically. Nipples pink and buttonlike when nulliparous, elongated and gray in more mature, multiparous females. First pregnancy at about six years of age; full size reached about seventh year for females.	Over 5	5 ^a (menarche)
Subadult male	Development of secondary sexual characteristics; mantle, long canine teeth, large size, greater musculature than females. Scrotum (testes) larger than in juvenile-2. White streaks on muzzle. Canine ridges.	7 to 10	5½ or 6 to 8 or 9
Adult male	Secondary sexual characteristics fully developed.	Over 10	Over 8 or 9

^aIndividuals viewed at a distance (males) or not observed regularly over several weeks (females), as in most censuses of non-study groups, will not usually be recognized as having the characteristics of the older age class until they are, on the average, 5½ yrs old, because, for example, small scrotal bulges, extended canines, and evidence of sexual cycles may be missed.

ages during population censusing. Natal coat color probably remains the best feature for identifying infants in censuses, but skin coloration, particularly that of the paracallosal skin, provides much better aging criteria when animals can be observed at close range. Likewise, we shall continue to seek better calibration of changes in standing height of immatures relative to adults for use in population censusing of many groups in a short time or of unhabituated groups; but age estimates by that method will probably remain crude and not highly reliable. Scrotal color, facial wrinkling, and presence of canine ridge, when age variability is better documented, will be the best characteristics for age estimation of older immatures but of little use for animals viewed for short periods and not at close range.

Another difference between age class boundaries used for censusing of unidentified animals and those used for known individuals is well illustrated by the age of menarche. Once a female reaches menarche she is no longer considered a juvenile. In censusing groups of unknown individuals, however, it will not always be recognized that a young female without a sex skin swelling has reached menarche, because she will be smaller than most adults and will not have elongated nipples. Moreover, because a baboon female will not become pregnant for about a year, she is in some sense not fully an adult [see eg, Rowell, 1977 for a discussion of criteria for adulthood in primates]. In censuses on groups of unknown individuals, such a young female will sometimes (when menstruation or sex skin swelling is visible) be called an adult and other times a large juvenile. Therefore the juvenile age class for population censuses should extend about another half year beyond average age of menarche.

In presenting data from our longitudinal study of savannah baboons, *Papio cynocephalus*, we have considered how some of the commonly used age classes can be refined by identifying the most behaviorally and biologically meaningful physical changes in baboons. In this context it is important to consider whether the most appropriate age categories and physical characteristics to use as criteria will vary with the particular topic at hand, not just between studies but also within them, as in our Amboseli baboon work. For demographic investigations the most useful physical characteristics are those that correlate well with rates of natality, mortality, and migration. For accurate age estimation one looks for closely spaced age characteristics for each of which the transition occurs over a short age span and for which interindividual variance is low. For work with unknown groups that cannot be observed at close range it is desirable from a practical standpoint to have all three of these previous criteria plus characteristics that are conspicuous at a distance.

Although narrow age classes are desirable for age estimations, for behavioral or other biological work with the small groups in which most primates usually live, use of age classes that span only a short period will often result in very small sample sizes if, say, each 6-month or year class were distinguished from the next. Under these demographic conditions, which typify captive groups as well as the nonexpanding natural groups that have been the subjects of some intensive and longitudinal research, the researcher will hope that some pooling over ages will be reasonable.

In general, the distinction in meaningful age class divisions for different purposes warrants closer attention in the future.

Factors Affecting Maturation

Snow's [1967] study of growth and physical development in captive baboons (mixed and hybrid species) provides a good basis for comparison with the Amboseli data partly because it is one of the few such laboratory investigations that included characteristics that are also observable under field conditions. A consistent picture emerges from the comparison. The ratio of the age at which captive baboons versus Amboseli baboons reach developmental markers is approximately 3 to 5 (Table II). Initial reports of age at sexual maturity from longitudinal primate field studies suggested that the delay of maturation is not restricted to declining environmental conditions, as at Amboseli, but rather is characteristic of a wide range of field conditions, perhaps only excluding those of extensive artificial feeding [see also Mori, 1979 for Japanese macaques, *Macaca fuscata*]. For a number of primate species, field data that have become available in recent years demonstrate longer interbirth intervals and especially later age at sexual maturity under field conditions than in captivity. These studies include those of Dittus [1975, 1977] for toque monkeys, *Macaca sinica*, Pusey's studies of chimpanzees, *Pan troglodytes* [1978], Packer's of olive baboons, *Papio anubis* [1979], and ours of yellow baboons [eg, Altmann et al, 1977].

TABLE II. Ages at Which Developmental Markers Were Reached in Three Groups of Baboons

	Laboratory data	Field data	
	Mixed <i>Papio</i> species	<i>P. anubis</i> ^a	<i>P. cynocephalus</i> ^b
Rapid testes enlargement	2.8 ^c	5.3-5.8	5.0-6.0
Male=adult female size	3.5-4.0 ^c		5.0-5.5
Male exceeds size of same-age female	2.5-3.0 ^c		3.0-4.0
Permanent canines extend beyond tooth row, males	4.0-4.5 ^d 5.0-5.5 ^e	5.4-6	5.0-6.0
Menarche	3.0 ^c	4.5-5.6	4.0-5.5

^aData from Packer [1979].

^bData from Alto's Group, Amboseli, this study; see text for details.

^cData from Snow [1967].

^dBased on Reed [1973, Fig. 2 for primary eruption] and the following information: "The eruption process averages three months for all but the maxillary canine, in the male, which may take 6 to 8 months for complete eruption," [Reed, 1973] and "The criteria of primary eruption has been a tip of a cusp breaking the gingival crest. Complete eruption has been the reaching of occlusal (level) or functioning level with opposing teeth." [Reed, 1967].

^e10/14 male *Papio cynocephalus* had both (9) or only one (1) canine extend "significantly beyond height of dental row" between 5.0 and 5.5 years of age (unpublished data, courtesy of A. Coelho through personal communication, from ongoing developmental study).

Nutritional differences are strongly implicated as the cause of these developmental differences, as has long been suggested from studies of a wide range of wild and captive mammals [see review in Sadleir, 1969]. The most illuminating primate study that points to the importance of nutrition in causing these and other demographic differences is that of Mori [1979], who analyzed data from three periods differing in food provisioning regimes for the Japanese macaques of Koshima Island. Some results of that study are complicated by the fact that individuals in that study were not all of the same ages during the years of abundant vs sparse provisioning. For example, some animals who reached sexual maturity during the recent years of little artificial feeding had spent their whole lives under that condition, others had experienced artificial feeding during infancy, and so on. The long period of immaturity in primates as compared to that of most other mammals allows for temporally coarse-grained environmental effects on development that are not possible in most other animals. However, certain patterns emerge through Mori's repeated use of both cross-sectional and longitudinal analyses. Growth rates were slower in the absence of artificial feeding, sexual maturity was delayed and less weight gain occurred after the attainment of sexual maturity.

Weight was affected more than was trunk length. Consistent with the hypothesis of Frisch and Revelle [1970] regarding onset of menarche in human females, Mori found that females reached sexual maturity at approximately the same weight under artificial and non-artificial feeding conditions, but that this weight was not attained until an older age in the latter case. However, with the Japanese macaques of Mori's study, older females reached sexual maturity after a delay of 1 to 2 years even if they still were below the hypothesized threshold weight [see also Erwin & Erwin 1976]. Mori also found that in the absence of extensive provisioning, females did not continue to gain appreciable weight after the onset of menarche. They were, therefore, smaller as adults in general and when they produced their first infants in particular. Lower-weight females, both multiparous and primiparous, produced infants with poorer chances of survival. Adult weight and age of menarche apparently were a function of nutritional conditions during the first year or two of life as well as those during the prepubertal period. Growth and fat storage during good years may provide buffers that improve animals' ability to survive and reproduce in poor years.

In summary, the picture that emerges from the Amboseli studies and from the recent literature on other primates is one of slower growth rates and, perhaps consequently, delayed maturation in all field conditions in the absence of extensive artificial feeding. There remains variability in development within a primate group at any one time or between years of less dramatic food changes than those produced by captivity or artificial feeding. In terms of within-group variability during any period, for the Cayo Santiago and La Paguera colonies of rhesus monkeys, *Macaca mulatta*, age at sexual maturity has been related to dominance rank [Drickamer, 1974; Sade et al, 1977]. However, for the most part the sources or even correlates of this within-group variability remain unknown and constitute a major area in which research is needed. Whereas nutritional factors are strongly implicated in the major differences described above, social factors which may or may not be partially mediated through differential nutrition may be particularly effective within groups [see Dittus, 1979], as has been demonstrated so dramatically within other taxonomic groups such as rodents and canids [see the reviews in Cohen et al, 1979; Sadleir, 1969]. What are now needed are data allowing within-species comparisons within and between populations.

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