Preparation and activation: determinants of age at reproductive maturity in male baboons

Abstract. Age at maturity is a particularly important life history trait, but quantified data are rare for males in natural populations of primates. Here we provide information on three mating-related milestones and their social and demographic correlates among 43 wild male baboons, Papio cynocephalus, in a natural population in Amboseli National Park, Kenya. We examined (1) age at testicular enlargement, which marks puberty and the onset of adulthood, and (2) age at attainment of adult dominance rank, which we consider to be the beginning of adulthood, and (3) age at first sexual coitus, which is the best measure available for age at first reproduction in a baboon. Testicular enlargement (median age = 5.69 years) occurred earlier among sons of high-ranking mothers, and was not influenced by rainfall or seasonality. Attainment of adult dominance rank (mean age = 7.41 years) was also accelerated among sons of high-ranking mothers, and among males whose mothers had died while the males were juveniles. First sexual consortship (median age = 7.86 years) was not influenced directly by maternal characteristics, but attainment of adult dominance rank always preceded first consortship. The lag time between attainment of adult rank and first consortship (median = 2.5 months; range = 5.536 days) was predicted by the number of sexually cycling females in the group when the male attained rank, and by how high ranking the male became in his first years as an adult. We suggest that the age at which a male baboon is ready to begin reproducing is influenced by a relatively stable maternal characteristic that exerts its influence early in development, but the timing with which this potential is realized depends on activation by more proximate, often stochastic triggers such as female availability. This two-level organization of influences is likely to contribute to the variance both in age at first reproduction and in life span. Differences in the relative magnitude of the two levels will lead to both intra- and interspecific variability in the opportunity for maternal selection and sexual selection.

Key words. Reproductive maturity · First reproduction · Dominance rank · Female availability · Baboons

Introduction

Individual fitness is often more sensitive to changes in age at maturity than to changes in any other life history trait (Cole 1954; Longino 1965; reviewed in Stearns 1992; Roff 1992), and age at maturity has consequently been the subject of much theoretical and empirical investigation. In increasing populations, individuals that mature relatively early will have a reproductive advantage, while in decreasing populations, individuals that mature relatively later will have a selective advantage (Mertz 1977; Caswell 1982; reviewed in Stearns 1992, Roff 1992). Delayed maturity may also be selected for if it results in higher fecundity or lower mortality rates (Bell 1982; Less 1982; Rubenstein 1993), or it may evolve as a correlate of larger body size or longer life span (Harcourt and Zammuto 1982; Charnov and Perrigo 1989; Pagel and Harvey 1993). Delayed maturity has evolved in all classes of vertebrates (Bell 1982),
and primates are notable among mammals in having unusually long pre-reproductive periods (Watts 1985). Hypotheses for the evolution of this long juvenile period in primates include re-examinations of the symmetric and lifehistory arguments (Page and Harvey 1993; Rubenstein 1993), as well as the argument that rapid growth entails risks not experienced by slower-growing juveniles (Altmann and Alberts 1987, Janzen and van Schaik 1993).

Here we examine age at physical maturation and first reproduction for wild male savannah baboons (Papio ursinus), and identify social and demographic correlates of age at maturation as potential influences on physical and social development. Male baboons reach adulthood between 7 and 10 years of age (Altmann et al. 1977, 1981), and have a maximum life span in the wild of roughly 20-25 years (L. Altmann and S. Alberts, unpublished work). Thus, male baboons spend a remarkable 30-50% of their maximum life span as juvenile males. Males who begin reproducing relatively early should experience net Luus advantages as long as early maturity does not also entail higher mortality or lower fecundity.

Proximity in male primates is signaled by enlargement of the testes, which coincides with the production of viable sperm (Plant 1968; Caillaud et al. 1986; Boursin 1989; Berovest and Goy 1990). However, while pubertal male primates are physically capable of fathering offspring, evidence (Wagenfeld and Catchpole 1956; Erwin and Mitchell 1975; Pong 1982) and this reproductive potential is not realized during the prepubertal adolescent period, during which males in natural social groups are reproductively inactive. Coinciding with this period of reproductive inactivity, males may undergo a growth spurt lasting several years that results, in some species, in an adult male body mass nearly double that of adult females (Cowles 1985; Watts 1985, Altmann and Alberts 1987; Berovest and Goy 1990; Smuts 1991). For males of many primate species, it is not until after this growth spurt, as they approach adult size, that they gain access to reproductive females and achieve full reproductive maturity. Thus, while testes and pubertal development are equivalent markers of physiological maturity for females and males respectively, and testicul development occurs only slightly later than menarche (e.g., compare data for males and females in Dittus 1977; Cornwell 1987; Pong 1982; Berovest and Goy 1990), most primate species exhibit bipuberty (Wiley 1974), in which males and females achieve first reproduction at different ages. Bima Jursen is pronounced in sexually dimorphic species such as baboons (Shen 1990), in which males directly compete with each other for access to females, and in which both fighting ability (Hamerstrom 1978; Panczak 1979; Hamilton and Bulger 1990), and social experience (Schaep 1982; Smuts 1985) contribute to male reproductive success.

Very little is known about intraspecific variability in age at maturity for male primates, both because of the longer pre-reproductive period of males, and because age at first conception is more difficult to ascertain for males than for females. Age at testicular enlargement has been described in a few captive populations (e.g., captive rhesus macaques, van Wagenfeld and Simonds 1954; captive or provisioned Japanese macaques, Muri 1979; Wolfe 1979; captive talapoin and patas monkeys, Rowell 1977), and data on some male maturation patterns are beginning to emerge from a few long-term studies of wild primates as well (Howe 1977; chimpanzees, Goodall 1966; Frey 1990; gorillas, Watts 1991; Watts and Poe 1993; howler monkeys, Crockett and Pope 1993). However, full reproduction patterns of wild male primates have remained largely undocumented, and sources of intraspecific variability have not been identified. In the current study, we examined ages at attainment of three developmental milestones among male baboons, based on long-term demographic and behavioral records. These milestones included: (1) testicular enlargement, which signals the onset of the period termed subadulthood, (2) first attainment of aggressive dominance rank among adult males, which we consider to terminate the subadult period, and (3) first sexual cooccurrence, which is the best measure available for age at first reproduction for male baboons. We examined both the distribution of ages at which these milestones were attained, and potential sources of variance in their attainment. Age at first departure, another important developmental milestone, is treated extensively elsewhere (Altmann and Altmann 1995; see also Discussion).

Methods

Study population

We studied male baboons from three wild baboon social groups, Amboseli and Bush’s groups, living in Amboseli National Park, in southern Kenya. This population has been under continuous, well-documented study by J and S. Altmann and colleagues since 1971 (Altmann et al. 1977; Altmann et al. 1981; Altmann et al. 1989; Nóbl and Wurfl 1990). All subjects were identified visually and reliably by all observers using behavioral patterns such as personality and coat color. Although this population, densly concentrated in a 5 square kilometer area during the 1970s, the cattle predominate in the context of a relatively stable population (Altmann et al. 1983).

The analyses included 33 males, ranging in age from 17 to 34 years. All the male baboons during the study period from were collected from 1971 to 1980 in 27 males born after 1 January, 1966, in Amboseli Group, and from 1977 to 1981 in 16 males born after 1 January, 1972 in Bush’s Group. In addition, two males that were born to the study groups, but that immigrated before they were adults, are included in the analyses on attainment of adulthood and first conception. The histories of these subjects were known since birth, as a result of daily records on demographic events, birth
effective circles, and social interactions. The remaining two variables were also assessed at birth and at 4 years, and were administered continuously throughout the study.

Data analysis: The analyses presented below were based on all available data at each stage of development. This approach allowed for an understanding of the relationships between different variables. In addition, data analysis focused on the development of each group, considering the sample size for each group. The data were analyzed using multivariate analysis of variance (MANOVA) for the development of each group. Following this, the relationships between the variables and developmental milestones were examined using regression analysis.

### Table 1: Developmental Milestones

<table>
<thead>
<tr>
<th>Variables</th>
<th>Notes</th>
<th>Group</th>
<th>Birthweight</th>
<th>Age at first walk</th>
<th>Age at first conversation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measures taken at birth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stature</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intelligence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Language Speech</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Motor Skills</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Social Behavior</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Dependent Variables

Factors such as growth and development were assessed using physical measurements and behavior. All data were analyzed using MANOVA. Among the variables assessed, the relationship between age and most of the variables was found to be significant. The results indicated that the age at which a child achieves developmental milestones is positively correlated with age.
period in each female and at the moment of dispersal and reproduction. Both males and females were observed for 14 months from the first occurrence of mating behavior. In the adult phase, the males lived for about 2.5 years. During this period, males were observed to disperse and interact with other males. The dispersal behavior of males was similar to that of females, but males tended to disperse in a more dispersed pattern.

Several social behaviors were observed, including agonistic behaviors and alloparental care. During the adult phase, males were observed to disperse and interact with other males. The dispersal behavior of males was similar to that of females, but males tended to disperse in a more dispersed pattern.

In addition to the dispersal and social behaviors, the males also engaged in harem maintenance and mating behavior. The harem maintenance behavior included sleeping with females and engaging in courtship activities. The males were observed to use scrotal swelling and vocalizations to attract females and maintain dominance over other males. The mating behavior included courtship displays and copulation.

The data collected during the study were used to analyze the social and reproductive behaviors of the males, including harem maintenance, dispersal, and mating behavior. The results showed that the males were highly aggressive and competitive, with intrasexual competition being the main driver of social behavior. The males also engaged in intersexual competition, with females playing a role in the determination of male social status.

The study also examined the effects of environmental factors on the social and reproductive behaviors of the males, including habitat quality, food availability, and climate. The results showed that habitat quality and food availability were the main determinants of social and reproductive behavior, with males in better quality habitats and with high food availability demonstrating higher levels of aggression and mating success.

In conclusion, the study showed that the adult male B. a. athalassos engaged in complex social and reproductive behaviors, including harem maintenance, dispersal, and mating behavior. The results also highlighted the importance of environmental factors in determining social and reproductive behavior, with habitat quality and food availability playing a critical role in shaping male behavior. The study provides valuable insights into the social and reproductive ecology of this primate species and contributes to our understanding of primate behavior and evolution.
Results

Testicular enlargement: onset to reproductive potential and subadulthood

Testicular enlargement occurred at a median age of 5.69 years (6–32, range = 4.96–8.21 years; Fig. 1a). Maternal dominance rank predicted age at testicular enlargement (r = 0.72, P < 0.004; Fig. 2a). Sons of high-ranking mothers attained this development milestone significantly earlier than sons of low-ranking mothers, with an average advantage of 1.35 yrs per rank position. No other independent variables, including rainfall measures, contributed significantly to the variance in age at testicular enlargement. No testicular enlargement occurred on a seasonal basis, total cumulative rainfall in the month preceding testicular enlargement varied from 6 mm to 126.4 mm (mean = 38.9, SD = 35.1), which encompassed nearly the whole range of monthly rainfall values for Amboseli, and testicular enlargement occurred with roughly equal frequency all seasons.

Attachment of dominance rank, adulthood

Subadulthood was considered to begin with testicular enlargement and to end with the attainment of age-specific dominance rank among the adult males in the group. Rank attainment occurred at a median age of 4.41 years (range = 3.54–5.85 years; Fig. 1b). The shortest period of subadulthood lasted 11.1 months, and the longest 21.2 months, with a mean of 22.7 months (SD = 5 months).

Wilcoxon and logrank tests for determining covariates of censoring data revealed that maternal dominance rank and death of mother by male’s 50th birthday (age at onset of puberty for the developing males) both affected age at rank attainment (Wilcoxon test: maternal rank, P = 0.0366; mother’s death, P = 0.025; logrank test: maternal rank, P = 0.001; mother’s death, P = 0.011). Sons of high-ranking mothers attained rank earlier, as did males orphaned before they were 6 years old (Fig. 3b). No other independent variables, including female availability, contributed significantly to age at rank attainment.

First sexual coparship: full reproductive maturity

First coparships in the total group occurred at a median age of 7.92 years (range = 6.73–8.91 years; Fig. 1d). First coparships were always preceded by rank attainment, and age at rank attainment strongly predicted age at first coparship (r² = 0.47, P = 0.009; Fig. 3). Although maternal rank predicted age at rank attainment, neither maternal rank nor any other maternal characteristics, either alone or in a multiple.
regression with age at rank attainment, directly predicted age at first cohabitation. Similarly, number of older or younger maternal siblings alive in the group did not predict age at first cohabitation.

The median age time between rank attainment and first cohabitation was 2.5 months (range 1.5–3.0 years), and this age time was independent of age at rank attainment. The slope of the regression line was not significantly different than one (0.92 > β > 0.81) for the null hypothesis that the slope of the regression line was one (Sokal and Rohlf 1981, p. 474). The age time was predicted both by average number of cycling females in the 3 months before the male attained rank, and by his dominance rank-based ability to gain access to those females (see Methods). Males whose age time between rank attainment and first cohabitation was below the median of 2.5 months had higher numbers of cycling females in the group during the first 3 months after rank attainment (Mann-Whitney U-test, P = 0.04; Fig. 3). They also had greater access to those females, based on their access measures (Mann-Whitney U-test, P < 0.01). In fact, all but one ‘fast’ male (those who attained rank less than the median time to begin cohabitation) had positive or zero access measures, while rank numbers smaller than or equal to the number of cycling females, while all ‘slow’ males had negative access measures. In contrast, the number of males in the group did not predict either age times or cohabitation ranks attained by ‘fast’ males.

Discussion

Maturational readiness among male baboons, the ability to produce viable sperm and to compete for access to reproductive females, appears to depend on relative maternal characteristics such as rank and stress status. Indeed, much of the variability among males on the row in adulthood can be predicted during the early juvenile period, or even as birth, due to the pervasive effects of maternal rank. However, the actual triggers for first reproduction include demographic characteristics of the social group that have a large stochastic component. The strongest predictors of how quickly a male begins to consort after he reaches adulthood are aspects of group structure, including the number of reproductive females and the maturational status of dominance-based ability to gain access to those females, which is influenced by both individual and group characteristics.

The idea that first reproduction is influenced by conspecific individuals as well as by genetic and environmental factors is a central one. Among non-human primates, sex maturity may be either accelerated or delayed, depending on the frequency and intensity of contact with conspecific males versus females (Vandenbergh and
Among cooperative breeders, comprising hundreds of species of birds and mammals, young male adults experience a considerable delay between physiological maturity and first reproduction, primarily because of constraints on mate availability, or because suitable habitat is filled by conspecifics (Dunlap 1986). Among primates, the most extreme version of this pattern is found in the New World callicebids, in which cooperative breeding is prevalent (Gockellen 1983), and is associated with the behavioral or physiological suppression of reproductive behavior among young low-ranking individuals by higher-ranking reproductive individuals (Abbott 1984, 1987; Epple and Katz 1984; Freidich et al. 1984). In addition, acceleration of puberty among females exposed to adult males has been reported for callicebids (i.e., Cebus apella in Ziegler et al. 1990). Thus, the onset of reproductivity for callicebids depends both on physiological readiness and on the presence of reproductive opportunities signaled by the absence of suppressing behavior or chemosignals or by the opportunity to breed elsewhere (see also Gockellen and Terborgh 1985; Savage et al. 1986).

As with many animals, ovulation patterns in which preparation for and execution of reproductive behavior are separate processes, and in which reproduction is triggered by social stimuli. These stimuli are effective triggers only when animals are physiologically capable of reproducing, and are not at earlier stages. For male baboons the triggers consist of demographic characteristics of the social group that are influenced by stochastic as well as determinate processes, including male immigration, emigration, and female reproductive schedules. Accordingly, the variance in age at first reproduction will be unaccounted for by individuals, familial, or early developmental characteristics. On average, sons of high-ranking males have a head start as they approach first reproduction because they are poised at a relatively early age. When many reproductive females are available, sons of high-ranking fathers may retain this advantage, but in general, the variance in age at first reproduction will be significantly smaller for males.

For a number of primate species or populations, first reproduction is probably the vulnerable to stochastic influences. In low and medium provisioner, expanding populations of chimpanzees and Japanese macaques, maternal rank is a strong influence throughout much development, not indirectly through rank effects (high maternal rank promotes high male rank and thus increased mating success; Kofoed 1983; Kay 1979; Durieux and Yassa 1983; Sugiyama 1976; Sade et al. 1975; Chapman 1983) and directly through increased reproductive success of sons of high-ranking mothers (Smith and Smith 1988). The pattern is different in wile baboons, where maternal rank, even among juvenile males, predicts offspring rank only partly (Cheney 1977; Lee and Oliver 1979) or not at all (Lamson 1980; Petrie 1989). In the extent that these represent demographic differences between baboons and macaques, they may be due in part to the fact that baboon mothers exhibit less extreme body size dimorphism than baboons, which means that macaque mothers can sometimes directly interfere in assisting their sons in attracting females (Feraboschi 1983; W. Leuen and Seyfarth 1987; Petrie 1992).

Although baboon mothers have a limited ability to influence the dominance ranks of their sons, maternal rank did influence both the age at which males entered puberty and the age at which males entered the adult male dominance hierarchy (i.e., became adults). This early maturation for sons of high-ranking mothers parallels the effects of maternal rank on maturing females of a number of primate species (Johansson 1987), including Amboseli baboons (Altmann et al. 1988), and may, cause males poised to take advantage of dispersal opportunities and as females of reproductive opportunities. In Amboseli, dispersal entails both substantial mortality risks and opportunity costs, because baboon density is low and predation risk is appreciable (Alberts and Altmann 1995). However, these dispersal risks appear to be offset by an increasingly risk, which, with the result that 50% of males leave the natal group without mating. Dispersal is more likely to occur when female availability is low in the natal group and males tend to enter groups in which female availability is high (Alberts and Altmann 1995).

Thus, for males, like females, maternal factors are important at a number of developmental stages. However, in contrast to females, male development had stochastic components that are influenced by maternal influences. The extent to which these factors maintain their influence in the face of these stochastic components remains to be fully elucidated.

Our findings clearly demonstrate the social constraints on reproductive maturation for male baboons, and they limit the potential range of complexity of these constraints. Neither reproductive potential as signaled by testes enlargement, nor physical strength in intrasexual competitive ability as signalized by rank attainment, were sufficient to predict consort attainment and full reproductive maturity. Nor were simple measures of the demographic context such as the number of adults or other males in the group. Rather, the important characteristic was a measure of access that incorporated both a male's own readiness and his position. Scores of other males and the number of cycling females. Likewise, in our study of both male and subsequent dispersals, we found that female availability, which was a function of both the number of males and the number of cycling females, was a strong predictor of dispersal (Alberts and Altmann 1993). Future efforts to understand the effects of the demographic and social contexts on male reproduction might profitably explore factors that contribute to reproductive attainment and to the complex 'calculation' that males
may use in making dispersal decisions. Likely candidates for such refinement might include discounting, among following males, those with whom existing is less desirable (such as maternal relatives, with whom mating generally does not occur; Alberts and Altmann 1985) or evaluating those with whom the male is more likely to mate with as “friends.” Simms 1985). These considerations highlight the extent to which the composition of social groups, in terms of age, sex, and kinship, affect opportunities for mating and other aspects of behavior (Altmann and Altmann 1970).

The two-level organization of influences on maturation for male primates, in which preparation for and activation of first reproduction are subject to different influences, can result in a wide range of inter- and intraspecific maturation patterns. Conditions in which proximate demographic influences are minimal provide the greatest opportunity for maternal selection, in which traits may be transmitted through non-Mendelian mechanisms and the fitness of offspring depends on that of the mother (Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990), so that the evolution of male life history traits is influenced by maternal traits. Conditions in which proximate demographic influences are many and complex will result in a decrease of maternal influences and a concurrent increase in selection on traits that increase individual competitive ability across a wide variety of conditions.

Acknowledgments We thank the Office of the President of Kenya and the Kenya Wildlife Service, formerly the Wildlife Conservation and Management Department, for permission to work in Amboseli, and the wardens and staff of Amboseli National Park for cooperation and assistance. We also thank D. E. Price, V. Tschirch, and the staff at the Primate Research for medical and equipment care. A number of people have collected data in Amboseli during the last 20 years, and we are grateful for their contributions: S. A. Altmann, C. R. B. Altmann, A. E. A. Altmann, S. Altmann, J. Altmann, M. Altmann, P. Altmann, A. Altmann, K. Altmann, M. Altmann, and M. Altmann provided helpful comments on earlier versions of the manuscript, and S. Altmann provided helpful references. R. Zimmerman generously provided additional data collected in Tanzania, S. C. A. was supported by the National Science Foundation Division of Environmental Research Grant No. DEB-84056914; M. D. H. was supported by the Ford Foundation’s “Primates” of the Future” grant; and J. V. was supported by the National Science Foundation’s “Primates” of the Future” grant.


