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

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**Abstract** Age at maturity is a particularly important life history trait, but maturational data are rare for males in natural populations of mammals. Here we provide information on three maturational 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 signals puberty and the onset of subadulthood, (2) age at attainment of adult dominance rank, which we consider to be the beginning of adulthood, and (3) age at first sexual consortship, which is the best measure available for age at first reproduction in male baboons. 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 (median 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 = 7.92 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 = 5–526 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 months 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 lifetime fitness. 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; Lewontin 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 selective advantage, while in decreasing populations, individuals that mature relatively late will have a selective advantage (Mertz 1971; 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 1980; Lessels 1991; Rubenstein 1993), or it may evolve as a correlate of large body size or long life span (Harvey and Zammuto 1985; Charnov and Berrigan 1990; Pagel and Harvey 1993). Delayed maturity has evolved in all classes of vertebrates (Bell 1980),

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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 allometric and life history arguments (Pagel 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; Janson and van Schaik 1993).

Here we examine age at physical maturation and first reproduction for wild male savannah baboons (*Papio cynocephalus*), and identify social and demographic correlates of, and 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 (J. Altmann and S. Alberts, unpublished work). Thus, male baboons spend a remarkable 30–50% of their maximum life span as pre-reproductives. Males who begin reproducing relatively early should experience net fitness advantages as long as early maturity does not also entail higher mortality or lower fecundity.

Puberty in male primates is signalled by enlargement of the testes, which coincides with the production of viable sperm (Plant 1988; Castracane et al. 1986; Bronson 1989; Bercovitch and Goy 1990). However, while pubescent male primates are physically capable of fathering offspring (van Wagenen and Catchpole 1956; Erwin and Mitchell 1975; Foerg 1982), this reproductive potential is not realized during the protracted 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 (Coelho 1985; Watts 1985; Altmann and Alberts 1987; Bercovitch and Goy 1990; Strum 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 menarche and testicular development are equivalent markers of physiological maturity for females and males respectively, and testicular development occurs only slightly later than menarche (e.g., compare data for males and females in Dittus 1977; Rowell 1977; Wolfe 1979; Bercovitch and Goy 1990), most primate species exhibit bimaturism (Wiley 1974), in which males and females achieve first reproduction at different ages. Bimaturism is pronounced in sexually dimorphic species such as baboons (Shea 1990), in which males directly compete with each other for access to females, and in which both fighting ability (Hausfater 1975; Packer 1979; Hamilton and Bulger 1990), and social experience (Strum 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 Wagenen and Simpson 1954; captive or provisioned Japanese macaques, Mori 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 (toque macaques, Dittus 1977; chimpanzees, Goodall 1986; Pusey 1990; gorillas, Watts 1991; Watts and Pusey 1993; howler monkeys, Crockett and Pope 1993). However, full maturation 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 agonistic dominance rank among adult males, which we consider to terminate the subadult period, and (3) first sexual consortship, 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 dispersal, another important developmental milestone, is treated extensively elsewhere (Alberts and Altmann 1995; see also Discussion).

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## Methods

### Study population

We studied male baboons born into two wild-feeding social groups, Alto's and Hook's Groups, living in Amboseli National Park, in southern Kenya. This population has been under continuous, near daily observation by J. and S. Altmann and colleagues since 1971 (e.g., Altmann et al. 1977; Altmann et al. 1981; Pereira 1988; Noë and Sluiter 1990). All subjects were identified visually and reliably by all observers, using individual physical characteristics such as physiognomy and coat color. Although the population decreased dramatically in size during the 1960s, the animals in the current study matured in the context of a relatively stable population (Altmann et al. 1985).

The analysis included 43 males, comprising all those who reached puberty during the study period. Data were collected from 1971–1990 on 27 males born after 1 January, 1966 in Alto's Group, and from 1977–1991 on 16 males born after 1 January, 1972 in Hook's Group. In addition, two males that were not born in the study groups, but that immigrated before they attained adulthood, are included in a subset of the analyses on attainment of dominance rank and first consortship. The histories of 33 subjects were known since birth, as a result of daily records of demographic events, repro-

ductive cycles, and social interactions. The remaining ten subjects were first seen as infants or juveniles between 1 and 5 years, and were monitored continuously from that age.

Sample sizes vary among the analyses presented below because males dispersed or died at all stages of development, reducing sample size between successive milestones. In addition, some males had incomplete records for exact ages at milestone attainment, particularly in the early stages of study for each group when developmental monitoring was less fine-grained (see Table 1). Following conventions in the literature, males living in their group of birth

will be called natal males; immigrants will be called non-natal males. Departure of a male from the natal group will be termed natal dispersal.

#### Dependent variables

*Testicular enlargement* records were based on monthly visual assessments of scrotal size and shape for all non-adult males in the study groups. Among infants and juveniles the scrotum appears as a transverse, concave flap of skin. As puberty begins, the testes begin a

**Table 1** Developmental variables for natal males in Hook's and Alto's Groups (ages are expressed in years)

Name	Group	Birthdate	Age at testicular enlargement	Age at rank attainment	Age at first consortship
<b>A. All markers attained in natal group</b>					
BEN	Alto	01Jan66(est.)	Attained	Attained	Attained
EVEN	Alto	01Jul66(est.)	Attained	Attained	Attained
RED	Alto	01Jul67(est.)	Attained	Attained	Attained
RUSS	Alto	01Jul67(est.)	Attained	Attained	Attained
STU	Alto	01Jul67(est.)	Attained	Attained	Attained
FRED	Alto	01Jan75	5.67	7.50	7.72
BRISTLE	Alto	17Aug75	5.25	7.38	7.45
HANS	Alto	15Oct75	6.13	8.05	8.41
GRENDEL	Alto	27Jan76	5.09	7.59	7.92
PEANUT	Alto	25Jul77	5.77	8.35	8.54
NAMI	Hook	19Mar78	6.12	7.37	7.87
PUTZ	Alto	16Aug79	5.96	7.38	7.39
NOGGIN	Hook	12May81	5.72	7.80	7.82
NEPTUNE	Alto	17Aug81	4.96	6.87	7.42
SEZNA	Alto	11Oct81	5.39	7.23	8.45
PEPO	Hook	08Dec81	5.15	7.56	8.07
ELFU	Alto	22Apr83	6.06	8.11	8.24
INZI	Alto	26May83	5.52	7.35	7.47
<b>B. Rank attained in natal group, but dispersal before first consortship</b>					
OZZIE	Alto	24Dec74	5.69	7.02	Not attained
SPIKE	Alto	24Jul77	6.11	7.85	Not attained
RASTA	Hook	30Aug79	5.34	7.26	Not attained
WIMBI	Hook	31Jan82	5.20	6.83	Not attained
KWANZA	Hook	03May84	4.99	7.16	Not attained
<b>C. Dispersal before rank attainment and first consortship</b>					
STIFF	Alto	01Jul67(est.)	Attained	Not attained	Not attained
RAYMOND	Hook	01Sep72(est.)	Attained	Not attained	Not attained
RALPH	Hook	19Sep74(est.)	Attained	Not attained	Not attained
MANFRED	Hook	20Jan76(est.)	Attained	Not attained	Not attained
CYMBAL	Alto	25Nov80	5.68	Not attained	Not attained
FAVAS	Alto	20Sep81	5.78	Not attained	Not attained
KUZA	Hook	21Sep82	6.15	Not attained	Not attained
POLE	Alto	29Nov82	6.21	Not attained	Not attained
POSHO	Hook	19Jul83	5.37	Not attained	Not attained
VUMBI	Alto	25Sep83	5.72	Not attained	Not attained
TAMU	Hook	19Dec84	5.95	Not attained	Not attained
<b>D. Still maturing as of Dec 1991, or died while maturing</b>					
TOTO	Alto	01Jul70(est.)	Attained	Censored	Censored
DOGO	Alto	06Aug71	Attained	7.41	Censored
JAKE	Alto	25Aug73	6.02	Censored	Censored
HODI	Alto	06May77	5.82	6.74	Censored
MSWAKI	Hook	04Sep83	5.66	Censored	Censored
JITU	Alto	18Sep83	6.16	Censored	Censored
PASCAL	Hook	13Mar85	5.16	Censored	Censored
KOBOL	Hook	21Mar85	5.14	Censored	Censored
TUZO	Hook	23May85	5.51	Censored	Censored

(*Attained* indicates that the marker was attained in the natal group but at an unknown age. *Not attained* means the male dispersed before attaining that marker. *Censored* means the male died, was still maturing, or remained in the natal group as an adult by 31 Dec 1991)

period of rapid enlargement and the scrotum becomes rounded and pendulous. Both onset of slight rounding, when the scrotum ceased to be concave, and completion of rounding, when the scrotum was completely convex and well rounded with visible testicular bulges, were recorded by observers. Completion of rounding usually occurred about 5 months after onset of slight rounding.

*Attainment of dominance rank* was defined as the first unreversed win by the subadult over any adult male in an agonistic interaction (i.e., the first win over an adult male that was not followed by a loss to that same male within the next month), and was considered to end the subadult period. In theory, a single win by a subadult male over an adult male was sufficient to designate him as an adult. In practice, this first win virtually always heralded the onset of a period of rapid rank rise, involving fights with many adult males (see also Hamilton and Bulger 1990). Agonistic behaviors were recorded on an ad libitum basis during all years of the study and were defined as in Hausfater (1975). Males were assigned rank numbers according to the absolute ranking they achieved in the adult male hierarchy. Thus, a male of rank one consistently won agonistic encounters over all other adult males; a male of rank 8 consistently lost encounters with seven males, and so on. Rank relationships, while not particularly stable over long periods, were almost always linear, that is, transitive and connected; circularities were rare and brief.

*Sexual consortships* between adult males and cycling females were recorded whenever observers were with the group. Sexual consortships were defined as periods of sexual behavior and close, persistent following of an adult female when the female was in estrus (i.e., had a tumescent swelling of the sexual skin; the reproductive state of females was assessed visually during routine monitoring of social groups). In this as in other baboon populations (Packer 1979; Smuts 1985; Bercovitch 1987; Noë and Sluiter 1990; J. Altmann unpublished work), the vast majority of copulations took place within the context of consortships; consequently, the first consortship was taken as the onset of reproductive life span for males. We used first consortship rather than other more or less restrictive measures of first reproduction, such as first copulation with an estrous female, or first consortship during days of most likely conception, because it is a conspicuous milestone which observers were unlikely to miss, and because it signals the beginning of the period in which males are successfully gaining and maintaining access to estrous females. Consortships were typically quite obvious, with a clear beginning and ending, and lasted anywhere from 15 min to many days. The first date on which the male appeared in the consortship records was assigned as his date of first consortship.

#### Independent variables

In identifying influences on male maturation, we began with variables known to influence age at maturity for female primates and variables known to influence dispersal and reproduction for males of some primate species. These included:

1. Agonistic dominance rank of the mother at the male's conception, which influences age at menarche or first reproduction for females of some species (provisioned rhesus macaques, Drickamer 1974; Sade et al. 1976; captive Japanese macaques, Gouzoules et al. 1982; wild baboons, Altmann et al. 1988; Bercovitch and Strum 1993)
2. Mother's age at the male's birth, which influences age at dispersal in male baboons (Alberts and Altmann 1995)
3. Whether the mother was alive at the onset of puberty, which influences age at dispersal in both baboons and vervet monkeys (Cheney 1983; Alberts and Altmann 1995)
4. Seasonality in maturation patterns, as well as rainfall in the 1st year and 4th year of life (the year prior to puberty), because ages at menarche or first birth for females of several species are influenced by nutritional status and food availability, and rainfall is often considered a proxy for food availability (Frisch and

Revelle 1970; Frisch and MacArthur 1974; Loy 1988; Lyles and Dobson 1988; Bercovitch and Strum 1993)

In addition, we examined group structure as a predictor of rank attainment or first consortship for males, because competition for mates is influenced by the number of potential mates and the number of competitors for those mates. We therefore measured several specific aspects of group structure, including:

1. The number of cycling females in the group when the male attained adult rank, compared to the number of cycling females in the group when he reached the mean age for rank attainment; in this way we hoped to detect whether a male gained access to more females by attaining rank when he did than by accelerating or decelerating to the mean age
2. The average number of adult males in the group during the 3 months following adult rank attainment for each male
3. The average number of cycling females in the group during the 3 months following adult rank attainment for each male
4. The difference, for each male, between the number of cycling females in the group and his dominance rank, averaged across the 3 months following adult rank attainment

This last we refer to as the male's 'access measure'. Male dominance rank was incorporated into these analyses in addition to the number of other adult males because agonistic dominance rank predicts mating success among males in most baboon populations, including Amboseli (Hausfater 1975; see extensive review in Bulger 1994 and note references therein). The correlation between dominance ranks of male baboons and their mating success means that a male's access to estrous females will in general be diminished whenever his group includes fewer cycling females than males that outrank him. At such times, it is as if a male is waiting in a queue for reproductive opportunities (Altmann 1962; Hausfater 1975; Bulger 1994).

Finally, we examined structure of the maternal family, because the presence of kin may represent selective forces that are distinct from the presence of non-kin. In particular, for a male on the verge of adulthood, mature brothers in the social group represent reproductive competitors, while mature sisters represent reduced reproductive opportunities in the natal group (mature siblings avoid each other as mates; Alberts and Altmann 1995). In contrast, younger siblings represent potential opportunities for increasing inclusive fitness through investment. The three maternal characteristics we examined (age, survival, and dominance rank) were not correlated with each other (e.g., mother's age and survival status, Spearman rank correlation  $r_s = -0.07$ ,  $n = 35$ ,  $P = 0.67$ ; mother's age and rank,  $r_s = -0.03$ ,  $n = 35$ ,  $P = 0.86$ ). However, as one might expect, mothers who survived past the male's 6th birthday had more surviving offspring *younger* than the male ( $r_s = 0.66$ ,  $n = 35$ ,  $P = 0.0001$ ), and older mothers showed a non-significant tendency to have more surviving offspring *older* than the male ( $r_s = 0.26$ ,  $n = 35$ ,  $P = 0.13$ ).

Males exhibited no group-specific differences in any developmental milestones or independent variables, with the exception of maternal rank: males in Hook's Group tended to have higher-ranking mothers than males in Alto's Group, in part because Hook's Group had fewer members throughout the study period. Consequently, after dominance ranks and developmental milestones were calculated within groups, further analyses were done by pooling data across groups. In cases where maternal rank was found to be an important predictor, we confirmed that trends in each group were similar by examining data for Hook's and Alto's Groups separately.

#### Statistical methods

We obtained descriptive statistics for age at testicular enlargement, and used simple and multiple linear regressions to examine effects of independent variables on this developmental milestone. We

treated age at rank attainment and first consortship as failure time data that were randomly censored on the right, indicating that some males had not yet attained these milestones by the study's end, or had died before attaining them. We employed survival analysis to produce (1) estimates of medians and ranges for age at attainment of each of these milestones, and (2) a survival function, representing the proportion "surviving" (i.e., the proportion not yet attaining the milestone in question) for each age interval (Kalbfleisch and Prentice 1980; Lee 1992). Survival analyses were done in SAS, using the "Lifetest" procedure (SAS Institute 1988). Two tests, the Wilcoxon test and the logrank test (Lee 1992; SAS Institute 1988), were employed to examine effects of independent variables on age at rank attainment and first consortship.

## Results

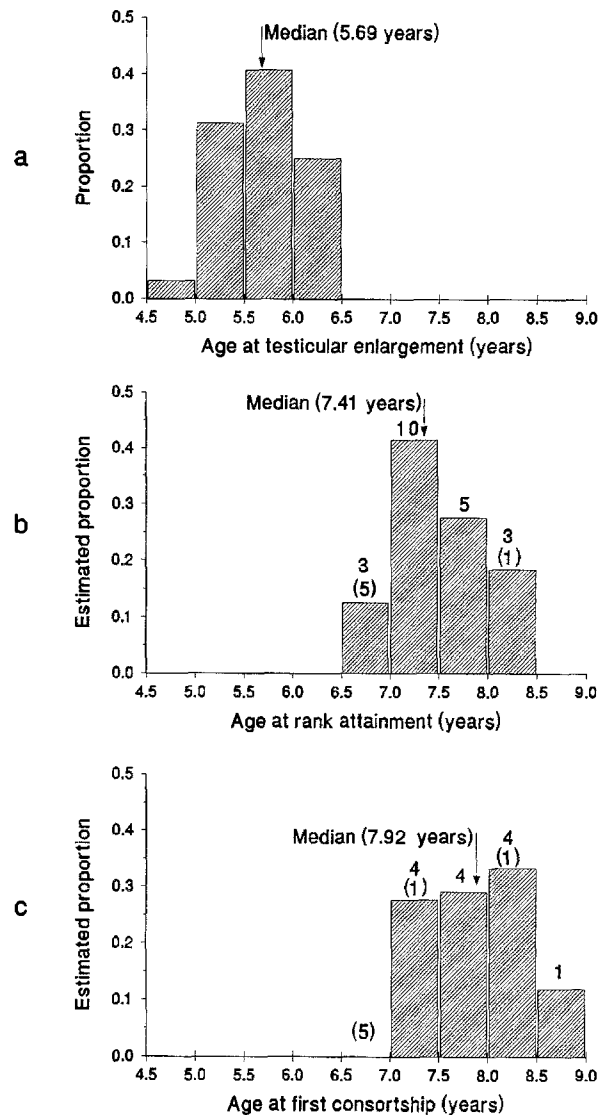
### Testicular enlargement: onset of reproductive potential and subadulthood

Testicular enlargement occurred at a median age of 5.69 years ( $n = 32$ , range = 4.96–6.21 years; Fig. 1a). Maternal dominance rank predicted age at testicular enlargement ( $n = 32$ ,  $r^2 = 0.25$ ,  $P < 0.004$ ; Fig. 2a). Sons of high-ranking mothers attained this developmental milestone significantly earlier than sons of low-ranking mothers, with an average advantage of 13.5 days per rank position. No other independent variables, including rainfall measures, contributed significantly to the variance in age at testicular enlargement. Nor did testicular enlargement occur on a seasonal basis; total cumulative rainfall in the month preceding testicular enlargement varied from 0 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 in all seasons.

### Attainment of dominance rank: adulthood

Subadulthood was considered to begin with testicular enlargement and to end with the attainment of agonistic dominance rank among the adult males in the group. Rank attainment occurred at a median age of 7.41 years (range = 6.74–8.35 years; Fig. 1b). The shortest period of subadulthood lasted 11.1 months, and the longest 31.2 months, with a mean of 22.7 months (SD = 5 months).

Wilcoxon and logrank tests for determining covariates of censored data revealed that maternal dominance rank and death of mother by male's 6th birthday (age at onset of puberty for the latest-developing males) both affected age at rank attainment (Wilcoxon test: maternal rank,  $P < 0.006$ ; mother's death,  $P < 0.025$ ; logrank test: maternal rank,  $P < 0.0015$ ; 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. 2b). No other independent vari-

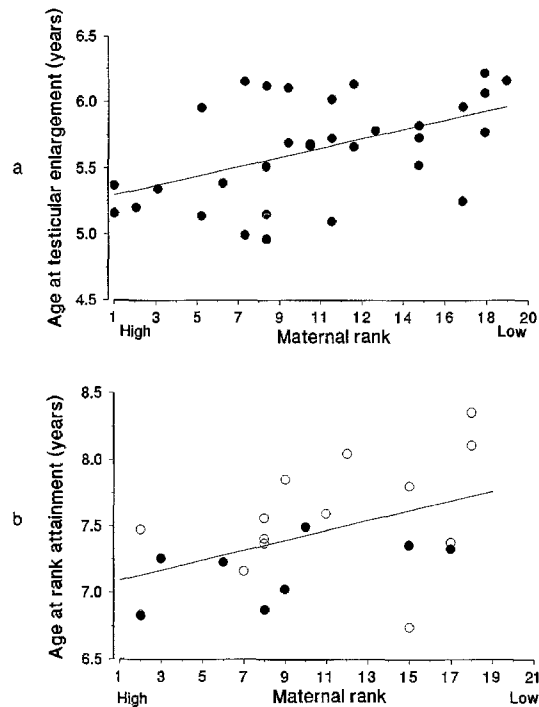


**Fig. 1a–c** Ages at which developmental milestones were reached. **a** Proportion of males reaching testicular enlargement in each age interval. **b** Estimated proportion of males attaining rank and **c** estimated proportion of males attaining first consortship in each age interval, based on survival analyses (see text). For **b** and **c**, numbers above bars represent a count of males attaining rank in each age interval; numbers in parentheses represent a count of males censored in that interval

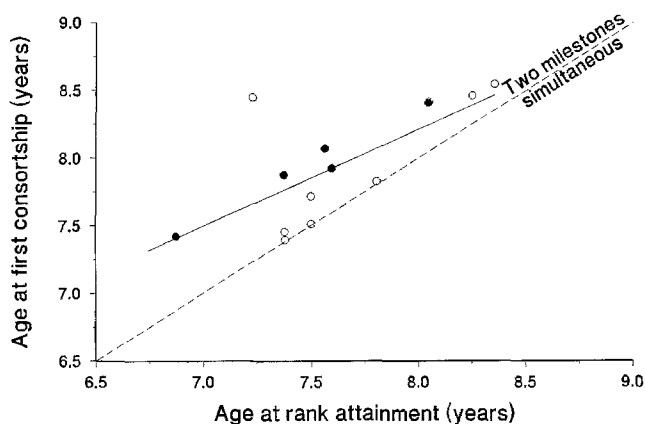
ables, including female availability, contributed significantly to age at rank attainment.

### First sexual consortship: full reproductive maturity

First consortships in the natal group occurred at a median age of 7.92 years (range = 7.39–8.54 years; Fig. 1c). First consortship was always preceded by rank attainment, and age at rank attainment strongly predicted age at first consortship ( $r^2 = 0.47$ ,  $P = 0.009$ ; Fig. 3). Although maternal rank predicted age at rank attainment, neither maternal rank nor any other maternal characteristics, either alone or in a multiple



**Fig. 2a, b** Effects of maternal characteristics on developmental milestones. **a** Effects of maternal rank on age at testicular enlargement (linear regression,  $r^2 = 0.25$ ,  $P < 0.004$ ). **b** Effects of maternal rank and maternal death on age at which males attained adult dominance rank. *Closed circles* represent males whose mothers died before the males' 6th birthdays; *open circles* represent males whose mothers survived past that point. See text for details about statistical tests employed



**Fig. 3** Linear regression of age at first consortship on age at rank attainment ( $r^2 = 0.47$ ,  $P = 0.009$ ). The *solid line* is the regression line, the slope of which is not significantly different from 1. The *dashed line* represents the line of simultaneous rank attainment and first consortship. *Closed circles* represent males for whom the average number of cycling females in the group during the 3 months following rank attainment was five or less; *open circles* represent males for whom the average number of cycling females was more than five. Note the correspondence between rank-to-consortship lag times and number of cycling females (Mann-Whitney  $U$ -test,  $P = 0.04$ )

regression with age at rank attainment, directly predicted age at first consortship. Similarly, number of older or younger maternal siblings alive in the group did not predict age at first consortship.

The median lag time between rank attainment and first consortship was 2.5 months (range = 5–526 days), and this lag time was independent of age at rank attainment: the slope of the regression line was not significantly different than one ( $0.2 > P > 0.1$  for the null hypothesis that the slope of the regression line was one; Sokal and Rohlf 1981, p. 474). The lag time was predicted both by average number of cycling females in the 3 months after the male attained rank, and by his dominance rank-based ability to gain access to those females (see Methods). Males whose lag time between rank attainment and first consortship 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 waited less than the median time to begin consorting) had positive or zero access measures (i.e., had 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 lag times or dominance ranks attained by maturing males.

## Discussion

Maturation readiness among male baboons, the ability to produce viable sperm and to compete for access to reproductive females, appears to depend on relatively stable maternal characteristics such as rank and survival status. Indeed, much of the variability among males on the road to adulthood can be predicted during the early juvenile period or even at 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 maturing male's 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 growth has analogs in many other taxa. Among mice, female sexual maturity may be either accelerated or delayed, depending on the frequency and intensity of contact with conspecific males versus females (Vandenbergh and

Coppola 1986). Among cooperative breeders, comprising hundreds of species of birds and mammals, young mature 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 (Emlen 1991). Among primates, the most extreme version of this pattern is found in the New World callitrichids, in which cooperative breeding is prevalent (Goldizen 1987), 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; French et al. 1984). In addition, acceleration of puberty among females exposed to unrelated adult males has been reported for callitrichids (reviewed in Ziegler et al. 1990). Thus, the onset of reproduction for callitrichids depends both on physiological readiness and on the presence of reproductive opportunities, signalled by the absence of suppressing behavior or chemosignals or by the opportunity to breed elsewhere (see also Goldizen and Terborgh 1989; Savage et al. 1988).

Hence, many animals exhibit maturation patterns in which preparation for and activation of reproductive behavior are distinct processes, and in which reproduction is triggered by social stimuli. These stimuli are effective triggers only when animals are physiologically capable of reproducing, and 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 deterministic processes, including male immigration and emigration and female reproductive schedules. Accordingly, much of the variance in age at first reproduction will be unaccounted for by individual, familial, or early developmental characteristics. On average, sons of high ranking mothers have a head start as they approach first reproduction because they are primed relatively early. When many reproductive females are available, sons of high ranking mothers may retain this advantage, but in general the waiting period will be similarly uncertain for all males.

For a number of primate species or populations, first reproduction is probably less vulnerable to stochastic influences. At least in food provisioned, expanding populations of rhesus and Japanese macaques, maternal rank is a strong influence throughout male development, both indirectly through rank effects (high maternal rank promotes high male rank and thus increased mating success; Koford 1963; Koyama 1970; Drickamer and Vessey 1973; Sugiyama 1976; Sade et al. 1976; Chapais 1983) and directly through increased reproductive success of sons of high ranking mothers (Smith and Smith 1988). The pattern is different in wild baboons, where maternal rank, even among juvenile males, predicts offspring rank only partly (Cheney 1977; Lee and Oliver 1979) or not at all (Johnson 1987;

Pereira 1989). To the extent that these represent taxonomic differences between baboons and macaques, they may be due in part to the fact that macaques exhibit less extreme body size dimorphism than baboons, which means that macaque mothers can sometimes directly intervene in assisting their sons to attain high rank (Koford 1963; Chapais 1983; Walters and Seyfarth 1987; Pereira 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 adult). This early maturation for sons of high-ranking mothers parallels the effects of maternal rank on maturing females of a number of primate species (Silk 1987), including Amboseli baboons (Altmann et al. 1988), and may leave males poised to take advantage of dispersal opportunities as well as 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 inbreeding risk, 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 has stochastic components that are overlaid on maternal influences. The extent to which maternal factors maintain their influence in the face of these stochastic components remains to be fully elucidated.

Our findings clearly demonstrate the social constraints on full reproductive maturity for male baboons, and they hint at the potential range of complexity of these constraints. Neither reproductive potential as signalled by testes enlargement, nor physical strength in intrasexual competitive ability as signalled by rank attainment, were sufficient in predicting consort attainment and full reproductive maturity. Nor were simple measures of the demographic context such as the number of adults of either sex in the group. Rather, the important characteristic was a measure of access that incorporated a male's own readiness and his position vis a vis other males and the number of cycling females. Likewise, in our study of both natal 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 1995). Future efforts to understand the effects of the demographic and social context on male reproduction might profitably explore further the factors that contribute to reproductive attainment and to the complex 'calculus' that males

may use in making dispersal decisions. Likely candidates for such refinement might include discounting, among cycling females, those with whom mating is less desirable (such as maternal relatives, with whom mating generally does not occur; Alberts and Altmann 1995) or overvaluing those with whom the male is more likely to mate (such as "friends"; Smuts 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 1979).

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 intra- and interspecific maturational 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 concomitant increase in selection on traits that increase individual competitive ability across a wide variety of conditions.

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