



Testicular Size, Mating System, and Maturation Schedules in Wild Anubis and Hamadryas Baboons

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Received April 30, 2001; accepted December 29, 2001

We report body mass and testicular size in 258 anubis (Papio anubis or P. hamadryas anubis) and 59 hamadryas (P. hamadryas or P. h. hamadryas) baboons, live-trapped in Ethiopia. As predicted by theories of sexual selection by sperm competition, among hamadryas baboons, which are monandrous, fully adult males have absolutely and relatively smaller testes than those of comparable males among anubis baboons, which are polyandrous. Male hamadryas are also ca. 10% smaller in bodily mass as adults. The intertaxonal difference in adults is due entirely to the fact that in male anubis baboons, testicular and bodily mass continue to grow up to full adulthood—the age at which most males emigrate from their natal troop and initiate a confrontational breeding strategy among unrelated animals. By contrast, male hamadryas baboons, which are usually philopatric, attain adult body mass and testicular size as subadults. In both species, juveniles experience rapid testicular growth peaking in rate at ca. 12kg body mass, but testicular descent and growth starts earlier in hamadryas than in anubis baboons. Juvenile hamadryas baboons have relatively larger testes than their anubis equivalents, perhaps because male philopatry allows the mating strategy of male hamadryas baboons to be initiated during juvenile life and therefore permits some sperm competition between juveniles and adults.

KEY WORDS: baboons; Ethiopia; testes; growth and development; sperm competition; Papio.

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INTRODUCTION

The relative size of the adult testis in primates, as in other mammals, has been related to patterns of mating, especially to polyandrous mating that is likely to cause sperm competition (Harcourt, 1997; Harcourt *et al.*, 1981; Møller, 1988). We examined testicular size in two closely related, similarly-sized primate taxa with contrasting mating systems. In hamadryas baboons, mating is often polygynous but generally monandrous (Kummer, 1968), while in olive or anubis baboons, as in most papionin monkeys, mating is regularly promiscuous, *i.e.*, both polygynous and polyandrous (Smuts, 1985; Strum, 1994). As predicted by the sperm competition model (Harcourt *et al.*, 1981, Harvey and Harcourt, 1984), *Papio hamadryas* had been reported to have smaller testes as adults than other *Papio* spp. (Harcourt *et al.*, 1981; Møller, 1988), but this conclusion was based on small samples of uncertain provenience, and the developmental trajectory resulting in the distinctive proportions had not been documented in wild animals. We present data on bodily and testicular size from a substantial sample of wild-caught baboons and include observations on the ontogeny of the relevant variables, derived from cross-sectional data.

Sperm Competition and Male Gametic Investment

If, as seems to be the case (Møller, 1988), testicular size in anthropoid primates is correlated with the quantity of sperm produced per ejaculate or the rapidity with which sperm are replenished between ejaculations, or both, then larger testes are predicted under one or both of two conditions: (1) when a female often mates with more than one male within a single conceptional cycle, forcing their gametes to compete within her reproductive tract: sperm competition, or (2) when successful reproduction requires a male to serve a number of females within a limited space of time: potential sperm depletion. Since sperm competition is a consequence of polyandry, and sperm depletion of polygyny, the largest testes are expected in species where both sexes are polygamous within a single female breeding cycle and the smallest testes are predicted in species in which both sexes usually mate monogamously, so that sperm competition is absent and sperm depletion is inconsequential. In monandrous, polygynous—one male group—species, testicular size is expected to be adapted to the interval between females' optimally fertile periods. Synchronous or seasonal breeding will favor larger testicular size in such societies, even in the absence of sperm competition, and there is some evidence (Zinner *et al.*, 1994) that females in the largest harems of hamadryas baboons may experience delayed conception, presumably

because of their mate's sperm depletion. However, Møller (1988) concluded from inter-specific comparisons that in primates sperm competition is more influential than sperm depletion in determining relative testicular size.

Hamadryas and Anubis Baboons

The two baboon populations live in permanent, multimale, multifemale social groups, numbering between 20 and 150 individuals. Their breeding is non-seasonal. The two taxa are sufficiently closely related, and evidently share enough components of their mate recognition systems to hybridize freely in the wild (Nagel, 1973; Phillips-Conroy and Jolly, 1986), yet they exhibit mating and dispersal behaviors that differ in ways relevant to the male gametic investment model.

In relevant aspects of behavior, anubis baboons resemble other savanna, i.e., non-hamadryas, baboons, which, contrary to morphological and genetic evidence (Jolly, 1993; Newman *et al.*, in press; Williams-Blangero *et al.*, 1990) are often united as a single species, *Papio cynocephalus*. Most male anubis baboons emigrate from their natal group and join another before breeding. Groups usually include more than one male of breeding age, and the reproductive success of a male depends critically upon the rank he attains among the largely unrelated adult males of his adoptive group. Most mating, especially periovulatory mating most likely to result in conception, occurs in the context of intense but short-term pairings: consortships. A periovulatory female, whose condition is advertised by a swollen perineum, is closely followed, groomed, and mated by an adult male consort over a period of hours or days. A male's ability to form and to maintain a consortship with a fertile female is influenced by several factors, including his familiarity to, and affiliative relationship with, the female (Smuts, 1985). However, his success is, determined largely by his agonistic interactions with other fully adult males. Consorting pairs are harassed by other males, both individually and in coalition, resulting in frequent turnovers. A female thus commonly mates with a succession of adult males during a single fertile period. Typically, young adult males in prime condition are more likely to mate during the female's peak—periovulatory—swelling, while subordinate and post-prime males are more likely to mate during the periods of inflation and deflation of the sexual skin. The short-term nature of most anubis baboon consortships, the polyandrous mating that precedes most conceptions in multimale groups, and the presumably low relatedness of rival males, all predict strong sperm competition, and consequent selective pressure in favor of larger testes.

In hamadryas baboons, the fertile period of the female cycle is similarly signaled by a perineal swelling, but the social context in which most

conception occurs is very different. Every female of reproductive age is socially bonded to a single adult male (Kummer, 1968, 1995), who attempts, usually successfully, to enforce his exclusive relationship by herding and if necessary by physically restraining his female(s) and by attacking them if they fail to follow him or if they approach another male. Mate-guarding is maintained throughout the female's reproductive cycle, with little if any intensification during her periovulatory period (Kummer, 1968; Nystrom, 1992). Female behaviors that contribute to the stability of the male-female bond include intensive attention to the male's luxuriant shoulder-manes. The resultant one-male units (OMU) are highly coherent spatially and persistent over time. They may include as many as 9 adult females, their young offspring, and often a socially peripheral, young adult or subadult male. Adult males, especially OMU leaders, rarely conflict in the context of mating, and most disputes between them are resolved by avoidance, or by ritualized, mutual appeasement and greeting behavior, instead of fighting (Kummer, 1968). Unlike a male anubis baboon, a male hamadryas baboon generally remains within his troop of birth (Abegglen, 1984; Sigg *et al.*, 1982), and often joins an established OMU as a follower, presumably establishing a social vantage point for eventually taking over as leader. Although followers have little social contact with the OMU females, strong circumstantial evidence indicates that they sometimes succeed in copulating, and may beget some of the OMU offspring.

Maturing among kin, a male hamadryas baboon does not need to establish a position in an unfamiliar group and can initiate his long-term breeding strategy as a juvenile. Even as an adult, a hamadryas male's mating success depends less upon his ability to physically dominate or to displace other fully adult males, and far more upon his ability to hold the allegiance of the females of his OMU by coercion, attraction or both (Jolly, 1963; Kummer, 1968). A female hamadryas baboon's mating is usually confined to her OMU leader. Such extra-OMU matings as occur are likely to be with the follower male, who is believed often to be a close relative of the leader (Sigg *et al.*, 1982). Both these factors should minimize sperm competition as a selective force.

MATERIALS AND METHODS

We gathered data on body mass, dental development and testicular size from 258 anubis and 59 hamadryas baboons in the Awash National Park, Ethiopia, in short (2–6 week) trapping seasons between 1984 and 1998. Unlike those sampled in the drought year of 1973 (Phillips-Conroy and Jolly, 1986), all these subjects were examined in years of normal rainfall and food availability. They showed no sign of emaciation or malnutrition. Neither

absolute nor relative testicular size differed significantly according to the season of capture (dry: January, February or rainy: July, August).

The anubis baboons belonged to social groups whose ranges were situated in the valley of the Awash River, immediately above the Awash Falls (Nagel, 1973; Phillips-Conroy *et al.*, 1991). We sampled 44 hamadryas baboons from 3 large groups (Swedell, 2000) whose range included the hot springs (Filwoha), about 30 km northeast of the capture site of the anubis baboons. The hamadryas sample also included 15 data sets from individuals that had migrated into one or other of the anubis groups (Phillips-Conroy *et al.*, 1991; unpublished data). They did not differ from the Filwoha hamadryas in any relevant variable.

Hamadryas and anubis baboons are physically and behaviorally adapted to semidesert and savanna habitats, respectively, (Kummer, 1968). However within the Awash National Park differences in the quality of their respective ranges are minimal. Apart from some evergreen, riparian woodland in the range of the anubis baboons, and groves of doum palms (*Hyphaene thebaica*) in the Filwoha area, the environments of the two populations consisted of very similar *Acacia* scrub and savanna grassland (Jacobs and Schloeder, 1993). It seems most unlikely that the minor habitat differences determined the divergent patterns of growth and development we observed.

We captured subjects in baited, manually operated cage-traps and tranquilized, weighed, measured, sampled, and released them (Brett *et al.*, 1982; Phillips-Conroy *et al.*, 1991, 1992). Since birth-dates were unknown, we estimated age from dental emergence, assigning each animal to one of 5 age classes. The approximate chronological ages corresponding to the dental stages have been estimated from animals of known age in this and other wild populations by Phillips-Conroy and Jolly (1988):

Age class 1: Infants: No permanent molar visible (<24 mo) (Not included in this study).

Age class 2: Younger juveniles: One or more first molars visible, no M2s (24–50 mo).

Age class 3: Older juveniles: One or more second molars visible, no M3 (50–80 mo).

Age class 4: Subadults: One or more third molars visible, but dental eruption not complete (80–100 mo).

Age class 5: Full adults: Dentition (including canines) completely erupted (>100 mo).

We measured body mass in kg on a spring scale, and Phillips-Conroy measured the left testis through the scrotal skin with a dial caliper. Length (in mm) was the longest dimension; breadth was the larger of the two dimensions orthogonal to length. Most of the testes measured were scrotal, but we also

measured a few young animals with inguinal testes. No infant had measurable testes. All animals in age classes 3–5 had scrotal testes, but younger juveniles (age class 2) varied, and it seems that testicular descent normally occurs during this phase of development. Except where noted, we included only subjects with measurable testes in the body mass sample.

We expressed testicular volume in cm^3 , as: $10^{-3} \times (\text{testicular breadth}/2)^2 \times (\text{testicular length}/2) \times 4\pi/3$ (Glander *et al.*, 1992). Following previous usage (Clutton-Brock and Harvey, 1984; Harcourt *et al.*, 1981; Short, 1979) we related testicular to somatic size by a simple ratio: relative testicular volume = testicular volume (in cm^3)/body mass (in kg). We also investigated the relationship between testicular volume and bodily mass by linear regression of Log_e -transformed data (Stockley and Purvis, 1993). To compare relative testicular size between taxa within age classes, we recorded residuals from the linear regression of log_e testis volume on log_e body mass for that age class, with taxa combined. We expressed rates of change as the slope of the linear regression of log_e testis volume on log_e body mass for each age class, with taxa treated separately.

The distribution of absolute and relative testicular size in age class 5 of both populations is strongly unimodal with low skew and kurtosis, but is more irregular in the other age classes. Thus, although we include mean values for comparison in Tables I–III, we used the non-parametric Mann-Whitney test to investigate age- and taxonal differences in absolute testicular size, absolute bodily mass, and relative testicular size. We obtained identical results (not shown) by assuming that the variables were normally distributed and using *t*-tests to compare mean values.

RESULTS

Figure 1 shows the distribution of primary data. Locally-weighted linear (LOWESS) regressions (fitted to 50% of points, with 5 iterations; SPSS statistical package) indicate the trajectory of the bodily mass—testicular volume relationship while minimizing assumptions about the overall mathematical relationship between the variables. In Tables I and II we summarize and compare absolute and relative testicular size and body mass by age class and taxon. Table III includes expressions of the linear relation between testicular volume and bodily mass, both converted to log_e , within each of the age classes.

As the LOWESS regression lines in Fig. 1 suggest, the relationship between testicular size and body mass in each taxon describes an approximately sigmoid curve, with its steepest slope corresponding to rapid increase in both absolute and relative testicular size in the late juvenile period. However,

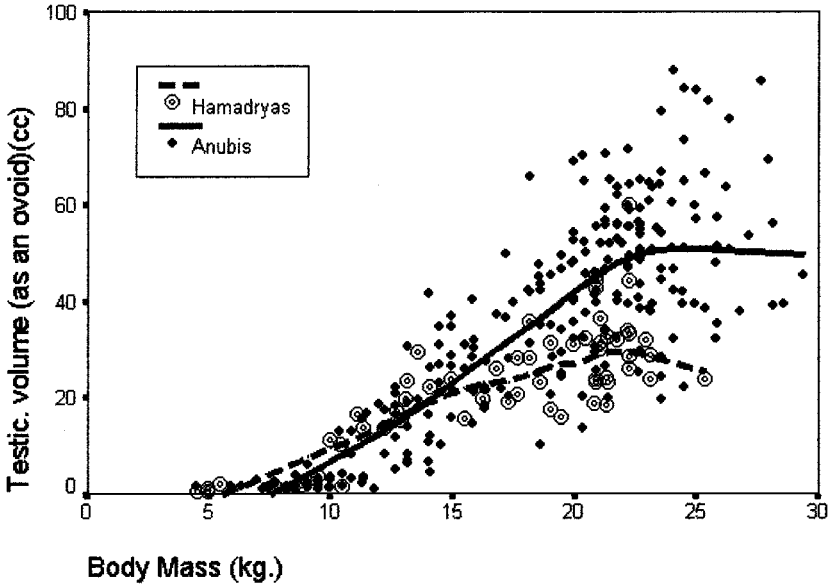


Fig. 1. Testicular volume (as an ovoid, ccs.) plotted against body mass (kg.) in hamadryas (open symbols, dashed line) and anubis (closed symbols, solid line) baboons. Lines are locally-weighted linear (LOWESS) regressions, fitted to 50% of points, with 5 iterations (SPSS statistical package).

there are intertaxonal differences at both ends of the trajectory of testicular growth. The phase of rapid increase in absolute and relative testicular size begins and terminates earlier in hamadryas baboons, while increase in both body mass and testicular volume are prolonged in anubis baboons.

In both taxa, there is a strong, positive linear correlation between body mass and testicular size within age classes 3, 4, and 5 (Table III), which presumably reflects both age-related variation and individual variation in mass-for-age. In the absence of independent criteria of age by which to rank individuals within the classes, one can not separate the two effects completely. However, we assume that variation in size-for-age remains more or less constant over the growth trajectory and that changes in the slope of the regression from one interval to the next predominantly reflect age-related change in relative growth rates.

The developmental trajectories of the two taxa, as expressed in residuals from the bi-taxonal log-log regression, are contrasted in Fig. 2. Rapid increase in testicular size begins at a lower body mass and presumably earlier in time in hamadryas baboons. Hamadryas baboons in Age Class 3 have significantly higher (more positive) values of the residual from the log-linear,

Table I. Absolute and relative measures of bodily mass and testicular size in anubis and hamadryas baboons

	Age class	Anubis				Hamadryas				Mean diff	Sig.
		Mean	Std D.	N	% AD	Mean	Std D.	N	% AD		
Testic. vol.	2	1.78	0.93	14	3.6	1.25	0.64	6	4.3	0.53	NS
	3	14.43	12.03	78	29.2	13.91	8.29	13	47.5	0.52	NS
	4	33.50	12.28	31	67.7	26.40	7.75	9	90.1	7.10	NS
	5	49.49	14.95	135	100.0	29.31	9.70	31	100.0	20.18	0.0001
Body mass	2	7.28	1.31	14	32.1	6.09	1.76	6	29.3	1.19	NS
	3	12.83	3.05	78	56.5	11.75	1.85	13	56.5	1.08	NS
	4	17.83	2.70	31	78.5	17.87	3.45	9	86.0	-0.04	NS
	5	22.71	2.36	135	100.0	20.78	1.99	31	100.0	1.93	0.0000
Rel. testic. vol.	2	0.25	0.12	14	11.5	0.20	0.09	6	14.2	0.05	NS
	3	1.00	0.73	78	45.9	1.12	0.57	13	79.4	-0.12	NS
	4	1.87	0.58	31	85.8	1.49	0.33	9	105.7	0.38	NS
	5	2.18	0.63	135	100.0	1.41	0.43	31	100.0	0.77	0.0000

Note. Mean diff. = anubis mean minus hamadryas mean. % AD = value as a percentage of the adult (Age Class 5) value in this taxon. Sig = Probability of no difference between hamadryas and anubis, Mann-Whitney test, 2-tailed. Testic. vol. = testicular volume, calculated as an ovoid (cm³). Rel. testic. vol. = Testicular volume (in cm³)/bodily mass (in kg).

bitaxonal regression (Table III). Most of the intertaxonal difference occurs in the body mass range of 9–13 kg, which is close to the average bodily mass of a fully adult female. In this range, the LOWESS regression line for hamadryas baboons lies above the anubis baboon line (Fig. 1), and the 10 hamadryas points have significantly higher residuals from the log-linear,

Table II. Differences between age classes

	Classes	Anubis			Hamadryas		
		Abs diff	Fract.	Sig diff	Abs diff	Fract.	Sig diff
Testic. vol.	2 to 3	12.67	8.10	<0.001	12.66	11.15	<0.001
	3 to 4	18.41	2.27	<0.001	12.49	1.90	0.002
	4 to 5	16.51	1.50	<0.001	2.77	1.11	NS
Body mass	2 to 3	7.15	2.25	<0.001	6.13	2.09	<0.001
	3 to 4	4.76	1.37	<0.001	6.12	1.52	<0.001
	4 to 5	5.09	1.29	<0.001	2.87	1.16	0.04
Rel. testic. vol.	2 to 3	0.75	3.99	<0.001	0.92	5.59	0.001
	3 to 4	0.85	1.85	<0.001	0.37	1.33	NS
	4 to 5	0.33	1.18	0.007	-0.08	0.94	NS

Note. Classes = successive age classes compared. Abs. diff. = absolute difference between means of successive age classes (cm³). Fract. = mean value for older of successive age classes divided by mean value for younger age class. Sig. diff. = probability of no difference between successive age-classes, Mann-Whitney test, 2-tailed. Testic. vol. = testicular volume, calculated as an ovoid (cm³). Rel. testic. vol. = testicular volume (in cm³)/body mass (in kg).

Table III. Details of linear regression of Log_e -transformed testicular volume on Log_e - transformed bodily mass within age classes

	Age class			
	2	3	4	5
Anubis				
Corr	0.21	0.86	0.60	0.28
p	0.47	<0.001	<0.001	<0.001
Slope	0.06	4.02	1.30	0.94
SE slope	0.78	0.28	0.32	0.28
N	14	78	31	135
Hamadryas				
Corr	0.71	0.76	0.58	0.40
p	0.11	0.002	0.05	0.01
Slope	1.58	4.40	0.74	1.29
SE slope	0.78	1.07	0.39	0.56
N	6	13	9	31
Combined				
Corr	0.37	0.83	0.49	0.41
p	0.06	<0.0001	0.001	<0.001
Slope	0.90	3.95	1.02	1.49
SE slope	0.54	0.28	0.30	0.26
N	20	91	40	166
Comparison				
Higher resid.	[Anubis]	Hamadryas	[Anubis]	Anubis
Sig. diff.	0.32	0.005	0.06	0

Note. Corr = Pearson correlation coefficient, Log_e testicular volume and Log_e bodily mass. SE slope = Standard Error of slope. p = probability that Corr = 0. Higher resid. = Taxon with more positive mean residual from linear regression of Log_e . Testicular volume on Log_e bodily mass in this Age Class. Brackets enclose cases where residuals do not differ significantly ($p > 0.05$) between taxa. Sig. diff. = probability of no difference between taxa for residuals; Mann-Whitney test, 2-tailed.

bitaxonal regression than those of the 36 anubis points (Mann-Whitney U, 2-tailed $p = 0.03$). Hamadryas baboons of 9–13 kg body mass have reached, on average, 67% of the relative testicular size of adults, while anubis baboons have reached only 30%. The difference is highly significant (Mann-Whitney U = 59, 2-tailed $p = 0.0013$).

Even greater differences between the taxa are apparent immediately before adulthood. In both age classes 4 and 5, anubis residuals from the log-linear, bitaxonal regressions are significantly more positive than those of hamadryas baboons (Table III). Among subadults, the slope of the regression of testis upon body mass is twice as steep in anubis baboons as in hamadryas baboons, presumably because in hamadryas baboons, testicular growth is slowing during this interval, while the anubis baboons are still experiencing rapid growth. This pattern continues into full adulthood. Among anubis baboons, age class 5 individuals have much larger testes than males in age class 4, while among hamadryas baboons, full adults show only a very

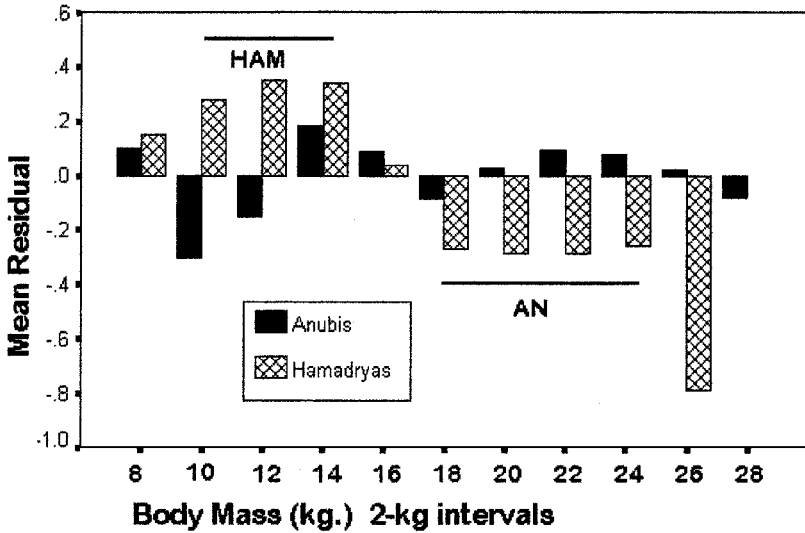


Fig. 2. Mean residual, by 2-kg. intervals, of individual testicular volume values from overall, log-log, bi-taxon linear regression of testicular volume on bodily mass, for hamadryas (hatched) and anubis (solid) baboons. Horizontal bars indicate ranges of bodily mass in which hamadryas (HAM) or anubis (AN) residuals, respectively, are significantly higher.

modest, statistically insignificant, increase over subadults in testicular size. The late growth spurt in anubis males results in an adult testicular size nearly 70% greater, on average, than in hamadryas baboons. A similar, though less extreme, contrast is apparent in body mass. Fully adult hamadryas males are not significantly heavier than young adults, but among anubis baboons, fully adult males are much heavier. The difference in body mass between fully adult anubis and hamadryas baboons (*ca.* 10%) results entirely from growth in this phase. The combination of somewhat greater body mass, and much greater testicular volume, results in an average relative testicular size *ca.* 45% greater in anubis than in hamadryas baboons (Table I).

DISCUSSION

The most immediate implication of our results is that relatively smaller testes in full-grown males are indeed a taxon-specific characteristic of hamadryas baboons, as predicted by the male gamete investment (sperm competition) model. However, since fully adult male anubis baboons are heavier than hamadryas males, it is possible that the difference is not adaptive, but simply represents the differential expression of a common allometric

trend. If this were the case the largest hamadryas baboon should have relatively the largest testes, and the smallest anubis baboon should tend to show hamadryas-like proportions. No such trends are apparent; though absolute testicular volume is positively correlated with body mass in age class 5, relative testicular volume is not, either in anubis (Pearson's $r = -0.05$, one-tailed $p = 0.54$) or in hamadryas baboons ($r = 0.08$, $p = 0.67$). Accordingly, the very weak positive correlation ($r = 0.11$, $p = 0.17$) that is evident when hamadryas and anubis baboons are pooled can be attributed solely to the intertaxonal difference in proportions. The explanatory hypothesis invoking a common allometric trend can be rejected, and relatively and absolutely small adult testicular size can be considered a taxon-specific attribute of hamadryas baboons, as predicted by the primary sperm competition model.

In addition, our developmental data suggest differences between the taxa in the timing of maturation, with earlier onset of maturation in the hamadryas baboons, related adaptively to their mating strategy. However, an alternative interpretation must also be considered. Our age estimates for hamadryas baboons are based upon eruption of the permanent molars. It is thus possible that the ontogeny of testicular and somatic growth is similarly timed in the two taxa, and that the only real developmental difference is in the age of molar eruption. This interpretation cannot be decisively rejected, in the absence of extensive longitudinal data from repeated trapping of wild hamadryas, comparable to that available for anubis and yellow (*Papio hamadryas cynocephalus*) baboons (Phillips-Conroy and Jolly, 1988), but a number of observations make it unlikely.

Body mass growth curves for captive hamadryas baboons (Crawford *et al.*, 1997) conform closely to our findings, showing male body mass plateauing at about 21 kg at about 8 years of age, and dropping slightly in males of ≥ 12 -years-old. Testicular volume data from the same colony (Crawford *et al.*, 1997) also match our results, with rapid increase occurring between about 3.8 and 6 years (corresponding to our estimated age range of age class 3), but little growth thereafter. We know of no comparably detailed work on anubis baboons, but Packer (1979) mentioned the onset of puberty between 5 and 6 years in anubis baboons at Gombe, Tanzania. Alberts and Altmann (1995) reported longitudinal observations of testicular enlargement in yellow baboons at Amboseli, Tanzania. Individual males underwent a period of *ca.* 5 mo rapid testicular growth, with a median age of onset of 5.69 yr. The earliest individual age of onset in the yellow baboon sample was 4.96 yr, by which time eruption of second molars is normally complete. Even allowing for the probability that observation from a distance was less sensitive than in-hand measurement to detect the onset of testicular enlargement, this suggests a real difference between hamadryas baboons and the two polyandrous, male-dispersing taxa. Moreover, information on

a few individuals of known chronological age in ANP (Phillips-Conroy and Jolly, unpublished) and elsewhere (Sigg *et al.*, 1982), does not suggest that hamadryas baboons experience a chronology of molar eruption distinct from that of other baboons, and none is assumed in the following discussion.

Our results suggest ontogenies of somatic and testicular development that are similar, but not identical, in anubis and hamadryas baboons. Since our data are entirely cross-sectional, we can assume a smoothing effect produced by averaging. The patterns of change and intertaxonal distinctions, would presumably be even more sharply defined if we could align individual developmental profiles, which are known to vary considerably (Alberts and Altmann, 1995).

Male anubis baboons undergo a major increase in body mass, starting about the time that the third molars begin to emerge, at about 6.6 years, and continuing into full adulthood. This period entails an even greater increase in testicular size, full eruption of the canine teeth, a voice break that gives them a deep rather than a shrill alarm-bark, and a more bulky body profile. The last feature is due to full development of the shoulder mane as well as to increased muscularity. These developments occur immediately before the age at which a male normally leaves his natal group and attempts to join the breeding hierarchy in another. Successful new immigrants tend to be high in rank, as defined by the traditional criterion of their ability to displace other males from contested resources, including fertile females (Packer, 1979; Popp and DeVore, 1979). A male's ability to immigrate successfully—by intimidating other males and perhaps by impressing the group's females—is thus crucial to his reproductive success. Our (unpublished) data suggest that the additional body mass acquired by male anubis baboons at this stage consists largely of muscle, especially in the upper body. For example, mean arm circumference, increases from 21.1 ± 1.9 cm in age class 4, to 24.2 ± 2.2 cm in age class 5 ($p < 0.001$). At the same life stage, the young adult anubis baboon acquires the large testes that are advantageous in sperm competition during polyandrous mating.

The anubis developmental program would be selectively favored because impressive body size and muscularity are advantageous at the time of intergroup migration, but the other side of this developmental coin may also be important. By delaying fully adult bodily and testicular size until shortly before emigration, the young adult anubis baboons may more easily keep a low profile—both literally and figuratively—among the unrelated and potentially hostile males of his natal group.

By contrast, male hamadryas baboons apparently add very little body mass after a period of rapid growth at about 7–8 yr, in which body mass almost doubles (Sigg *et al.*, 1982). Up to this stage, their growth curve is virtually indistinguishable from that of anubis males, at least on our relatively coarse,

dentally-based scale. It is evidently this drastic slowing of growth during early adulthood that results in the lower body mass at full maturity. Presumably, selection for a late growth spurt has been relaxed in the context of male philopatry. Testicular growth is also completed about the same time, so that both absolute and relative testicular size remain in the late subadult range, which is adequate for a mating regime that is predominantly monandrous, and entails virtually no sperm competition among adults.

Although his body mass and testicular volume apparently increase little beyond the size attained in late subadulthood, the physical development of full adulthood in a male hamadryas involves more striking changes in external appearance than occur in anubis males. The mane and cheeks continue to whiten, and the naked pink buttock pads become more prominent (Sigg *et al.*, 1982). These epidermal structures are involved with behaviors—mostly affiliative—that are peculiar to hamadryas males and are used in establishing, maintaining, and defending an OMU (Kummer, 1968).

The simple sperm competition model does not explain our second finding—that testicular growth in hamadryas males begins earlier in juvenile life, with signs of testicular enlargement appearing even before the eruption of the second molars, and proceeding rapidly in the earlier part of age class 3. The result is that by the time his second molars have fully erupted, and his body mass just exceeds the mean for fully adult females, the young hamadryas male has testes that are, relative to bodily mass, as large as an adult male. We can think of two possible explanations, both related to the long-term reproductive strategy of male hamadryas baboons, and not mutually exclusive.

Unlike those of male anubis baboons, the lifetimes of philopatric male hamadryas baboons are not sharply divided between immature years among matrilineal kin and breeding years typically among unrelated and often hostile members of an adopted group. A hamadryas male grows up among male kin with which he will continue to interact as an adult. Presumably related to this condition is the fact that the strategies used to acquire mates are predominantly affiliative rather than confrontational towards males of breeding age. In particular, a young male hamadryas usually attaches himself as a follower to a mature adult male, especially to an OMU leader. A juvenile female from the unit often eventually becomes the foundation of the younger male's OMU (Abegglen, 1984). Whereas a male anubis baboon has neither incentive nor opportunity to initiate his confrontational reproductive strategy until full physical maturity and (usually) after migration, a male hamadryas baboon presumably increases his chances of becoming an OMU leader by initiating a long-term program of ingratiation as early as possible. In fact, even young (age class 2) juvenile hamadryas baboons follow and show great interest in adult males and their accompanying females. This behavior is

especially striking when exhibited by a juvenile male hamadryas immigrant into an anubis group, where it contrasts with the peer-oriented behavior of juvenile anubis baboons (S. Beyene, personal communication, 1993). If the respective male reproductive programs of anubis and hamadryas baboons are initiated by hormonal signals from the maturing gonads, it is likely that sexual precocity in hamadryas males should be associated with somewhat accelerated testicular maturation. It remains to be determined whether the androgen profile of male hamadryas baboons also matures earlier than that of anubis males.

The reproductive program of a hamadryas follower is not purely prospective and affiliative, which suggests a second explanation for precocious testicular growth in hamadryas males. To the extent that he can sneak copulations despite the vigilance of the OMU leader, relatively large testes presumably enhance the chances of a large juvenile or subadult in sperm competition with the adult leader, and selection should favor both early testicular maturation, and relatively large testes in subadults.

This explanation is related to the model proposed by Stockley and Purvis (1993), following Parker (1990a,b), which predicts a different intraspecific relationship between testicular size and adult male bodily size, according to mating behavior in mammals. To the extent that male mating success is correlated with bodily size, natural selection will favor relatively greater gametic investment by smaller-sized members of the breeding male cohort, and hence little or no intraspecific body-size/testicular size correlation. For example, nonseasonal breeding makes fertile females more monopolizable (Harcourt, 1997), and the predicted flatter, weaker, bodily-testicular size correlation occurs in fully-grown adult males of non-seasonally breeding species versus their seasonally-breeding relatives (Stockley and Purvis, 1993).

Both focal baboon taxa are nonseasonal breeders, and fully-grown adults of both taxa (Age Class 5) show low correlations and comparatively flat (though significantly positive) testicular/body mass regressions (Table III). Presumably, the similar outcome results because in anubis both agonistic and sperm competition are operating among full-grown adults, while in hamadryas baboons neither factor is important in this age class.

Stockley and Purvis (1993) clearly intend their model to apply only to fully-grown, sexually mature adult males, which avoids complications arising from its application to developmental series, especially in species such as baboons and many other catarrhine primates, in which sexual maturity—the ability to beget offspring—is reached long before the completion of somatic growth (Alberts and Altmann, 1995). The difficulty with stretching the Stockley Purvis (1993) model to include males that are sexually mature but not fully-grown, is that the slope and position of the log-log regression

will be strongly influenced by data points representing the most problematic individuals: maturing males that in real life do little mating, and enter the breeding population at different ages and sizes (Alberts and Altmann, 1995).

Accordingly, the definition of the breeding population becomes critical. Including individuals that are too young to breed will simply tend to reproduce the overall, infant-to-adult growth trajectory, obscuring the effects of subadult mating, while too conservative a definition will omit some subadults whose reproductive success influences selection for testicular size at different life stages.

By arbitrarily including as potential breeders all males with bodily mass ≥ 12 kg. (the approximate size at which rapid testicular enlargement begins), we find that both taxa exhibit a significant, positive testicular/bodily mass correlation. However, because of the much higher end point on the testicular size scale in anubis baboons their regression slope is twice as steep (1.85 ± 0.124 S.E. vs. 0.90 ± 0.214 S.E.) and the correlation twice as strong (0.54 vs. 0.29), as in hamadryas baboons. Raising the threshold of sexual maturity to 15 kg. produces values more closely approaching those of full adults, as might be expected (slopes: 1.40 ± 0.16 and 1.04 ± 0.38 , respectively; correlation: 0.53 and 0.40 , respectively). It seems most unlikely that these values reflect adaptation to sperm competition between larger guarders (full adults) and smaller sneaks (juveniles) in the two taxa. The trajectories they describe may be partly the product of taxon specific rates of competition among adults and between subadults and adults, but they must also reflect the rates of growth needed to attain adaptive adult values.

If the Stockley-Purvis (1993) model is to be applied, it seems more meaningful to restrict the analysis to the age classes known or suspected to be involved in mating, and hence in sperm competition. In anubis groups, subadults and juveniles are effectively excluded from fertile matings, so an individual's sperm production and testicular size before full maturity are irrelevant to sperm competition in the current cohort of fully adult breeding males, and are likely to be influenced entirely by developmental constraints. Among hamadryas males there is virtually no sperm competition among full adults, but subadult followers have a low but real chance to mate, bringing them into sperm competition with an adult. If these differences in social structure are incorporated, we obtain, as expected, regressions of very similar slope, though different elevation (Fig. 3).

The distinctive hamadryas adaptive complex presumably evolved from a condition resembling that of anubis baboons and most other papionin monkeys (Jolly, 1963, 1993), though the reverse has also been suggested by Eisenberg *et al.* (1972). As the hamadryas socio-ecological complex emerged, natural selection would have favored a male developmental program and

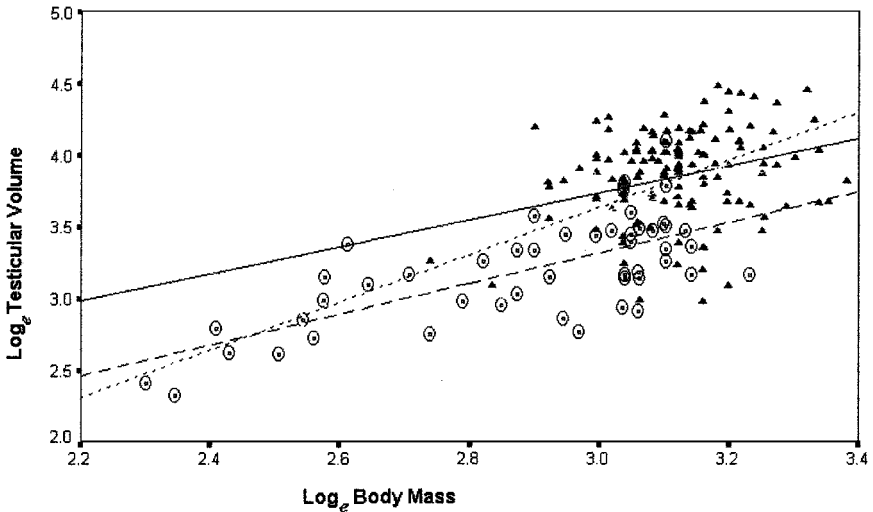


Fig. 3. Log_e testicular volume plotted against Log_e bodily mass, including only males assumed to participate in mating (and hence sperm competition): Anubis full adults (solid line; triangles); hamadryas ≥ 12 kg bodily mass (dashed line, open symbols). The dotted line is the regression obtained by including all anubis baboons of bodily mass ≥ 12 kg (individual points not shown).

physiology that, in full adults, invests in behaviors and structures, such as the spectacular mane (Jolly, 1963), related to the maintenance of the OMU, while de-emphasizing gametic productivity and structures related to agonistic interactions between males. Although sperm competition theory seems adequately to explain the derived features of hamadryas testicular size and development, it must be remembered that the testes are not simple sperm factories, but also endocrine organs that contribute hormones whose complex interplay controls growth, sexual differentiation and development, and, ultimately, mating and other social behavior (Sapolsky, 1991). For instance, we have previously shown (Kaplan *et al.*, 1999; in press) that male anubis and hamadryas baboons differ in mean levels of neurotransmitter metabolites in cerebrospinal fluid. In particular, 5-HIAA, the serotonin metabolite, is higher at all ages in hamadryas than in anubis baboons. Further recent analysis (Jolly and Phillips-Conroy, unpublished results) suggests that among fully adult males, relative testicular size is correlated with CSF serotonin metabolite levels positively in hamadryas, but negatively in anubis. Such subtle differences point to complex relationships between testicular size and function, on the one hand, and the endocrine factors related to male growth, maturation and social behavior, on the other, which are beyond the explanatory reach of the sperm competition model.

ACKNOWLEDGMENTS

We gratefully acknowledge the contribution of the many volunteers and colleagues who have helped to gather the data presented here; the financial support of the National Science Foundation (NSF SRB 9615150), the Harry Frank Guggenheim Foundation, Earthwatch, Washington University and New York University; the research permission granted by successive General Managers of the Ethiopian Wildlife Conservation Organization; the collaboration of Addis Ababa University; and the invaluable practical assistance of the Wardens and Staff of the Awash National Park. We also thank two anonymous reviewers for valuable insights and suggestions.

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