CHAPTER TEN

Ontogeny, Life History, and Maternal Investment in Baboons

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CHAPTER SUMMARY

This chapter compares the ontogeny of *Papio* baboons to other papionin primates through a theoretical perspective that prioritizes ontogeny in the study of life history. This viewpoint anticipates that life history variables are dissociable, or capable of responding to selection independent of one another. The result is diversity in how primate life histories unfold. *Papio* baboons provide excellent evidence for this view of life history, illustrating a mode of life history with clear ties to female reproduction. Specifically, relative to other papionins, life history in *Papio* baboons involves tightly coordinated patterns of development for somatic variables, including body mass, skeletal dimensions, and dental eruption. Growth hormones in *Papio* baboons are highly intercorrelated. However, brain growth follows a distinct pattern from other systems, ceasing very early in *Papio* baboons.

This life history mode reflects heavy metabolic burdens on baboon mothers to produce "high-quality" offspring that can cope with intense selection during early postnatal development. Brain growth is dissociated from

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development of other somatic systems, inducing high maternal gestational costs, but possibly reflecting the neural capabilities to survive the infant period. These costs appear to have selectively favored an integrated pattern of somatic, dental, and hormonal development, along with large female adult size. Ties between reproduction and life history are integral to understanding baboon evolution.

1. INTRODUCTION

Our understanding of primate life history variation and evolution relies on broad-scale interspecific analyses (Harvey et al., 1987; Ross, 1988, 1998). These studies provide a robust understanding of primate life history, generally finding that a continuum, ranging from "fast" to "slow," reasonably describes life history patterns (Ross and Jones, 1999). However, recent advances point to deficiencies with regard to how well this notion addresses basic questions about primate variation and evolution, particularly with regard to the relations between fitness components and life history. In general, analyses of life history in relation to behavior (Garber and Leigh, 1997; Janson and van Schaik, 1993), diet (S. A. Altmann, 1998; Godfrey et al., 2003; Leigh, 1994), demography (Altmann and Alberts, 2003; DeRousseau, 1990; Johnson, 2003; Sade, 1990; Stucki et al., 1991), endocrinology (Finch and Rose, 1995), and morphology (Pereira and Leigh, 2002; Leigh, 2004) have generated insights that are incompatible with hypotheses shaped by the concept of a "fast versus slow" continuum. The inherent limitations of comparative methods typically used in life history analyses compound these emerging theoretical difficulties (Altmann and Alberts, 2003; Martin, 2002). At a more specific level, broad-scale interspecific analyses may not provide the kinds of close-grained information necessary for assessing the relations of reproductive adaptations or strategies to the scheduling of life history.

Moving beyond traditional theoretical perspectives on primate life histories requires attention to ontogenetic processes (Shea, 1990). Consequently, the present study seeks to advance our understanding of life history evolution by investigating links between life history, reproduction, and morphological and hormonal ontogeny in baboons (*Papio*) and other papionins (*Macaca, Mandrillus, Cercocebus, Lophocebus)*. We conduct these analyses within a theoretical framework predicting that life history "modes" are fundamental to primate life history evolution (Leigh and Blomquist, 2006; Pereira and Leigh, 2002). The concept of a life history mode contrasts with a simple "fast versus slow" continuum by stipulating that primate life history adaptations can be understood in terms of qualitatively and quantitatively different ways of reaching maturation and adulthood, ultimately driving life history variation in primates. More explicitly, this concept predicts that primate life history does not merely reflect a sliding scale of "faster" or "slower" pathways to maturation and reproduction. While differences in age at maturation are, of course, vitally important (Charnov and Berrigan, 1993), the concept of a life history mode suggests that adaptations involving rates of growth (Janson and van Schaik, 1993; Godfrey et al., 2003; Leigh, 1994) and sequences of development (Smith, 2002; Watts, 1985, 1990) contribute significantly to the structure of primate life histories. Rates of growth and sequences of development can respond to evolutionary forces, potentially leading to an array of ontogenetic configurations that vary both by sex and species. These life history variables are influenced either independently or together by factors that modify ontogenetic programs, including physiological mechanisms such as hormones. The ways in which morphological and hormonal ontogenies are structured comprise life history modes, and these modes may vary predictably among species. In effect, life history modes reflect alternative ways of "assembling" and integrating morphological and behavioral systems during development: They comprise different pathways to adulthood, representing evolutionary responses to selection throughout the life course.

Baboons present outstanding opportunities to investigate the concept of a life history mode as well as the relations of life history modes to reproductive strategies mainly because a remarkable body of research has concentrated directly on baboons during ontogeny (J. Altmann, 1980, 1983; S. A. Altmann, 1998; J. Altmann and Alberts, 1987, 2003; J. Altmann et al., 1977, 1978, 1993; Bercovitch and Strum, 1993; Johnson, 2003, this volume; Moses et al., 1992; Pereira and Altmann, 1985; Strum, 1991). This research has myriad implications for understanding baboon life history adaptations in social and ecological contexts, and provides insight into life history evolution more generally. Baboons are especially important in this regard, given Stuart Altmann's findings that selection encountered by yearling baboons virtually determines lifetime reproductive success (1998). This pioneering research presents opportunities to assess life history theory, increases our understanding of how juvenile periods evolve, and evaluates the relations between reproductive strategies and ontogeny. Consequently, the present study hypothesizes that baboons have evolved a distinctive life history mode relative to other papionin primates. Compared to closely related species, we expect that the baboon life history mode involves major prenatal maternal investment in offspring brain growth, a coordinated pattern of morphological and hormonal ontogeny, high but consistent growth rates, and, finally, large body size. The timing of maturation may be intertwined with aspects of this life history mode, both in baboons and in other papionins. We can note that the attributes of infancy are poorly known in other papionins, precluding more definitive expectations for other species. However, we anticipate that baboons are exceptional in their highly eclectic foraging style relative to these other species.

2. MATERIALS AND METHODS

2.1. Materials

Defining and understanding the baboon life history mode requires detailed study of numerous developing systems. Rates, time spans, and sequences of ontogeny must be analyzed, with attention to variation both within and among behavioral, anatomical, and hormonal systems. Consequently, this analysis explores links between life histories and reproductive strategies by analyzing the ontogeny of specific anatomical and physiological features, including brains, teeth, body mass, somatometrics, and hormones.

Details on data sources must, regrettably, be cast aside in the interest of brevity. However, data are derived from a variety of sources, including literature, museum-curated wild-shot specimens, and live captive primates (Table 1; see also Bernstein, 2004; Buchanan, 2006; Leigh, 2004; Leigh et al., 2003). The majority of live captive data were collected during an ongoing comparative study of ontogeny in papionin primates (see Leigh et al., 2003; Leigh, 2006). When possible, we investigate three or more papionin species, so as to avoid certain inherent limitations of two-species comparative studies (Garland and Adolf, 1994). However, two-species comparisons are, by necessity, conducted in some cases, particularly for hormonal analyses. Our most detailed comparisons rely on longitudinal somatometric and hormonal data for captive baboons (*Papio hamadryas*, Southwest Foundation for Biomedical Research) and sooty mangabeys (*Cercocebus atys*, Yerkes Regional Primate Research Center). These data represent measurements obtained every 6 months from core groups of 20 baboons and 20 sooty mangabeys

Table 1. Data type, taxa represented, and data sources

Data type	Species	Source	Comments
Prenatal brain mass growth	*Papio hamadryas*	Hendrickx and Houston, 1971	All necropsy, captive
	Papio hamadryas	Tame et al., 1998	
	Macaca mulatta	Cheek, 1975	
Postnatal brain growth, cranial capacity	*P. hamadryas*, *M. mulatta*, *Cercocebus* sp., *Lophocebus* sp.	This study; Leigh, 2004	Cranial capacities of wild-shot specimens
Postnatal brain mass growth	*P. hamadryas*	Mahaney et al., 1993a,b	Necropsy, captive
Postnatal relative brain size growth	*P. hamadryas*, *M. mulatta*, *Mandrillus* sp., *Cercocebus* sp., *Lophocebus* sp.	Leigh et al., 2003	Cranial measures of wild-shot specimens
Age at first birth	*P. hamadryas*	Williams-Blangero and Blangero, 1995	Captive
	P. hamadryas	Bercovitch and Strum, 1993; Cheney et al., this volume; Sigg et al., 1982; Altmann et al., 1981	Wild
	M. mulatta	Bercovitch and Berard, 1993; Sade, 1990	Provisioned
	Cercocebus atys	This study	Captive
	M. sphinx	Setchell et al., 2002	Provisioned
Dental development	*P. hamadryas*	Bernstein et al., 2000	All captive or provisioned
	Cercocebus atys	Bernstein et al., 2000	
	M. mulatta	Cheverud, 1981	
Mass ontogeny	*P. hamadryas*	This study	
	C. atys	This study	
	M. mulatta	Leigh, 1992	
Body length	*P. hamadryas*, *C. atys*	This study	
	M. sphinx	Setchell et al., 2001	Crown-rump length
Hormones analyzed	*P. hamadryas*, *C. atys*	This study	IGF-I, IGFBP-3, DHEAS, estradiol, radioimmunoassay

over a 5-year time span (1997–2002 for baboons, 1998–2003 for mangabeys) (Table 2). Core group individuals were replaced as needed (usually upon death or transfer of the animal), and both sexes are equally represented in the core groups. Additional cross-sectional data were collected from

Table 2. Life history and morphometric variables for papionin primates

Species	Age at first birth (years)	Adult size (kg)	Adult size at first birth (%)	Adult length at first birth (%)	Sample source
Papio h. anubis	6.32[a]	15.96	89	~100	SFBR
Papio h. anubis	6.92[b]	15.2[c]	–	–	Noncaptive
Papio h. ursinus	6.75[d]				Noncaptive
Papio h. hamadryas	6.1[e]				Noncaptive
Papio h. cynocephalus	6[f]				Noncaptive
Papio h. papio	–	14.3[g]	–	–	Captive
Macaca mulatta	4.1[h]	8.37[9]	77	–	Captive, free ranging
Cercocebus	4.88	7.90	79	90	Yerkes, captive
Mandrillus[i]	4.63	9.91	74	94	Free ranging
Mandrillus		16.4[9]			Captive

[a] Williams-Blangero and Blangero (1995). [b] Bercovitch and Strum (1993). [d] Cheney et al. (this volume). [e] Sigg et al. (1981). [f] Altmann et al. (1981). [h] Bercovitch and Berard (1993). [i] Mandrill values from Setchell et al. (2001, 2002). weighted average of "founder" and "colony born" animals (12.8 and 9.1 kg, respectively). [c] Asymptotic parameter for nongarbage raiding animals from Strum (1991). [g] Leigh (1992). All other values estimated from the current study.

other animals (Leigh, 2006). Sex, age, subspecies, and general condition of each animal were recorded. Most of the baboons are olive baboons (*P. h. anubis* > 75 percent), with most of the remainder representing olive–yellow hybrids. Unless otherwise specified, baboon subspecies are combined in these analyses in order to maximize samples. Dental analyses are based on visual inspection of teeth.

Serum samples for hormone assays were obtained from core group animals (both species) at the time of measurement. These enable hormone analyses focusing on insulin-like growth factor I (IGF-I), IGF-binding protein-3 (IGFBP-3), 17β-estradiol (E2, or estradiol), testosterone, and dehydroepiandrosterone sulfate (DHEA-S). IGF-I is active in postnatal growth and exerts potent mitogenic action on the cells of connective tissues, organs, and bones (Liu and LeRoith, 1999). IGFBP-3 (Yu et al., 1999) is the principal carrier of IGF-I and IGF-II in serum (binding 90–96 percent of these growth factors), often traveling in a ternary complexed form with ALS (acid-labile subunit). IGFBP-3 actions in vivo include enhancing IGF-I actions in bone, muscle, and visceral growth (Baxter, 2000). Both testosterone and estrogen appear to have a stimulatory effect on IGFBP-3, possibly through indirect effects on GH secretion (Hall et al., 1999; Pazos et al., 2000). Estradiol plays an essential role in the control of development of secondary sexual characteristics in most female vertebrates, and in the regulation of female reproductive function (Bentley, 1998). Dehydroepiandrosterone sulfate (DHEA-S) is the sulfate of another steroid (DHEA), produced by the adrenal cortex, and can function as a major precursor of testosterone and estradiol in peripheral tissues (Hadley, 2000).

2.2. Methods

Patterns of brain growth are assessed by regression techniques. First, we describe both prenatal and postnatal absolute brain growth by nonparametric loess regression (Leigh, 2004, 2006). To assess postnatal brain ontogeny, we use summary statistics for baboon necropsy data (reported by Mahaney et al., 1993a,b) and measurements of cranial capacity from wild-shot specimens (Leigh, 2004; Pereira and Leigh, 2002). Second, relative growth trajectories compare allometric growth among papionin genera. Here, we present reduced major axis regressions of neurocranial size plotted against facial size (Leigh et al., 2003). Dental comparisons between baboons and sooty mangabeys are based on calculated average completed eruption age for each tooth represented by a 52-stage scale (Bernstein et al., 2000).

Analyses of somatic growth concentrate on a large data set compiled from baboons and mangabeys (Leigh, 2006). Mass (in kg) is estimated directly from weight measures of both core- and noncore-group animals. Additional mass data for baboons were provided by Mahaney (Mahaney et al., 1993a). Mass data for macaques are derived from captive colonies (Leigh, 1992). The remaining somatometric dimension, body length (vertex to ventral base of tail), was measured to the nearest millimeter. All data are treated cross-sectionally, including the multiple observations from core group animals. The vast majority of noncore group baboons were measured only once, but most noncore group mangabeys contribute longitudinal observations. Treating longitudinal data cross-sectionally poses problems in significance testing but does not generally affect estimates of central tendencies (Leigh, 1992). Formal investigations of longitudinal data are pending. Statistics for age at first birth in several papionins are derived from literature sources (Table 1). Data for mangabeys are calculated from colony records for 12 births during a period when females in the colony were at risk of pregnancy. Since several sources represent captive data, management practices may influence these estimates. We limit analyses to female patterns of ontogeny.

We mainly employ nonparametric regression techniques to describe ontogenetic variation (Efron and Tibshirani, 1991; Leigh, 1992; Mahaney et al., 1993a). Loess regression has been used extensively for analyses of primate growth (Leigh, 1992, 1996, 2001, 2004, 2006; Leigh and Park, 1998). This approach estimates a locally weighted regression line by successively analyzing small segments or "windows" of a bivariate data scatter (Efron and Tibshirani, 1991). Age at growth cessation is estimated visually, following earlier procedures (Leigh, 1992).

Hormone analyses utilize radioimmunoassay methods. To dissociate the IGF from its binding proteins (IGFBPs), serum samples (500 μL) are chromatographed in 0.2 M formic acid on a 0.9 × 100-cm column containing Sephadex G-50 beads (Pharmacia Fine Chemicals, Piscataway, NJ). IGF-I, estradiol, and DHEA-S are measured by radioimmunoassay. IGFBP-3 is measured using immunoradiometric assay. Changes in hormone levels with age were analyzed using protocols used for somatometric data, particularly nonparametric regression. Correlations among hormones and between hormones and measures of size (body mass and body length) are analyzed to assess the degree of hormonal integration, among hormones and between hormones and morphology. All statistical analyses are performed using Systat (version 9.01) statistical software (Wilkinson, 1999).

3. RESULTS

3.1. Brain Ontogeny

Nonparametric loess regressions illustrate that both baboons and macaques begin brain growth at about the same gestational age (Figure 1a). Macaque brains are marginally larger early in development, but are exceeded after baboons initiate a brain growth spurt at about 120 gestational days, or the beginning of the third trimester. This leads to neonates with large brains compared to macaques. Adjusting for average female adult size (Table 2) indicates that fetal brain sizes as a percentage of adult female body mass are smaller in baboons than macaques (Figure 1b).

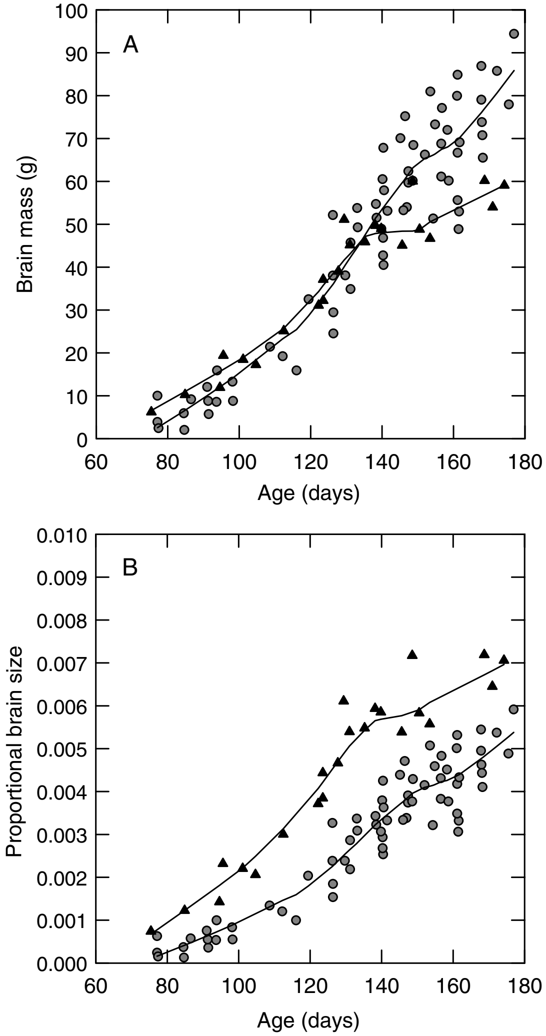

Figure 1. (A) Absolute brain growth in baboons (circles) and rhesus macaques (triangles). (B) Fetal brain size divided by average female body size for baboons (circles) and rhesus macaques (triangles).

Allometric comparisons of postnatal relative brain size ontogeny further demonstrate that baboons are born with brains that are large relative to the remainder of the skull, as illustrated by separation of regression lines (Figure 2a). It is important to note that mandrills, which reach adult body

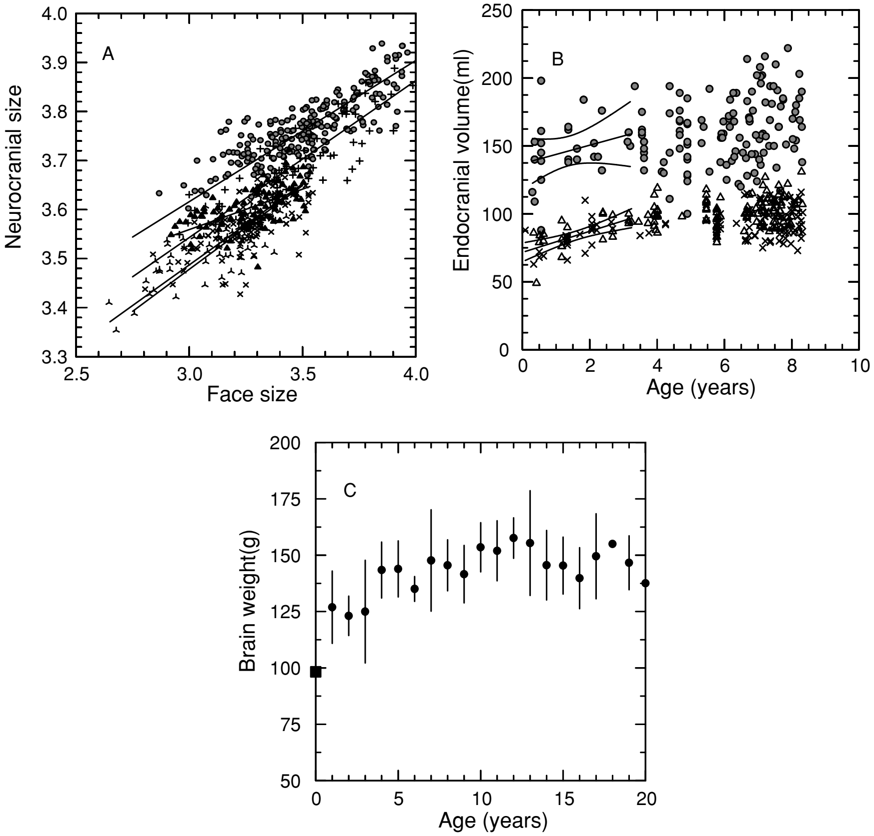

Figure 2. (A) Relative postnatal brain growth (neurocranial size plotted against facial size) for papionins. *Papio* is represented by filled circles, rhesus macaques by filled triangles, mandrills by +, *Lophocebus* by inverted "Y" symbols, and *Cercocebus* by "X" symbols. (B) Endocranial volume against estimated age for baboons (filled circles) and a combined sample of *Lophocebus* (X) and *Cercocebus* (triangles). Lines represent least squares regressions with 95 percent confidence intervals. (C) Postnatal brain size in female baboons from Mahaney et al., 1993a,b. Circles represent means, and bars denote standard deviations.

and brain sizes comparable to baboons, have smaller relative brain sizes early in life. Postnatal relative brain growth rates are low in baboons.

Absolute postnatal brain growth trajectories are difficult to interpret, given reliance on either wild-shot data of estimated chronological age or necropsy data. Wild-shot baboons show no statistically significant change in the relation between brain size and age during the first 3 years of postnatal life (Figure 2b; Pereira and Leigh, 2002). However, we find statistically significant postnatal brain size increases in some other papionins, notably in mangabeys (*Cercocebus* and *Lophocebus*). Samples for mandrills are small and difficult to interpret. Unfortunately, necropsy data for baboons are ambiguous (Figure 2c). Data are sparse for young specimens, but summary statistics are consistent with an interpretation of limited postnatal changes in brain size.

In summary, baboons have relatively and absolutely large brains that increase size dramatically during later gestation. At birth, some may fall within the adult size range. In contrast, other papionins appear to complete brain growth later in the postnatal period, with mangabeys possibly extending brain growth well into the postnatal period.

3.2. Age at First Birth

Age at first birth in the Southwest Foundation baboon colony averages 6.3 years (Williams-Blangero and Blangero, 1995), while noncaptive olive baboons achieve first birth at 6.9 years, on average (Bercovitch and Strum, 1993), chacmas at 6.75 (Cheney et al., this volume), and hamadryas at 6.1. Mangabeys first give birth at an average age of 4.9 years (Table 2). A t-test indicates that means for captive baboons and mangabeys are significantly different ($p < 0.05$), despite the small mangabey sample size. First birth in Cayo Santiago rhesus macaques (*Macaca mulatta*) occurs at an average of 4.1 years (Bercovitch and Berard, 1993; Sade, 1990). Free ranging mandrill females average 4.63 years for age at first birth, ranging between 3.29 and 6.14 ($N = 19$, Setchell et al., 2002). Baboons show an absolutely later age at first birth than these papionins. Literature reported values for noncaptive animals are consistent with these values (Ross and Jones, 1999). We urge caution in interpreting these results, given the variety of data sources (Table 1).

3.3. Dental Development

Patterns of tooth eruption show some distinctions between baboons and mangabeys (Figure 3). This and several subsequent plots show average ages

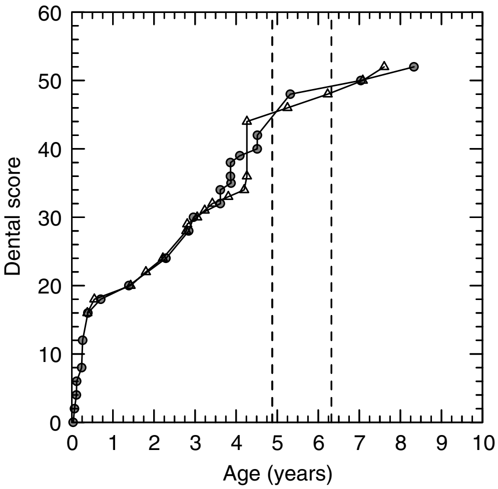

Figure 3. Dental scores for baboons (filled circles) and sooty mangabeys (triangles). Mean ages at first birth are designated by the dashed lines.

at first birth, so that results can be referenced to this important life history milestone. Female dental scores show identical progressions between the two species until about 3.75 years of age. At this point, the baboon premolar complex erupts very suddenly, with several teeth emerging in close succession. Mangabeys erupt premolars later, simultaneously erupting several teeth. Consequently, baboon dental development is accelerated relative to age at first birth in comparison to mangabeys. Analyses of macaques show that by age at first reproduction, eruption of adult teeth is nearly complete (with the exception of M3s) by 4 years of age (Cheverud, 1981).

3.4. Somatic Ontogeny

3.4.1. *Body Mass*

We find substantial similarities in the timing of body mass growth among baboons, mangabeys, and rhesus macaques, with all species reaching adult size between 6 and 7 years of age (Figure 4a–c). However, baboons grow at faster rates to become larger than either of the other two species. Female baboons older than 6 years of age average nearly twice the size of rhesus macaques and mangabeys (Table 2). Average age at first birth occurs when baboons are close to adult size (89 percent of adult value), but macaques, mangabeys, and mandrills are relatively much smaller (Table 2).

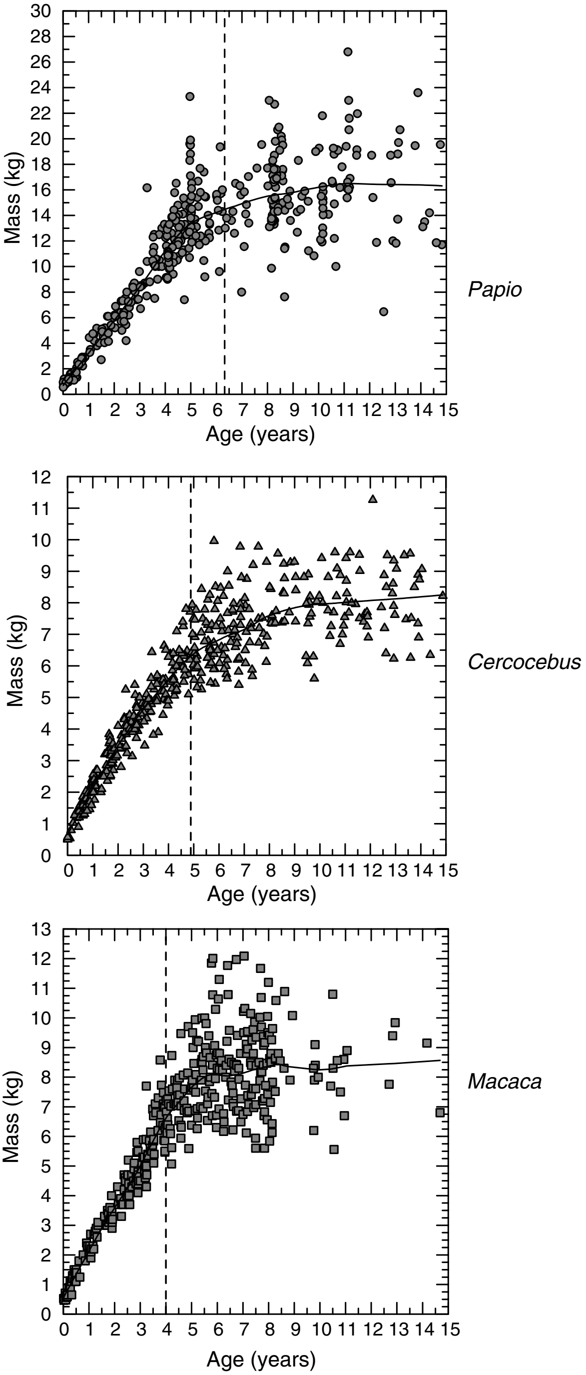

Figure 4. Body mass plotted against age for papionin primates. Growth curves are calculated with loess regressions, dashed lines denote average ages at first birth.

3.4.2 Body Length

Baboons increase body length at higher rates than mangabeys and actually may reach adult body length slightly before mangabeys (Figure 5; Table 2). Mangabeys can be expected to attain adult length well after average age at first birth. By average age at first birth, mangabeys have reached 90 percent

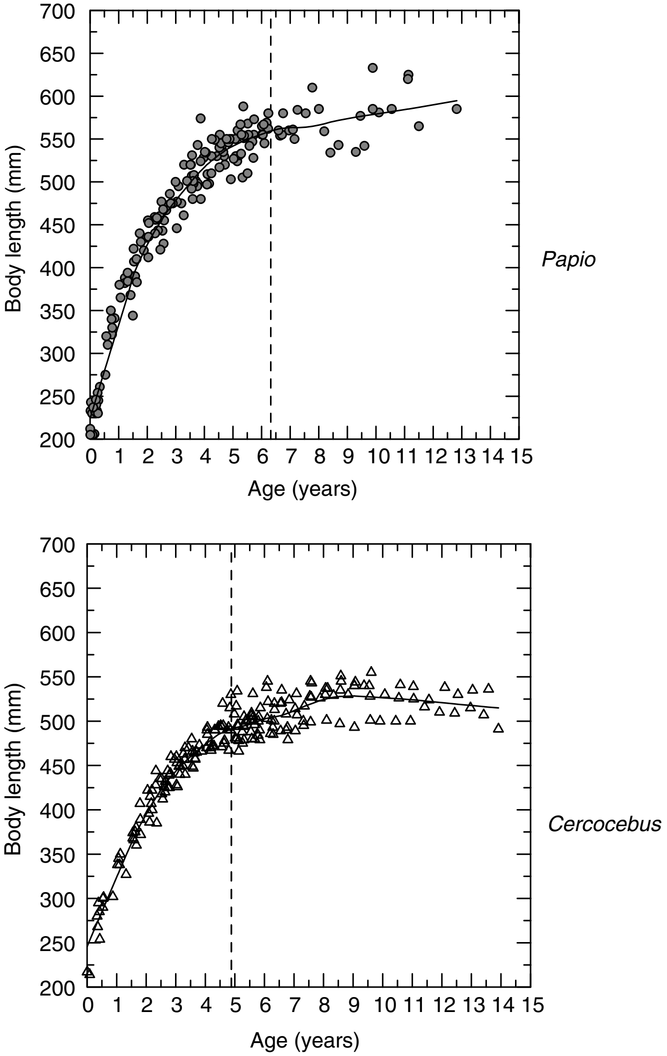

Figure 5. Body length growth in baboons and sooty mangabeys estimated by loess regression. Dashed lines represent age at first birth.

of adult size (523 mm), but baboon body length growth is virtually complete (adults average 571 mm). On a comparable measure of body length, mandrill females fall between these values (Table 2) (Setchell et al., 2001). It should be noted that mangabeys have long trunks relative to mass when compared to baboons. Although this study examines only body length growth, previous research indicates that baboons show few differences in the ages at which skeletal elements cease growth compared to macaques (Leigh, 2006). Specifically, overall skeletal growth appears to be better synchronized in baboons than in macaques (and possibly mangabeys). For example, macaque trunk dimensions apparently cease growth up to 2.5 years later than limbs (Cheverud et al., 1992; Turnquist and Kessler, 1989), with macaque species generally growing slower for longer periods of time than baboons. These patterns may be related to different management conditions, but this is unlikely because the macaques differ most in these terms. Thus, these patterns seem to represent species differences between baboons and macaques, implying that baboon skeletal growth is highly integrated. Preliminary analyses suggest that mangabeys show greater levels of growth rate variation than baboons. Males in particular show prominent growth spurts in numerous skeletal dimensions that are not apparent in baboons (Buchanan, 2006).

3.5. Hormonal Ontogeny

Hormonal analyses are restricted to baboons and mangabeys. Age-related changes in baboon hormone profiles are characterized by more regularity than those of mangabeys. For example, age-related changes in IGF-I in baboons are steadier than in mangabeys (Figure 6a and b). Estradiol is generally uncorrelated with age in each species, with young pregnant mangabeys showing high levels. In addition, serum concentrations for both hormones are notably lower in baboons than in mangabeys. IGFBP-3 levels are correlated with age in each species (Pearson $r = 0.64$ for baboons, $r = 0.63$ for mangabeys), although mangabey values are overall slightly higher than baboons.

Female baboons show strong, statistically significant correlations between IGF-I, IGFBP-3, and body mass and length (Table 3). Female mangabeys show significant correlations between IGFBP-3, mass, and length; additionally, estradiol and mass show a modest correlation. For both species, DHEA-S showed negative, nonsignificant correlations with both body mass and length and these values are therefore not shown.

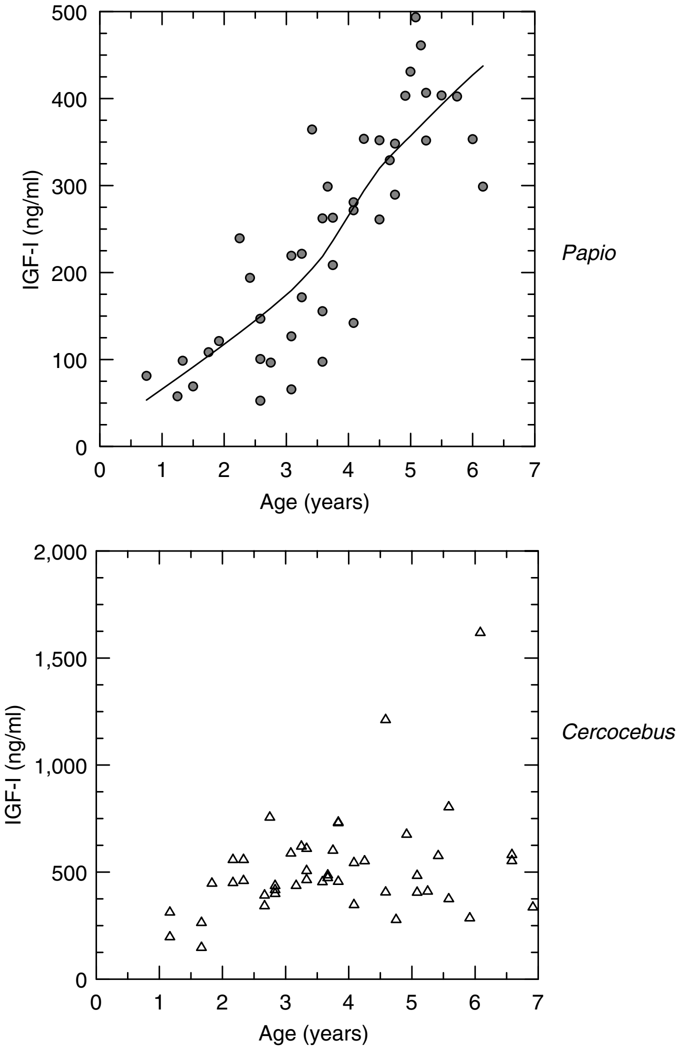

Figure 6. Hormone concentrations for IGF-I plotted against age for baboons and sooty mangabeys. The *Papio* regression line is calculated by loess regression.

Differences between species are evident when considering the correlations among the hormones themselves. Female baboons show strong and statistically significant correlations between IGF-I and IGFBP-3, and estradiol and IGFBP-3 (Table 4). Although not statistically significant, the positive correlation between estradiol and DHEA-S in female baboons is moderately strong, while correlations between DHEA-S and all other hormones (and all

Table 3. Correlations among hormones and size measures

	IGF-I		IGFBP-3		Estradiol	
	Papio	Cerco	Papio	Cerco	Papio	Cerco
Weight	0.841	0.593	0.696	0.658	0.367	0.507
Crown rump length	0.834	0.483	0.685	0.655	0.319	0.393

Table 4. Pearson correlations among hormones for *Papio*, below the diagonal, and *Cercocebus*, above the diagonal

	IGF-I	IGFBP-3	Estradiol	DHEA-S
IGF-I	–	0.028	0.195	–0.201
IGFBP-3	0.767	–	0.141	–0.78
Estradiol	0.106	0.561	–	–0.201
DHEA-S	–0.162	–0.134	0.333	–

hormones for mangabeys) are negative. Mangabeys do not show any significant correlations among any hormones.

4. DISCUSSION

4.1. Life History

These findings have important implications for understanding baboon ontogeny and maternal investment, as well as primate life history in a more general sense. Comparisons among papionins reveal that the level of integration among developing systems may vary during ontogeny. Furthermore, these results point to a complex and distinctive life history mode in baboons. This mode is characterized by brain and tooth ontogeny that is complete relatively early, high somatic growth rates, large size, and, probably, deferred age at first reproduction. Brain size, dental eruption, body mass, and somatic dimensions present a range of variations in ontogeny when compared across species. Female baboons show consistently high correlations between IGF-I, IGFBP-3, and size variables, and hormones appear to be integrated. Taken together, these findings indicate high degrees of diversity both among and within developing systems.

Our results have implications at general and specific levels. At the broadest level, papionin ontogenetic variation is consistent with recently established theoretical advances in developmental biology (Raff, 1996). Specifically, dissociability, or the capacity of developing systems to respond independently to selection, is now recognized as a major source of evolutionary diversity (Gould, 1977; Needham, 1933; Raff, 1996). Dissociability leads to modularity in ontogeny. Our comparative investigations reveal a prominent role for modularity in the organization of papionin ontogeny and life history. The presence of modularity is notable for at least three reasons. First, theoretical concepts in developmental biology have traditionally focused on the earliest phases of ontogeny (Raff, 1996). Modularity during postnatal periods implies that ideas about dissociability apply to all phases of ontogeny, including life histories. Second, the traditional view of life history as a "fast versus slow" continuum is incompatible with the concept of modularity. This continuum requires high levels of ontogenetic integration such that life history variables comprise a "suite" (Alberts and Altmann, 2002) of inter-related traits, running on either fast or slow trajectories with linkages to body size. Differing time scales of growth among variables recorded by our study compromise this assumption. Third, standard life history theory anticipates that selection on either maturation age or the duration of body size growth drives size differences among species (Charnov and Berrigan, 1993). Our analyses demonstrate that size, age at first reproduction, and age at body size growth cessation can be decoupled: Differing sizes may be reached in comparable time periods (see also Garber and Leigh, 1997; Leigh, 1992; Leigh and Terranova, 1998; Watts, 1990).

These basic points strongly imply that life history theory must accommodate both patterns of morphological ontogeny and the division of the life course into phases. We suggest that the concept of a life history mode accomplishes this goal by recognizing phases and components of life history (Figure 7). Two phases of life history traditionally have been recognized, including ontogenetic and reproductive periods. Classic life history theory focuses on explaining the allocation of the life course to these phases (Charnov and Berrigan, 1993; Cole, 1954), but life history components have received little theoretical attention. Components are, however, critical because they represent targets of selection on morphological, hormonal, or behavioral attributes during these life history phases. The rate and timing of ontogeny for various components or traits may differ considerably, and components can respond to selection in a modular fashion. Our "components" can be fitness components (Altmann and Alberts, 2003; Hughes and Burleson, 2000), although we use this term in a broader sense, referring to

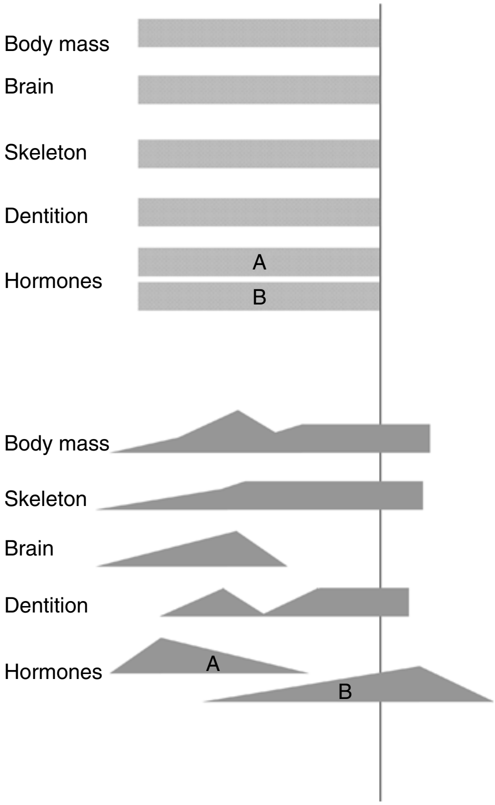

Figure 7. Alternative modes of life histories. Top panel represents a species in which patterns of ontogeny are well synchronized, and growth is complete by age at maturation (vertical line). Growth rates and periods are consistent among developing components. The bottom panel portrays a species in which components are dissociated, with some components growing past age at maturation. Vertical changes qualitatively represent changes in growth rates or changes in hormone concentrations.

the skeletal system, the brain, body mass, and hormones. The ways that components grow through different phases comprise life history modes. We suggest that attention to life history modes undermines a traditional "fast versus slow" continuum.

Analyses of baboons illustrate key features of life history modes, facilitating conceptualization of life history phases and components. First, the temporal organization of ontogeny varies among components, producing variable levels of integration among components. In baboons, somatic growth and dental eruption cease at about the time of average age at first birth, but the period of brain growth is well separated from the reproductive phase. Consequently, the brain growth period overlaps minimally with the growth periods of other components, but all components grow over similar time frames in other papionins. Investigations of baboons indicate that selection on individual components may have limited consequences for other components. Second, diversity in temporal patterning of ontogeny is complemented by variable levels of integration within each developing component. Components in baboons appear to be internally well integrated, particularly hormones and skeletal growth (Leigh, 2006). Baboons contrast with mangabeys and possibly macaques (Watts, 1990) in this regard, given that lower levels of integration are apparent in these taxa. Third, phases are distinct in baboons, with a clear switch between growth and reproduction, possibly stemming from hormonal integration. Taken together, these dimensions of variation indicate that components behave in a modular fashion, with interspecific differences in life history modes produced by differing configurations of components and phases.

Consideration of brain growth patterns in relation to other components provides direct insight into these processes. The case of brain size growth is especially significant given the emphasis accorded on the relations between brain size and life history (Allman and Hasenstaub, 1999; Deaner et al., 2002; Harvey et al., 1987; Sacher, 1959; Sacher and Staffeldt, 1974). Although much better data are needed for understanding patterns of brain growth, baboons seem to illustrate large increases in brain size over an abbreviated ontogenetic period. Baboon neonatal brain size is very large, even though gestation periods in papionins are strikingly uniform, ranging from 165 to 183 days across the clade (Table 5) (see also Martin and MacLarnon,

Table 5. Gestation lengths in papionin primates

Taxon	Approximate gestation length (days)	Reference
Macaca mulatta	165	Cerroni et al., 2003
Macaca	180	Ardito, 1976
Cercocebus	167	Gordon et al., 1991
Mandrillus	168–176, 175 (mean, *n* = 61, range 168–183)	Carman, 1979; Setchell et al., 2001
Lophocebus	175	DePutte, 1991
Papio	177 (mean, *n* = 59)	Hendrickx, 1967

1990). This finding suggests that evolutionary changes in brain size need not entail increases in gestation length (*contra* Sacher and Staffeldt, 1974), either through selection directly on gestation length, or as a result of more general selection for a "slow" life history. Postnatally, baboons seem to reach adult brain size very soon after birth, in contrast to mangabeys. Differences among papionins are apparent, despite a strong tendency for Old World monkeys to complete brain growth early in life (Leigh, 2004).

Comparative analyses of ontogeny suggest that baboons could be described as a "fast" species in terms of some aspects of morphological ontogeny by reaching large body and brain sizes during growth periods comparable to those of smaller papionins. Baboons are also legitimately considered a "slow" species in terms of age at first reproduction. However, consistency in the amount of time allocated to size growth among papionins precludes categorization of a particular species as "fast" or "slow." Furthermore, in baboons, the time period of brain growth and body size growth overlap minimally. Skeletal growth in baboons and, apparently, other papionins, occupies a shorter time frame than skeletal growth in macaques (cf. Cheverud et al., 1992; Turnquist and Kessler, 1989). Other papionins seem to reach adulthood very differently from baboons. For example, mangabeys can be described as "slow" in terms of brain growth, but "fast" in terms of age at first reproduction. Mangabey brain growth occupies a substantial portion of the postnatal period, attaining brain sizes absolutely and relatively smaller than in baboons. In addition, somatic growth rate variation is evident in mangabeys, but growth rates are generally lower than in baboons. These examples suggest that the concept of a life history mode, with attention to components and their allocation to different phases, helps account for life history variation. In baboons, patterns of brain growth, somatic growth, dental eruption, and levels of hormonal integration are related, but not directly through selection solely on the pace of life histories.

4.2. Baboon Life History Evolution and Reproduction

These findings, while providing general insights into primate life history theory, have specific implications for understanding the baboon life course. We define the baboon life history mode as one comprising discrete life history phases, with little overlap between the periods of ontogeny and reproduction. The brain follows an abbreviated time schedule, while maturation age appears to be deferred. However, anatomical and hormonal components appear to be relatively well integrated both internally and with one another. Mangabeys, and possibly other papionins, seem to show a contrasting mode, lacking clear separation among life history phases and a different pattern of relations among components. It is important to recognize that high levels of variability have been shown to characterize baboon life history attributes (Altmann and Alberts, 2003), so our inferences must be regarded in the context of species differences.

We hypothesize that the baboon life history mode is ultimately a response to severe selection during the juvenile period, based largely on S. Altmann's results illustrating major fitness consequences of foraging success in yearling baboons (1998). Selection seems to have favored heavy investment in offspring, especially production of absolutely and relatively large-brained infants. The large brain of infant baboons may, in turn, provide the necessary infrastructure for their highly eclectic foraging style (assuming that brain morphology relates to cognitive traits). Aspects of dental and somatic development may be organized around this heavy maternal metabolic investment. In other words, completion of female ontogeny is a precondition for this investment. Our model suggests that selection has favored large body size through growth at high rates, and completion of ontogeny prior to reproduction as a maternal reproductive strategy supporting infant brain growth costs. Thus we see both direct effects of selection on offspring—brain size and cognitive precocity—and indirect effects of this selection on females—a coordinated pattern of somatic development and discrete separation of life history phases (see also Leigh, 2004).

Attributes of the baboon life history mode are explicable in terms of maternal metabolic costs and resultant adaptations. For example, rapid dental and somatic ontogeny may represent a way to ensure that the costs of gestation can be met without the competing demands of maternal somatic growth. Accelerated dental eruption in baboons also ensures functional competence of adult dentition by age at first reproduction. High somatic growth rates in baboons may play a similar role, yielding large body size without trade-offs against reproductive phase duration. Large body size may also reduce the relative costs of fetal brain growth during gestation. Although detailed data exist for estimating reproductive costs in baboons (J. Altmann, 1980, 1983), such data are lacking for other papionins.

The relations between morphology, hormones, and life histories may be largely structured by the selective landscape for female baboons, particularly selection on maternal characteristics. Morphologically, baboon growth seems to be keyed to producing mothers that are capable of heavy investment in offspring, especially during late gestation and early postnatal life. Coordination among hormones may reflect selection on female baboons favoring clear distinctions between growth and reproductive periods. Intense selection on juveniles should be expected to result in a finely tuned system that controls growth and development. This model explains selection on both mothers and offspring. For female baboons, reproduction requires an individual that is hormonally and morphologically adult. Alternatively, mangabeys and other papionins apparently pay the costs of continued growth along with those of gestation and lactation. These other species appear not to face expensive trade-offs between growth and reproduction that may characterize baboons.

Accepting these hypotheses requires evaluation of numerous alternatives drawn from traditional life history theory. While more detailed tests are beyond the scope of this analysis, we anticipate that predictions from traditional theories would perform poorly in explaining baboon life history. First, variation in ontogenetic time scales of various components is not well accommodated by existing theoretical notions. For example, a "fast" life history should result in early cessation of brain and body growth, coupled with high coordination among developing systems and early reproductive maturation. Instead, we see "fast" life history species with early maturation such as mangabeys that may show relatively extended periods of brain and body ontogeny. Second, baboons unambiguously violate a fundamental assumption of traditional life history theory by reaching a body size larger than most other papionins absent a longer growth period. Thus, size differences need not be produced exclusively by variation in age at maturation, as assumed by some models (see Leigh, 2001). Growth rates respond adaptively to selection (Garber and Leigh, 1997; Godfrey et al., 2003; Janson and van Schaik, 1993; Leigh, 1994), combining with maturation age to produce size variation. Overall, standard life history theories fail to make predictions about growth rates, patterns of growth in components, and the allocation of component growth to different life history phases.

Despite our limited ability to appraise alternatives, we can suggest that the mangabey (*Cercocebus*) life history mode provides an instructive contrast to baboons. Most importantly, mangabeys blur separations among components and phases, apparently investing relatively little in prenatal brain growth, but growing brains well into the postnatal period (Leigh, 2004). Pregnancies in mangabeys are common prior to either completion of dental or somatic ontogeny. For example, during this study, Yerkes female mangabeys typically presented mixed deciduous/adult dentitions throughout their first pregnancy. In many cases, females had shed only deciduous incisors at the time of conception, actually erupting first molars during pregnancy. Obviously, female mangabeys can simultaneously meet the metabolic costs of both their own growth as well as costs of pregnancy despite incomplete adult dentition. The mangabey mode is characterized by production of a small-brained infant, prolonged brain growth into the postnatal period, indistinct life history phases, and loosely coordinated components. Unlike mangabeys, female baboons shoulder most of the costs of offspring brain growth, either during gestation or during a short postnatal brain growth period. Relative to body size, these costs may be comparatively low, but large size is also partly a product of maternal investment (Johnson, 2003, this volume), particularly when high growth rates occur. By age at first birth, baboons possess most of their adult teeth, and have completed the vast majority of body mass and length ontogeny. It should be noted that large brain size in young organisms can be a product of selection solely on size (Gould, 1971). This possibility has been considered for baboons, and while an evolutionary size increase in and of itself may be a factor, it cannot fully account for variation in brain size among papionins (Leigh et al., 2003). Finally, these results indicate that ties between brain ontogeny and life history involve both direct and indirect factors (see Leigh, 2004).

These analyses strongly imply that ontogenetic variability is fundamental to life history evolution and reproductive strategies. Ultimately, brain growth differences may relate to ecological and cognitive demands on these species. In baboons, the response to selection involves discretely separated life history phases along with coordinated development among certain components. Selection related to foraging in young animals has favored females that can support infant brain growth costs. Coordinated somatic ontogeny at high rates, followed by cessation of growth prior to age at first reproduction, may facilitate this adaptation. In contrast, other papionins may encounter a selective regime that favors very early first birth rather than production of "high-quality" offspring. Earlier age at first reproduction is possible because selection apparently has not favored large, rapidly developing brains in offspring, enabling female reproductive opportunities despite continued investment in maternal growth. Baboons follow a contrasting pathway, with an alternative pattern of growth among components and clear shifts between life history phases, possibly stemming from expensive trade-offs between growth and reproduction.

5. CONCLUSIONS

Investigations of ontogeny in papionin primates, with special emphasis on baboons, show that life histories in these species depart substantially from expectations of traditional life history theory. Specifically, information about growth and development suggests that predictions regarding "fast versus slow" life histories in primates cannot account for ontogenetic variability among taxa. We propose that the concept of a life history mode, which predicts that there are qualitatively and quantitatively different ways of reaching adulthood, better accounts for baboon and papionin life histories. The concept of a life history mode forces attention to phases and components of ontogeny. Most papionins seem to present a life history mode without clear separations of ontogenetic and reproductive phases. Developing systems, including the brain, skeletal dimensions, and hormones, appear to be only loosely coordinated. In contrast, the baboon life history mode involves discrete separation of ontogenetic and reproductive phases, with apparently high levels of integration among components. This life history mode may be a response to intense selection during the juvenile period involving both ontogeny and maternal reproductive strategies. The baboon life history mode may reveal expensive trade-offs between ontogeny and reproduction that are not faced by other papionins.

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