Primate Life Histories and Dietary Adaptations: A Comparison of Asian Colobines and Macaques

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ABSTRACT   Primate life histories are strongly influenced by both body and brain mass and are mediated by food availability and perhaps dietary adaptations. It has been suggested that folivorous primates mature and reproduce more slowly than frugivores due to lower basal metabolic rates as well as to greater degrees of arboreality, which can lower mortality and thus fecundity. However, the opposite has also been proposed: faster life histories in folivores due to a diet of abundant, protein-rich leaves. We compared two primate taxa often found in sympatry: Asian colobines (folivores, 11 species) and Asian macaques (frugivores, 12 species). We first described new data for a little-known colobine (Phayre's leaf monkeys, *Trachypithecus phayrei crepusculus*) from Phu Khieo Wildlife Sanctuary, Thailand. We then compared gestation periods, ages at first birth, and interbirth intervals in colobines and macaques. We predicted that heavier species would have slower life histories, provisioned populations would have faster life histories, and folivores would have slower life histories than frugivores. We calculated general regression models using log body mass, nutritional regime, and taxon as predictor variables. Body mass and nutritional regime had the predicted effects for all three traits. We found taxonomic differences only for gestation, which was significantly longer in colobines, supporting the idea of slower fetal growth (lower maternal energy) compared to macaques and/or advanced dental or gut development. Ages at first birth and interbirth intervals were similar between taxa, perhaps due to additional factors (e.g., allomothering, dispersal). Our results emphasize the need for additional data from wild populations and for establishing whether growth data for provisioned animals (folivores in particular) are representative of wild ones. Am J Phys Anthropol 144:286–299, 2011.   ©2010 Wiley-Liss, Inc.

There is general consensus that primate life histories are slow compared to other mammals of similar body mass (Harvey and Clutton-Brock, 1985; Read and Harvey, 1989; Charnov and Berrigan, 1993; Kappeler and Pereira, 2003) likely due to the higher degree of encephalization in primates (Clutton-Brock and Harvey, 1980; Harvey et al., 1980; Barton, 1999; Barrickman et al., 2008). During development, slow somatic growth should reduce the risk of starvation by enabling immatures to cope with periods of seasonal food scarcity, consequently enhancing their chances for survival (ecological risk aversion, Janson and van Schaik, 1993; brain malnutrition avoidance, Deaner et al., 2003). Whether the extra time primates spend as immatures is also necessary for acquiring social and ecological skills is not yet clear (e.g., Stone, 2006; Jaeggi et al., 2010).

More generally, a strong effect of body mass on life history has been documented (e.g., Charnov, 1991), hence, controlling for body mass is essential in life history studies (Harvey et al., 1987; Deaner et al., 2003). Furthermore, certain life history traits display a phylogenetic signal, for instance, litter size, neonatal mass, or growth rates (Martin, 1990; Charnov and Berrigan, 1993; Fleagle, 1999; Deaner et al., 2003). Thus, life history comparisons should be conducted within narrowly defined taxa or using methods that control for phylogeny.

The availability and quality of food is another major influencing factor, with faster life histories documented for nutritionally enhanced populations (Sadleir, 1969; Lee, 1987; Asquith, 1989; Watanabe et al., 1992; Borries et al., 2001; Altmann and Alberts, 2005). However, while such nutritional effects *within* a given species seem to be straightforward, it has proven difficult to evaluate the impact of different dietary patterns, such as folivory versus frugivory, on life history *across* primate species. For example, folivorous primates exhibit dietary adaptations such as molars with relatively sharp cusps and large crushing surfaces (Kay and Hylander, 1978; Lambert, 1998; Godfrey et al., 2001) and a specialized digestive tract to aid in the break down of hard-to-digest food components such as cellulose (Bauchop and Martucci, 1968; Lambert, 1998). These adaptations might improve food digestibility in folivores (Sakaguchi et al., 1991), which could accelerate life histories. Indeed, Leigh (1994a) documented a faster weight gain and an earlier

attainment of adult body mass in captive, folivorous primates. Likewise, in captivity, gorillas (the most folivorous ape) gained weight faster than chimpanzees or bonobos (Leigh and Shea, 1996).

In contrast, folivorous species have commonly been assumed to have lower basal metabolic rates than frugivores (McNab, 1978; Ross, 1992a), which should slow life histories. However, few data exist to support this assumption, perhaps due to the fact that an active digestive system means fermenters (folivores) rarely assume the strictly defined, neutral metabolic state essential in determining the standardized basal metabolic rate (McNab, 1997). Often we rely on indirect evidence of basal metabolic rate such as the much longer gut retention times in folivores (Clauss et al., 2008). Other indirect measures include relative brain mass and absolute muscle mass. Brain tissue requires more energy and a higher basal metabolic rate than that of most other organs, and skeletal muscle can be metabolically demanding simply because it makes up such a large portion of total body mass (Aiello and Wheeler, 1995). While relative brain mass is known to be lower in folivores compared to frugivores (Clutton-Brock and Harvey, 1980; Harvey et al., 1980, 1987; Harvey and Clutton-Brock, 1985; but see McNab and Eisenberg, 1989), it remains difficult to distinguish cause from effect. In other words, it is not clear whether brain mass is constrained by basal metabolic rate or vice versa (maternal energy hypothesis, Martin, 1996).

Furthermore, arboreal (often folivorous) species experience a more sedentary lifestyle, resulting in significantly lower muscle mass, and they are therefore likely to have a lower basal metabolic rate (Snodgrass et al., 2007; Raichlen et al., 2010). However, because folivorous mammals usually live arboreally, the effects of arboreality and folivory are difficult to disentangle (McNab, 1978). In addition, mortality is often lower in arboreal species (Mumby and Vinicius, 2008; see Cords and Chowdhury, 2010 for the most recent example in primates). These low mortality rates should lead to lower fecundity, resulting in slower life histories (Charnov, 1991; Ross, 1992b; van Schaik and Deaner, 2003; but see Clutton-Brock and Harvey, 1980). Thus, while earlier comparative studies on life history did not find differences between primate leaf-eaters and fruit-eaters (Harvey and Clutton-Brock, 1985; Ross, 1988, 1998), metabolic factors seem to suggest slower life histories in folivorous primates. This trend has recently been confirmed for Malagasy lemurs and some cercopithecids (Bolter, 2004; Godfrey et al., 2004).

Conversely, based on the ecological risk aversion hypothesis, it has been suggested that folivores grow more rapidly due to reduced feeding competition associated with a less seasonal food supply (Janson and van Schaik, 1993), which also tends to be rich in protein relative to fruits. It has become clear, however, that feeding competition is not necessarily low in folivorous primates (Koenig, 2000; Robbins 2008; overview in Snaith and Chapman, 2007) and food availability can be highly seasonal (Koenig et al., 1997; Harris et al., 2010). These findings weaken the idea that leaves are an ever-abundant food source. Currently, there does not seem to be much supporting evidence for faster life histories in folivorous primates.

Additional effects on primate life history have been proposed that might override or reinforce differences attributed to dietary adaptations. For example, the degree of nonmaternal care seems to accelerate life history via faster infant growth and birth rates (e.g., small-bodied New World primates, Garber and Leigh, 1997; Ross and MacLarnon, 2000). Yet while nonmaternal care tends to shorten infancy (weaning age) across primate species, it does not influence the age at first reproduction, which instead, is strongly influenced by brain size (Ross, 2003). Another potentially confounding factor for life history is prebreeding dispersal by females, which seems to be more common in folivores (Moore, 1984; Isbell, 2004). Dispersal can delay the onset of reproduction (age at first birth) because, unlike philopatric females, dispersing females need to establish themselves in a new group (often with little or no support) before they can reproduce.

In sum, the overall lack of consensus for the effect of general dietary adaptations across primate species might be attributable to poorly defined life history variables, phylogenetic constraints, confounding factors, and/or stochastic effects based on small sample sizes. In addition, major differences in climate, phenological patterns, and nitrogen concentrations in food across continents (Ganzhorn et al., 2009) might mask existing effects. Thus, as previously mentioned, life history comparisons should be conducted within narrowly defined taxa or should control for phylogeny (as well as body mass). To minimize stochastic effects, sample sizes should be as large as possible and small datasets should be avoided.

Here we present results from a comparison of life history traits for Asian colobines (folivores) and Asian macaques (frugivores). Within both taxa, species are more or less similar in body mass (advantageous for cross-taxa comparisons, Leigh, 1994b) and should have evolved under roughly similar ecological conditions (Delson, 1975, 1980, 1994). Thus far, only a few Asian colobine species have been used for morphological (*Trachypithecus cristatus*, Leigh, 1994a) or behavioral (*Semnopithecus entellus*, Harley, 1988; Sommer et al., 1992; Borries et al., 2001) analyses of life history. Extensive datasets for additional Asian colobine species in the wild have only recently become available (e.g., *Presbytis thomasi*, Wich et al., 2007; *Rhinopithecus roxellana*, Qi et al., 2008; *Trachypithecus poliocephalus*, Jin et al., 2009; *Trachypithecus phayrei*, our present study) allowing for a revised compilation and a comparison with the better known genus *Macaca*. Compared to macaques, Asian colobines have a lower neonatal brain mass relative to neonatal body mass and a lower neonatal mass relative to maternal mass (Harvey and Clutton-Brock, 1985). The colobine neonate, therefore, achieves a higher proportion of its somatic growth postnatally to become, on average, a slightly heavier adult. This should reinforce the trends described above and we therefore expect to find slower life histories for the folivores in our sample (but see Leigh, 1994a).

We chose three life history variables with unequivocal definitions that are frequently reported: gestation length, age at first birth, and interbirth interval after a surviving infant (to control for infant mortality). An additional life history variable, age at weaning, could not be used, because it was rarely reported, most likely due to the gradual nature of the weaning process (Kappeler et al., 2003). Moreover, definitions of weaning were found to be inconsistent across studies (Harvey and Clutton-Brock, 1985; Lee and Kappeler, 2003).

In the following, we a) present data for a little-known Asian colobine, the Phayre's leaf monkey; b) compare

TABLE 1. *Study periods and basic sample sizes until January 2009 (inclusively)*

Group	Start	Contact months	Contact days	Contact hours	n infants born
PA[a]	Jan 2001	91	864	8,397	32
PB[b]	Jun 2003	65	777	8,268	36
PO[c]	Aug 2005	40	245	2,157	17
PS[d]	Mar 2002	81	519	4,855	20
Total	Jan 2001	277	2,405	23,677	106[e]

[a] No data for September 2001 to January 2002 and July 2008.
[b] No data for July 2008.
[c] No data for February 2007 and July 2008.
[d] No data for May and June 2002.
[e] One additional infant was born while its mother resided in a nonfocal group.

gestation, age at first birth, and interbirth interval for Phayre's leaf monkeys with those of other Asian colobines (expecting it to fall within the range of published results); and c) analyze the effects of body mass, nutritional regime (wild/unprovisioned versus provisioned/captive) and feeding adaptation (folivory/colobines versus frugivory/macaques) on these life history variables in Asian colobines and macaques. In accordance with the facts and arguments laid out above we expect: 1) heavier species to have a longer gestation, be older at the time of first birth, and reproduce at a slower rate; 2) individuals from provisioned populations to have a shorter gestation, be younger at the time of first birth, and reproduce at a faster rate; 3) the more folivorous colobines (compared to the more frugivorous macaques) to have a longer gestation, be older at the time of first birth, and reproduce at a slower rate. By providing data for a rarely studied, wild Asian colobine species, we further contribute to the still small pool of studies on this taxon (Harvati, 2000; Kappeler and Pereira, 2003; Kirkpatrick, 2007).

METHODS

Phayre's leaf monkeys: Study site, durations, definitions, and sample sizes

We studied Phayre's leaf monkeys at Phu Khieo Wildlife Sanctuary, Northeast Thailand (16°5′-35′ N, 101°20′-55′ E; 300 - 1300 m a.s.l., 1,573 km^2). The site within the sanctuary, called Huai Mai Sot Yai, is located at around 16°27′N, 101°38′E at 600 to 800 m a.s.l., and consists of dry evergreen forest with patches of dry dipterocarp forest (Borries et al., 2002). Mean annual temperature is 21.2°C (mean minimum temperature = 18.3°C, mean maximum temperature = 25.4°C, 2001 through 2008) and the annual rainfall averages 1,144 mm (2003 through 2008). The highest protection status for Thailand (Wildlife Sanctuary) was granted in 1979 to the area and an efficient patrolling system and regular surveys by helicopter have limited illegal logging, bark-stripping, and poaching. With 30 species, the carnivore community in the sanctuary is diverse (Kumsuk et al., 1999; Grassman et al., 2005).

From January 2001 through January 2009, we observed four habituated groups of Phayre's leaf monkeys for a total of 277 group months (group month refers to demographic data available for a particular group in a particular calendar month) and 23,677 contact hours (Table 1). Adult females devote 46.3% of their annual feeding time to the consumption of leaves (S.A. Suarez pers. com.) which means that this species fits the criterion for a folivo-

rous primate (40–45%, Leigh, 1994a). All group members were individually identified based on coat color, crest, tail, and muzzle shape as well as scars from former injuries. During contact with a group, basic information such as presence/absence (including births) was recorded daily. In total, 106 infants were born (to 43 adult females) of which the birth of 97 was either known to the day ($n = 26$), the month ($n = 66$) or within two months ($n = 5$). The remaining nine birth estimates were less precise and were excluded from the analysis. The 97 births led to 40 complete interbirth intervals following a surviving infant. An additional 14 intervals when the infant had died prematurely were not considered here (comprehensive life history data for the study population will be published elsewhere). Interbirth intervals were calculated to the month.

Gestation length in Phayre's leaf monkeys was previously determined based on hormonal data extracted from feces (Lu, 2009; Lu et al., 2010). This period lasted from the estimated day of ovulation during the conceptive cycle (based on a significant rise in fecal estrogen metabolite levels) until the day prior to parturition and was calculated in days. Details are provided by Lu (2009) and Lu et al. (2010).

In the study population, dispersal was strongly female biased (Borries et al., 2004) and all but one natal female dispersed prior to first parturition. As a result, we know the exact age at first birth for only three females (dispersing between habituated groups). In addition, 14 nonadult females immigrated into and subsequently bred in our study groups. Their ages were estimated based on direct comparisons with females of known age. In addition, nipple length as well as body proportions helped to distinguish nulliparous from pluriparous females (Koenig et al., 2004). Because the three known ages at first birth did not differ from the 14 estimated ages (Mann-Whitney U-test, $U = 15.0$, $z_{adj} = -0.76$, $P_{exact} = 0.51$) we pooled the data.

The study was approved by IACUC Stony Brook University (IDs: 20001120 to 20081120) and complied with the current laws of Thailand and the USA.

Comparative life history data

Data on gestation length (in days), age at first birth (in years), and the interbirth interval following a surviving infant (in months) were extracted from the literature. Published, cross-species compilations served as guides but every data point was taken from the original literature. Recently published data for captive *Rhinopithecus brelichi* were not included due to a possible effect of inbreeding in the colony leading to a late age at first birth (8.6 years) and a reduced reproductive rate (interbirth interval: 38.2 months; Yang et al., 2009: p 269). We further evaluated these data points by regressing all available data on body mass. The standard residuals for both life history values for *R. brelichi* deviated by more than two standard deviations from the mean values for the other populations included in our analysis supporting our decision to exclude these unusual values from the analysis.

Gestation length estimates based on hormonal data (11 cases) were generally preferred over those determined by other methods (11 cases) even if sample sizes were smaller. Other estimates were based on the temporal pattern of sexual behavior plus data on menstruations, swellings (some macaques), vaginal swabs or isolated days of housing with a male (some captive studies). Cruder estimates (e.g., based on birth peak versus mating peak or days after male takeover) were not considered.
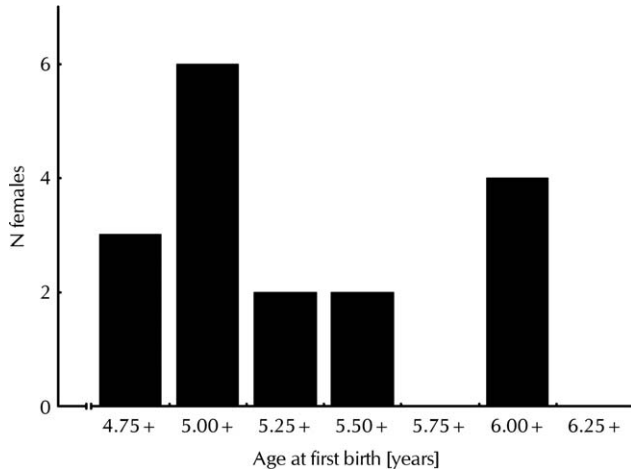
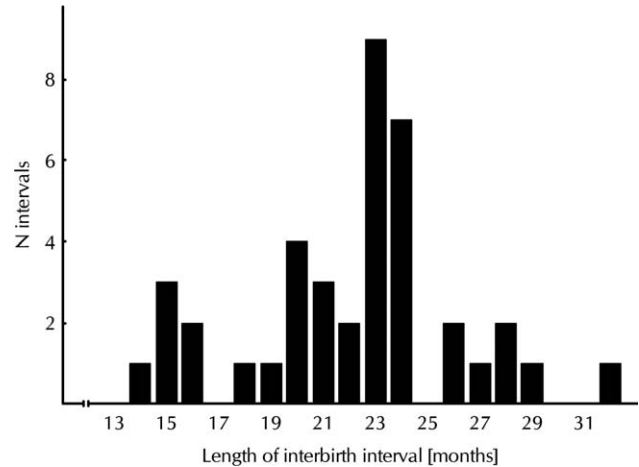**Fig. 1.** Distribution of age at first birth in Phayre's leaf monkeys.

Fig. 2. Distribution of interbirth interval in Phayre's leaf monkeys following a surviving infant.

Mean age at first birth was provided for many populations. In one case (*Macaca tonkeana*, Thierry et al., 1996) we calculated the value by adding the mean gestation length to the mean age at first observed consort.

We collected information on interbirth intervals following a surviving infant. If this information was not available (5 out of 26 cases) we used the overall interbirth interval instead. This value is somewhat shorter because it includes the often shorter intervals after early infant loss. To control for a possible effect, the analysis was run twice, once with all 26 cases and once with the 21 cases following a surviving infant.

Because high quality food can have an accelerating effect on growth and reproduction, we distinguished two nutritional regimes: i) *wild* with no access to human derived food throughout the year, and ii) *provisioned* encompassing all other nutritionally enhanced conditions (free-ranging but provisioned regularly by people, crop raiding or captive; Leigh, 1994b). We note that the diets of colobines classified as "folivorous" may contain less than 50% leaves (Bennett and Davies, 1994; Koenig et al., 1997; Kirkpatrick, 2007) with fruits and seeds often preferred over leaves (Dasilva, 1994). However, the basic dietary adaptations allow for a seasonal inclusion of a large amount of leaves and Asian colobines fulfill the criterion set for a folivorous primate (40–45% leaves in the annual diet, Leigh, 1994a).

If data for the same species were available for more than one study site and the same nutritional regime, the larger sample was chosen (with data from outdoor preferred over indoor housing). Several colleagues (see acknowledgements) helped in locating the relevant data and in selecting the most reliable values for species and populations for which multiple datasets were available. Each species was considered twice at the most, once for each nutritional regime. Note that all African colobines as well as the only African macaque (*Macaca sylvanus*) were excluded because continental differences could potentially introduce additional confounding variables (cf. Introduction).

The taxonomy followed Groves (2001) and body mass values for adult females (the majority from wild animals, Smith, pers. com.) were taken from Smith and Jungers (1997). For only one species in our sample, the Hanuman langur (*Semnopithecus entellus*), do Smith and Jungers (1997) list weights for two subspecies (*Semnopithecus*

entellus schistaceus 14.80 kg, and *Semnopithecus entellus entellus* 9.89 kg), and both subspecies were represented in our sample (*S. e. schistaceus* as the nonprovisioned and *S. e. entellus* as the provisioned population). These values were averaged (12.35 kg), but all analyses were run twice, once with the average weight and once with two different weights for *Semnopithecus*, the latter leading to identical results and slightly improved statistical values. We present the more conservative results based on average body mass. Because no weight was available for *Trachypithecus poliocephalus*, we assigned the weight of the taxonomically closest species (Roos et al., 2007; Osterholz et al., 2008) for which data were available (*T. francoisi*). Note that, per species, only one value for weight (wild individuals) was used, even for captive populations, to simulate the body mass conditions under which the respective life history variables likely evolved. Further testing of body mass influences (wild versus provisioned) was precluded because the respective data were unavailable.

We ran separate general regression models for each of the three dependent life history variables: gestation (log), age at first birth (log), and interbirth interval (log). For all three, female body mass (log), nutritional regime, and taxon served as predictor variables. Before calculating general regression models, all dependent variables and log body mass were tested for outliers (Grubb's test, Iglewicz and Hoaglin, 1993) and normality (Kolmogorov-Smirnov test, all $Ps > 0.2$, Siegel and Castellan, 1988). All tests were run in STATISTICA 6.1 at an alpha level of 0.05.

RESULTS

Life history of wild Phayre's leaf monkeys

At the time of first birth, female Phayre's leaf monkeys averaged 5.3 years of age (median = 5.2, range = 4.8–6.2, $n = 17$, Fig. 1). Gestation lasted 205.3 ± 1.41 days on average (median = 204.0, range = 201–211, $n = 7$; Lu, 2009; Lu et al., 2010). The interbirth interval following a surviving infant averaged 22.3 ± 3.99 months (median = 23.0, range = 14–32, $n = 40$, Fig. 2) with a notably large range of 18 months.

All three variables for Phayre's leaf monkeys fell within the range for other Asian colobines (data in Table 2). The *t* tests comparing a single observation with

TABLE 2. Life history parameters of Asian macaques and Asian colobines included in the analysis (sample sizes in parentheses)

Species	w/p	Gestation Mean (days)	m	Gestation Reference	Age at first birth Mean (yrs)	Age at first birth Reference	Interbirth interval after surviving infant Mean (mos)	Interbirth interval after surviving infant Reference	Body mass[a] Mean (kg)
Macaca silenus	w				6.6 (5)	Kumar 1987 in Lindburg and Harvey, 1996			6.10
"	p	170.0 (28)	?	Lindburg, 2001	4.9 (39)	Lindburg et al., 1989	17.3 (119)	Lindburg et al., 1989	6.10
Macaca nemestrina	p	171.0 (56)	o	Hadidian and Bernstein, 1979	4.5 (?)	Ha et al., 2000	13.3 (44)	Hadidian and Bernstein, 1979	6.50
Macaca tonkeana	p	173.0 (27)	h	Thierry et al., 1996	5.2 (8)	Thierry et al., 1996			9.00
Macaca nigra	p	170.0 (51)	h	Thomson et al., 1992	5.4 (3)	Hadidian and Bernstein, 1979	17.8 (13)	Hadidian and Bernstein, 1979	5.47
Macaca fascicularis	w	163.0 (6)	h	Engelhardt et al., 2006	5.2 (22)	van Noordwijk and van Schaik, 1999	29.3 (33)	van Noordwijk and van Schaik, 1999	3.59
"	p	162.7 (10)	o	MacDonald, 1971	3.9 (252)	Petto et al., 1995	12.8 (22)	Hadidian and Bernstein, 1979	3.59
Macaca arctoides	p	177.5 (10)	o	MacDonald, 1971	3.5 (58)	Petto et al., 1995	23.5[b] (102)	Petto et al., 1995	8.40
Macaca mulatta	w				5.0 (?)	Melnick and Pearl, 1987	26.0[b] (?)	Melnick and Pearl, 1987	5.37
"	p	166.5 (709)	o	Silk et al., 1993	4.1 (769)	Bercovitch and Berard, 1993	12.2 (661)	Rawlins and Kessler, 1986	5.37
Macaca cyclopis	p	163.0 (98)	o	Hsu et al., 2001	3.9 (63)	Petto et al., 1995	13.7 (223)	Hsu et al., 2001	4.94
Macaca fuscata	w	176.3 (9)	h	Fujita et al., 2004	6.1 (17)	Takahata et al., 1998	26.9 (42)	Takahata et al., 1998	8.03
"	p	173.0 (17)	o	Nigi, 1976	5.4 (182)	Koyama et al., 1992	17.5 (770)	Koyama et al., 1992	8.03
Macaca sinica	w	168.0 (?)	o	Dittus pers. com. in Bercovitch and Harvey, 2004	4.8 (?)	Dittus, 1975	19.1 (?)	Dittus pers. com. in Bercovitch and Harvey, 2004	3.20
Macaca radiata	p	166.0 (315)	h	Rao et al., 1998	4.2 (47)	Silk, 1990	15.1 (120)	Silk, 1990	3.85
Macaca thibetana	p				5.4 (7)	Li et al., 1994	16.3[b] (25)	Wada and Xiong, 1996	9.50
Semnopithecus entellus	w	211.6 (7)	h	Ziegler et al., 2000	6.7 (26)	Borries et al., 2001	32.4 (45)	Borries and Koenig, 2000	12.35[c]
"	p	200.3 (31)	o	Sommer et al., 1992	3.5 (12)	Sommer et al., 1992	17.2 (82)	Sommer et al., 1992	12.35[c]
Trachypithecus vetulus	w	197.6 (4)[d]	o	Rudran, 1973			23.5 (4)	Rudran, 1973	5.90
Trachypithecus cristatus	p	194.6 (7)	o,h	Shelmidine et al., 2009	2.9 (8)	Shelmidine et al., 2009	15.4 (45)	Shelmidine et al., 2009	5.76
Trachypithecus phayrei	w	205.3 (7)	h	Lu, 2009; Lu et al., 2010	5.3 (17)	this study	22.3 (40)	this study	6.30
Trachypithecus pileatus	w	200.0 (4)	o	Solanki et al., 2007	5.0 (?)	Solanki et al., 2007	23.0[b] (?)	Solanki et al., 2007	9.86
Trachypithecus francoisi	p	184.0 (16)	o	Mei, 1991	5.4 (3)	Gibson and Chu, 1992	16.3 (12)	Gibson and Chu, 1992	7.35
Trachypithecus poliocephalus	w				5.4 (3)	Jin et al., 2009	25.0 (23)	Jin et al., 2009	7.35[e]
Presbytis thomasi	w				5.4 (9)	Wich et al., 2007	26.8 (28)	Wich et al., 2007	6.69
Pygathrix nemaeus	p	210.0 (1)	h	Lippold, 1981	4.7 (6)	Lippold, 1989	22.0[b] (27)	Lippold, 1989	8.44
Rhinopithecus roxellana	p	202.7 (3)	h	Yan and Jiang, 2006	5.6 (16)	Qi et al., 2008	23.3 (36)	Qi et al., 2008	11.60
Rhinopithecus bieti	p	203.7 (3)	h	He et al., 2001	5.0 (?)	Ji et al., 1998	23.2 (12)	Cui et al., 2006	9.96

Species listing follows the sequence in Groves (2001); w/p = nutritional regime, w = wild, p = provisioned (captive or wild but provisioned); m = method, h = hormonal, o = all other methods; ? = sample size or method not known.
[a] Mean for a wild, adult female (from Smith and Jungers, 1997).
[b] Independent of infant survival.
[c] Mean weight of two subspecies.
[d] Minimum estimate.
[e] Weight for *Trachypithecus francoisi*.

TABLE 3. *Results of the t test comparing a single observation (i.e., mean value for Phayre's leaf monkeys) with a sample mean (i.e., all other colobines listed in Table 2)*

Variable	Mean	SD	n	−95%	+95%	Phayre's	t	P
Gestation (days)	200.5	8.25	9	194.2	206.8	205.3	−1.746	0.119
Age at first birth (years)	4.89	1.13	9	4.03	5.76	5.30	−1.076	0.313
Interbirth interval (months)	22.56	4.92	11	19.25	25.86	22.3	0.173	0.866

Mean, SD, n, and 95% confidence limits refer to colobines (Phayre's exempt).
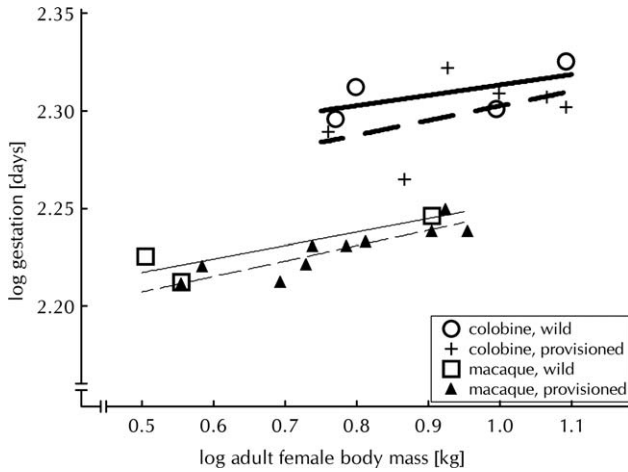
Fig. 3. Log duration of gestation period (days) in relation to log adult female body mass (kg) for Asian colobines and macaques (data in Table 2). Lines represent bivariate regressions and were included for demonstration purpose only; solid lines = wild populations, hatched lines = provisioned populations; bold lines = colobines, thin lines = macaques.
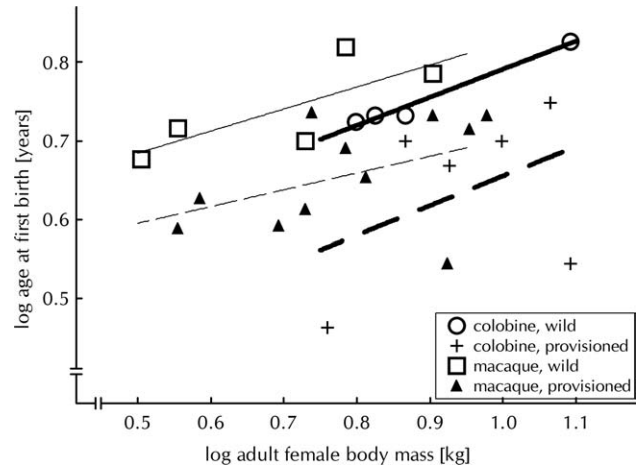

Fig. 4. Log age at first birth (years) in relation to log adult female body mass (kg) for Asian colobines and macaques (data in Table 2). Lines represent bivariate regressions and were included for demonstration purpose only; solid lines = wild populations, hatched lines = provisioned populations; bold lines = colobines, thin lines = macaques.

TABLE 4. *Results of the general regression models with sample sizes*

Independent variables	Dependent variables					
	Gestation		Age at first birth		Interbirth interval	
	F	P	F	P	F	P
Body mass	16.45	<0.001	7.61	0.012	9.80	0.005
Nutritional regime	3.45	0.080	17.06	<0.001	41.66	<0.001
Taxon	84.71	<0.001	2.47	0.131	0.21	0.650
I.A.	0.21	0.653	0.18	0.675	3.08	0.094
GRM ($df = 4$)	65.97	<0.001	5.05	0.004	14.40	<0.001
R^2	0.922		0.393		0.682	
n macaques	13		16		14	
n colobines	10		10		12	

I.A. = interaction of categorical variables "nutritional regime" and "taxon".

a sample mean (Sokal and Rohlf, 1995) yielded no significant differences (Table 3).

Life histories of Asian colobines and macaques

As expected, the length of the gestation period (see Fig. 3) was significantly influenced by female body mass, such that, on average, heavier females had longer gestation periods (Table 4). With the exception of one species (*Trachypithecus francoisi*), the data sorted along taxonomic lines: colobines had longer gestation periods than macaques. Within each taxon, wild populations tended to have longer gestation periods than provisioned ones (see Fig. 3). The model explained 92% of the variance (Table 4).

Age at first birth (see Fig. 4) covaried significantly with female body mass: heavier species began reproducing at later ages (Table 4). The nutritional regime also had a significant influence with earlier ages at first birth for provisioned populations compared to wild ones. There was no significant taxonomic influence as macaques and colobines started to reproduce at similar ages (see Fig. 4). The model explained 39% of the variance (Table 4).

The interbirth interval (see Fig. 5) was significantly influenced by female body mass, with longer interbirth intervals among heavier species (reproducing more slowly, Table 4). Provisioned populations reproduced significantly faster than wild ones. There was no taxonomic influence: macaques and colobines reproduced at the same speed. The model explained 68% of the variance (Table 4). If only interbirth intervals following a surviving infant were considered ($n_{macaques} = 11$, $n_{colobines} = 10$) the model explained 75% of the variance. While the effects of the same independent variables remained significant, the trend for the interaction effect disappeared (values not shown).

DISCUSSION

The data presented here for wild Phayre's leaf monkeys are consistent with those for other Asian colobines. Although the tests employed did not control for body mass or nutritional regime, all values fell within the range for the other Asian colobines included in this study (Table 3). The gestation period of wild Phayre's
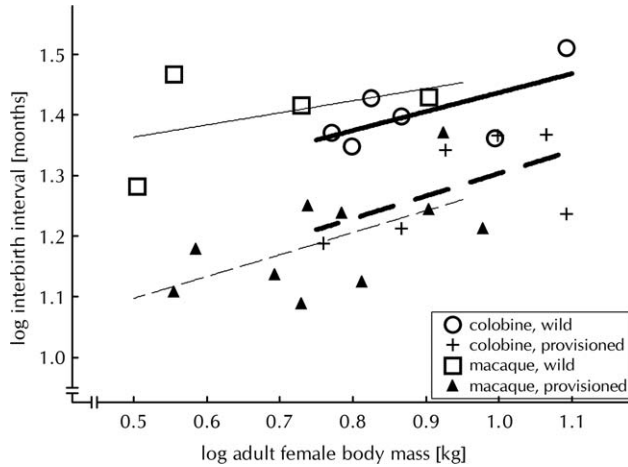
Fig. 5. Log interbirth interval following a surviving infant (months) in relation to log adult female body mass (kg) for Asian colobines and macaques (data in Table 2). Lines represent bivariate regressions and were included for demonstration purpose only; solid lines = wild populations, hatched lines = provisioned populations; bold lines = colobines, thin lines = macaques.

leaf monkeys is comparatively long but the value still falls within the 95% confidence limit.

Throughout our comparative analysis, female body mass had the predicted significant effect on all three life history variables investigated: the greater the body mass of a species, the longer the gestation period, the later the age at first birth, and the longer the interbirth interval (Table 4). This general trend in life history has been confirmed repeatedly (e.g., Charnov, 1991; Fleagle, 1999). In primates, brain size may be even more closely related to life history than body mass (Harvey et al., 1987; Ross and Jones, 1999; but see e.g., Deaner et al., 2003). However, brain size could not be considered here because the resolution in the data available is still too low for our taxonomically narrow approach.

In the following discussion, we compare the results of our analysis to previous investigations of primate life histories. In addition to the general effects of nutritional regime and dietary adaptations, we also discuss the underlying mechanisms hypothesized to cause differences in life history especially with respect to dietary adaptations. These factors and their proposed effects on gestation, age at first birth, and interbirth interval are summarized in Table 5. We note that our analysis did

TABLE 5. *Summary of factors hypothesized by earlier studies to influence life history*

Factors and their hypothesized effects	Taxon and life history variables affected	Example reference(s), for further sources see text	Colobines relative to macaques		
			G	age 1st	IBI
Low basal metabolic rate (assumed for folivores) slows down growth and reproduction	colobines: longer G, older age 1st, longer IBI	Martin, 1983, 1996	+	+	+
Advanced dental (or gut) development requires longer prenatal investment	colobines: longer G	Godfrey et al., 2003[a]	+		
Nursing during most of the subsequent gestation reduces energy available for the fetus	(colobines: longer G)	Borries et al., 2001	(+)		
Female dispersal may delay onset of reproduction	colobines: older age 1st	Ross, 1992b		+	
Arboreality reduces (infant) mortality, slowing down growth and reproduction	colobines: older age 1st, longer IBI	Charnov, 1991; van Schaik and Deaner, 2003		+	+
Infants ride on the back which is energetically more economical	macaques: shorter IBI	Nakamichi and Yamada, 2009			+
Infant head (large relative to maternal transversal pelvis diameter) abbreviates prenatal investment	macaques: shorter G, older age 1st	Leutenegger, 1970	+	-	
Improved digestibility of most foods due to extensive fermentation provides more energy for growth and reproduction	colobines: shorter G, younger age 1st, shorter IBI	Sakaguchi et al., 1991; Caton, 1999	-	-	-
Lower neonatal brain and body mass relative to maternal mass reduces prenatal investment	colobines: shorter G	Harvey et al., 1980	-		
Leafy diet and reduced feeding competition buffer seasonal food shortages	colobines: younger age 1st, shorter IBI	Janson and van Schaik, 1993		-	-
Allomothering of neonates saves maternal energy	colobines: shorter IBI	Ross and MacLarnon, 2000; Ross, 2003			-

[a] For gut development see discussion; G = length of gestation; age 1st = age at first birth; IBI = interbirth interval; + = longer or older in colobines; − = shorter or younger in colobines; parentheses = effect disputed, argument might not hold if more data become available. The first two columns describe the factors and their effects as originally hypothesized for colobines or macaques. Factors are sorted from top to bottom as: slowing colobine life histories, accelerating macaque life history, equivocal effects, accelerating colobine life histories. For ease of comparison, the last three columns on the right summarize the predicted effects for colobines relative to macaques. The current analysis found a longer gestation period for colobines, a similar age at first birth, and a similar interbirth interval, but did not test any of the individual factors listed here. For further explanations see Discussion.

not test any of these underlying mechanisms and, hence, these parts of the discussion must remain speculative.

Availability and quality of food (nutritional regime)

Provisioning had the predicted, accelerating influence on life history (Table 4) commonly found in primates and other mammals (Sadleir, 1969; Gilmore and Cook, 1981; Kiltie, 1982; Asquith, 1989; Hendrickx and Dukelow, 1995). The influence was weakest for gestation (Table 4). Our compilation contained only three species for which gestation periods of both provisioned and wild populations were available for a direct comparison of nutritional regimes (Table 2, *Macaca fascicularis*, *Macaca fuscata*, and *Semnopithecus entellus*). The values for provisioned populations were always (even if only slightly) lower. For Hanuman langurs, we previously found significantly shorter gestation periods in a provisioned population (11.3 days or 5.6%, Borries et al., 2001). On a broader, cross-taxonomic scale, however, nutritional differences in gestation length seem to be less pronounced than for *Semnopithecus*. Factors such as fetal growth rate, female metabolic rate, and neonatal body and brain mass (Sacher and Staffeldt, 1974; Martin, 1981, 1996; Harvey et al., 1987; Pagel and Harvey, 1988) might override any general nutritional influence.

Taxonomic differences—Dietary adaptations

Gestation. Only one of the three dependent variables included in our comparison was related to taxon and thus perhaps to dietary adaptations: Asian colobines had a significantly longer gestation period compared to Asian macaques (Fig. 3, Table 4). The result supports the more recent findings that primate brain size and gestation length are not related (Deaner et al., 2003; see also below) or at least not strongly related (Catlett et al., 2010), but stands in contrast to other analyses (Sacher and Staffeldt, 1974; Pagel and Harvey, 1988; Barrickman et al., 2008).

Longer gestation periods for colobines are unexpected perhaps because previous work often listed underestimated values of around 165 days (e.g., Ardito, 1976; Harvey et al., 1987; Kappeler and Pereira, 2003; but see e.g.; Martin, 2007) despite early indication to the contrary. More than 70 years ago, Hill had determined the gestation period for *Semnopithecus priam* as 196 days and commented: "It is, therefore, highly probable that all the Colobidae have a longer gestation period than the Cercopithecidae" (Hill, 1937: p 370). Much later, a gestation length of around 200 days or more was confirmed for Hanuman langurs with various methods and for different populations (Jayaraman et al., 1984; Sommer et al., 1992; Ziegler et al., 2000; Borries et al., 2001). Data for several more colobine species have since become available (cf. Table 2), all confirming Hill's conclusion. Gestation in colobines is about one month or 18% longer than in macaques. It is likely that past estimates of the day of conception, which were mainly based on observed mating behavior, were less precise because pregnant colobines continue to mate regularly and often lack external signs of receptivity or gestation (Hrdy and Whitten, 1987). In general when working with life history data, we need to be aware that past compilations might be outdated. Existing databases need to be maintained and updated regularly.

Still, the result might seem counterintuitive: colobines, with a slightly larger female body mass (Smith and Jungers, 1997), require more time to produce a lighter neonate (relative to female body mass) with a smaller brain (Clutton-Brock and Harvey, 1980; Harvey and Clutton-Brock, 1985; Harvey et al., 1987; Isler et al., 2008)! Brain tissue in particular is expensive to produce (Aiello and Wheeler, 1995). However, the taxon with the smaller absolute and relative neonatal brain mass in our sample requires longer gestation periods. This could be explained if energy transfer to the fetus were lower in colobines as assumed (cf. Introduction) even though basal metabolic rate per se does not seem to influence gestation length in mammals in general (Pagel and Harvey, 1988). An additional constraint on maternal energy transfer could be that pregnant colobines regularly nurse the previous infant almost until its next sibling is born (Borries et al., 2001; Shelmidine et al., 2009), which could reduce the energy available for the fetus. At present, however, it is unclear whether macaque females nurse for a smaller portion of gestation than colobines. Rhesus macaques at Sabana Seca for example, nurse almost until subsequent parturition (K.J. Hinde pers. com.). A clear, standardized definition of weaning along with weaning ages for species from both primate taxa is needed to resolve this issue.

Significantly longer gestation periods have previously been found in other folivorous primates and comparisons across multiple taxa suggest an association with a more advanced dental schedule relative to infant age (Godfrey et al., 2003). Growing teeth early and rapidly might be essential for a young folivore's nutritional independence when dealing with fibrous foliage and seeds in the diet (Godfrey et al., 2001, 2004). In light of these prior findings, longer gestation in colobines could similarly be related to additional maternal investment in prenatal dental development. Unfortunately, no data seem to be available for colobines on fetal tooth development. In one colobine species (*Semnopithecus entellus*) crown formation of the first permanent molar (M1) starts comparatively late, around the time of birth (Schwartz et al., 2005) and thus cannot account for the long gestation as seems to be the case with folivorous lemurs (no data on M1 crown formation are available for other colobine species). However, colobines tend to have advanced dental development at four months of age and also at the time of weaning (Godfrey et al., 2001). Furthermore, early eruption of the first deciduous molar was recently documented for *Trachypithecus cristatus*, *Presbytis rubicunda*, and *Nasalis larvatus* (Bolter, 2004: p 145) supporting an accelerated dental schedule in colobines. Because it is not yet clear whether or not the colobine fetus is already on an advanced dental schedule, we can only speculate as to whether maternal investment in dental tissue is associated with the longer gestation periods found in Asian colobines. Data on the prenatal development of deciduous and permanent teeth are required to investigate this hypothesis.

Alternatively, gut tissue, which is considered to be as metabolically expensive as brain tissue (Aiello and Wheeler, 1995; Fish and Lockwood, 2003), could play a role. Adult colobines have a significantly larger gut and an even larger stomach relative to body mass than all other primate taxa (Martin et al., 1985; Martin, 1990). Therefore, it seems plausible that colobine females may invest more in fetal gut development, which could explain the longer gestation periods. Once more, comparative data on prenatal development are required but currently not available.

Macaques might face very different constraints with respect to gestation length based on their different energetic and growth patterns. In captivity, macaques show a high prenatal maternal investment in combination with low postnatal brain growth and a low overall postnatal growth velocity (Leigh, 2004), supporting the idea of a much higher energy transfer to the fetus in this taxon (Martin, 1996). Given this fast prenatal growth, it is conceivable that infants need to be born before they become too big for the mother, particularly their brain or head, thereby limiting gestation length in macaques. Indeed, among Old World primates, the genus *Macaca* has an unfavorable ratio of the breadth of the infant's head to the transversal pelvic diameter of the adult female; only humans and some New World primates have a worse ratio (Leutenegger, 1970).

Taken together it seems that colobines can afford to invest longer in prenatal infant development (particularly teeth and guts) than macaques perhaps because more time to grow means that the fetus requires less maternal energy per unit time, the infant is smaller at birth, and birth is less constrained by maternal pelvic anatomy.[1]

Age at first birth and interbirth interval. Why are age at first birth and the interbirth interval similar in the two taxa? After all, the already heavier macaque neonates have to reach a lower adult weight and metabolic rates in macaques are supposedly higher (Martin, 1996). In addition, macaques might save energy by riding their infants on their backs instead of carrying them ventro-ventrally as colobines do (Nakamichi and Yamada, 2009). Furthermore, the more terrestrial lifestyle of macaques (MacKinnon and MacKinnon, 1980) should lead to higher infant mortality, thus reducing the interbirth interval (Ross, 1988; Charnov, 1991; Ross and Jones, 1999; van Schaik and Deaner, 2003). Concerning age at first birth, macaque females might gain additional time due to female philopatry, allowing them to breed in their natal group among kin providing agonistic support and a matrilineal rank (Chapais and Belisle, 2004). In contrast, most female colobines disperse prior to first reproduction (Isbell and van Vuren, 1996; Borries et al., 2004; Sterck et al., 2005). Establishing themselves in a new social environment often in the absence of close kin and with minimal support might delay the onset of breeding.

However, other factors suggest life histories should be faster in colobines. Frequent allomaternal care, which is typical for colobines but not macaques (Mitani and Watts, 1997) might ease a mother's energetic burden (Ross and MacLarnon, 2000). The onset of reproduction could occur sooner because colobine females can have their first infant before they are fully grown (captive, Shelmidine et al., 2009; wild, Borries, personal observations). Bolter (2004) had several pregnant females from three different colobine species (see above) in her sample. While all had fused pelvic bones (p 119), she notes that "... pregnancy can occur before trunk height, body mass and skeletal fusion is completed, ..." (p 139). Macaques, on the other hand, have relatively larger infants with big heads (see above) so that perhaps a stable, fully grown pelvis could be essential in supporting the birth process. Higher mortality in

first-time mothers (Mori, 1979; Ross, 1992b) as well as high infant mortality (Sade, 1990) has indeed been reported for some macaque populations but not for others (Bercovitch and Berard, 1993).

In sum (Table 5), some of the factors and their effects are hypothesized to reduce and others to increase age at first birth and interbirth interval in colobines relative to macaques. Our finding of similar life histories might just indicate that these effects counterbalance each other. At birth, colobines lag behind macaques (perhaps with the exception of tooth and/or gut development), but seem to catch up postnatally perhaps because they are less energetically constrained. Energetic measures (also during gestation but not restricted to it) are needed to understand the constraints and capabilities of the two taxa.

We note that differences between the two taxa might simply be masked due to the imprecise nature of most life history variables (Deaner et al., 2003). Datasets much larger than the one considered here would be required to investigate this issue.

Colobines: Disproportionately faster when provisioned?

We found similar ages at first birth for colobines and macaques (see Fig. 4), which is surprising given Leigh's (1994a) finding that folivorous anthropoid primates reach adult body mass sooner than frugivores and are thus likely to start reproducing at an earlier age. Leigh's (1994a) analysis is based on a very large sample size (n = 2,706 from 42 species) and is restricted to captive subjects to minimize environmental influences—a research design that leaves little room for errors. Even though the measures compared (age at first birth versus age at adult body mass) are not identical, we assume for colobines and macaques alike that the age at first birth is reached first. Theoretically, the younger age at attainment of adult mass for colobines in Leigh's sample should also be indicative of a younger age at first birth, all things being equal. Alternatively, colobines might start reproducing only after completion of growth while macaques are able to start prior to completion. Under such a scenario, Leigh's (1994a) and our results would not contradict each other, because attainment of adult body mass would not be a predictor of age at first birth. As discussed above, however, the few data currently available point in the opposite direction with colobines reproducing prior to completion of skeletal growth and attainment of adult body mass.

Assuming that a mismatch does exist between Leigh's and our results, we would like to suggest a different, plausible explanation involving taxonomic differences in responding to provisioning. That is, growth speed and growth patterns in the two taxa might be fundamentally and differentially altered by the better nutritional regime under provisioned conditions. Colobines seem to react in two extreme ways to provisioning and either flourish or perish. In the latter case, they may suffer from inadequate nutrition, and in fact colobines (folivores in general) are considered difficult to keep and breed (Hill, 1964; Collins and Roberts, 1978). Mechanical stomach injuries (Ensley et al., 1982) and acidosis (Kay and Davies, 1994; Lambert, 1998) are among the complications faced by provisioned colobines.

The opposite extreme seems to occur with the few species that have been maintained successfully and, consequently, these are overrepresented in the literature

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[1]These results also offer an explanation for the significantly longer gestation periods in species with male philopatry (Lee and Kappeler, 2003), a result that did not seem to make sense at the time. This could be a secondary, taxonomic effect because folivorous primates (with their longer gestation periods) are more likely to exhibit female dispersal and to some degree male philopatry (Moore, 1984).

(Harvey and Clutton-Brock, 1985). The silvered leaf monkey is one such example. In captivity the species retains a body mass similar to wild animals (Shelmidine et al., 2009) or even lighter (Leigh, 1994b). Individuals grow faster and reach adult size sooner than captive frugivorous primates of similar body mass (Leigh, 1994a). Females can deliver their first infant when just 21.3 months of age (youngest age recorded, Shelmidine et al., 2009). Another successful species is the Hanuman langur. Provisioned females give birth for the first time three years earlier, at about half the age as their wild, unprovisioned counterparts (3.5 versus 6.7 years, Borries et al., 2001). Perhaps this accelerated schedule can be explained by the efficient digestive system characteristic of colobines. Not only is the forestomach capable of microbially enhanced fermentation and soluble components pass through it quickly (Cork, 1996), but the colon plays a prominent role in fermentation as well (gastrocolic fermentation, Caton, 1999), perhaps allowing additional energy and nutrients to be extracted from a provisioned diet relatively high in calories and rich in nutrients. In a comparison of captive Japanese and rhesus macaques with silvered leaf monkeys, the latter had significantly higher digestibility for all components analyzed (Sakaguchi et al., 1991). Furthermore, silvered leaf monkeys have the largest stomach in relation to body mass of all colobines (Bolter, 2004), which might render their digestion even more efficient. It is possible that those colobine species that survive and breed successfully in captivity use the atypically nutritious food so efficiently as to allow for exceptionally fast growth and reproductive rates. However, it remains unclear why only some colobine species survive well in captivity.

If the arguments above turn out to be correct as well as applicable to other folivorous species, it will no longer be sufficient to restrict growth analyses to a single nutritional regime, for example, investigating only data from provisioned animals. Different nutritional regimes would have to be analyzed separately. At present, however, growth data for wild (unprovisioned) populations are still rare, although first noninvasive measures based on double laser optics have been performed successfully (Bergeron, 2007; Rothman et al., 2008). It is conceivable that taxon-specific growth patterns are differentially sensitive to nutritional conditions and, thus, data from captivity might not consistently inform us about growth in wild animals.

CONCLUSIONS AND PERSPECTIVES

The results presented here suggest very similar life histories with respect to dietary adaptations in the two primate taxa investigated. However, the underlying mechanisms and their strengths have yet to be thoroughly tested (they were only discussed here) and it remains unclear as to *why* the life history variables are similar. For one, these traits could be linked to constraints other than feeding adaptation that distinguish the two taxa. Additional analyses of the influence of feeding adaptations are needed for many more taxa before conclusions can be drawn. In particular, the suggested mechanisms warrant future research. Data on the energetic requirements and the development of tissues such as teeth, brains or guts during the pre- and postnatal phase could prove especially useful in this context.

Gestation length is the only variable found to be significantly longer in Asian colobines compared to macaques. We assume that this fundamental difference was not recognized sooner, because gestation length has rarely been considered in past analyses. In cases where it was included, the data for colobines were often flawed, which serves as a reminder to treat even published data with caution and to regularly update existing life history compilations. The differences in gestation period compared to the two other similar life history traits further emphasizes that life histories may not fall along a slow-fast continuum and that this concept might be outdated (see e.g., Godfrey et al., 2001; Leigh and Blomquist, 2007). The different life history variables may be influenced by entirely different factors and, for example, a taxon with a comparatively long gestation period does not necessarily also reproduce at a slow rate.

Our analysis further suggests the possibility of major differences in growth speed and pattern between provisioned and wild populations, which should be tested with growth data for wild animals. We might find that we can learn less from provisioned animals (and colobines in particular) than we had hoped. If so, future analyses need to control for the nutritional regime (as defined here). Finally, in terms of understanding life history variables, mortality rates likely have very high explanatory value (Ross, 1988; Charnov, 1991; Janson, 2003) especially for the length of juvenility (Ross and Jones, 1999). Although such data are notoriously difficult to obtain, future life history research will greatly benefit from efforts to determine these rates for wild primate populations.

ACKNOWLEDGMENTS

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