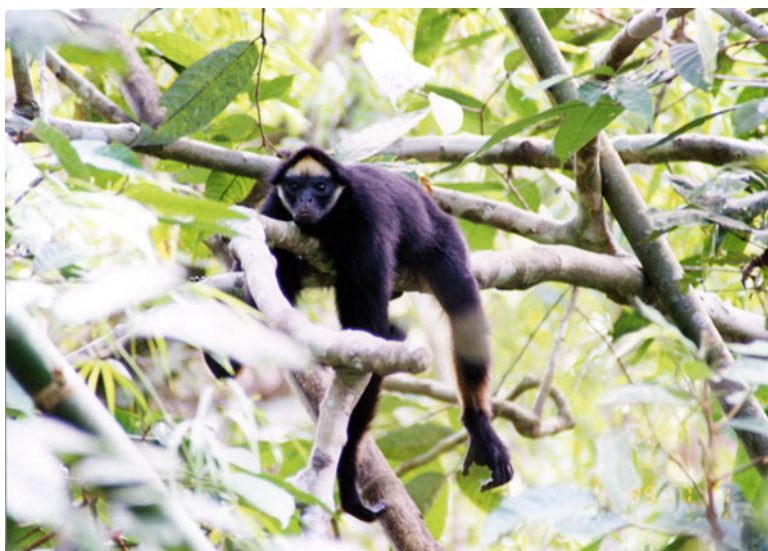


## Chapter 9

# Life History Tactics in Monkeys and Apes: Focus on Female-Dispersal Species

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**Abstract** Primates show life history traits similar to those of cetaceans, such as small litter size, long gestation, long lactation, and long lifespan, in spite of striking contrasts in habitats, diet, mobility, and range size between them. Ecological factors (food and predation) may influence their life history traits in various ways, but social factors (social structure and reproductive strategies) may be more important for the life history of primates, in which both sexes live together even outside the breeding season. Group-living primates are classified into female-bonded species and female-dispersal species, based on the patterns of female dispersal after maturity. A comparison of life history parameters shows that female-dispersal species have a slower life history (gestation length, weaning age, age at first reproduction, and interbirth interval) than the female-bonded species, except for neonatal weight and weaning weight, which may be determined in relationship to female body weight. To elucidate factors promoting the slow life history, we focus on Atelinae and Hominidae (female-dispersal species) and examine their interspecific and intraspecific variation in social structure and male reproductive tactics in relationship to life history traits. Most Atelinae species form multimale and multifemale groups, and variation in their life history features may reflect relationships among males and their reproductive tactics. In howler monkeys, both males and females disperse, and infanticide by males may lead to a fast life history. In other Atelines, infanticide rarely occurs, although it has the effect of reducing interbirth interval. Forcible copulation by males occasionally occurs in spider monkeys. Variations in grouping among females reflecting their flexible foraging efforts according to distribution of high-quality foods may have some effects on the fast–slow continuum in the life history features of female Atelinae. Hominidae exhibit larger variations in life history features than Atelinae, probably because of their diverse social structure. Solitary nature and male reproductive tactics may have great influences on the life history of female great apes. Female orangutans, who usually live a solitary life, show the slowest life history. Maturing female orangutans need a longer time to establish their own home range and relationships with reproductive mates than female chimpanzees and gorillas, who transfer into other groups immediately after emigration. Female gorillas show the lowest age at first reproduction and the shortest interbirth interval. Intensive caretaking of the immature by male gorillas may facilitate early weaning, and infanticide by males may promote a prolonged bonding between a protector male and females to shorten the interbirth interval. Similar life history traits have been found in four long-term study sites of chimpanzees. Only females at Bossou show a fast life history, probably the result of high-quality foods and single male group composition under isolated conditions. The more frequent and stable association between females and males and more promiscuous mating in bonobos may facilitate the search for mating partners and lead to a shorter interbirth interval than chimpanzees. Frugivorous orangutans and chimpanzees may suffer more costs of female dispersal through decreased foraging efficiency than folivorous gorillas, and chimpanzees with fission–fusion grouping may suffer more social stress than gorillas in highly cohesive groups. Such differences may generally shape the fast–slow continuum of life history in female-dispersal primate species.

**Keywords** Age at first reproduction • Atelinae • Female-dispersal species • Hominidae • Interbirth interval • Life history

## 9.1 Life History Traits of Cetaceans and Primates

Life history is expressed as a scheduling of development and reproduction within a life cycle (Stearns 1992). Parameters of life history, such as gestation length, prenatal and postnatal growth rate, weaning age, age to first reproduction, interbirth interval, and lifespan, vary allometrically with body size (Read and Harvey 1989; Charnov 1991, 1993; Purvis and Harvey 1995). In mammals, large species take longer to grow to maturity, have a longer gestation, have a longer interval between births, and have fewer young per litter than smaller species. This “fast–slow continuum” in the speed of life is also found among cetaceans and primates.

A cetacean is characterized by its large body size (for the blue whale, a body length of 31 m) and large neonatal mass (more than 15 % of maternal mass) because of its aquatic habitats and advanced feeding techniques, such as the filtering observed in mysticetes (Whitehead and Mann 2000). Among cetaceans, life history traits differ between mysticetes and odontocetes (Fig. 9.1). Although no difference is found in neonatal weight relative to adult female body weight, weaning age and age at first parturition of mysticetes are lower than those of odontocetes. The mysticetes show fast life history patterns and no obvious correlation between body size and the speed of their life history processes (Martin and Rothery 1993; Kasuya 1995). By contrast, the odontocetes generally follow the fast–slow continuum, possibly caused by predation pressure and food availability being variable with body size (Whitehead and Weilgart 2000; Whitehead and Mann 2000). Duration of lactation is extremely variable among cetacean species, ranging from 6 months in baleen whales to 6 years in bottlenose dolphins (Connor et al. 2000). Mysticetes produce milk with the highest fat content (30–53 %) among mammals and wean offspring at an earlier age than most of the odontocetes, irrespective of body length (Ofstedal 1997). In odontocetes, the length of lactation has a positive correlation with body length, and weaning occurs gradually, probably the result of the necessity of learning how to feed on highly mobile prey (Mann and Smuts 1999). Food supply may affect the duration of lactation, which constitutes a constraint factor on the future reproduction of mothers (Martin and Rothery 1993; Mann et al. 2000). Cetaceans are gregarious and socially diverse, but most of their social structure is matrilineal, in which males disperse from their natal groups (Kasuya 1995). As observed in bottlenose dolphins and striped dolphins, kin-related females tend to associate and cooperate in rearing calves in a school (Miyazaki and Nishiwaki 1978; Shane et al. 1986). In some matrilineal social structures (e.g., pilot whales and killer whales), menopause has been found (Whitehead 1998). Patrilineal social structure has been found in Baird’s beaked whales, in which males reach maturity earlier and live longer than females (Kasuya and Jones 1984). Male Baird’s beaked whales care for weaned offspring, which is exceptional among cetaceans (Kasuya et al. 1997).

Primates show life history traits similar to those of cetaceans, such as small litter size, long gestation, long lactation, and long lifespan, in spite of striking contrasts in habitats, diet, mobility, and range size between them (Harvey et al. 1987; Read and Harvey 1989; Ross 1998; Whitehead and Mann 2000). Primates lie at the slow end of the fast–slow continuum (Fig. 9.1; Table 9.1). Haplorhines have a slower life history than strepsirrhines of the same size (Purvis et al. 2003). Recent arguments

**Fig. 9.1** Life history traits of cetaceans and primates among mammals relative to female body weight: neonatal weight (a), weaning age (b), and age at first parturition (c). *Open squares*, mysticetes; *filled squares*, odontocetes; *open triangles*, anthropoids; *filled triangles*, prosimians; *filled diamonds*, other mammals. (Data from the list by Purvis and Harvey 1995)



have proposed determinant factors of the slow life history in primates, such as large brain size (Allman et al. 1993; Martin 1996), high risk of juvenile mortality (Janson and van Schaik 1993), nutritional risk (Borries et al. 2001; Altmann and Alberts 2003; Anderson et al. 2008), and arboreal lifestyle (Eisenberg 1981; Martin 1995), but no single factor seem to fully explain this (Harvey and Purvis 1999; van Schaik and Deaner 2002).

Ecological factors may influence the life history traits of primates in various ways (Kappeler et al. 2003). The low growth rate of primates may be caused by a negative association between mortality rates and growth rates, and juvenile vulnerability to food shortage and predation may shape their life history traits (Janson and

**Table 9.1** Species averages for mammalian life history variables

Common name	Scientific name	Adult weight (g)	Neonatal weight (g)	Weaning age (day)	Age at first parturition (days)
Nutria	<i>Myocaster coypus</i>	5,300	227	56	257
Uinta ground squirrel	<i>Spermophilus armatus</i>	266		21	365
Belding's ground squirrel	<i>S. beldingi</i>	257		27	365
Daurian ground squirrel	<i>S. dauricus</i>	200			365
Golden-mantled ground squirrel	<i>S. lateralis</i>	156	7	33	523
Yellow-bellied marmot	<i>Marmota flaviventris</i>	2,510	34	29	1,100
Eastern chipmink	<i>Tamias striatus</i>	95	3	35	223
Eastern grey squirrel	<i>Sciurus carolinensis</i>	568	16	63	306
Red squirrel	<i>Tamiasciurus hudsonicus</i>	200	7	62	413
East African mole rat	<i>Tachyoryctes splendens</i>	195	15	43	159
Meadow jumping mouse	<i>Zapus hudsonius</i>	19	1	28	365
Western jumping mouse	<i>Z. princeps</i>	26	1	25	478
Yellow-necked mouse	<i>Apodemus flavicollis</i>	27	2	21	89
Bank vole	<i>Clethrionomys glareolus</i>	17	2	20	58
White-footed mouse	<i>Peromyscus leucopus</i>	24	2	23	63
Deer mouse	<i>P. maniculatus</i>	18	2	23	70
Pika	<i>Ochotona princeps</i>	140	10	24	303
Brown hare	<i>Lepus europaeus</i>	3,730	115	26	243
European rabbit	<i>Oryctolagus cuniculus</i>	1,550	38	23	175
Eastern cotton-tail rabbit	<i>Sylvilagus floridans</i>	1,270	35	22	129
Greater horseshoe bat	<i>Rhinolophus ferrumequinum</i>	23	6	48	1,100
Big brown bat	<i>Eptesicus fuscus</i>	23	3	29	365
Eastern (U.S.) pipistrelle bat	<i>Pipistrellus subflavus</i>	7			730
Common pipistrelle bat	<i>P. pipistrellus</i>	6	1		730
European mole	<i>Talpa europaea</i>	85	4	31	365
European hedgehog	<i>Erinaceus europaeus</i>	771	16	40	365
Giant panda	<i>Ailuropoda melanoleuca</i>	120,000	106	183	1,170
Black bear	<i>Ursus americanus</i>	87,200	293	253	1,830
Ringed seal	<i>Phoca hispida</i>	69,700	4,400	40	1,530
Grey seal	<i>Halichoerus ursinus</i>	182,000	14,100	18	1,810
Elephant seal	<i>Mirounga leonina</i>	558,000	40,600	23	1,900
Fur seal	<i>Callorhinus ursinus</i>	42,400	4,930	82	1,700
River otter	<i>Lutra canadensis</i>	4,600	149	122	1,180
European skunk	<i>Mustela putorius</i>	646	10	38	365
Striped skunk	<i>Mephitis mephitis</i>	2,000	26	53	365
American badger	<i>Taxidea taxus</i>	4,100	104	54	593
Grey wolf	<i>Canis lupus</i>	27,000	404	43	365
Grey fox	<i>Urocyon cinereoargenteus</i>	3,300	102	42	393
Red fox	<i>Vulpes vulpes</i>	3,650	100	59	365
Arctic fox	<i>Alopex lagopus</i>	3,000	70	70	328
Domestic cat	<i>Felis catus</i>	2,620	97	56	365
Bobcat	<i>Lynx rufus</i>	7,100	317	60	460

(continued)

**Table 9.1** (continued)

Common name	Scientific name	Adult weight (g)	Neonatal weight (g)	Weaning age (day)	Age at first parturition (days)
Wild boar	<i>Sus scrofa</i>	54,800	817	98	687
Warthog	<i>Phacochoerus aethiopicus</i>	54,000	720	111	776
Hippopotamus	<i>Hippopotamus amphibius</i>	1,360,000	42,800	304	2,010
Impala	<i>Aepyceros melampus</i>	44,400	4,830	154	733
Waterbuck	<i>Kobus ellipsiprymnus</i>	188,000	13,000	211	654
Kob	<i>K. kob</i>	59,200	4,470	197	641
Topi	<i>Damaliscus lunatus</i>	128,000	11,300		898
Cape buffalo	<i>Syncerus caffer</i>	547,000	40,300	304	1,800
Chamois	<i>Rupicapra rupicapra</i>	26,100	3,070	183	843
Himalayan tahr	<i>Hemitragus jemlahicus</i>	35,200	2,000	149	965
Dall's sheep	<i>Ovis dalli</i>	60,000	3,620	149	1,010
Chinese musk deer	<i>Moschus berezovskii</i>	10,900	648		1,100
Red deer	<i>Cervus elaphus</i>	109,000	8,800	216	1,030
European roe deer	<i>Capreolus capreolus</i>	23,000	866	136	733
Moose	<i>Alces alces</i>	408,000	13,200	131	897
Caribou	<i>Rangifer tarandus</i>	93,600	5,720	111	1,210
Mule deer	<i>Odocoileus hemionus</i>	56,300	2,800	69	677
Horse	<i>Equus caballus</i>	410,000	41,500	238	1,460
Plains zebra	<i>E. burchelli</i>	268,000	32,200	294	1,090
African elephant	<i>Loxodonta africana</i>	2,770,000	115,000	1,886	5,460
Blue whale	<i>Balaenoptera musculus</i>	105,000,000	7,250,000	210	3,650
Humpback whale	<i>Megaptera novaeangliae</i>	35,000,000	2,000,000	150	2,008
Grey whale	<i>Eschrichtius robustus</i>	31,466,000	500,000	210	3,285
Sperm whale	<i>Physeter macrocephalus</i>	20,000,000	1,016,000	720	4,088
False killer whale	<i>Pseudorca crassidens</i>	700,000	80,000	630	4,380
Beluga	<i>Delphinapterus leucas</i>	400,000	79,000	660	2,555
Bottlenose dolphin	<i>Tursiops spp.</i>	200,000	32,000	570	3,650
Eastern gorilla	<i>Gorilla beringei</i>	71,000	1,900	1,090	3,650
Chimpanzee	<i>Pan troglodytes</i>	34,300	1,740	1,900	4,310
White-handed gibbon	<i>Hylobates lar</i>	5,340	400	548	2,446
Gelada baboon	<i>Theropithecus gelada</i>	11,427	465	540	1,460
Guinea baboon	<i>Papio papio</i>	9,750	710	365	2,008
Rhesus macaque	<i>Macaca mulatta</i>	5,370	466	192	1,095
Toque monkey	<i>Macaca sinica</i>	3,590	446	391	1,730
Black and white colobus	<i>Colobus gueraza</i>	7,900	445	330	1,752
Savanna monkey	<i>Cercopithecus aethiops</i>	2,980	336	201	1,825
Spider monkey	<i>Ateles spp.</i>	8,440	425	760	1,825
Howler monkey	<i>Alouatta spp.</i>	4,670	295	372	1,679
Lion tamarin	<i>Leontopithecus rosalia</i>	559	50	90	876
Ring-tailed lemur	<i>Lemur catta</i>	2,210	65	105	730
Slender loris	<i>Loris tardigradus</i>	5,370	466	192	1,095
Allen's bushbaby	<i>Galago alleni</i>	255	10	170	548
Tarsiers	<i>Tarsius spp.</i>	173	12	84	256

Sources: Harvey et al. (1987), Purvis and Harvey (1995), Whitehead and Mann (2000), Kappeler and Pereira (2003)

van Schaik 1993). Primates may be adapted to the low mortality rates prevalent in their ancestral habitat (tropical forests), because other arboreal mammals, such as bats (Jones and MacLarnon 2001), also have low mortality rates. Primates living in the more unpredictable habitats have higher birthrates and earlier age at first reproduction (Ross 1998). The apes that are strictly distributed in and around the tropical forests have slow life history traits, whereas Old World monkeys living in variable habitats have relatively rapid life history traits. Forest macaques have a longer interbirth interval and a later age at first reproduction than opportunistic macaque species living in a variety of habitats, even in sympatric conditions (Ross 1992). However, the age of first reproduction in olive baboons is highly heritable (Williams-Blangero and Blangero 1995). Large intraspecific variations are also found in some life history traits. Female vervet monkeys may respond to limited access to food resources by delaying reproduction (Cheney et al. 1988). Female Japanese macaques and savanna baboons with high rank tend to mature earlier than females with low rank (Altmann et al. 1988; Gouzoules et al. 1982; Takahata et al. 1999). These observations may suggest that life history traits of primates may have evolved as a species-specific strategy as well as the immediate responses to environment changes.

Social structure and social behavior are also important for life history traits. Among mammals, primates have a unique social feature in that the two sexes live together even outside the breeding season. This lifestyle may result in diversity of social structure and may characterize the fast–slow continuum in relationship to social systems. Group size and sociometric sex ratio (the number of adult males per female within a group) can change feeding and reproductive strategies of both sexes and thereby affect life history parameters (Dunbar 1988; Sterck et al. 1997; Nunn and Pereira 2000). Female gregariousness, social relationships, or alloparental care of dependent infants may also change life history traits such as postnatal growth rate, weaning age, and interbirth interval (Fairbanks 1990; Stanford 1992; Van Noordwijk and van Schaik 2005). High infant growth rates do not appear to be correlated with environmental factors (diet, climate, or habitat) but with nonmaternal care, which allows mothers to increase birthrates by decreasing interbirth interval (Ross and MacLarnon 1995). Male reproductive strategies may constitute a strong selective force on life history traits. Infanticide by males promotes prolonged male–female association (van Schaik 2000) and complex male–infant relationships (Paul et al. 2000) and affects patterns of female movements between groups (Steenbeck 2000; Yamagiwa and Kahekwa 2001) and female reproductive biology (Watts 2000; van Noordwijk and van Schaik 2000; Yamagiwa et al. 2009). Recent findings show large variations in social structure and behavior between species and within species (Barton et al. 1996; Henzi and Barrett 2003; Doran et al. 2002; Yamagiwa et al. 2003). Life history traits are also easy to change, relatively independently, via selection (Kappeler et al. 2003). However, it is still unclear how such social variation is linked with life history variation.

In this chapter, we focus on female dispersal as the limiting factor of life history parameters. Group-living primates have been classified into female-bonded species and female-dispersal species (Wrangham 1980). Most of the macaques, cercopithecines, and *Cebus* monkeys form a group in which females remain during their entire life.

They usually associate with kin-related females and form coalitions with them in agonistic contexts (Watanabe 1979; Silk 1982; Dunbar 1988; Harcourt 1992; Henzi and Barrett 1999). Cooperation and support of kin-related females increase female reproductive success. The linear dominance rank is stable among females and between kin-groups of females. Females of the kin-groups with higher rank have higher birth-rates, younger age at first parturition, and lower infant mortality than females of kin-groups with lower rank (Drickamer 1974; Silk 1987; Itoigawa et al. 1992; Paul and Kuester 1996), although these tendencies are not consistent in some species (Cheney et al. 1988; Takahata et al. 1999). On the other hand, females of Hominidae and Atelinae usually leave their natal groups and spend their reproductive life without related females (Wrangham 1987; Yamagiwa 1999; Strier 1999a). Social relationships with males or unrelated females that they join are important for their reproductive success. The elder females or females joining earlier are dominant to younger females or those joining later (Goodall 1986; Watts 1991a; Idani 1991; Crockett and Pope 1993; Printes and Strier 1999; Nishimura 2003). However, intervention by males in conflicts (Watts 1997), sociosexual behavior among females (Kano 1992), and the fission–fusion nature of grouping (Wrangham and Smuts 1980; Goodall 1986; Strier 1992) reduce dominance effects and prevent females from having prolonged antagonistic interactions. Because of the lack of support from kin-related females, male reproductive strategies including infanticide may affect life history parameters in female-dispersal species (Strier 1999a; Harcourt and Stewart 2007). Here, we also examine inter- and intraspecific variation in social structure and male reproductive tactics in relationship to life history traits.

## 9.2 Life History Tactics of Female-Bonded and Female-Dispersal Species

Anthropoid primates form either female-bonded or female-dispersal groups, except for orangutans, in which both females and males spend a solitary life after maturity. Among them, we selected primate species with medium and large body size for comparisons of life history traits: 20 species for female-bonded and 15 species for female-dispersal (Table 9.2). The orangutan was included in the female-dispersal species because all females separate from their mothers before maturity. As life history parameters, gestation length, neonatal weight, weaning age, weaning weight, age at first parturition, and interbirth interval were used for interspecific comparison with reference to female body weight. We used the database constructed by Kappeler and Pereira (2003) and added to it some reliable data from recent reports. Most of the data were from observations on wild populations, but some data were from observations on provisioned or captive individuals. For statistical tests, we used the analysis of covariance (ANCOVA) in the Analyze/Fit Model section in JMPs.

Gestation length of female-dispersal species was significantly longer than that of female-bonded species ( $F=69.05$ ,  $p<0.0001$ ; Fig. 9.2a). Length of gestation of Atelinae (*Ateles*, *Brachyteles*) was far longer than that of Cercopithecinae



**Table 9.2** Life history parameters of female-bonded and female-dispersal primate species

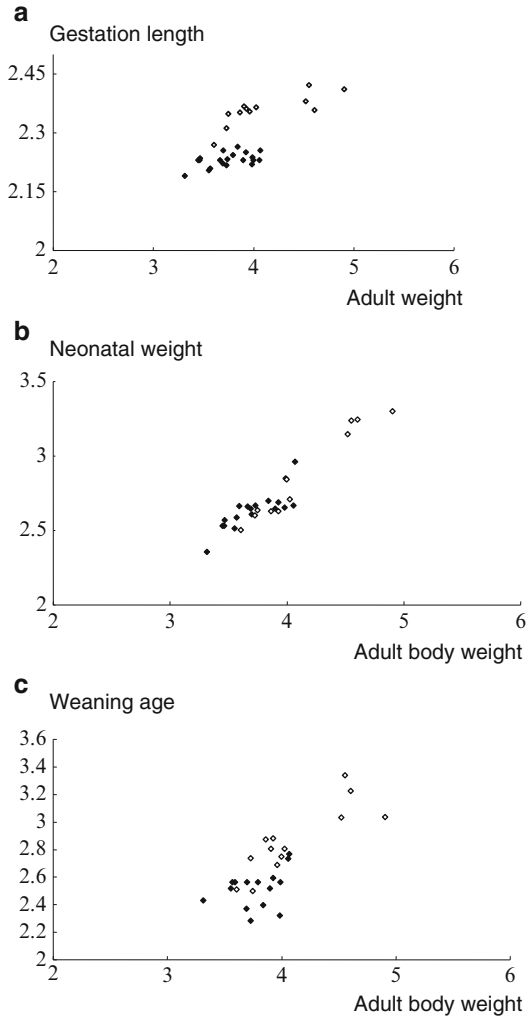
Species	Female-bonded (M) or female-dispersal (P)	Adult female body weight (g)	Gestation length (day)	Neonatal Weight (g)	Weaning age (day)	Weaning weight (g)	Age at first reproduction (years)	Interbirth interval (months)
<i>Cebus abifrons</i>	M	2,067	155	228	269		4	18
<i>Alouatta palliata</i>	P	4,020	186	320	325	1,100	3.6	20
<i>Ateles fusciceps</i>	P	9,160	226		486		4.9	
<i>A. Geoffroyi</i>	P	7,290	225	426	750	2,000	7	37
<i>A. paniscus</i>	P	8,440	230	425	760	3,790	5	24
<i>Brachyteles arachnoides</i>	P	8,070	233		638		7.5	34
<i>Lagothrix lagotricha</i>	P	5,585	223	432	315		5	24
<i>Cercopithecus ascanius</i>	M	2,920	172	371			5	
<i>C. cephus</i>	M	2,805	170	339			5	
<i>C. diana</i>	M	3,900		460	365		5.3	12
<i>C. pogonius</i>	M	2,900	170	339			5	
<i>Macaca arctoides</i>	M	8,400	178	489	393	2,300	3.8	19
<i>M. fascicularis</i>	M	3,574	160	326	330	1,700	3.9	13
<i>M. mulatta</i>	M	5,370	165	466	192	1,454	3	12
<i>M. nemestrina</i>	M	4,900	167	444	234	1,417	3.9	14
<i>M. nigra</i>	M	4,600	170	457			5.4	18
<i>M. radiata</i>	M	3,700	162	388	365	2,000	4	12
<i>M. silenus</i>	M	5,000	180	407	365		4.9	17
<i>Lophocebus albigena</i>	M	6,209	175		365	2,170	4.1	
<i>Cercocebus torquatus</i>	M	5,500	171				4.7	
<i>Papio anubis</i>	M	11,700	180	915	584		4.5	25
<i>P. cynocephalus</i>	M	9,750	173	710	365	2,500	5.5	23
<i>P. hamadryas</i>	P	9,900	170	695	561	3,100	6.1	24

(continued)

Table 9.2 (continued)

Species	Female- bonded (M) or female- dispersal (P)	Adult female body weight (g)	Gestation length (day)	Neonatal Weight (g)	Weaning age (day)	Weaning weight (g)	Age at first reproduction (years)	Interbirth interval (months)
<i>Theropithecus gelada</i>	M	11,427	170	465	540	3,900	4	24
<i>Colobus gereza</i>	M	7,900	170	445	330	1,600	4.8	20
<i>Semnopithecus entellus</i>	M	6,910	184	500	249	2,100	3.4	17
<i>Nasalis larvatus</i>	M	9,593	166	450	210	2,000	4.5	18
<i>Hylobates lar</i>	P	5,340	205	400	548	1,070	6.7	30
<i>H. syndactylus</i>	P	10,568	232	513	639		5.2	50
<i>Pongo pygmaeus</i>	P	35,700	264	1,728	2,190	11,000	15	96
<i>Gorilla gorilla beringei</i>	P	80,000	258	1,996	1,090		10	51
<i>Pan paniscus</i>	P	33,200	240	1,400	1,080	8,500	14	75
<i>P. troglodytes</i>	P	40,400	228	1,750	1,680	8,500	14	69

Sources: Anderson et al. (2008), Fedigan and Rose (1995), Furuichi and Hashimoto (2002), Harcourt and Stewart (2007), Kappeler and Pereira (2003), Nishida et al. (2003), Nishimura (2003), Shimooka et al. (2008), Wich et al. (2004)



**Fig. 9.2** Life history traits of female-bonded and female-dispersal primate species (relative to female body weight): gestation length (a), neonatal weight (b), weaning age (c), weaning weight (d), age at first parturition (e), interbirth interval (f). *Filled diamonds*, female-bonded species; *open diamonds*, female-dispersal species



**Fig. 9.2** (continued)

(*Cercopithecus*, *Macaca*, *Cercocebus*, *Lophocebus*, *Papio*, *Theropithecus*) and Colobinae (*Colobus*, *Semnopithecus*). Gestation length of Hominae was diverse and did not correlate with body weight among the four species. Neonatal weight tended to increase relative to female body weight, and no difference was found here between the female-bonded and the female-dispersal species ( $F=106.86$ ,  $p=0.3877$ ; Fig. 9.2b). Although no difference was found in weaning weight ( $F=45.05$ ,  $p=0.9586$ ; Fig. 9.2c), weaning ages of female-dispersal species were significantly

higher than those of female-dispersal species ( $F=34.28, p<0.01$ ; Fig. 9.2d). In primate species, weaning generally occurs around the time when infants reach about one third of adult body weight (Lee et al. 1991; Lee 1996). Female-dispersal species tend to have a higher age at first parturition ( $F=23.97, p<0.05$ ; Fig. 9.2e) and longer interbirth interval ( $F=56.63, p<0.0001$ ; Fig. 9.2f) than female-bonded species. These results suggest that female-dispersal species may have slower life history traits than female-bonded species. Neonatal weight and weaning weight may be determined in relationship to female body weight irrespective of female movement patterns. However, female dispersal and reproduction without help from kin-related females may result in a slow life history.

Female-dispersal species form various social structures, such as solitary, monogamous, polygynous, or multimale/multifemale groups. Which aspects of female dispersal or social features lead them to slow life history? To answer this question, we compared life history traits between genera, between species, and between populations within species of Atelinae and Hominidae, which have been extensively studied at several sites.

### 9.3 Factors Leading to Slow Life History of Atelinae and Hominidae

Atelinae and Hominidae are typical taxa in which all genera have common social features, such as the lack of female kin bonding and female dispersal from the natal group or mother (Goodall 1986; Rosenberger and Strier 1989; Strier 1999b; Harcourt and Stewart 2007). Atelines live in the tropical forests of Central and South America and are divided into four genera: howler monkeys (*Alouatta*), spider monkeys (*Ateles*), woolly monkeys (*Lagothrix*), and muriquis (*Brachyteles*). Hominidae (great apes), except for humans, are divided into three genera and live in the tropical forests of Asia (orangutans, *Pongo*) and Africa (gorillas, *Gorilla*; chimpanzees, *Pan*). Atelines usually form groups including multiple females and males. Although male howler monkeys also disperse from their natal groups, males of the other three Atelines remain in their natal groups to associate with kin-related males, as observed for chimpanzees and bonobos (Symington 1988; Strier 1999a). The social structures of the great apes are highly differentiated. Both male and female orangutans usually live alone and partially overlap their home range with neighboring individuals of the same sex (Galdikas 1984; Delgado and van Schaik 2000; van Schaik 1999). Gorillas form a cohesive group consisting of a mature male and several females with their offspring. Both female and male gorillas tend to emigrate from their natal groups, and only females immigrate into other groups in which they start reproduction (Yamagiwa and Kahekwa 2001; Stokes et al. 2003; Robbins et al. 2009). Chimpanzees form large groups including multiple males and females, and only females emigrate from their natal groups (Nishida 1979; Goodall 1986; Boesch and Boesch-Achermann 2000).

**Table 9.3** Life history parameters of atelines

Species	Body weight (kg)	Age at first reproduction (years), average (range)	Interbirth interval (years), average (range)	Source
<i>Alouatta seniculus</i>	5.6	5.2	(17–20)	Crockett and Pope (1993)
<i>Lagothrix lagotricha</i>	5.8	9	34.7	Nishimura (2003)
<i>Ateles geoffroyi</i>	7.5	7	34.7	Fedigan and Rose (1995)
<i>Brachyteles</i> sp.	9.5	(8–14)	36.0	Strier (1996)

Analogous to the great apes, Atelines are characterized by the largest body weight and the slowest life history among neotropical primates (Table 9.3). The slower reproductive traits of woolly monkeys compared to howler monkeys, which have a similar body size, may reflect their differences in female reproductive costs in relationship to social features. Female howler monkeys can have more diverse options than female woolly monkeys, such as transferring into other groups, joining males to establish a new group, or remaining in their natal group to breed (Crockett and Pope 1993; Strier 1999a). Aggressive interactions among males over mating partners are frequent, and infanticide by males occurs in howler monkeys (Crockett and Seklic 1984; Agoramorthy and Rudran 1995; Crockett and Janson 2000). In the Venezuelan red howler monkeys (*Alouatta seniculus*), infanticide reduces the interbirth interval, and the risk of infanticide increases with the number of females within a group (Crockett and Rudran 1987; Crockett and Janson 2000). Infanticide may prompt female emigration and lead to a fast life history. In the other three Ateline genera with male philopatry, however, infanticide rarely occurs. On the other hand, coalitional aggression by males to other males, including killing of immature males and forced copulations by males, have been reported in spider monkeys (Campbell 2003, 2006; Valeo et al. 2006; Gibson et al. 2008). There are large variations in the average interval between consecutive viable births of spider monkeys among long-term study sites [32.0 months in Mexico (Ramos-Fernandez 2003); 34.5 months in Peru (Symington 1988); 43.7 months in Columbia (Y. Shimooka, unpublished data)]. Within-group competition among males and their mating strategies, including sexual coercion, may change the interbirth interval of spider monkeys (Gibson et al. 2008; Shimooka et al. 2008).

A comparison of life history parameters in female great apes indicates that orangutans have the slowest and gorillas have the fastest life history (Table 9.4). These differences are inconsistent with female body weight, and the life history parameters vary with male mating strategies. There are two types of sexually mature male orangutan: “flanged” males, with fully developed secondary sexual features, cheek pads, long hair, and a throat sack, and “non-flanged” males, looking younger without these sexual features but actually having reached the adult age. Flanged males emit loud calls and maintain antagonistic relationships with each other, competing over access to females (Galdikas 1985; Rodman and Mitani 1987; van Schaik and van Hooff 1996). Non-flanged males occasionally travel in groups to follow the same females (van Schaik et al. 2004). The strong female mating preference for the dominant flanged males facilitates their exclusive mating, but roaming non-flanged

**Table 9.4** Life history parameters of the great apes

Species/subspecies	Study site	Age at first reproduction (years), average (range)	Interbirth interval (years), average (range)	Source
<i>Pongo abelii</i>	Ketambe	15.4 (13–18)	9.3 (6.3–11.6)	Wich et al. (2009)
<i>Pongo pygmaeus</i>	Tanjung Putting	15.7 (15–16)	7.7 (5.3–10.4)	Galdikas and Wood (1990), Tilson et al. (1993)
<i>P. pygmaeus</i> (rehabilitant)	Sepilok	10.9 (7–16)	6.2 (5.0–7.6)	Kuze et al. (2008), Kuze et al. (2012)
<i>Pongo abelii</i> (zoo-born, captive)		16.4 (15–17)	5.8	Anderson et al. (2008)
<i>Pongo pygmaeus</i> (zoo-born, captive)		15.5 (14–16)	6.3	Anderson et al. (2008)
<i>Gorilla beringei beringei</i>	Virunga	10.1 (9–13) <sup>a</sup>	3.9 (3.0–7.3)	Watts (1991a, b)
<i>Gorilla beringei graueri</i>	Kahuzi	10.6 (9–12)	4.6 (3.4–6.6)	Yamagiri et al. (2003)
<i>Gorilla gorilla gorilla</i> (captive)	Mahale	9.2 (6–19)	4.2 (2.4–6.4)	Kirschofer (1987), Sivert et al. (1991)
<i>Pan troglodytes schweinfurthii</i>	Gombe	13.2 (12–23) <sup>a</sup>	5.7 (5.3–7.3) <sup>a</sup>	Nishida et al. (2003)
<i>Pan troglodytes schweinfurthii</i>	Bossou	13.3 (11–17)	5.2 (3–8)	Goodall (1986), Wallis (1997)
<i>Pan troglodytes verus</i>	Tai	10.9 (10–14)	5.3 (4–11)	Sugiyama (2004)
<i>Pan troglodytes verus</i>	River Gambia	14.3 (13–19)	5.8 (4–10)	Boesch and Boesch-Acherermann (2000)
<i>Pan troglodytes</i> (provisioned)	Japan	14.3 (13–18)	5.7 (2–9)	Marsden et al. (2006)
<i>Pan troglodytes</i> (captive)	CIRMF (Gabon)	11.6 (5–37)	4.2	Udono et al. (1989), Yoshihara (1999)
<i>Pan troglodytes</i> (captive)	Wamba	11.2 (8–17)	4.2 (2.8–5.2)	Tutin (1994)
<i>Pan paniscus</i>		14.2 (13–15)	4.8	Kuroda (1989), Furuichi et al. (1998), Furuichi and Hashimoto (2002)

<sup>a</sup>Median

males occasionally force females to mate with them. Females do not form prolonged consorts with either flanged or non-flanged males. Females with dependent infants rarely associate with males, which never take care of infants. The lack of the male's care and protection may promote the female's solitary travel and preclude early weaning and reproduction.

Gorillas form a cohesive group and have no territoriality with neighboring groups (Schaller 1963; Watts 1998; Tutin 1996; Yamagiwa et al. 1996; Bermejo 2004). High cohesiveness and one-male group composition may have promoted a rapid life history compared to other apes. The leading male monopolizes most of the copulations with fertile females and takes intensive care of the offspring before and after weaning (Fossey 1979; Stewart and Harcourt 1987; Fletcher 2001; Stewart 2001). These social features may facilitate weaning at an earlier age, shorter interbirth interval, and female reproduction at an earlier age for gorillas than for chimpanzees. Furthermore, infanticide by male gorillas occurs as a mating tactic to resume female estrus and thereby shorten interbirth interval (Watts 1989; Yamagiwa et al. 2009).

Female chimpanzees and bonobos copulate with multiple males and take care of their infants by themselves (Tutin 1979; Goodall 1986; Kano 1992). Female chimpanzees tend to associate or interact with other adults less frequently than males, and mothers with dependent infants rarely join males (Wrangham 1979; Nishida 1979; Boesch and Boesch-Achermann 2000). Infanticide occurs in chimpanzees, but promiscuous mating may reduce it, as do female tactics, with paternity confusion (Hasegawa 1989; Van Noordwijk and van Schaik 2000). Fission–fusion features and promiscuous mating may prevent males from monopolizing mating and lead to a slower life history than gorillas.

Life history parameters in female great apes vary with their social features. Female orangutans, who usually live a solitary life, show the slowest life history. Maturing females need to establish their own home range and relationships with reproductive mates after separation from their mothers. They need a longer time to attain these tasks than female chimpanzees and gorillas, who transfer into other groups immediately after emigration. Solitary travel for weeks or months by female chimpanzees or gorillas has rarely been observed (Wrangham 1979; Nishida 1979; Goodall 1986; Boesch and Boesch-Achermann 2000; Watts 2003; Stokes et al. 2003; Yamagiwa et al. 2003). Female chimpanzees and gorillas may easily find mates for reproduction in the group they join and thus may not need to establish their own ranging areas. Instead, they need to establish social relationships with unrelated conspecifics within the new group. Immigrant females usually are harassed by resident females in both chimpanzees and gorillas (Goodall 1986; Idani 1991; Furuichi 1997; Watts 1991a, 1994; Harcourt and Stewart 2007). Female gorillas get support from the leading males, who frequently intervene in conflicts among females (Watts 1997; Harcourt and Stewart 2007). Immigrant female bonobos first establish affiliative relationships with resident females through sociosexual behavior (Idani 1991; Kano 1992; Furuichi 1997; Hohmann et al. 1999). Although group life may facilitate female chimpanzees in starting or resuming reproduction earlier than do female orangutans, more complex social relationships within a group and unassisted caretaking may prevent them from having a fast life history.



The costs of female transfer may also prevent Atelinae from having rapid reproduction (Strier 1999a). Female woolly monkeys transfer between groups and give birth seasonally, and immigrant females are usually accepted peacefully (Nishimura 1994, 2003). The most frequent fission–fusion in grouping is found in spider monkeys (Symington 1990; Strier 1992). Female muriquis transfer throughout the year, and immigrant females are occasionally threatened by resident females and start copulation several months after immigration (Printes and Strier 1999; Strier and Ziegler 2000). Variations in grouping and relationships among females are the driving force of the fast–slow continuum in the life history of Atelinae.

#### 9.4 Ecological Factors Versus Social Factors Influencing Life History Parameters in Hominidae

Ecological factors, such as nutritional conditions and predation risks, may also change life history parameters. Ecological risk aversion theory predicts that seasonal fluctuation in the availability of high-quality foods, increasing intraspecific feeding competition, and low predation risk, reducing mortality rate, may lead to a slow life history (Janson and van Schaik 1993). In this respect, great apes with low predation risk have a slower life history than *Cercopithecus* monkeys, and frugivorous orangutans and chimpanzees have a slower life history than folivorous gorillas. Spider monkeys, relying most heavily on fruits with the most frequent fission–fusion grouping, have the slowest life history among Atelinae (Symington 1990; Strier 1992; Shimooka 2005). Local variation within a genus or species in relationship to different environmental conditions may elucidate the ecological role in shaping life history parameters. The great apes have been intensively studied for many years at different sites and are the best subjects for examining these local variations.

Sumatran orangutans are more frugivorous and tend to associate more frequently than Bornean orangutans (van Schaik 1999; Wich et al. 1999; Delgado and van Schaik 2000). The association rate and time tend to increase with an increase in fruit availability (Sugardjito et al. 1987). However, the association of female orangutans or an increase in association of mother–offspring units along with an increase in food availability may not be linked with fast reproduction but does extend the inter-birth interval (Wich et al. 2004). Two models tried to explain these tendencies. The ecological energetic model predicts that the lower and unpredictable energy availability in Borneo may lead to reproductive output scheduled according to sufficient energy availability during the period of fruit abundance (Knott 2001; Knott et al. 2009). The ecological life history model predicts that the higher energy availability and lower mortality in Sumatra may lead to slow life history (Wich et al. 2004, 2009). Another explanation is that the difference in life history may be caused by female response to the ratio of flanged/non-flanged males and to their different mating strategies. In Sumatra, where more non-flanged males (trying forcible mating) are available, females may have slow reproduction (Delgado and van Schaik 2000). In Borneo, where more flanged males (trying monopolization of mating) are

available, females may have fast reproduction. However, more detailed observations on mating and reproduction are needed to verify these interpretations.

The slower physical maturation of frugivorous western gorillas compared to folivorous mountain gorillas may support the risk-aversion hypothesis (Breuer et al. 2009). The longer interbirth interval is also suggested for western gorillas, although no difference is observed in other reproductive parameters between them (Robbins et al. 2004). Between the subspecies of *Gorilla beringei*, some differences are observed in life history parameters (Table 9.4). In the montane forest of Kahuzi, *G. b. graueri* live at a lower altitude and have a more frugivorous diet than does *G. b. beringei* in the Virungas; they show slightly longer interbirth intervals and lower infant mortality than *G. b. beringei* (Yamagiwa et al. 2003). However, this difference may be caused by the presence or absence of infanticide by males, rather than ecological factors. Killing of infants by males occurred frequently in the Virunga gorilla population as a male reproductive tactic to hasten resumption of female estrus (Fossey 1984; Watts 1989). To avoid infanticide, females tend to travel with silverbacks (fully matured males) and to join a group with multiple males to seek more reliable protection (Watts 1996; Robbins 1999). These female strategies may reduce interbirth intervals in the Virungas. By contrast, infanticide has not been observed until recently in Kahuzi, and females occasionally form all-female groups for a prolonged period after the death of the leading silverbacks (Yamagiwa and Kahekwa 2001). Infant mortality (until the second year from birth) is higher for Virunga gorillas (33.9 %) than for Kahuzi gorillas (26.1 %), and 37 % of infant mortality in the Virungas was the result of infanticide (Watts 1991b; Yamagiwa et al. 2003). The interval between the death of an infant and a next birth for Virunga gorillas (1.0 years) is shorter than that for Kahuzi gorillas (2.2 years) (Yamagiwa et al. 2003). Female Virunga gorillas may find mates and resume reproduction more rapidly after the death of infants. Three cases of infanticide have recently been observed in a group of Kahuzi gorillas, and the birthrate in the groups is very high (Yamagiwa et al. 2009, 2011). The occurrence of infanticide may promote the fast life history of gorillas.

A comparison among four study sites of chimpanzees in natural habitats shows a similarity in interbirth interval (5.2–5.8 years on average). Age at first reproduction is also relatively constant among sites (13.2–14.3 years on average), except for chimpanzees at Bossou (10.9 years). Sugiyama (2004) attributed these findings to nutritional conditions. In Bossou, high-quality foods, such as fruits and nuts, are concentrated in the study group's core area, and their tool using behavior may mitigate low nutrition during the period of fruit scarcity (Sugiyama 1997, 2004; Yamakoshi 1998). Small group size and isolated conditions may also speed the start of female reproduction in Bossou. Group size of Bossou chimpanzees is kept around 20, which is far smaller than those of Gombe, Mahale, and Tai (30–100). The study group of Bossou has been isolated from neighboring groups for 26 years, and most of the females started their first reproduction in their natal groups (Sugiyama 2004). The study group included only one adult male for more than 10 years (who stayed as an alpha male for 20 years), and the maturing males emigrated, probably because of increased competition with the leading male (Sugiyama 1999). Isolation from

neighboring populations and the polygynous composition of the study group may have limited female mate choice to a single male and promoted their earlier start of reproduction. Females who gave birth in their natal group also were younger at their first birth than immigrant females in Mahale (Nishida et al. 2003). Females emigrating from their natal groups may suffer several costs for reproduction, such as reduced foraging efficiency in unknown ranges or harassment by resident females in the unfamiliar groups (Pusey 1980; Goodall 1986; Williams et al. 2002; Nishida et al. 2003).

Nutritional conditions also constitute limiting factors on the life history of great apes. Orangutans in captivity show faster reproduction than those in natural habitats (Knott and Kahlenberg 2007). Artificial feeding and grouping may permit faster growth and reproduction of orangutans than in their solitary natural habitats (Knott 2001). Rehabilitant free-ranging female orangutans also show an earlier age at first birth and a longer interbirth interval than wild females (Kuze et al. 2012). High energy intake from provisioning may enable their faster reproduction. The life history parameters of gorillas in natural habitats have been considered to be similar to those in captivity. A folivorous diet may supplement fruit scarcity, and the cohesive group formation with a one-male mating system may facilitate faster female reproduction at a level closer to their evolutionary potential (Tutin 1994; Harcourt and Stewart 2007). However, data on life history have come from folivorous mountain gorillas, and data in captivity are from frugivorous western gorillas. Recent studies on western gorillas in their natural habitats show a slower life history than captive gorillas, and regular provisioning may promote the faster life history of gorillas (Robbins et al. 2004; Breuer et al. 2009)

Female chimpanzees in captivity also tend to start reproduction earlier and have shorter interbirth intervals (Table 9.4). A rich nutritional condition from regular feeding, the limited selection of mates, and restricted movement may facilitate fast reproduction, as observed for Bossou chimpanzees. However, the interbirth interval at Bossou is longer than those in captivity and similar to those in natural habitats. Provisioned but free-ranging chimpanzees from the rehabilitation project in River Gambia National Park show a similar age at first reproduction and interbirth interval to those in natural habitats, rather than to those in captivity (Marsden et al. 2006). These observations suggest that limited movement under confined conditions may promote the shorter interbirth intervals of female chimpanzees in captivity.

## 9.5 Discussion

### 9.5.1 *Costs of Female Transfer*

In contrast to cetaceans, characterized by high mobility and animal diets in aquatic environments, the life history traits of primates with vegetarian diets are strongly linked with dispersal patterns of females. As primate socioecology predicts (Sterck et al. 1997), food availability and predation pressure shape female gregariousness

and association between sexes, which in turn change life history parameters. Most cetaceans form matrilineal social groups, and kin-related females tend to cooperate in rearing calves in a school (Kasuya 1995; Shane et al. 1986). Food availability relative to body size may affect the duration of lactation and thereby female reproductive strategies (Martin and Rothery 1993; Whitehead and Weilgart 2000; Mann et al. 2000). By contrast, some primate species (Atelinae and Hominidae) form nonmatrilineal groups in which females transfer, and female dispersal may promote slow life history (Strier 1999a; Kappeler et al. 2003; Harcourt and Stewart 2007). Our study suggests that male reproductive tactics, adding to ecological factors, may affect the cost of female transfer and shape the fast–slow continuum in the life history traits of female-dispersal species.

In both Atelinae and Hominidae, high gregariousness among females observed in howler monkeys and gorillas is linked with faster life history than fission–fusion grouping in spider monkeys, marmosets, and chimpanzees and solitary travel in orangutans. In female-dispersal species of primates, in which females usually start reproductive life after separation from their mothers or from their natal groups, frequent association with other conspecifics and high group cohesiveness may reduce costs of female foraging and promote rapid reproduction. Solitary travel is costly in terms of the need for vigilance against predators and for finding and occupying high-quality food patches, and these costs may lead to delayed age at first reproduction and a longer interbirth interval. Association with other adults, especially with a single male that positively takes care of an infant, will decrease these costs and enable them to develop a faster life history.

In male philopatric species such as woolly monkeys, spider monkeys, marmosets, and chimpanzees, differences in life history may reflect a female's flexible foraging efforts, according to the different spatiotemporal distribution of high-quality foods, as a means to attain reproductive success. Female atelines show large variations in grouping within and between species according to the distribution of high-quality foods (Symington 1990; Strier 1992; Shimooka 2005), and female chimpanzees also show large variations in grouping between and within species (Goodall 1986; Kano 1992; Boesch and Boesch-Achermann 2000). Female great apes may promote these variations as a way of coping with strong feeding competition because of their lower digestive ability for unripe fruits and mature leaves compared with Old World monkeys (Yamagiwa 2004). In both orangutans and chimpanzees, females with dependent infants tend to travel without other adult conspecifics (van Schaik 1999; Wrangham 1979), probably because of the higher costs of feeding competition. Female bonobos form larger parties than female orangutans and chimpanzees, and even females with dependent infants usually associate with other adult females and males. Large fruit patches available throughout the year and abundant fallback foods such as terrestrial herbs may mitigate the cost of grouping among bonobos (Wrangham 1986). Frequent sociosexual behavior may also reduce social tension induced by feeding competition among them (Kuroda 1980; Kano 1989; Kitamura 1989; Parish 1994). Female gorillas do not alter their grouping patterns in response to fruit availability, although they extend their daily path length with an increasing frugivorous diet (Goldsmith 1999; Doran et al. 2002; Yamagiwa et al. 2003).

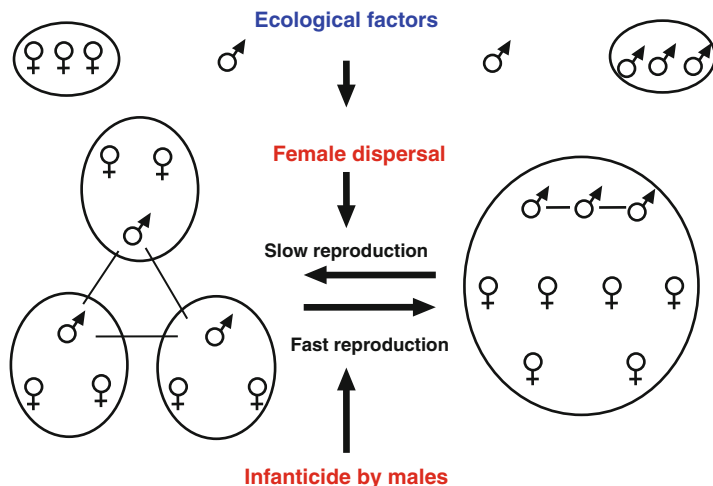
### 9.5.2 *Male Reproductive Tactics and Life History of Female Great Apes*

Sexual coercion of males may have strong influences on life history traits in female-dispersal species of primates. Infanticide by males promotes faster life history in howler monkeys and gorillas (Crockett and Janson 2000; Harcourt and Stewart 2007; Yamagiwa et al. 2011). To avoid infanticide, females move and choose males with which to associate, and they stay with males who have the ability to protect their infants. These movements result in stable associations between females and the protector males that lead to a fast life history.

Infanticide may shape local variation in group composition within the genus *Gorilla* through female strategies against it. In the Virungas, where infanticide by extra-group males frequently occurs, females tend to transfer into multiple male groups, seeking more protection against infanticide (Watts 1989, 1996). The female preference for multimale groups may have increased the number of females within the multimale groups and enabled maturing males to have a mating opportunity (Robbins 1995, 2001; Watts 1996, 2000; Robbins and Robbins 2005). The dominant males tend to tolerate mating by kin-related subordinate males and cooperate to defend their groups against solitary males or other groups (Robbins 2001; Watts 2003). A recent genetic analysis of paternity in four multimale groups in the Virungas indicated that both dominant and subordinate males enjoyed reproductive success, with the dominants siring an average of 85 % of group offspring (Bradley et al. 2005). Philopatric males tend to start reproduction earlier and to sire more offspring than dispersal males (Robbins and Robbins 2005). Female choice of multimale groups may have prevented male dispersal from the natal group and consequently promoted faster life histories of both males and females at Virungas (Harcourt and Stewart 2007).

By contrast, eastern lowland gorillas rarely form multimale groups and females occasionally transfer with other females and immatures at Kahuzi, where infanticide has rarely been reported (Yamagiwa et al. 1993; Yamagiwa and Kahekwa 2001). Although long-term studies have not yet been conducted on western gorillas in the lowland tropical forests, very little infanticide has been reported (Stokes et al. 2003). Frugivorous diets may prevent gorillas from forming large multimale groups in the lowland forests, and females may not have the option of transferring into multimale groups (Yamagiwa et al. 2003). Females tend to prefer to transfer into smaller groups and remain together to accept new males after the death of the leading male (Stokes 2004). Recent DNA analysis suggested a network among related males in separate but neighboring groups instead of forming multimale groups in the population of western lowland gorillas at Mondika (Bradley et al. 2004). Consequently, by forming a network of related males in neighboring one-male groups, rather than forming multimale groups, frugivorous western gorillas may be able to avoid infanticide (Fig. 9.3).

Although infanticide rarely occurs in species with male philopatry, it functions to reduce interbirth interval and may shape interspecies variation in spider monkeys



**Fig. 9.3** Variation in social structure and life history of *Gorilla beringei*

(Gibson et al. 2008; Shimooka et al. 2008). Their fission–fusion grouping is characterized by frequent associations among kin-related males within a group and communal defense by these males (Symington 1990, 1988; Strier 1992; Shimooka 2005). Within-group aggression among males and forced mating by males tend to occur in the groups of spider monkeys in which operational sex ratios were highly skewed toward males (Gibson et al. 2008). These observations suggest that competition among males over mates and male coercive mating may promote faster life history traits in atelines, although long-term data on individual demography are needed for further speculation.

By contrast, sexual coercion may promote a slow life history in the genus *Pan*. As do spider monkeys, both chimpanzees and bonobos form fission–fusion grouping and males tend to remain in their natal groups after maturity (Nishida 1979; Goodall 1986; Kano 1992). Females show promiscuous mating patterns, but their gregariousness and male mating tactics vary between species and across populations (Tutin 1979; Tutin and McGinnis 1981; Furuichi 1987). Male chimpanzees are generally more gregarious than females, and the most dominant males try to monopolize mating (Tutin 1979; Hasegawa and Hiraiwa-Hasegawa 1983; Boesch and Boesch-Achermann 2000). Males form a coalition for communal defense that occasionally results in fatal communal attacks in eastern chimpanzees (Goodall et al. 1979; Nishida et al. 1985; Watts et al. 2006). Infanticide by extra-group males also occurs as an extension of their territorial aggression (Goodall 1977; Hamai et al. 1992; Arcadi and Wrangham 1999; Watts and Mitani 2000; Muller 2007). Consequently, male eastern chimpanzees sire most of their offspring within their communities (Constable et al. 2001; Inoue et al. 2008; Wroblewski et al. 2009; Newton-Fisher et al. 2010). Infanticide by females was also observed in Gombe and Budongo and is considered as a female tactic for increased conflict over

resources with new immigrants (Goodall 1977; Townsend et al. 2007; Muller 2007). These aggressions may promote solitary travel of females, especially females with suckling infants, to avoid infanticide, and thus may lead to slow reproduction.

There are considerable differences in coalitional formation and intergroup attacks by males between western and eastern chimpanzees (Goodall et al. 1979; Nishida et al. 1985; Herbinger et al. 2001; Wilson and Wrangham 2003; Watts et al. 2006; Lehman and Boesch 2003). Female western chimpanzees tend to associate and groom with each other frequently at both Bossou and Tai compared to eastern chimpanzees (Sugiyama 1988; Boesch 1991; Lehmann and Boesch 2008). Nevertheless, the interbirth interval parameters of female chimpanzees at both Tai and Bossou and the age of first reproduction at Tai are similar to those of female eastern chimpanzees (Table 9.4). However, the age of first reproduction at Bossou is far earlier than those of other sites, reflecting the conditions observed in captivity. The uniqueness of Bossou chimpanzees is shown by their one-male group composition, where only one male monopolizes mating for a prolonged period (Sugiyama 2004). This social situation is similar to that in captivity, where most groups include only one adult male. Variations in social features between western and eastern chimpanzees are also explained by the distribution of defendable high-quality food resources and predation risk (Wittig and Boesch 2003; Lehmann and Boesch 2008). High nutritional conditions lead to a shorter interbirth interval in captivity than in the wild (Table 9.4). The age of first reproduction may be influenced by both nutritional conditions and male mating tactics, especially the degree of mating monopolization.

The influence of male mating tactics on the speed of life history is distinct between the two species of *Pan*. Male bonobos tend to associate with females rather than with other males, and their ranks reflect their mothers' ranks because of the mothers' strong support in agonistic conflicts between males (Kano 1992; Parish 1994; Furuichi 1997; Hohmann et al. 1999). Different groups of bonobos sometimes intermingle to stay together, and both females and males exhibit affiliative social interactions between groups (Idani 1990; Hashimoto et al. 2008). Weaker competition among male bonobos enables females to maintain stable association with males and may facilitate the search for mating partners and lead to a shorter interbirth interval than chimpanzees (Fig. 9.4).

In summary, male mating tactics may change the life history of the great apes in different ways. Female dispersal and independent reproduction from related conspecifics may enable them to form various social structures and flexible life history traits according to male mating strategies. Ecological factors basically shape the gregariousness of females in female-dispersal species, but they can choose from a wide variety of feeding strategies, from individual foraging to moving in cohesive groups. Males also take various mating tactics according to female movement and association patterns, which in turn also vary with male associations and mating strategies. Although the influences of these ecological and social factors on the life history of great apes differ between genera, between species, and between populations, the solitary nature may urge females to choose a slower life history, whereas stable associations between males and females may promote a faster life history (Fig. 9.5). Frugivorous orangutans and chimpanzees may suffer more costs of

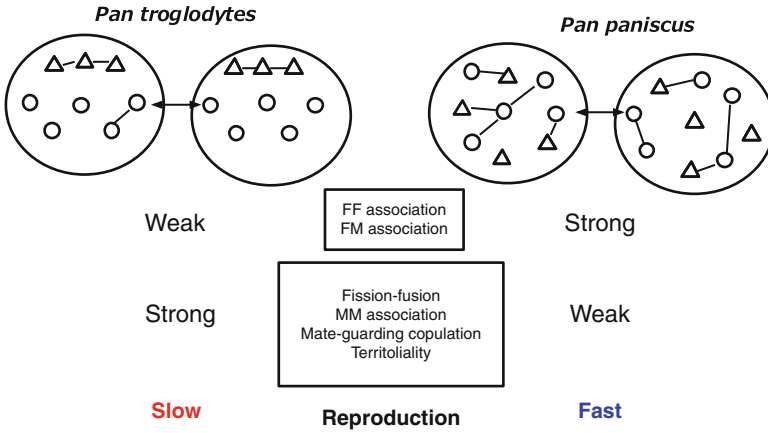


Fig. 9.4 Variation of social features and life history of *Pan*

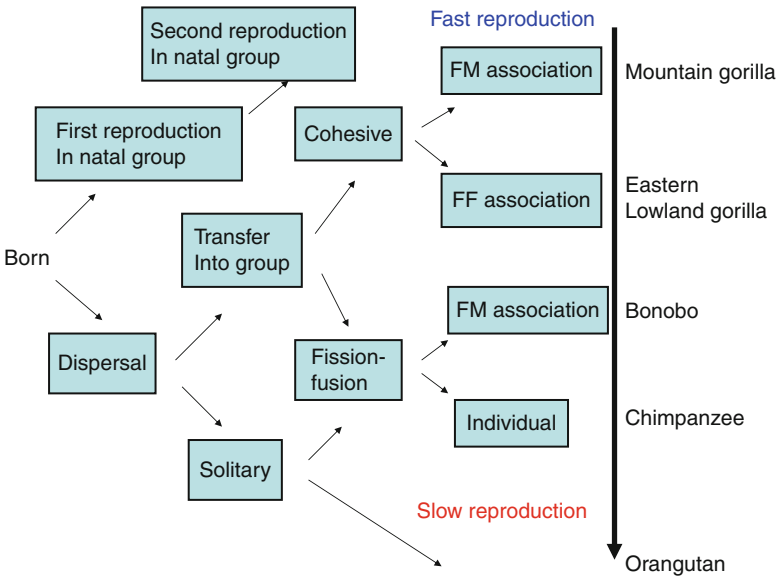


Fig. 9.5 Costs of female transfer and fast–slow continuum of life history

female movement through decreased foraging efficiency than folivorous gorillas, and chimpanzees with fission–fusion grouping may suffer more social stress than gorillas in highly cohesive groups. Such differences may generally shape the fast–slow continuum of life history in female-dispersal primate species.



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