Chapter 11
Evolution of Hominid Life History Strategy and Origin of Human Family

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Female Dispersal and Life History Traits in Primates

Group-living primates are classified into female-bonded species and female-dispersal species, based on the patterns of female dispersal after maturity (Wrangham 1980). Most of cercopithecines, including *Macaca*, *Papio*, *Theropithecus*, *Erythrocebus*, and *Cercopithecus*, form a group in which females remain during their entire life (Strier 1994). Kin-related females usually associate 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 reproductive success than females of kin-groups with lower rank (Drickamer 1974; Silk 1987; Itoigawa et al. 1992; Paul and Kuester 1996). On the other hand, females of Hominidae (orangutans, gorillas, chimpanzees, and bonobos) and Atelinae (howler monkeys, wooly monkey, spider monkeys, and muriquis) 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 dynamics of grouping (Wrangham and Smuts 1980; Goodall 1986; Strier 1992) reduce dominance effects and prevent

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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, b; Harcourt and Stewart 2007).

Female-dispersal species tend to have a slower life history (gestation length, weaning age, age at first reproduction, and inter-birth interval) than the female-philopatric species, except for neonatal weight and weaning weight, which may be determined in relationship to female body weight (Strier 1999a; Kappeler et al. 2003; Harcourt and Stewart 2007; Yamagiwa et al. 2014). Adding to ecological factors such as food availability and predation pressure, male reproductive tactics may affect the cost of female transfer and shape the fast–slow continuum (the degree of speed in reproduction and growth) in the life history traits of female-dispersal species. Female-dispersal species form various social structures, such as solitary, monogamous, polygynous, or multi-male/multi-female groups. Among female-dispersal species, Hominidae have the most diverse social structure and large variation in life history features.

Female orangutans, who usually live a solitary life, show the slowest life history in the wild (15.4 years old as the mean age at first reproduction and 9.3 years as the mean inter-birth interval for Sumatran orangutans, Wich et al. 2009). Maturing female orangutans need a longer time to establish their own home range and relationships with reproductive mates than female gorillas, chimpanzees, and bonobos, who transfer into other groups immediately after emigration. Female mountain gorillas show the lowest age (10.1 years old) at first reproduction and the shortest inter-birth interval (3.9 years) (Watts 1991a, b). Intensive caretaking of 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 inter-birth interval (Harcourt and Stewart 2007; Robbins et al. 2009; Yamagiwa et al. 2014).

Recent advances in DNA and isotope analyses have revealed a tendency of female dispersal and male philopatry in Pliocene–Pleistocene hominins, such as *Australopithecus africanus*, *Paranthropus robustus*, and *Homo neanderthalensis* (Copeland et al. 2011; Lalueza-Fox et al. 2011). Modern societies of hunter-gatherers are also characterized by female dispersal, although both sexes tend to disperse in most of them (Marlowe 2004; Alvarez 2004; Hill et al. 2011). However, human social structure has different features (multileveled based on family units, extended kinship, and daily fission–fusion dynamics) from those of great apes (Chapais 2011; Foley and Gamble 2009. Life history traits of modern humans are also different from those of great apes (later age at first reproduction, while shorter inter-birth interval). When and how did these traits emerge in human clade? The relationship between social and life history features unique to humans should be considered by reconstruction of human evolutionary history. In this chapter, I analyze the order of these features' emergence and the factors shaping them by considering those of great apes, fossil evidence, and the subsistence of foragers.

Uniqueness of Human Life History

Among mammals, primates show the slowest life history, such as long gestation, small litter size, long lactation, long juvenile period, long inter-birth interval, and long life span (Harvey et al. 1987; Read and Harvey 1989; Ross 1998). Modern humans have features similar to those of other primates but also have earlier age at weaning, shorter inter-birth interval, later age at sexual maturity, and longer life span compared to the great apes (Kaplan et al. 2000; Robson et al. 2006). Menopause (reproductive senescence) and an extended post-reproductive period are only found in human females (Thompson et al. 2007). These features unique to humans have possibly emerged with human-specific social features, such as communal breeding, strong parental investment, extended kinship, division of labor, and multilevel social structure (Foley and Gamble 2009; Chapais 2011). There have been many arguments over when and how these life history features unique to modern humans emerge in the evolutionary history of hominids.

Fossil evidence shows bipedal locomotion as the first morphological feature in the human clade after differentiation from *Homo–Pan* latest common ancestor (LCA) (Brunet et al. 2002). It may have decreased the energetic costs of terrestrial locomotion to expand daily range (Leonard and Robertson 1997). A dietary shift is expected in this period from vegetative foods to widely dispersed and nutrient-dense resources, such as nuts and underground tubers (Foley and Lee 1989; Laden and Wrangham 2005). Bipedalism also led to low-cost transport and complex tool use in the early stage of human clade (Kaplan et al. 2000). Sequential use of different woody tools by chimpanzees for collecting honey or termites has been observed in the wild (Boesch et al. 2009; Sanz and Morgan 2010; Wilfried and Yamagiwa 2014). Similar or more complex tool use is expected for bipedal hominins in later Miocene. Reduction of canine size in the early stage of human evolution suggests a reduction in aggressive interactions and a preference for cooperative intra- and intersexual relationships (Plavcan and van Schaik 1997; Plavcan 2000; Lovejoy 2009). The first sign of an increase in brain size (*Homo habilis* at 2 Ma) followed the emergence of stone tools for cutting meat from carcass (possible increase in meat consumption) at 2.3–2.6 Ma (Foley and Gamble 2009; Prat et al. 2005). The appearance of delayed maturation, which coincided with the increase in brain size, has been estimated from patterns of dental development (Smith 1994).

Delayed maturation is a common feature of great apes and humans, compared to other primates, but it is also the most conspicuous human feature. As a possible cause, the size of the birth canal may have imposed a constraint on brain growth in the course of human evolution. Bipedalism transformed the human pelvis so that it could support upper body weight with a narrow canal, through which a large brain could not pass (Rosenberg and Trevathan 1995; Lovejoy 2005). A human mother could not have a baby with a large enough brain to develop into adult size at the same speed as the brain of great apes. This obstetrical dilemma was solved by delivery of the fetus at a much earlier stage of development (Rosenberg and Trevathan 1995). The human brain functions at a high energy cost (Aiello and Wheeler 1995). In particular, the brain of a human child in the growing stage imposes the highest costs, and a large volume of fat supports the rapid brain development of a human baby (Cunnane and Crawford 2003). Providing much energy for brain development may have resulted in delayed maturation within human life history.

The earlier age at weaning and the short inter-birth interval may have interacted with each other and evolved in the early stage of human evolution (Lovejoy 1981). In order to increase fecundity, female mammals can adopt two reproductive strategies: (1) giving birth to multiplets and (2) increasing the number of births during the limited reproductive span. Among primates, some prosimians and new world monkeys tend to have twins or triplets. But old-world monkeys and great apes usually have a single baby at birth, and human ancestors may have adopted this second strategy. Early weaning leads to cessation of suckling and to resumption of cycling. Therefore, it may have shortened the inter-birth interval and increased the number of births and offspring.

Why did human ancestors increase fecundity? This is because since the late Miocene they have expanded their habitat into arid areas including fragmented forests, woodlands, and savanna (Reed 1997; Elton 2008), where they faced higher predation pressure than in the forest (Fig. 11.1). Terrestrial predators, such as lions and hyenas (more species with larger body size than the modern species in Africa in the late Miocene; see Hart and Sussman 2005), may have increased mortality of human ancestors, especially the mortality of immatures. They needed to compensate for this high mortality risk by increasing fecundity (Lovejoy 1981). Higher predation pressure leads primates to rapid life history traits (Janson and van Schaik 1993). Primates living in savanna and secondary forests (more unpredictable habitats) have higher birth rates and earlier age at first reproduction than in tropical rain forests (Ross 1988). Macaque species living in a variety of habitats, including open areas, have a shorter inter-birth interval and an earlier age at first reproduction than macaques living in the forest (Ross 1992). As with these nonhuman primates, high predation pressure led to rapid life history of human ancestors in the arid areas.

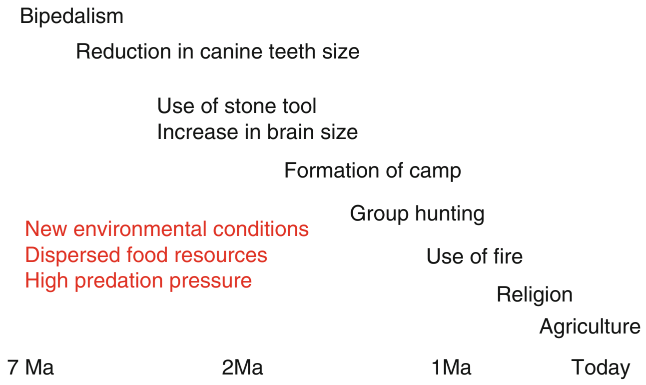

Fig. 11.1 Emergence of human-specific features

The uniqueness of human life history is its mix of slow (delayed maturation, later age at parturition, and long life span) and rapid traits (early age at weaning, short inter-birth interval). Such a complex combination of life history traits coincided with bipedalism and encephalization to solve various socio-ecological problems that human ancestors faced outside of tropical forests. Consequently, they acquired the ability to raise many independent children who grow up slowly. The formation of the human family might have been one of the strategies they took to survive such risky environments. Social features characterizing human family, such as monogamy, multilevel community structure, daily fission–fusion dynamics, exogamy, incest taboo, extended kinship, and division of labor (Imanishi 1961; Murdock 1965; Lovejoy 1981; Furuichi 2006; Aureli et al. 2008; Foley and Gamble 2009; Chapais 2011), might have coevolved with the unique life history traits of humans. However, direct comparisons between humans and great apes have been difficult until recently due to the lack of long-term data on great apes (Nishida et al. 2003; Wich et al. 2009; Yamagiwa et al. 2014). It is still unknown how the human family was created from common social and life history features among humans and great apes, although some authors tried to explain the relationships between life history traits and social features in the evolutionary history of hominids (Foley and Gamble 2009; Hill et al. 2009; Grueter et al. 2012; Chapais 2013).

In this chapter, I attempt to find strong links between particular social features and life history traits of humans as their survival strategies under fluctuating environments through comparisons with social and life history traits of great apes (orangutans, gorillas, chimpanzees, and bonobos). Unlike human ancestors, great apes have evolved within the tropical forests and have never extended their range far into the savanna. They all have relatively slow life history traits and common social and cognitive features, such as female dispersal and self-recognition (Goodall 1986; Kano 1992; Russon et al. 1998; Harcourt and Stewart 2007; Wich et al. 2009). These findings suggest that females reproduce independently from their relatives and that they have ability of intentional decision making. However, they also differ from each other in social features: solitary life of orangutans, polygynous and cohesive group of gorillas, and multi-male and multi-female groups with a high degree of fission–fusion dynamics of *Pan* species. The life history traits of hominids may have evolved with such variable social features of hominoids. Thus, I first compare life history traits among great apes and humans in order to find variability of traits within and between species in their evolution.

Comparison of Life History Traits Among Great Apes

The ancestral type of great apes first appeared in the early Miocene in Africa, differentiated into many species, and dispersed into Asia and Europe (Fleagle 1999). However, during these 20 Ma, the diversity of Cercopithecine monkeys increased, while the diversity of hominoids decreased (Andrews 1981). The reasons for this shift may be attributed to differences in feeding and life history strategies between cercopithecoids and hominoids, under the large climatic changes in the late Miocene and Pleistocene periods. Like modern great apes, fossil hominoids have larger body size than fossil cercopithecoids, possibly due to their weaker digestive abilities.

Great apes are less able to digest unripe fruit and mature leaves than are Cercopithecine monkeys, who have evolved specialized gut systems in which microbial fermentation precedes digestion and absorption (Parra 1978; Chivers and Hladik 1980; Lambert 1998, 2002). These dietary constraints may have forced great apes to broaden their diet and to increase their social flexibility. All great apes have a strong preference for ripe fruit and show various fallback food strategies during periods of fruit scarcity (Yamagiwa 2004). Vegetative foods, such as leaves, bark, and terrestrial herbs, constitute their fallback foods (Galdikas 1988; Knott 1999; Doran et al. 2002; Marshall and Wrangham 2007; Yamagiwa and Basabose 2009). Some fruits with a prolonged availability, such as figs, are used as filler fallback fruits by orangutans and chimpanzees (van Schaik 1999; Wrangham et al. 1993). Animal foods and tool-using behavior may also supplement the scarcity of fruit for chimpanzees (Yamakoshi 1998; Yamagiwa and Basabose 2009). Their grouping patterns basically reflect their tactics to mitigate ecological constraints (food shortage and predation) in the natural habitats. Large annual fluctuation in fruit availability may prevent arboreal and frugivorous orangutans from a prolonged group life (Galdikas 1988; van Schaik 1999). A folivorous and herbivorous diet enables terrestrial gorillas to form a cohesive group without territoriality between neighboring groups (Watts 1996; Yamagiwa et al. 2003; Doran-Sheehy et al. 2004). Fluid grouping of chimpanzees and frequent sexual interactions of bonobos mitigate the social tension caused by feeding competition (Wrangham 1986; Newton-Fisher et al. 2000; Boesch and Boesch-Achermann 2000; Basabose 2004; Kuroda 1984; Furuichi 1987). These differences in their socio-ecological features are linked to life history traits (Fig. 11.2).

As with other mammalian taxa, larger primates tend to show slower life history than smaller primates (Charnov 1991, 1993; Purvis and Harvey 1995). Besides, among primates, female-dispersal species show slower life history traits than female-philopatric species with the same body weight (Yamagiwa et al. 2014). The cost of female transfer may affect the fast–slow continuum in the life history traits of female-dispersal species. All female great apes tend to avoid reproduction in their natal groups. They need to choose a suitable range where they can get enough food and suitable mates for reproduction at their own discretion. Unlike some Cercopithecine monkeys that usually associate and form coalition with kin-related females, female great apes need to reproduce alone or among unrelated conspecifics. Such reproduction independent from their kin may delay the start of reproduction. As with the present great apes, the fossil hominoids may have social features of female dispersal and slow life history. Later age at first reproduction and longer inter-birth interval prevent great apes from having a swift increase in population size and, in particular, a rapid recovery from population crush. These differences in the speed of life history may have caused the shift from domination by hominoids to domination by cercopithecoids during the large climatic changes in the Miocene and Pleistocene.

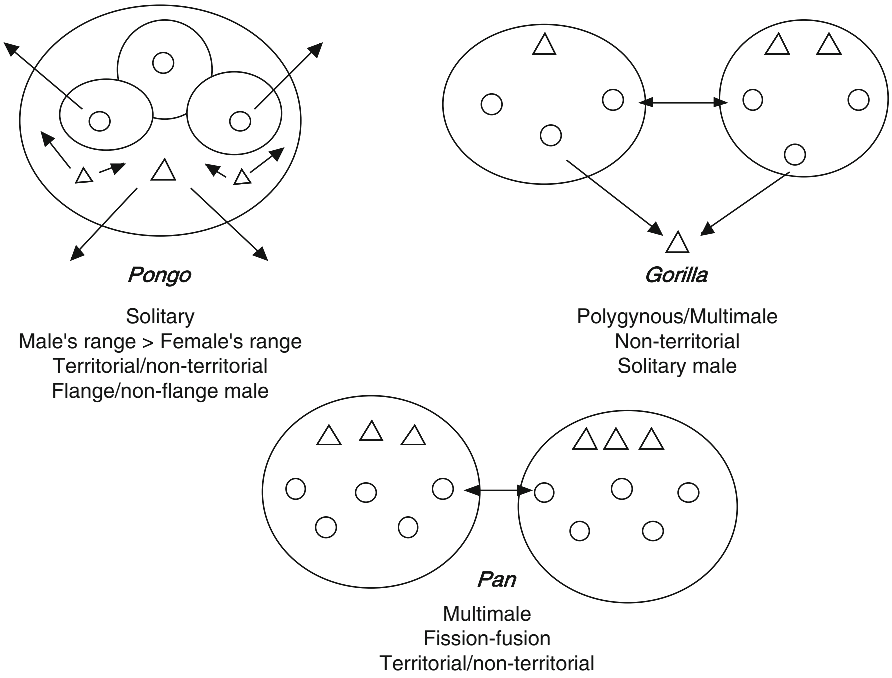

Fig. 11.2 Social structure of great apes

The differences in life history traits among great apes are inconsistent with female body weight (Table 11.1). The largest female gorillas have the lowest age at first reproduction and the shortest inter-birth interval. Although ecological factors, such as frugivorous diet and arboreal lifestyle, may promote a slow life history among extant apes (Doran et al. 2002; van Schaik and Deaner 2002; Wich et al. 2004), social factors may also influence the life history parameters of female apes (Furuichi 1997; Williams et al. 2002; Nishida et al. 2003; Harcourt and Stewart 2007; Wich et al. 2009; Yamagiwa et al. 2014). Female independent travel may have great influences on the fast–slow continuum in the life histories of female apes (Fig. 11.3). Female orangutans usually spend a solitary life and have the slowest life history. Solitary travel for weeks or months has rarely been seen for female chimpanzees, bonobos, or gorillas, who may easily find mates for reproduction in the group they join, and association with males may promote faster reproduction than orangutans (Goodall 1986; Boesch and Boesch-Achermann 2000; Watts 2003; Stokes et al. 2003).

Stable association between males and females and the male's care of infants may promote faster life history. The high dependence of female gorillas on a particular male with high protective abilities may hasten female reproduction, and the male gorilla's intensive care of infants, such as protection against predators or infanticidal males, tolerance for immature to feed close to him, playmate, and

Table 11.1 Life history traits of great apes and modern humans

Species	Adult female body mass	Neonatal mass	Endocranial volume	Gestation length	Age at weaning	Age at menarche	Age at first molar emergence	Age at first reproduction	Inter-birth interval	Maximum life span
	kg	kg	cm^3	Day	Year	Year	Year	Year	Year	Year
Orangutan	37.8	2	346	260	7	12	3.5–4.6	15.6	8.5	58.7
Gorilla	95.2	2.1	433	255	4.1	9	3.2	10	4.4	54
Chimpanzee	35.4	1.8	356	225	4.5	12	3.1–4.1	13.3	5.5	53.4
Bonobo	33.4	1.4	326	240	4.5	8.5		14.2	4.8	50
Modern human	45.5	3.3	1,212	270	2.8	16	4.7–7.1	19.5	3.7	85

Source: Robson and Wood (2008), Humphrey (2010), Marlowe (2012), van Schaik and Isler (2012), and Yamagiwa et al. (2014)

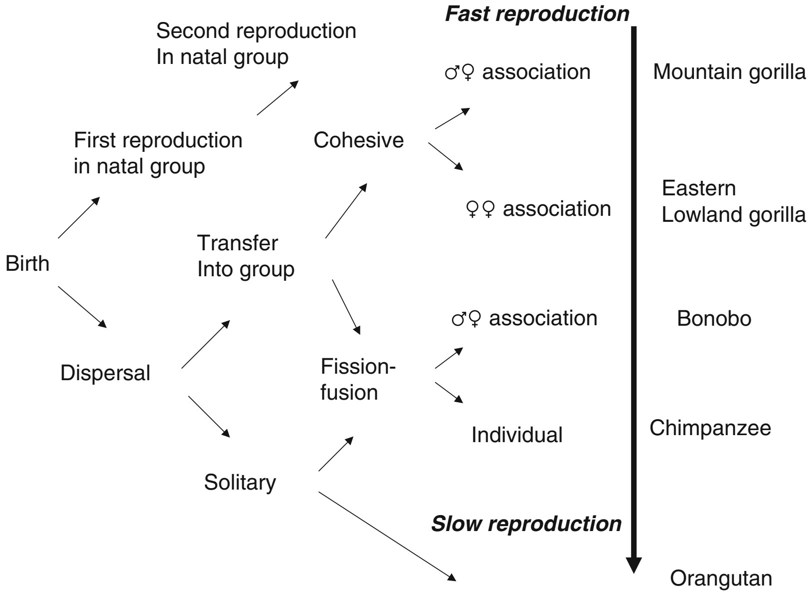

Fig. 11.3 Costs of female transfer and fast–slow continuum of life history

intervention of conflicts between immature, may facilitate weaning at an earlier age (Watts 2000; Harcourt and Stewart 2007). Although *Pan* species usually form a large group including females and males, they have longer life history traits than gorillas, probably due to the lack of the male's care of infants. Bonobos show lower degree of fission–fusion dynamics than chimpanzees (Goodall 1986; Kano 1992). High gregariousness and promiscuous mating in bonobos may facilitate their search for mating partners and lead to a shorter inter-birth interval than chimpanzees (Kano 1992; Furuichi and Hashimoto 2002; Yamagiwa et al. 2014). There are two types of sexually mature male orangutans (Galdikas 1985; Rodman and Mitani 1987; van Schaik and van Hooff 1996). A flanged male, with fully developed secondary sexual features, has his own territorial range and maintains antagonistic relationships with other males. A non-flanged male, mature but without these sexual features, roams between ranges of flanged males and occasionally forces females to mate with him. Female orangutans with dependent infants rarely associate with either type of male. The lack of the male's care of infants and protection may promote the female's solitary travel and preclude early weaning and reproduction (Delgado and van Schaik 2000; Wich et al. 2009).

Sexual coercion of males may have a strong influence on life history traits. Killing of infants by the male is regarded as his reproductive strategy to resume the mother's cycling, to increase mating opportunity, and thus to increase his reproductive success (van Schaik 2000; Kappeler et al. 2003). Infanticide by males has occurred in chimpanzees and gorillas (see below), while it has rarely been reported in gibbons, orangutans, and bonobos (van Schaik 2000). The high probability of paternity with pair bonding (gibbons), lack of estrous sign and less probability of prolonged consort with females in solitary life (orangutans), and confused paternity with highly promiscuous mating (bonobos) may have prevented males from developing infanticide as reproductive tactics. The male's tendency to increase the probability of paternity and the female's choice of multiple mating partners in chimpanzees and gorillas may constitute causal factors of infanticide. This has occurred frequently in mountain gorillas in the Virungas, while it has rarely been reported in other populations (Fossey 1984; Watts 1989; Yamagiwa et al. 2009). Mountain gorillas in the Virunga population are characterized by large group size and multi-male group composition. The risk of infanticide is highest in the absence of a mature male within a group (Watts 1989). In order to avoid infanticide, females tend to join a group with multiple males to seek more reliable protection, and this female choice may enable males to remain in their natal groups after maturity (Watts 1996; Robbins 1999). A comparison between Virunga (infanticide) and Kahuzi (no infanticide) populations shows higher infant mortality (34 % vs. 26 %), shorter interval between consecutive viable births (3.9 vs. 4.6 years), and shorter interval between the death of an infant and the next birth (1.0 vs. 2.2 years) in Virunga than in Kahuzi (Yamagiwa et al. 2003, 2014). Infanticide by males has occurred in eastern chimpanzees but not in western chimpanzees (Takahata 1985; Newton-Fisher 1999; Watts and Mitani 2000; Murray et al. 2007). However, this may not affect the inter-birth interval. A comparison among four long-term study sites (eastern chimpanzees, Gombe and Mahale; western chimpanzees, Taï and Bossou) shows a similarity in inter-birth interval (5.2–5.8 years on average). On the other hand, the age at first reproduction in Bossou (10.9 years on average), where no infanticide has been reported, is earlier than those of other populations (13.2–14.3 years). Highly nutritional foods and isolated conditions may influence the age of first reproduction in Bossou (Sugiyama 1997, 2004). The study group of Bossou has been isolated from neighboring groups for 26 years. Most of the females had first reproduction in their natal group, and a single mature male monopolized copulation with females for more than 10 years (Sugiyama 1999, 2004). These observations suggest that a male's monopolized copulation promote rapid reproduction, while conflicts among males that cause coercive copulation and infanticide may lead to slow reproduction.

Based on comparisons of these variations in social and life history features among great apes, we can imagine possible features for human ancestors, when they started a new life outside tropical forests. First, our human ancestors may have had female-dispersal features, since all female great apes tend to disperse from their mothers. Second, they might have had from the beginning a slow life history (later age at weaning, later age at first reproduction, and longer inter-birth interval) as observed in all great apes. Third, the possible ecological factors promoting rapid life history traits of human ancestors include high predation pressure, which increased infant mortality, and provisioning, which improved the nutritional conditions of females and immatures. Fourth, the possible social factors promoting rapid life history traits of human ancestors include stable associations among females and prolonged associations of females with the particular males that protected them against predation and infanticide. The male's abilities of protection and infant care would have been important for human ancestors to survive in open land with high predation pressure and sparse distribution of high-quality foods.

Suggestions from Fossil Evidences of Human Ancestors

The arguments for the social structure of human ancestors have been based on sexual dimorphism in body weight and canine teeth, due to the high correlation between them (Lovejoy 1981; Plavcan 1993). Among modern primate species, large sexual dimorphism in body weight is linked to a polygynous social structure, and the height of canine teeth indicates the intensity of the male's aggression (Clutton-Brock et al. 1977; Plavcan 1993; Fleagle 1999). However, the relation of the two indexes in human evolutionary history is still unclear; sexual dimorphism in body weight decreased gradually, while the height of canine teeth was already low in the early stage of human evolution such as *Ardipithecus ramidus* (Plavcan and van Schaik 1997; Suwa et al. 2009). The body weight of male *Australopithecus afarensis* (3–3.5 Ma) was estimated to be more than 1.5 times that of the female by comparison, although much smaller dimorphism was estimated (Fleagle 1999); this ratio is 1.1–1.2 for modern humans, 1.2–1.3 for modern chimpanzees, and 1.5–1.7 for modern gorillas (McHenry and Coffing 2000). On the other hand, the height of canine teeth in *A. afarensis* was very small, as also observed in modern humans. Recent findings of *Ardipithecus ramidus* (6 Ma) show low height of canine teeth in both sexes, similar to the canine size of female chimpanzees (Suwa et al. 2009). Plavcan (2000) explained such inconsistencies by citing different selections for body weight and canine teeth: Predation pressure favored large sexual dimorphism in both traits, but frequent use of tools such as weapons for fighting may reduce the function of the male's canine teeth.

Recent studies on *A. afarensis* using random sampling methods show smaller sexual dimorphism in body mass similar to modern humans (Reno et al. 2003, 2010). Moreover, the body mass of *A. ramidus* is considered as nearly monomorphic (Lovejoy et al. 2009; White et al. 2009). These reports support the prediction that human ancestors such as *A. ramidus* in the early stage of evolution had already acquired bipedalism, reduced sexual dimorphism, and monogamous social structure with provisioning by males (Lovejoy 1981). Although there are still many arguments over sexual dimorphism in *A. afarensis*, we can hypothesize that the *Homo–Pan* LCA had a social structure with female dispersal similar to chimpanzees, but with more monomorphic characteristics than chimpanzees. White et al. (2009) predicted that the large canine teeth of male chimpanzees had appeared after differentiation from the human lineage and that terrestrial locomotion and high predation pressure in open land had increased sexual dimorphism in the body mass of *A. afarensis*.

One of the distinct features in the life history of humans is early weaning (Table 11.1). Modern humans living in traditional and natural-fertility societies without birth control wean at 2–3 years, which is younger than great apes based on the estimation from inter-birth intervals (gorillas: 3–4 years, chimpanzees: 5–6 years, orangutans: 7–9 years). Early weaning has the function of stopping the lactational suppression of ovulation and thus reducing inter-birth interval, but it increases risks such as infant mortality and morbidity from infectious and parasitic diseases that potentially restrict growth and development (Taylor et al. 1999; Kennedy 2005). In nonhuman primates, weaning tends to occur when the infant reaches about 33 % of adult body weight (Charnov and Berrigan 1993) or when the first molar (M1) erupts (Smith 1992). Based on these assumptions, the weaning age of modern humans is 5–7 years, far older than the actual weaning age. Apparently our ancestors selected rapid population growth by early weaning, despite its high risks (Martines et al. 1994). This feature has probably evolved in open land with high predation pressure, as observed in nonhuman primates (Ross 1992; Janson and van Schaik 1993). The feature of early weaning had already started in *Homo neanderthalensis*, from analysis of barium distributions in teeth on cessation of breast-feeding at 1.2 years (Austin et al. 2013). It has also coevolved with encephalization. Kennedy (2005) argued that selection in humans had favored not merely the survival but also the intellectual potential of the child and, moreover, suggested that the early shift to adult foods had been necessary at a critical period of neurological development. However, if early weaning was the tactic used to increase fecundity as compensation for increased mortality in open lands, it had possibly started in the early stage of human evolution, when human ancestors extended their range into the savanna (Fig. 11.4). In the savanna environment, population growth

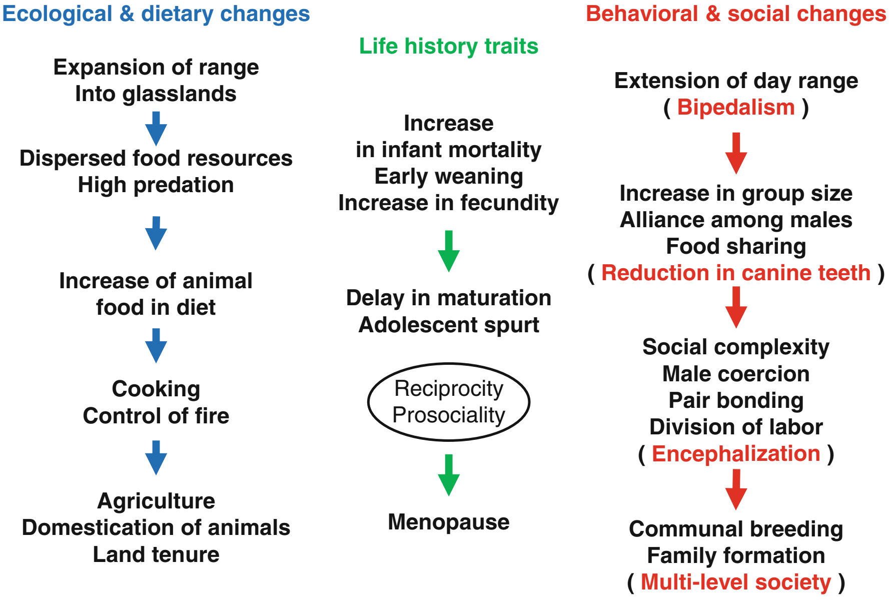

Fig. 11.4 Evolutionary history of hominids

is not expected to have occurred with the late weaning and long inter-birth interval that are characteristics of the modern great apes living in tropical forests with more stable food availability and security (Galdikas and Wood 1990; Nishida 1990; Watts 1991b). Early weaning, therefore, would have been accompanied by innovations in foods and improvement of security in the savanna.

Some important behavioral shifts possibly occurred in the evolutionary history of humans. First, the division of labor for gathering foods appeared as an extension of food sharing before encephalization (Lovejoy 1981). Food sharing or transfer is observed in nonhuman primates, especially in great apes and callitrichids (Feistner and McGrew 1989; Price and Feistner 1993; Huck et al. 2004). In chimpanzees, meat and plant foods are frequently shared among the same community's members, and food transfer has been suggested as a means of trade for social commodities such as grooming, coalition, and sexual access (McGrew 1975; Nishida et al. 1992; Boesch and Boesch-Achermann 2000). The high level of food transfer in callitrichids may be related to their cooperative breeding system. From phylogenetic analyses of food transfer in primates, Jaeggi and van Schaik (2011) predicted that food sharing among adults only evolved in species already sharing with offspring, regardless of diet. However, nonhuman primates rarely transport foods to share with their conspecifics. Great apes and humans have no cheek pouch to temporarily stock foods being processed as do some Cercopithecine monkeys, and their feeding is limited to food patches. In the savanna, where human ancestors extended their range, dispersed foods and high predation pressure may have forced them to select safe feeding places for immatures. Adult individuals changed association patterns with daily fission–fusion dynamics for gathering, transporting, and sharing foods with their offspring and exchanged information in the limited safe site, which led to information center, central place for foraging, and home base (Isaac 1978; Potts 1984; Marlowe 2006; Aureli et al. 2008). Bipedalism may have promoted such tasks as using hands for transporting foods (Lovejoy 1981). Early weaning implies the presence of effective parental provisioning (Galdikas and Wood 1990). Frequent food sharing may have improved nutritional conditions to increase fecundity, which in turn promoted cooperative breeding and food sharing. High-quality foods such as nuts and underground tubers were also exploited using tools for provisioning and sharing (Wrangham and Conklin-Brittain 2003; Wood and Strait 2004).

A second type of behavioral shift probably occurred prior to encephalization. A larger brain needs more energy intake from high-quality foods, and this requirement possibly increased animal foods in the diet of human ancestors (Aiello and Wheeler 1995). The first increase in brain size appeared in *Homo habilis* at approximately 2 Ma. Evidence of the first stone tools was found in Ethiopia and dated at 2.3–2.6 Ma, and these are assumed to have been used as knifelike wedges (Kimbel et al. 1996; Semaw et al. 2003). Bones bearing cut marks found nearby indicate that these stone tools were used for butchery and carcass manipulation. These findings suggest that the shift to tool-assisted butchery and scavenging appeared prior to the distinct increase in brain size (Asfaw et al. 1999; Semaw et al. 2003).

The third behavioral shift may have preceded the final increase in brain size to the level of modern humans at 0.6 Ma. The large brain of modern humans (three times larger than that of gorillas) needs more than 20 % of basal metabolic rate compared to 13 % on average for nonhuman primates, while there is no evidence of an increase in basal metabolism due to an enlarged brain (Aiello and Wheeler 1995). Aiello and Wheeler (1995) compared organ mass and shape of the rib cage among humans, nonhuman primates, and *Australopithecus afarensis*, and they hypothesized that a possible solution to this dilemma was the compensation of energy by a reduction in gut size. Since gut size is associated with diet and digestibility of food (Milton 1986; Martin 1990), the increase in meat consumption and cooking by using fire may have contributed to the supply of more energy to the brain by improving food quality and digestibility (Aiello and Wheeler 1995; Wrangham 2006, 2009). The evidence of fossils and their remains shows the gradual increase in the use of tools and fire for processing animal tissue by *Homo erectus* (Shipman and Walker 1989; Goren-Inbur et al. 2004; Berna et al. 2012).

The last behavioral shift was agriculture and domestication of animals to produce nutritious and digestible foods around the beginning of the Holocene. These remarkable innovations in human-specific foods promoted settlement and formation of communities, which led to systematic activities to improve life history strategies of *Homo sapiens*. However, life history traits unique to humans, such as early weaning, late eruption of molar teeth, delayed somatic development, short interbirth interval, and long post-reproductive period, had already appeared before the emergence of agriculture. The important questions, therefore, are when these traits appeared and which social features were created to support them.

Encephalization undoubtedly led to delayed somatic development, since the rapid growth of the human brain requires allocation of energy to brain growth. Using the volume of the braincase as a proxy for brain size, Zollikofer and Ponce de Léon (2010) concluded that large neonate brains and high sustained growth rates after birth were already present in the LCA of *H. sapiens* and *H. neanderthalensis* at least 0.5 Ma. Recent reports indicate that *H. erectus* had a somatic growth trajectory more similar to chimpanzees than to modern humans, although they attained body sizes in the range of modern humans, as observed in the Nariokotome boy (Anton 2003; Gurven and Walker 2006; Dean 2007). Rapid brain growth and delayed somatic growth brought *H. erectus* and *H. neanderthalensis* immobile infants and an adolescent growth spurt (Leigh and Shea 1996; Leigh 2001; Gurven and Walker 2006).

The adolescent growth spurt also occurs in great apes, but at earlier ages than in modern humans (Leigh and Shea 1996). It occurs in the somatic growth trajectory of both female and male humans, while it is only distinct in male apes (Bogin 1999a, b, 2001; but see Hamada and Udono 2002). Analyses of growth trajectories in skeletons of *H. neanderthalensis* show the presence of an adolescent growth spurt in both sexes (Ruff et al. 1997; Churchill 1998; Zollikofer and Ponce de Léon 2010). Adolescence includes the long period (10–18 years for girls, 12–21 years for boys) of postpubertal growth in modern humans, and teenage girls and boys remain immature in terms of sociocultural knowledge and experience (Schlegel and Barry 1991; Kaplan et al. 2000; Bogin 2009). The adolescent growth spurt may cause many problems for human children, who start to have various social interactions outside their families in complex societies.

The problems after the early weaning and during the adolescent growth spurt required alloparental care and facilitated cooperation within and between groups, which probably led to a new organization of human society. If early weaning evolved to increase the fecundity of hominids, frequent food transfer and communal breeding may have developed to support it, as observed in tamarins and marmosets (Ruiz-Miranda et al. 1999; Huck et al. 2004; Rapaport 2006). Hawkes et al. (1998) hypothesized that selection for lower adult mortality and greater longevity (extension of postmenopausal period) allowed for evolution of prolonged growth in hominids (the "grandmother hypothesis"). However, while data on modern hunter-gatherers indicate the great contributions of post-reproductive women to child care, tool making, and food processing, there is no evidence of reproductive success in post-reproductive women (Kaplan et al. 2000). Fossil and archaeological data suggest no evidence that a sufficient number of older individuals survived to provide significant aid in child care (Kennedy 2003). A comparison of the ratio of older to younger adults in Paleolithic and Neanderthal fossil sites suggests that a distinct survivorship of older individuals appeared in the Upper Paleolithic and that it is not a biological attribute but reflects cultural adaptations (Gaspari and Lee 2006). Bogin (2009) proposed an alternative hypothesis that the development of increased biocultural resilience during the years of human growth and development promotes greater survival to adulthood, adult survival, longevity, and reproductive success (reserve-capacity hypothesis). Based on these arguments, we can conclude that first the early weaning occurred to increase fecundity in the evolutionary history of hominids, then the adolescent growth spurt followed the increase in brain size, and finally the extension of longevity after menopause appeared in recent times.

Social Evolution and Emergence of Human Family

As described previously, common social features among great apes suggest that our *Homo–Pan* LCA may have had a society characterized by female dispersal (Table 11.2). Due to its high costs, female dispersal occurs in primate species living in and around tropical forests, in which high-quality foods such as fruit are available during the whole year and arboreal life protects them against terrestrial predators (Yamagiwa et al. 2014). An exceptional example is *Hamadryas* baboons living in grasslands within a multilevel society, in which small polygynous groups aggregate to form a large band or troop and females transfer within bands (Kummer 1968). The lack of competitive food resources in grasslands may prevent females from forming kin-based coalitions, and the high predation pressure may lead to frequent association and alliance formation among males of different polygynous groups (Barton et al. 1996). Adding to these ecological factors, sexual coercion, including infanticide, may have promoted cooperation among kin-related leader males of different groups and facilitated modular society (Grueter et al. 2012). When early hominids extended their range into open land, they may have faced the same problems as papionins in promoting a multilevel social system.

Table 11.2 Social features and mating strategies of great apes and modern humans

Species	Social structure	Dispersal/philopatry	Sexual dimorphism in body mass	Mating system	Sign of estrus	Paternal care	Infanticide
Orangutan	Solitary	♂ ♀ dispersal	2.2	Temporal consort	None	None	None
Gorilla	Unimale or multi-male polygyny	♀ dispersal, ♂ dispersal/philopatry	1.6	Prolonged consort	Slight swelling	Frequent	Occasional
Modern human	Multileveled with families	♂ ♀ dispersal/philopatry	1.2	Prolonged consort	None	Frequent	Occasional
Chimpanzee	Multi-male and multi-female	♀ dispersal, ♂ philopatry	1.2	Promiscuous	Exaggerated swelling	Rare	Occasional
Bonobo	Multi-male and multi-female	♀ dispersal, ♂ philopatry	1.3	Promiscuous	Exaggerated swelling	Rare	None

Source: Mitani et al. (1996), Furuichi and Hashimoto (2002), Lindenfors (2002), Harcourt and Stewart (2007), Utami et al. (2009), and Marlowe (2012)

The distinct difference in social organization among great apes is male dispersal (orangutans and gorillas) or philopatry (chimpanzees and bonobos), although local variation in the degree of male dispersal is found in gorillas. Male orangutans tend to disperse in a wider range than female orangutans (Singleton and van Schaik 2002; Knott et al. 2008; Morrogh-Bernard et al. 2011), while male gorillas tend to remain near the range of their natal groups or to breed in their natal groups (Robbins et al. 2004; Bradley et al. 2004; Stoinski et al. 2009; but see Inoue et al. 2013). Although the recent isotopic and genetic analyses of fossil hominids predict the tendency of female dispersal and male philopatry (Copeland et al. 2011; Lalueza-Fox et al. 2011; Vigilant and Langergraber 2011), it is not a strong tendency and the dispersal patterns of both sexes is dominant in the present hunter-gatherers (Marlowe 2004; Alvarez 2004; Hill et al. 2011). These may suggest that the strict male philopatry of *Pan* species is derived after the differentiation of the chimpanzee and human clades and that patrilocality in humans became more prevalent with food production by agriculture and livestock raising (Destro-Bisol et al. 2004; Koenig and Borries 2012).

Which factors have promoted multilevel social structure with kin-based male coalition and a particular male–female pair bonding unique to humans? High predation pressure possibly strengthened coalition among males against predators, and increased fecundity led to food sharing and communal breeding in early hominids (Fig. 11.5). Group size along with the number of mates for copulation should have increased. In such a situation, papionins increased sexual dimorphism to reinforce the male’s ability of mate guarding (Grueter et al. 2012). Another choice was to increase promiscuity as observed in chimpanzees and bonobos with overt

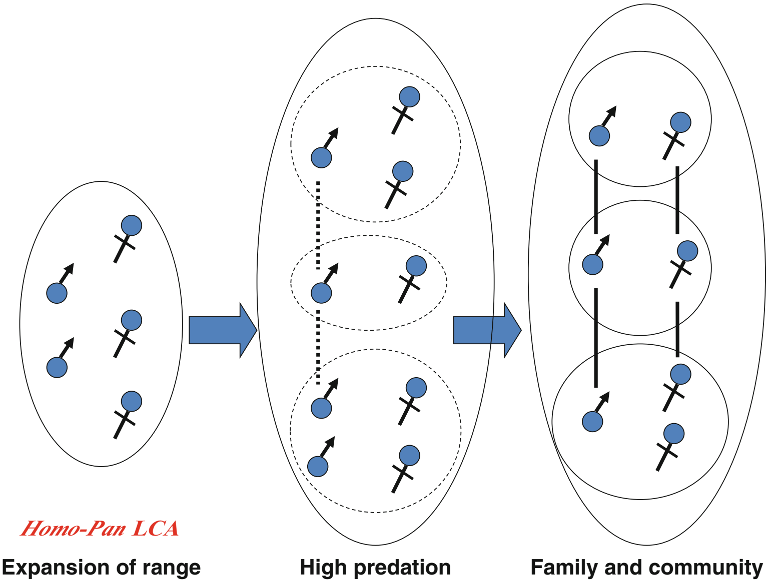

Fig. 11.5 Human ancestral society

sexual swelling (Nishida and Hosaka 1996; Kano 1992). However, human ancestors may not have adopted either option. Fossil evidence indicates that the height of the canine teeth was low in the early stage of human evolution (Plavcan 2000; Suwa et al. 2009), and the social structure of the present hunter-gatherers (Turnbull 1961; Marlowe 2003; Kaplan et al. 2009; Layton et al. 2012) suggests that a monogamous mating system has been common in human societies since before the emergence of agriculture and land tenure. Grueter et al. (2012) hypothesized two steps for emergence of multilevel human society. The first step was from the multi-female and multi-male group with promiscuous mating to the multiharem group with polygyny as observed in all multilevel societies of nonhuman primates, and the second step was from polygyny to monogamy in response to an increase in the dependency of children and in paternal investment. However, promiscuity was not the common feature of great apes and humans, and *Homo–Pan* LCA may not have showed overt sign of estrus. Sillén-Tullberg and Moller (1993) analyzed the relationship between monogamous mating systems and visual signs of ovulation in nonhuman primates phylogenetically, and they concluded that the lack of ovulatory signs is more likely to promote monogamy than vice versa. These findings suggest that large canine teeth and the overt swelling of sexual skins observed in *Pan* species are features derived after differentiation from the human clade. The *Homo–Pan* LCA may have had a society in which sexual dimorphism was low and females did not show visual signs of ovulation.

An increase in brain size and the subsequent delay in somatic growth may have increased parental investment in offspring to a longer period. The brain size (1,400 g) of modern humans is 3.5 times larger than that of chimpanzees. It is approximately 2.3 % of the body weight and uses approximately 23 % of the body's daily energy requirement (Aiello and Wheeler 1995). The brain of a newborn infant needs 74 % of the body energy intake, and juveniles at the age of 10–11 years still need 34 % (Holliday 1971). Human babies are born with large body fat deposits as insurance for the developing brain (Cunnane and Crawford 2003). Just before birth, fat deposition on the human fetus accounts for 90 % of its weight gain (Battaglia and Meschina 1973). Therefore, human brain evolution depended on an abundant, reliable, and nutritious food supply for a long period during pregnancy and after birth. When the brain size of *Homo habilis* increased at 2 Ma, they did not hunt live game but collected high-quality foods such as carrion, marrow, and tubers. Use of fire and cooking may have gradually reduced gut size to provide more energy for brain development (Aiello and Wheeler 1995; Wrangham 2009). Provisioning would have been prevalent among adults, and the division of labor was promoted under the risky environments of large terrestrial predators. The complexities of diet and social life followed the increase in brain size (Jerison 1973; Clutton-Brock and Harvey 1980; Milton 1981; Dunbar 1996). Ripe fruits, extractive foods, tool use, and increasing group size with complex social interactions improved the memories and intellectual behavior of *H. erectus*, *H. neanderthalensis*, and *H. sapiens*. In the forager societies, human juveniles have a long dependency on adults, and men provide most of the energy surplus that is used to subsidize juveniles and reproductive-aged women (Kaplan et al. 2000).

These requirements from life history strategies unique to the *Homo* clade probably promoted the division of labor between sexes and reinforced the formation of family, the basic reproductive unit of humans, which had already been created in the early stage of human evolution. Division of labor in protection, gathering food, cooking, provisioning, and cooperative rearing of infants may have strengthened bonding between monogamous pairs and among related females (Wrangham 2009; Hrdy 2009).

Human sociality is strongly based on the abilities of empathy and other-regarding sentiments (Batson and Powell 1998; Fehr and Fischbacher 2005. Cooperation and reciprocating interactions observed in nonhuman primates imply deep roots of empathy in primate evolution (de Waal 1996; Silk 2007). In particular, chimpanzees show a wide range of cooperation in forming coalitions, hunting, sharing food, and patrolling their range borders (Nishida and Hosaka 1996; Mitani et al. 2000; Boesch and Boesch-Achermann 2000). They also show compassion and empathy for others in distress or injury (Boesch 1992; O'Connell 1995; Flack and de Waal 2000). However, most cooperative activities in nonhuman primates are limited among kin relatives or within a group, and the other-regarding behavior of chimpanzees is mostly based on selfish motivation (Jansen et al. 2006; Vonk et al. 2008; Yamamoto and Tanaka 2010; Silk and House 2011). By contrast, humans participate in a wide range of activities that benefit others including non-kin individuals and non-group members, and they show regard for the welfare of other people who are poor, sick, or aged (Fig. 11.6). The emergence of these prosocial behaviors would have been after the differentiation of the *Pan* and human clades.

Recent studies on callitrichids suggest that other-regarding preferences may have developed in cooperative breeding. Burkart and van Schaik (2011) compared social tolerance and service to other group members among Japanese macaques (independent breeding system), common marmosets (cooperative breeding system),

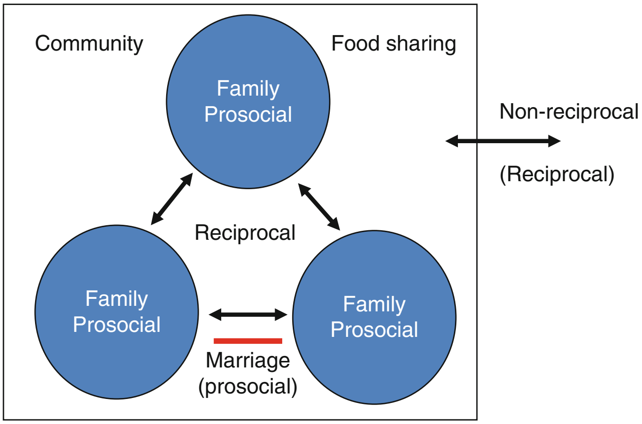

Fig. 11.6 A community structure of modern humans

and capuchin monkeys (an intermediate breeding system), and they concluded that social tolerance was slightly higher in marmosets than in capuchins and much higher in both compared to macaques, but only marmosets provided service to other group members. In common marmosets, the extent of expressed prosociality was positively correlated with the duration of the pair bond as well as with the number of offspring produced together (Burkart et al. 2007). The limited other-regarding behavior in great apes implies that the evolution of prosociality may not require advanced cognitive ability but rather evolved along with cooperative breeding. Early weaning and delayed maturation resulted in similar conditions to those of callitrichids in early hominids, as shown by caring for many independent infants in cooperation with other group members. Provisioning was indispensable for weaned infants with large, rapidly growing brains. The high risk of predation promoted an association of several family groups and division of labor between females and males and probably promoted male's collection and transportation of digestible and high-nutritional foods for females and infants at the safe place. These conditions facilitated the prevalence of food sharing among adults (Jaeggi and van Schaik 2011). Thus empathy, sympathy, and prosociality derived from communal breeding, and provisioning in risky habitats may have led to the formation of large groups including several families in human ancestral societies.

The first possible human family in human clade is assumed to be monogamous and polygynous groups that were associated loosely in a community. Females lacked any sign of estrus and transferred between family groups within or between communities, and males dispersed from their natal family groups to search for mating partners, but remained in a community to cooperate with kin-related males. A community with substructures of various compositions of families had a tendency of fission–fusion dynamics for different daily tasks (Aureli et al. 2008). Increased animal foods in the diet of *Homo* clade facilitated encephalization, and early weaning and subsequent delayed maturation further reinforced cooperative breeding and division of labor for provisioning their offspring, which had been created in the early stage of human evolution. Increased requirements of provisioning also promoted preparation of high-quality foods by using tools and fire in *Homo* clade. These changes in life history and feeding technology led to a multilevel community structure in which several families cooperated with each other in diverse tasks of subsistence. This formation might have been resilient against severe conditions in arid areas and enabled *Homo erectus* to expand their distribution out of Africa. The most important innovation in diet at this stage was cooking and control of fire. Cooking increased the digestibility of plants and meat and conserved energy and time for brain growth and social interactions (Wrangham et al. 1999; Wrangham and Conklin-Brittain 2003; Boback et al. 2007). It also facilitated bonding between individual females and males to facilitate a family formation within the larger community structure (Foley and Gamble 2009). These nested social structures in which family units were embedded within larger kin-based communities characterize human society at present (Chapais 2011). Brain size became equivalent to that of modern humans between 600 and 300 Ka (*Homo heidelbergensis* and *H. neanderthalensis*). Fossil evidence shows that both childhood and adolescent stages (early weaning and delayed maturation with a distinct spurt in somatic growth) emerged by 780 Ka (Thompson et al. 2003). Before reaching the brain size of modern humans, hominids would have established cooperative provisioning and care of offspring during a long dependency. Most of the life history traits unique to humans are found in both *H. neanderthalensis* and *H. sapiens* before the emergence of agriculture and the domestication of animals (Foley and Gamble 2009; Chapais 2013). The cognitive ability of modern humans grows rapidly to a peak of 26 years and then gradually decreases while maintaining a high level until 60–80 years of age (McArdle et al. 2002). This suggests the great contribution of aged individuals to the development of human children (Bogin 2009). However, a prolonged post-reproductive period is found only in the Upper Paleolithic (Gaspari and Lee 2006). Menopause is not found in great apes, and there is little evidence on the survival of aged or handicapped individual until the emergence of modern humans (Thompson et al. 2007; Bogin 2009). This implies that extension of the post-reproductive span necessitated additional social skills, such as language. Communication using language enabled aged people to transmit their past experiences and knowledge to younger generations and facilitated nursing behavior for aged people with strong other-regarding sentiments. Biocultural development would have enabled modern humans to acquire such features.

Conclusions

Modern humans have unique life history traits compared to great apes, such as earlier age at weaning, later age at sexual maturity, shorter inter-birth interval, and longer life span. These features did not emerge together in the evolutionary history of hominids but interacted with each other to promote human adaptive abilities to new environments out of tropical forests and out of Africa. I analyzed the order of these traits' emergence and the factors shaping each trait by considering the life history traits of great apes, fossil evidence, and the subsistence of foragers.

A comparison with great apes predicts that changes in diet and social features may have preceded or coincided with the development of human's life history traits. Based on a comparison of social features among great apes, the *Homo–Pan* LCA may have lived in a medium-sized group with a multi-male and multi-female social structure characterized by a strong tendency of female transfer between groups and a weak tendency of male philopatry. They also had small sexual dimorphism in body mass, with females showing no overt sign of estrus. Large climatic changes in the late Miocene forced the human ancestors to expand their distribution from tropical forests to open lands. The dispersed food resources and high predation pressure they faced in the new environments constituted the driving force behind provisioning and early weaning, which shortened the inter-birth interval and increased the fecundity of early hominids. The dietary innovation of collecting high-quality foods including meat preceded encephalization and promoted a division of labor between sexes in foraging. Increased brain size led to the allocation of energy to rapid brain growth and caused a delay in somatic growth. Such changes in life history traits resulted in the emergence of childhood and adolescence unique to humans. The long dependency inherent to these periods required cooperative breeding and pair bonding, while risky environments strengthened kin-based alliance among males. Cooking and control of fire increased digestive ability and expanded the dietary range of hominids. Reductions in the time energy spent on processing and consuming foods allowed them to expand their social interactions. The prevalence of provisioning and food sharing in adulthood solicited development of reciprocity and prosociality, which possibly led to the creation of a multilevel community structure consisting of families, as observed in modern foragers' societies. This social structure might have increased the resilience of the *Homo* clade to severe conditions in the new environments and led them in their first steps out of Africa. Menopause and extension of the post-reproductive period may have emerged recently, contributing to the increased survival of immatures and overall population growth. The development of speech using language and other cultural innovations played important roles in shaping this remarkable life history trait unique to modern humans.

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