

The attainment of independence from the mother in primate infants and its implications for the evolution of cooperative breeding in hominins

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ABSTRACT The infant process of attaining independence from the mother is directly related to the course of lactation and timing in resumption of cycling for mothers, which affect female reproductive rates. Understanding infant development patterns and variations across primates can allow us to evaluate their fitness implications and inform comparative life history models of hominoids. Here, factors leading to inter- and intra-species differences in development and lactation will be evaluated and contextualized relative to sources of life history and socio-ecological variation. Literature on maternal investment through lactation and on infant nutritional development in the *Primate* order will then be reviewed. Finally, the concept of alternative behavioral and nutritional perspectives on weaning will be introduced to emphasize that physiological and social needs within the mother-offspring relationship are mitigated, together and separately, to support primate infants in their attainment of independence. A layered perspective that distinguishes between social and physiological mother-infant relationships may be important to consider in evolutionary models aimed at understanding the appearance of cooperative breeding in hominins, as it puts extant nonhuman primates in a position more similar to the human pattern than previously anticipated.

This perspective can help us to more accurately determine the evolutionary steps leading to the unique life history traits of contemporary humans.

KEYWORDS cooperative breeding, infant development, mother-infant relationship, parental investment, primate life history, weaning

1 INTRODUCTION

Infancy is one of the most dangerous periods of a primate's life, and this is assumed to be partly because infants are unable to meet nutritional requirements independently (Janson & van Schaik, 1993). Mortality risks are highest during this time, as infants are vulnerable to the negative health effects of inadequate nutritional intake (Altmann & Alberts, 2005; Sellen, 2007). To reach feeding independence, primate infants transition through three developmental stages that are distinguished by two major life history markers: 1) the first ingestion of solid food marks the end of the exclusive suckling stage and beginning of transitional feeding (or complementary feeding in humans), and 2) the last nutritive nursing bout (with milk transfer) marks the end of *weaning*, and effectively ends infancy (Bădescu, Katzenberg, Watts, & Sellen, 2016a; Sellen, 2007, 2009). The rates at which primate infants go through the process of attaining feeding independence from the mother often varies by species according to differences in life history patterns, physiology and socioecology (Kennedy, 2005; Lee, 1997; Sellen, 2006). Moreover, infant development can differ considerably between and within populations of the same species. Variations in feeding development have been noted in the great apes (e.g., chimpanzees, *Pan troglodytes*: Bădescu et al., 2016a; Bădescu, Watts, Katzenberg, & Sellen, 2016b; Fahy et al., 2014; mountain gorillas, *Gorilla beringei*: Eckardt, Fawcett, & Fletcher, 2016), although to a lesser extent than in hominins. Contemporary humans seem to be adapted for greater flexibility in lactation, infant feeding and care. For example, infants may be weaned anytime from birth (no breastfeeding when maternal milk is substituted for infant formula) to several years after birth (Kennedy, 2005; Sellen, 2006), and no other extant primate species can sustain the demands of early infant growth with no breastfeeding whatsoever (Ken-

nedy, 2005; Sellen, 2006, 2009). Inter-specific variation suggests that numerous traits associated with infant development and growth in several primate species can show a degree of plasticity that may directly respond to differing social and environmental pressures (Lee & Kappeler, 2003).

The process of attaining independence from the mother is directly related to maternal reproductive parameters that affect female reproductive rates and growth of populations (Lee, 2012). Therefore, understanding the general patterns, while also highlighting the extent of variation in the development of extant primates, can help us to evaluate the fitness consequences of different developmental and parental investment strategies, and inform comparative evolutionary models that aim to delineate the evolutionary trajectories of early life history parameters across hominids (Hawkes, 2014; Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998; Hrdy, 2009; Kennedy, 2005).

In this chapter, factors leading to inter- and intra-species variation in development will be evaluated. The focus will be on the process of infant nutritional development, from complete dependence on maternal milk to nutritional independence. This is the time when primate infants are unequivocally connected to their mothers and other caregivers by access to food and care to meet basic needs. Thus, the attainment of feeding independence arguably forms the functional basis of an individual's overall growth and development during infancy. Firstly, patterns of infant growth, development and maternal lactation will be contextualized relative to sources of life history and socioecological variation. Secondly, what we know about the exclusive suckling stage of nutritional development in primates including maternal lactation and maternal milk, will be summarized. Thirdly, the transitional feeding stage of development will be described, and the ways by which primate infants develop the knowledge and ability to forage independently will be evaluated. Fourthly, the weaning process will be discussed – the theoretical and methodological challenges in measuring and describing weaning in wild primates, the variation in weaning across the primate order and hypotheses of mother-offspring weaning conflict. In this section, the distinction between physiological weaning separate from behavioral weaning in nonhuman primates will be introduced. Finally, the behavioral versus nutritional mother-infant relationship and the implications of this distinction to the

emergence of cooperative breeding in *Homo* during the Pleistocene will be discussed.

2 **LIFE HISTORY VARIATION, SOCIOECOLOGY AND DEVELOPMENT**

Mammalian life histories are comprised of parameters associated with rates of development and reproduction, such as the typical lengths of gestation and inter-birth intervals, age at first reproduction, life span, number and weight of offspring at birth, size and age at weaning and postnatal growth rates (Zimmermann & Radespiel, 2007). The scheduling and durations of nutritional development stages (i.e., exclusive suckling, transitional feeding, weaning) affect the lactational physiology of mothers, which mediate maternal trade-offs between investment in current offspring versus future reproduction, number versus quality of offspring, and influence the inter-birth intervals of females (Charnov, 1991; Charnov & Berrigan, 1993; Pusey, 2012; Sellen, 2006, 2009; van Noordwijk, 2012). Although primates generally exhibit slow life histories compared to most other mammals, showing low rates of birth, growth, mortality and long life spans, significant variation does exist within the primate order (Zimmermann & Radespiel, 2007). Several hypotheses that highlight inter-species differences in body size, diet, and social systems have been used to explain primate life history variation (Lee & Kappeler, 2003; Zimmermann & Radespiel, 2007). Large primates, like great apes, give birth to fewer offspring that have relatively slower rates of development, and reach sexual maturity relatively later than small primates like strepsirrhines (including lemurs, lorises and bushbabies, Lee & Kappeler, 2003; Zimmermann & Radespiel, 2007). The life histories of larger primates are therefore relatively slower than those of smaller primates, illustrating how body mass is a major predictor of life history parameters (Lee & Kappeler, 2003; Zimmermann & Radespiel, 2007). Maternal and neonatal body mass are correlated with weaning age, as mothers typically wean infants when they are roughly one-third of maternal body weight (Lee, 1997; Majluf & Gordon, 1991). While species of similar size are expected to have similar weaning ages, this is not always

the case (Lee et al., 1991). Differences in suckling patterns and in the nutritional quality of maternal milk produced can lead to differential rates of infant development, which can result in variation in the length of infant dependency and weaning age (Lee, 1997, 2012).

Inter-species differences in diet explain some of the life history variation exhibited by similarly-sized primates (Lee & Kappeler, 2003). Compared to *frugivores*, who predominantly eat fruit, and *omnivores*, who eat a variety of plant and animal sources, *folivores* may be less likely to risk starvation because they benefit from higher food availability, as their main food source, leaves, are spatially and temporally more abundant than fruit or prey (Lee & Kappeler, 2003). Since species at risk of starvation often exhibit slower infant growth rates (Altmann & Alberts, 2005; Janson & van Schaik, 1993; Leigh, 1994; Nowell & Fletcher, 2007; Wich et al., 2007), frugivores and omnivores generally have slower infant development than folivores of similar body mass, and this has been shown using multi-species comparative analyses (Leigh, 1994).

Variation in social systems may lead to life history variation among similarly sized species (Lee & Kappeler, 2003). Primates displaying *alloparenting* (i.e., infant care by individuals other than the mother) often exhibit faster postnatal growth rates and earlier weaning ages than species lacking alloparenting (Mitani & Watts, 1997; Ross & MacLarnon, 2000; van Noordwijk, 2012). Alloparenting may increase maternal foraging efficiency, enabling mothers to obtain the energy needed to support rapid infant growth and earlier weaning (Borries, Lu, Ossi-Lupo, Larney, & Koenig, 2011; Lee, 1997; Maestriperi, 1994; Tardif, 1994; van Noordwijk, 2012). Additionally, as infants spend more time away from their mothers during alloparenting, infant nursing rates and durations often decrease (Bădescu et al., 2016b; Fairbanks, 1990). A reduction in suckling stimulus releases mothers from hormonal inhibition, enabling them to return to estrus (i.e., become fertile) sooner than if alloparenting did not occur (Lee, 1997). Thus, in species with alloparenting, mothers have shorter inter-birth intervals and infants are weaned earlier. In humans, infants are provisioned extensively by alloparents, and mothers may also rely heavily on food provisioning by relatives and other group members during lactation (Hawkes, 2014; Hawkes et al., 1998; Kramer, 2010; Kramer & Otarola-Castillo, 2015; Piperata, 2009).

3 EXCLUSIVE SUCKLING, LACTATION AND MATERNAL MILK

Apart from human infants, who may be bottle-fed infant formula rather than breastfed, primate infants rely completely on maternal milk that is accessed through suckling during nursing (Nicolson, 1987; Sellen, 2007; see Figure 1). Patchy data on infant feeding across species indicate that the duration of exclusive suckling, and the age at which transitional feeding begins, is typically shorter than six months (e.g., black lemur, *Eulemur macaco*: 6 weeks, see Harrington, 1978; blue monkey, *Cercopithecus mitis*: 5 weeks, see Forster & Cords, 2002; patas monkey, *Erythrocebus patas*: 7 weeks, see Chism, 1986; yellow baboon, *Papio cynocephalus*: 5 months, see Altmann, 1980; Hanuman langur, *Semnopithecus entellus*: 3 months, see Rajpurohit & Mohnot, 1991; mountain gorilla: 6 to 8 months, see Watts, 1985; lowland gorilla, *G. gorilla*: 6 months, see Nowell & Fletcher, 2008; chimpanzee: 3 to 5 months, see Bădescu et al., 2016a; van de Rijt-Plooij & Plooij, 1987; human, *Homo sapiens*: 6 months recommended, see World Health Organization, 2001, but Reilly and Wells, 2007, suggest 3 months may be optimal), with the exception of the orangutan (*Pongo pygmaeus*), which can nurse exclusively for one year (van Noordwijk & van Schaik, 2005).

The exclusive suckling stage is critical for overall infant development, as this is when growth rates tend to be highest (Fairbanks, 2000; Lavenex, Banta Lavenex, & Amaral, 2007). Some primate infants can attain up to 70 percent of their adult body size within the first few months of postnatal development (e.g., black-and-white ruffed lemur, *Varecia variegata*: Pereira, Klepper, & Simons, 1987). Variation in the quantity and composition of maternal milk produced can influence infant growth and development rates (e.g., common marmoset, *Callithrix jacchus*: Tardif, Power, Oftedal, Power, & Layne, 2001; baboon, different species of *Papio*: Roberts, Cole, & Coward, 1985). In rhesus macaques (*Macaca mulatta*), the quantity of milk infants ingest can affect their ability to cope with environmental stressors later in life (Hinde & Capitano, 2010). Time spent suckling and the amount of milk transferred to infants can vary throughout the course of lactation and infant development, depending on several factors of the mother-infant dyad (Hinde & Milligan, 2011). These may include maternal health condition (Hinde, 2007a; Hinde, Power, & Oftedal, 2009; Prentice & Prentice, 1995; Roberts et al., 1985; Sellen,

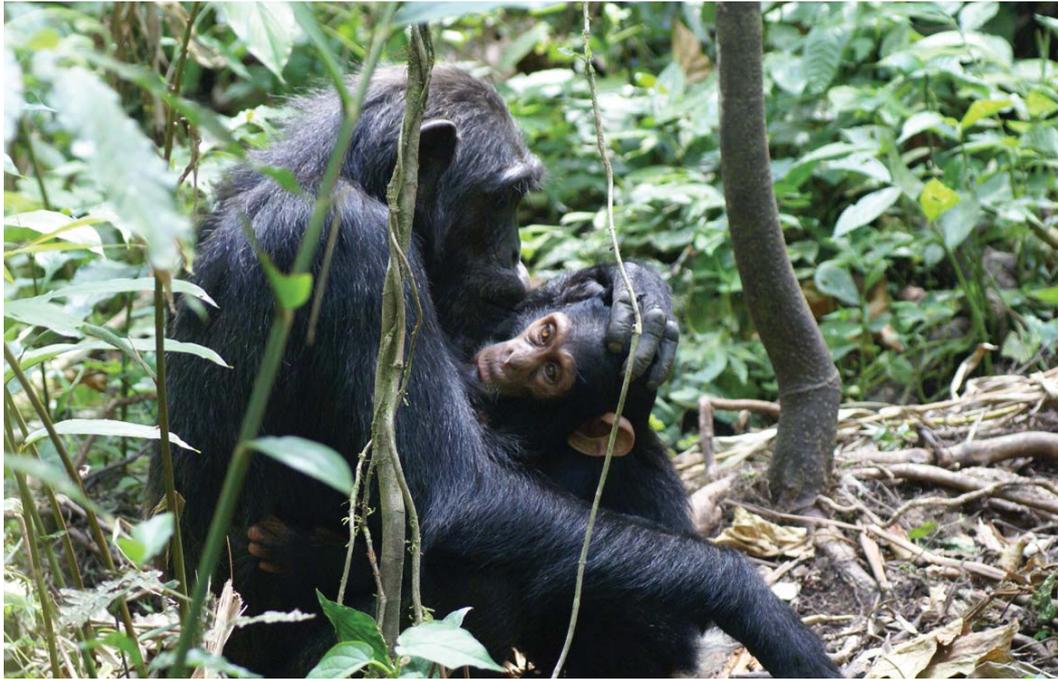


Figure 1. 2-year-old chimpanzee infant, Kozena, engaged in a nursing bout while her mother, Penelope, simultaneously grooms her at Ngogo, Kibale National Park, Uganda (photographed by Eva M. Luef).

2007; Tardif et al., 2001), reproductive experience (Hinde, 2009; Hinde et al., 2009) and the quality of milk produced (Gomendio, 1989; Hinde, 2009; Tanaka, 1997; Tilden & Oftedal, 1997; Whittier, Milligan, Nutter, Cranfield, & Power, 2011), as well as infant sex (Gomendio, 1990; Hinde, 2007b, 2009; Quinlan, Quinlan, & Flinn, 2005; Tanaka, 1997), hunger (Cameron, 1998; de Passillé & Rushen, 2006), age and nursing efficiency (Drewett & Woolridge, 1979). Nursing efficiency increases with age as infants develop the ability to coordinate suckling rate with swallowing and respiration, and consequently, while the time spent suckling can remain constant, the amount of milk transfer can actually increase as infants grow (Cameron, 1998).

While the quality of maternal milk shows little intra-specific variation, it can differ greatly across species (Oftedal, 2012; Oftedal & Iverson, 1995; Sellen, 2007). In some mammals, mothers produce energetically rich milk with a high fat content to support rapid development over a shorter time frame (e.g., hooded seal, *Cystophora cristata*: Bowen, Oftedal, & Boness, 1985). Relative to most mammals, primates produce di-

lute and low-energy milk, which enables mothers to support frequent nursing while minimizing maternal energetic costs of milk production (Hinde & Milligan, 2011). Variation in milk composition does exist among different primates. Strepsirrhines, and especially genera where infants are left unattended during prolonged periods of maternal absence (i.e., *infant parking*), and therefore nurse infrequently, tend to produce richer milk relative to other primates (Tilden & Oftedal, 1997).

The duration of lactation is influenced by infant nursing patterns, as mothers are often unable to reproduce again until their dependent offspring are weaned (Lee et al., 1991). This is the result of mechanical stimulation of the nipple that leads to the release of the hormone *prolactin*, which inhibits ovulation (i.e., *lactational amenorrhea*). Lactational amenorrhea may not be as clear-cut, as mothers in some primates (including *H. sapiens* and species of *Pan*, *Colobus*, *Semnopithecus* and *Macaca*) can continue to lactate and nurse their current offspring at low rates while resuming ovarian cycling, estrus, and even into their next pregnancy (Borries et al., 2011; Ellison, 1995; Pusey, 1983; Tanaka, 1992).

4 **TRANSITIONAL FEEDING**

Prior to the cessation of exclusive suckling and the beginning of *transitional feeding*, infants engage in exploratory foraging behaviors that include mouthing and handling of food objects. In blue monkeys, exploratory foraging can occur as early as four days after birth (Forster & Cords, 2002), whereas mountain gorilla infants may not engage in exploratory foraging behaviors until four months of age (Watts, 1985). While human infants are fed selected complementary foods during much of transitional feeding (Sellen, 2007), nonhuman primate infants acquire ecological competence through a combination of genetic and learned components (King, 1999). The mechanisms by which primate infants learn what transitional foods to ingest, and how to process them, vary depending on the species. In some primates, mothers may share food with their infants by permitting them to take some of their food (initiated by the infants, e.g., Temminck's red colobus, *Procolobus badius temminckii*: Starin, 2006; golden lion tamarin, *Leontopithecus rosalia*: Lefebvre, 1985; chimpanzee:



Figure 2. Older weanling, Gus, staring at (top) – and begging for honey from (below) – adult male, Bartok, at Ngogo, Kibale National Park, Uganda. Gus obtained left-over parts of the honey comb discarded by Bartok (photographed by author).

Bădescu, 2017, Silk, 1978, Ueno & Matsuzawa, 2004; capuchin, *Cebus* spp.: Fragaszy & Bard, 1997). While this type of food sharing occurs to some degree across the primate order, the active feeding of adult foods by mothers and other conspecifics to infants is rare and may only occur regularly in cooperative breeding primates, in which alloparenting and active provisioning is compulsory (i.e., humans: Sellen, 2006, 2007; spe-

cies in the family *Callitrichidae*: Brown, Almond, & van Bergen, 2004). Food sharing with infants encourages independent foraging (Silk, 1978), which can potentially lead to earlier weaning in primates (Lefebvre, 1985).

The predominant mechanisms by which most primate infants acquire information on transitional foods appear to be through trial-and-error, imitation and observational learning (e.g., mantled howler monkey, *Alouatta palliata*: King, 1999; mountain gorilla, chimpanzee, orangutan: Byrne, 1999, van Noordwijk & van Schaik, 2005). Infants may pay close attention to – and peer at – individuals feeding, and they may also ingest food items dropped by other individuals or be permitted to directly take food from others (Goldstone et al., 2016; Kopp & Liebal, 2016; Nicolson, 1987; van Noordwijk & van Schaik, 2005; Watts, 1985; see Figures 2a and 2b). The exact duration of the transitional feeding stage in many primates is not known, however, it typically lasts until the end of the weaning process and is thus quite long in species that give birth to single offspring that show a prolonged period of dependence on care-givers (Hayssen, 1993; Sellen, 2007). Therefore, while maternal food sharing and observational learning may encourage independent feeding, neither results in immediate nutritional independence.

5 WEANING

Weaning is generally a gradual and often lengthy process but can also be abrupt in some mammals (e.g., hooded seal: Bowen et al., 1985). Definitions of weaning can vary according to whether the focus is on infant development or maternal reproduction (Lee, 1997) and also depend on the academic discipline. For instance, human biologists define weaning as the final period of time when maternal milk provisioning is terminated (Sellen, 2009), whereas primatologists and archaeologists usually define weaning from the time the contribution of maternal milk in the diet of infants begins to decrease, to the last suckling bout with milk transfer (Bădescu et al., 2016a; Borries, Lu, Ossi-Lupo, Larney, & Koenig, 2014; Kennedy, 2005; Lee, 1997). Here, we defer to the latter definition more commonly used in primatology.

Determining the beginning and end of weaning, and thus the exact duration of the weaning process, is difficult to calculate from observations of wild primate infants. To demarcate the onset of weaning, studies have relied on a number of observable correlates, including the first intake of solid food, beginning in the decline of nursing rates, or time when maternal nursing rejections became repetitive (Borries et al., 2014; Martin, 1984; Nicolson, 1982). Inconsistent definitions of weaning onset across studies have led to unclear information on when the weaning process tends to begin for most species (Borries et al., 2014). For example, depending on the type of definition used, the weaning onset of chimpanzee infants ranges from 5 months to 2 years of age (Bădescu et al., 2016a; Clark, 1977; van de Rijt-Plooij & Plooij, 1987). An infant who has successfully completed the weaning process is able to digest adult foods and forage independently, even in the face of food supply fluctuations (van Noordwijk, 2012). The completion of weaning is usually behaviorally determined when the last nutritive nursing bout occurs, but observing this directly in the field is difficult. While weaning is often not complete until the birth of subsequent offspring (Chism, 1986; Nicolson, 1987; Pusey, 1983; Rajpurohit & Mohnot, 1991; Watts, 1991), in some primates, weanlings may continue to nurse, and mothers may tolerate this, even after the birth of a new sibling (e.g., orangutan: van Noordwijk & van Schaik, 2005). The age of weaning completion varies across primate species (e.g., gray mouse lemur, *Microcebus murinus*: 1 month; ring-tailed lemur, *Lemur catta*: 3.5 months; mantled howler monkey: 1.8 years; crab-eating macaque, *Macaca fascicularis*: 1.2 years; black colobus, *Colobus satanas*: 1.3 years; lar gibbon, *Hylobates lar*: 2 years, orangutan: 7 years; lowland gorilla: 2.8 to 4.6 years; chimpanzee: 4 to 5 years, see Alvarez, 2000; Bădescu et al., 2016a; Nowell & Fletcher, 2007; Watts, 1991). While data from human hunter-gatherers suggest a mean weaning age of 2.8 years, weaning ages of human infants range from birth (no breastfeeding) to several years (with extremes of 15 years, see Alvarez, 2000; Marlowe, 2010; Sellen, 2001). Weaning in humans can be gradual, or abrupt, and can occur to infants ranging in size from small to large (Sellen, 2007).

Most investigations of weaning in wild nonhuman primates use proxies of continued nursing behavior, such as the time spent by infants on the nipple or in ventral body contact, to identify the age at which infants are weaned and evaluate the termination of the mother-infant relation-

ship (e.g., grivet, *Chlorocebus aethiops*: Lee, 1987; chimpanzee: Clark, 1977, van Lawick-Goodall, 1967; gorilla: Nowell & Fletcher, 2007, Stewart, 1988; orangutan: van Noordwijk & van Schaik, 2005). However, nipple contacts without milk transfer do occur in some primates, and this may fulfill a social or affiliative function for infants, as opposed to a nutritive function (i.e., *comfort nursing*, Martin, 1984; see, e.g., rhesus macaque, *Macaca mulatta*: Harlow & Harlow, 1965; chimpanzee: Bădescu et al., 2016a; Hanuman langur: Rajpurohit & Mohnot, 1991). On the other hand, infants may appear completely weaned from daytime observations but they may continue to nurse nutritively at night when observations are not normally conducted. For example, Reitsemá (2012) used feeding observations and fecal stable carbon and nitrogen isotope ratios to evaluate dietary intake in a captive François langur infant (*Trachypithecus francoisi*), and revealed that milk constituted a small portion of the infant's diet even after the age when observational data indicated weaning was complete. This study showed that while primate infants can behave as weaned juveniles through self-foraging of adult foods and without nursing or ventral contact with the mother during the day, they can continue to rely nutritionally on milk beyond this stage, probably through nighttime suckling. In wild *P. troglodytes* at Ngogo, Uganda, the same method of fecal stable isotope ratios was used to evaluate the relative contributions of maternal milk to solid foods in infant diets at different ages (Bădescu, 2017; Bădescu et al., 2016a; Bădescu et al., 2016b). Individuals showed comfort nursing, without milk transfer, for up to two years after lactation had ended and physiological weaning was complete (Bădescu, 2017; Bădescu et al., 2016a). In this case, the offspring behaved as infants through continued nipple contacts with their mothers, but were no longer obtaining maternal milk and were nutritionally independent.

5.1 Weaning conflict

Maternal suckling rejections during the weaning process can be aggressive (e.g., hitting, biting, pushing, cuffing) or passive (e.g., mother obstructs access to nipple by changing position of arms or body; avoiding infant before they can attempt to access the nipple), which can lead to infant distress ranging from mild infant vocalizations and fear grins to prolonged temper tantrums (Nicolson, 1987; e.g., ring-tailed lemur:

Macedonia, 1993; patas monkey: Chism, 1986; Hanuman langur: Rajpurohit & Mohnot, 1991; lowland gorilla: Nowell & Fletcher, 2007). Three major hypotheses associated with the amount of parental investment (Trivers, 1974), timing of investment (Altmann, 1980) and honest signaling of nutritional need (Bateson, 1994; Wells, 2003) can explain mother-infant weaning interactions. Maternal rejections and infant distress are often outcomes of what is typically known as the *weaning conflict* between mothers and infants over access to maternal investment through lactation effort (Trivers, 1974). The production of maternal milk to energetically support a growing infant is an expensive form of maternal investment due to its energetic and reproductive costs (Lee, 1984). Conflict arises when infants become too large for mothers to energetically support via lactation, and to reduce the energetic burden on mothers, it becomes more beneficial for infants to feed independently (Trivers, 1974). Mothers can subsequently invest in the next offspring and enhance their reproductive success. However, while mothers may try to encourage independent feeding by rejecting nursing, infants may persist in their attempts to make nipple contact. While the weaning conflict hypothesis (Trivers, 1974) is traditionally accepted, some primate studies do not fully support it (Altmann, 1980; Barrett, Dunbar, & Dunbar, 1995; Chism, 1986; Nowell & Fletcher, 2007).

Conflict over the inappropriate timing of nursing, rather than over investment itself, can also lead to weaning conflict behaviors (e.g., gelada, *Theropithecus gelada*: Barrett et al., 1995). Over time, nursing behaviors of growing infants may impede the ability of mothers to fulfill their daily activities and nursing attempts made during inappropriate times (e.g., foraging, traveling) may be rejected so that infants learn to nurse when it is not a hindrance to maternal activities (Altmann, 1980). The weaning conflict and *timing over investment* hypotheses are not necessarily mutually exclusive, as mothers could initially change nursing patterns and later reduce the amount of investment (Barrett et al., 1995).

Another hypothesis suggests that mother-infant interactions typically associated with the weaning conflict may be a means for mothers to monitor their infants' energetic needs (Bateson, 1994; Wells, 2003). Mothers may reject infant nursing attempts but continue to monitor infant behavior, so that if infants show an honest energetic need through persistent distress and suckling attempts, they will permit infants to

suckle. In a population of geladas for example, weaning conflict behaviors only occur during times of low food availability, however, nursing rates actually increase, as mothers allow infants to nurse more during these times (Barrett, Henzi, & Lycett, 2006). Thus, in periods of low food availability, infant distress likely portrays an *honest signal* of inadequate nutritional intake, as weanlings are unable to meet their energetic needs through independent foraging (Barrett et al., 2006). A similar pattern of mothers monitoring infant distress to gauge honest nutritional need for maternal milk may also occur in wild lowland gorillas (Nowell & Fletcher, 2007).

A few factors can make it difficult to measure weaning conflict between mothers and infants. Firstly, the reasons for weaning conflict can be difficult to determine because nursing rejections can be coupled with maternal rejections in contexts other than nursing, such as over solicitations to be carried, groomed, in close proximity, or if the weanling wants access to food that the mother is eating (MacDonald, 2011). The ambiguity in the contexts of maternal rejections makes it challenging to establish whether infants are distressed over denied access to maternal milk or due to lack of maternal proximity, or another aspect of maternal care (MacDonald, 2011). Secondly, in addition to rejections, mothers in some species may initiate play with weanlings when they seek nipple contact (e.g., chimpanzee: Goodall, 1986; orangutan: van Noordwijk & van Schaik, 2005), and this may distract infants from pursuing nursing. Lastly, in the absence of an outright weaning conflict, infants may wean themselves when maternal milk becomes insufficient to nourish their growing body size and energy needs, which leads them to an adult food-based diet (e.g., lowland gorilla: Nowell & Fletcher, 2007; chimpanzee: Bădescu, 2017; human: Fouts, Hewlett, & Lamb, 2005).

6 THE SOCIAL VERSUS PHYSIOLOGICAL MOTHER-INFANT RELATIONSHIP AND ITS IMPLICATIONS FOR EVOLUTIONARY ANTHROPOLOGY

In preceding sections of this chapter, the mother-infant relationship, as it is often described in primatology, was reviewed within the parame-

ters of *parent-offspring conflict theory* introduced by Trivers (1974). The parent-offspring conflict paradigm operates mainly on the basis of a push-and-pull in the mother-infant relationship, as it focuses on mothers managing limited investment, mainly through lactation effort for current offspring, and on infants maximizing their own access to limited maternal resources, primarily milk. Evolutionary anthropological studies that rely on parent-offspring conflict theory often implicitly confound the social and physiological facets of the relationship between mothers and their offspring. This can be problematic when hypotheses are founded on expectations of how mother-infant relationships should be exhibited over time; different assessments may represent only some facets of the mother-infant relationship that may not completely or accurately depict its progression. Several studies featured in this chapter (e.g., Bădescu et al., 2016a; Harlow & Harlow, 1965; Martin, 1984; Rajpurohit & Mohnot, 1991; Reitsema, 2012) point to the notion that nutritional and behavioral relationships between nonhuman primate mothers and infants can develop separately from one another despite considerable overlap in ontogeny (Borries et al., 2014). Offspring may achieve nutritional independence before it is beneficial for the mother-infant behavioral relationship to end (Bădescu, 2017; Bădescu et al., 2016a; Rajpurohit & Mohnot, 1991; van Noordwijk & van Schaik, 2005). That is, there can be a need for weaned offspring to continue making ventral and nipple contacts, and their mothers may allow or even encourage these behaviors for some time after lactation ends (I. Bădescu, personal observation in chimpanzees at Ngogo 2013–2014). Alternatively, infants may reach behavioral and social independence from the mother during daytime interactions before they fully reach dietary independence, and milk may continue to fulfill nutritional and immunological needs for offspring even after the mother-infant behavioral relationship ends. This notion is supported by data showing that offspring who are seemingly weaned due to a lack of day-time suckling and ventral contact may continue depending on maternal milk to a low degree via night-time suckling, or even fall back on milk when food availability decreases (Barrett et al., 1995; Nowell & Fletcher, 2007; Reitsema, 2012; Smith, Austin, Hinde, Vogel, & Arora, 2017). These studies point to a need for wild primate research to more explicitly distinguish between the progressions of social and physiological mother-infant relationships, and to account for potentially distinct

nutritional and behavioral weaning processes. In addition, weaning conflict between mothers and offspring could be absent in primates where mothers maintain a steady level of investment through lactation effort over several years as infants effectively wean themselves during the prolonged transition to independent feeding (e.g., chimpanzee: Bădescu, 2017; human: Fouts et al., 2005).

A layered perspective on mother-offspring relationships in nonhuman primates may be important to consider in evolutionary models of parental investment and infant development, as it puts extant nonhuman primates in a more similar position to the human pattern than previously anticipated. Like humans, where infants are weaned relatively early off maternal milk but continue to require extensive support from parents and alloparents, nonhuman primates also show that nutritional and behavioral needs within the mother-infant relationship are mitigated together and separately, to support infants in their attainment of complete independence (Hrdy, 2009; Sellen, 2006, 2009). Moreover, social interactions through alloparenting in several nonhuman primate species can assist with the transition of infants away from maternal dependence (Bădescu et al., 2016b; Mitani & Watts, 1997; Ross & MacLarnon, 2000; van Noordwijk, 2012). Using the extant nonhuman primate data as a proxy, we can thus imagine a hominoid ancestor who may have exhibited similar features. What needs to be better understood are the progressive changes that occurred in the infant care and development patterns of successive hominoid species that eventually led to the cooperative breeding system of *Homo* in the Pleistocene (Kramer & Otarola-Castillo, 2015). Humans are arguably cooperative breeders, given the existence of the long childhood stage and our universally high rates of alloparenting that includes regular provisioning of infants and mothers with complementary foods, especially by siblings, grandmothers and fathers (Hawkes et al., 1998; Hrdy, 2009; Kramer, 2005, 2010; Kramer & Otarola-Castillo, 2015; Lee, 2012; Sellen, 2006). With the exception of the family *Callitrichidae* that evolved through convergent forces a system of cooperative breeding comparable to *H. sapiens*, this combined suite of adaptive characteristics makes humans unique among extant primates, and raises ultimate questions about when and how these features appeared in our lineage (Hawkes et al., 1998; Hrdy, 2009; Kramer, 2010).

The transition from more ape-like hominids, like *Australopithecus*, to the *Homo* genera was probably a seminal stage of important changes in the mother-infant relationship (Matsuzawa, 2006). With the distinction between behavioral and nutritional components of the mother-infant relationship likely already present, we would expect to see an emergence of features during the *Australopithecus* to *Homo* transition that would have made it possible to further widen the division between infant feeding and infant socio-emotional needs, which could have ultimately allowed for the life history traits characteristic of later *Homo*, such as a lengthening in the period of dependence on caregivers but shortening of infant nutritional dependence on maternal milk (Hawkes, 2014; Hrdy, 2005; Hrdy, 2009; Matsuzawa, 2006; Sellen, 2006). Fossil evidence from the *Australopithecus* to *Homo* transition points to a suite of general changes, including increasing brain volume, appearance of tool manufacturing, and likely appearance of more complex gestural and vocal communication, division of labor, and greater cooperation among group members, including potentially relying more on kin for alloparenting (Hrdy, 2009; Matsuzawa, 2006). During this transition, we may also have seen a decrease in the time that mothers and infants spent in direct ventral body contact; infants were either held by alloparents or left on their own, as they would now have been able to sit upright in a supine posture (Matsuzawa, 2006). The emergence of infant crying, making direct eye contact, and changes in the development of neonate cognition would have allowed infants to monitor and behaviorally engage their mothers and other caregivers during the prolonged period of dependence (Hawkes, 2014; Hrdy, 2005; Hrdy, 2009; Matsuzawa, 2006). Combined with the shift toward bipedalism already present, these changes may have presented situations in which mothers were regularly not in direct physical contact with their infants, which could have facilitated the need for *baby talk* or *motherese*: melodic, sing-song vocal communication used by mothers and other caregivers to draw infants' attention and to soothe them when they are not in direct maternal body contact (Falk, 2004; see also Filippi and Gingras in this volume). Social relationships of mothers and alloparents with infants during the transition to *Homo* would likely have been characterized by a combination of mutual gazing, manual-gestural signs during face-to-face communication and vocal exchanges at various levels of proximity (Falk, 2004; Hrdy, 2005; Matsuzawa, 2006). Some have

even pointed to these important changes in modes of communication between infants with their mothers and others as one of the stepping stones facilitating the transition to language in *Homo* (Falk, 2004).

For later *Homo*, important changes in the feeding patterns of infants and young children would have contributed to changing the nutritional physiology of weanlings, and consequently, the lactational physiology of mothers. Notably, the provisioning of young by caregivers with high-energy, easily digestible complementary foods would have played a crucial role in quickening weaning, shortening the lactation period of mothers, and in allowing females to invest in a subsequent infant long before present offspring reached complete independence (Sellen, 2006, 2007, 2009). The gradual appearance of these combined adaptive features formed part of the evolutionary backbone of the unique life history traits that appeared in Paleolithic hominins; namely, early weaning but relatively low infant mortality, short birth spacings, and increased female fecundity (Hawkes et al., 1998; Kennedy, 2005; Kramer, 2010; Kramer & Otárola-Castillo, 2015; Lee, 2012).

7 CONCLUSION

Rearing of young offspring played an important role in our evolutionary past. The shift toward shared infant care, including shared infant feeding through complementary foods given to infants by alloparents, added another prosocial motivation that allowed our species to transition from the more individualistic behavioral phenotypes likely present in ape-like hominids to the *shared intentionality* that is characteristic of later *Homo* (Burkart et al., 2014; Hrdy, 2009). The appearance of obligate cooperative breeding in our species therefore went hand-in-hand with our hyper-cooperation, increasing sociality and collaboration, and evolution of cognition enabling more complex modes of communication, including language and instructed learning (Burkart et al., 2014). That being said, humans are also characterized by considerable variability and flexibility in our strategies of infant and young child care, both within and between populations (Sellen, 2006, 2009). To help delineate the evolutionary forces responsible for the variable patterns of infant feeding and care

shown by ancient and contemporary humans, we need to understand the key differences and similarities between human and nonhuman primate infant feeding, care, and development.

Future studies in nonhuman primates should account for the possibility that the typical weaning conflict expected of mothers and their offspring, particularly over maternal milk, may not be apparent or visually exhibited. In addition, interpretations of mother-infant relationships should more explicitly evaluate the different facets associated with the social and physiological implications of development, weaning and attainment of independence in early life. The relationship of infants with their mothers was the focus in this chapter. However, fathers, older siblings, grandparents, aunts and even unrelated individuals often play crucial roles in the process of attaining independence in human and nonhuman primates. The expressions of infant relationships outside of maternal care, and the individual roles they played in the evolutionary histories of primate species, continue to deserve further detailed attention (Hawkes et al., 1998; Kramer & Otarola-Castillo, 2015; Mitani & Watts, 1997; Ross & MacLarnon, 2000).

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