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Female Reproductive Ecology of the Apes

Implications for Human Evolution

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Long-term research on great apes is now revealing that a wide range of variation exists both within and between species in reproductive parameters such as age at menarche, age at first birth, and interbirth interval. However, a clear understanding of what ecological factors may influence these female reproductive parameters and the relative importance of each factor has been lacking from great ape studies. We know much more about the ecology of reproduction in female humans than we do for any of the great ape species.

Owing to the close kinship between humans and great apes, research on the ecological context of human ovarian function is extremely relevant to understanding the variability in great ape reproductive parameters. I argue that recent evidence suggests that the same ecological variables that are regulating reproduction in humans also influence the great apes. Outside of lactation, the key ecological mediators of fecundity in human females are nutritional intake, energetic expenditure, and net energy balance (Ellison et al. 1993). A thorough understanding of the ecology of reproductive functioning in the great apes can help us make sense of interindividual variation, interpopulation variation, and to some extent, interspecies variability. Furthermore, if great ape and human reproductive physiology share similar adaptive responses to the environment, then we can develop more accurate models for human, as well as great ape, evolution.

I begin by reviewing the variability in reproductive parameters within each species of the great apes. Specifically, I examine age at menarche, length of adolescent subfecundity, age at first birth, and the components of the interbirth interval in wild as well as captive ape populations. Then, I outline evidence from my study of wild orangutans to demonstrate how female energy intake and expenditure influence hormonal functioning in the wild. I present evidence that orangutans experience dramatic changes in energetic status owing to fluctuations in fruit availability and that these changes result in significant differences in hormonal levels. I review evidence in the literature that supports the conclusion that chimpanzees are influenced by these same ecological factors. Finally, I discuss how parallels between ape and human reproductive functioning help us to understand human evolution. In particular, I explore changes in the interbirth interval and the period of juvenile dependency during hominid evolution.

VARIABILITY IN REPRODUCTIVE PARAMETERS

Apes of the same species living under different ecological conditions display wide variability in their reproductive timetables. This is true in the extreme in the altered ecological conditions of captivity. Most captive apes, living under conditions of nutritional abundance and low energy expenditure, have dramatically earlier ages at menarche and shorter interbirth intervals than are seen in any wild population. This variability in reproductive patterns demonstrates that the timing of reproduction occurs within a range for each species and is not a fixed parameter. We can no longer, for example, talk about the interbirth interval of "the" chimpanzee. Instead, it is much more informative to explore what causes this reproductive parameter to vary both within chimpanzees and among the great ape species.

Most studies of variability in reproductive patterns within great ape populations focus on males and the effectiveness of male mating strategies in achieving paternity (e.g. Tutin 1979; Tutin and McGinnis 1981). Until recently, there has been little focus on how ecological factors might influence a female ape's ability to conceive—largely because of the difficulty of measuring nutritional status and reproductive functioning in the field. Additionally, wild apes cannot be sampled as reliably as those in captivity. Tutin (1994) points out that female transfer in gorillas and chimpanzees makes it difficult to track these individuals longitudinally during development and to know the ages at which they go through menarche and reproduce. In orangutans, the size and fluidity of their residence patterns also makes tracking individuals over their reproductive lifespan extremely difficult.

Below I review what we know about female reproductive parameters in captivity and in the wild. New data are provided from my study of wild orangutans in Gunung Palung National Park, West Kalimantan, Indonesia. For gorillas, captive data come from members of the western lowland gorilla subspecies (*Gorilla gorilla gorilla*) whereas wild data are from mountain gorillas (*Gorilla gorilla beringei*). Where more than one study has taken place at a single field site, I only report the most recent figures. Medians are presented where available and data are converted into comparable units (e.g. years, months) to facilitate these comparisons when possible. Data are summarized in Table 18.1.

Age at Menarche

Unlike human studies, where first menstrual bleeding provides the obvious marker of menarche, great ape studies, particularly in the wild, normally rely on other indicators of reproductive maturity, such as first sexual swelling, sexual behavior, or first successful copulation with an adult male.

Orangutans. In captive orangutans menarche can be assessed through the presence of menstrual bleeding. Markham (1990, 1995) found that menarche occurred between 5.8 and 11.1 years. Within the seven individuals in her sample, menarche was earliest in a large, overweight female and latest in two females with eating disorders. Asano (1967) provides data for one female who reached menarche at 4.5 years and first began mating at 5.5 years. Lippert (1977) states that first sexual activity occurs at 7–9 years in captivity. The age of menarche is particularly difficult to determine in wild orangutans owing to the absence of a sexual swelling. Galdikas (1981) defines menarche as the advent of proceptivity and describes a wild female from Tanjung Putting, Borneo, who began approaching adult males at an estimated age of 10–11 years. In the future, with field application of chemstrips (Knott 1996), menarche may be able to be determined by the presence of blood in urine.

Gorillas. In captivity, the first menstrual flow reportedly occurs between 6 and 7 years of age (Dixson 1981). Menstrual bleeding has not been observed in wild mountain gorillas at Karisoke; thus menarche has been determined from the first evidence of labial tumescence (Harcourt et al. 1980) or first sexual activity (Watts 1991). After their first swellings, according to Harcourt et al. (1981) it took 5 months for two females to mate with a fully adult male. Watts (1991) reports that the first sexual activity among mountain gorillas occurs between 5.7 and 7.1 years (median = 6.3 years).

Bonobos. The median age at menarche for three captive-born females (known birth date) and six wild-born females (estimated birth date) was 7.7 years (Thompson-Handler 1990). Kuroda (1989) states that bonobo females at Wamba, Zaire, experience their first swellings at the age of 8 or 9 years. Females transferred into the intensively studied E-group at an estimated age of 13–15 years.

Table 18.1. Reproductive Parameters of Wild and Captive Female Apes. Means are given, followed by medians in parentheses. Ranges and sample sizes, when available, are provided in parentheses below (*n* is the number of samples or intervals and *f* is the number of females).

Species	*Site*	*Age at menarche (yrs.)*	*First Sexual Behavior (yrs.)*	*Adolescent Subfecundity (yrs.)*	*Age at First Birth (yrs.)*	*Interbirth Interval (yrs.)*	*Postpartum Amennorhea (yrs.)*	*Waiting Time to Conception (mths.)*
Orangutan	Captive	7.7 (7.6)[1,19,20,a,d] (4.5–11.1, n=8)	5.5–9[1,18]	0.8 (0.6)[1,19,d,f] (0.6–1.2, n=3)	9–9.9[20] (mode) (5.2–32.7, n=372)	6.3[19] (n=1)	4.7[19] (n=1)	1[17]–10[19] (n=1)[19]
Orangutan	Tanjung Putting	—	10–11[10] (estimated age, n=1)	1?–4[10,g] (n=2)	15.7 (16.0)[28] (15–16, n=3)	7.7 (7.7)[11,l] (5.2–10.4, n=23, f=11)	6+[8]	10.3 (2)[8,9,d] (1–28, n=3, f=3)
Orangutan	Ketambe	—	—	5[22,g] (n=1)	14.7 (16.0)[28] (12–16, n=3)	8.6(8.4)[29,k] (5.7–12.8, n=9, f=5)	—	—
Orangutan	Gunung Palung	—	—	—	—	7.0 (7.0)[2] (6–8, n=4, f=3)	5.7[2] (4.5–7, n=2, f=2)	2.5[2] (n=1)
Gorilla	Captive	6–7[6] (n=3)	—	2.1[6,j] (see text)	9.3[6] (7.5–10.4, n=8)	4.2 (4.0)[23] (2.3–6.4, n=16, f=13)	2.7 (2.4)[23] (1.5–5.2, n=13, f=8)	2.0 (2.0)[23] (0.07–8, n=9, f=8)
Gorilla	Karisoke	—	(6.3)[31] (5.7–7.1)	0.9–1.5[13,k] (n=3)	(10.0)[13,31] (8.7–12.7, n=13)	(3.9)[31] (3–7.2, n=26)	(3.2)[31] (2.2–4.2, n=12)	3–4 (5)[31] (1–10+)
Bonobo	Captive	8.2 (7.7)[27] (6.0–11.2, n=9)	—	4.4 (4.2)[27] (1.9–8.4, n=7)	10.8 (10.0)[16,27,d] (7.7–20.0, n=20)	3.6[27] or 5.1 (5.2)[14] (1.9–7.6, n=21, f=14)[14]	1.3–2.7[14] (n=3)	2.4–37.2[14,27] (calculated, see text)
Bonobo	Wamba	8–9[16]	—	5.0[16,h] (calculated)	14.2 (14.0)[16] (13–15, n=6)	4.5[26] (n=10)	1 or 3–4[15] (see text)	0–33.6[15] (calculated, see text)
Bonobo	Eyengo, Lomako	—	—	—	—	8.0 (9.0)[7,l] (4–9, n=19)	–	—
Chimpanzee	Captive	8.0[24,33,a,e,f] (6.3–10.2, n=25)	—	0.9[33,f] (0.3–1.4, n=7)	10.8[24] (n=17)	3.8[5] (1.5–6.3. n=15, f=8)	2.3[5] (1.2–3.2, n=11, f=7)	10.5[5] (calculated)
Chimpanzee	Gombe	10.8[30,c] (8.5–13.5, n=8)	—	2.4[30,i] (0.6–4.9, n=4)	13.3[30] (11.1–17.2, n=4)	5.5[12] (4.0–6.5, n=21, f=13)	3.9[30] (2.4–5.7, n=12)	4.7[30] (0.5–13.4, n=17)
Chimpanzee	Mahale	10.6 (10.0)[21,c] (9–13, n=33)	10.9 (10.7)[21] (9.1–13.4, n=20)	2.3 (2.1)[21,j] (0.3–6.9, n=13)	14.6 (15.0)[21] (12–20, n =22)	6.0 (6.0)[21] (4.4–7.3, n=19, f=16)	4.4 (4.6)[21] (2.5–5.6, n=18, f=15)	10.6 (8.9)[21,m] (1.4–32.4, n=18, f=15)
Chimpanzee	Tai	—	—	2.6 (2.2)[3,j] (1.4–5.7, n=7)	14.3 (14.0)[3] (12.5–18.5, n=8)	5.8 (5.4)[3] (4.0–10.0, n=33, f=19)	2.0 (1.9)[3,4] (0.2–5.1, n=26, f=19)	26.9[3,m] (n=33, f=19)
Chimpanzee	Kanywara, *Kibale*	11.1[32,c] (n=1)	11.1[32] (n=1)	1.6 (1.6)[32,j] (0.3–2.5, n=5)	15.4 (15.0)[32] (14–18, n=5)	6.2 (6.0)[32,l] (2.3–10.0, n=31)	4.4 (4.0)[32] (1.7–6.5, n=11)	15.3 (18.9)[32] (calculated)
Chimpanzee	Bossou	—	—	—	12–14[25]	5.1 (5.0)[25] (3.0–11.0, n=15)	–	—

Sources: [1]Asano, 1967; [2]author's data; [3]Boesch and Boesch-Achermann, 2000; [4]Boesch, pers. comm., 2000; [5]Courtney, 1987; [6]Dixson, 1981; [7]Fruth, pers. comm; [8]Galdikas, 1980; [9]Galdikas, 1981; [10]Galdikas 1995; [11]Galdikas and Wood, 1990; [12]Goodall, 1986; [13]Harcourt et al., 1981; [14]Harvey, 1997; [15]Kano, 1992; [16]Kuroda, 1989; [17]Lippert, 1974; [18]Lippert, 1977; [19]Markham, 1990; [20]Markham, 1995; [21]Nishida et al., 1990; [22]Schurrmann and van Hoof, 1986; [23]Sievert et al., 1991; [24]Smith et al., 1975; [25]Sugiyama, 1994; [26]Takahata et al., 1996; [27]Thompson-Handler, 1990; [28]Tilson et al., 1993; [29]Utami, pers. comm..; [30]Wallis, 1997; [31]Watts, 1991; [32]Wrangham, pers. comm.; [33]Young and Yerkes, 1943. [a]Age at first menstruation, [b]Age at first swelling, [c]Age at first *full* swelling, [d]The mean and median were calculated by pooling all the original raw data from multiple studies, [e]The raw data were not available from the multiple studies cited, thus I weighted the sample means by the sample sizes to calculate the overall mean, [f]Period between first menstruation and conception, [g]Period between first copulation and conception, [h]Period between first swelling and conception, [i]Period between first *full* swelling and conception, [j]Period between immigration and conception (thus these should be considered minimum values because menarche and first copulation occur prior to immigration), [k]Excluding data from one interval with a known miscarriage, [l]Median computed using a Kaplan-Meier analysis with censored and uncensored intervals, [m]Subtracting gestation length from published figures.

Chimpanzees. In captivity, mean ages of menarche (defined as first menstruation) in female chimpanzees have been reported as 7.6 (Smith et al. 1975) and 8.9 (Young and Yerkes 1943) years, although some individuals may show swellings as early as 5 years (Wallis, personal observation). Wallis (1997) reports that the first *full-sized* swellings in Gombe (Tanzania) chimpanzees occur at a mean age of 10.8 years. Menarche (first menstruation) occurs 1–3 years after the first sexual swelling (at age 11–14; Tutin and McGinnis 1981) and 1–6 months after the first *full- sized* swelling (Goodall 1986). At Mahale, Tanzania, the median age of first maximal swelling is 10.0 years (6 of 33 individuals are of known birth year; calculated from Nishida et al. 1990). Age at first mating occurred at a median age of 10.7 years. The apparent first menstrual blood was seen in one Mahale chimpanzee at 11 years of age (Nishida et al. 1990). At Kanyawara, in the Kibale Forest of Uganda, one female of known birth date had her first swelling at 10.2 years, and her first *full* swelling and first copulation at 11.1 years (Wrangham, personal communication 2000).

Adolescent Subfecundity

The terms *adolescent subfecundity* and *adolescent sterility* have both been used to describe the period between menarche or the beginning of sexual activity and conception. In most species there is normally only a brief period in which cycles are truly sterile. Succeeding cycles are variably fecundable, with ovulation sometimes occurring but often without an adequate luteal or follicular phase. As in humans, ovulation may occur but progesterone secretion may not be adequate to support pregnancy (Young and Yerkes 1943).

Orangutans. Markham (1990) reports on two captive females of known ages at menarche and first parturition. Asano (1967) provides similar figures for one female. From these I calculate a median period of adolescent subfecundity of 0.6 years (subtracting 8.1 months of gestation [Markham 1995]). Menstrual cycle lengths were longer in females during the first two years after menarche than in older females (Markham 1990). However, after analyzing urinary estrone, Masters and Markham (1991) found a pattern similar to adults in an adolescent female only eight months past menarche. In the wild at Tanjung Putting, Galdikas (1995) describes one female with an estimated age at first sexual activity of 10–11 years and first birth at 14–15 years, giving a four-year period of adolescent subfecundity. A second female had at least a one-year cycling period before conceiving. Schürmann and van Hooff (1986), working at Ketambe, Sumatra, have data on one female. She did not conceive for five years after the onset of sexual activity, despite an estimated 130–210 copulations.

Gorillas. Dixson (1981) reports a mean age at first conception of 8.6 years for captive gorillas. With an average age at menarche of approximately 6.5 years (Dixson 1981), this indicates a period of adolescent subfecundity of about 2.1 years. At Karisoke, wild mountain gorillas experienced adolescent subfecundity for 10.5–18.5 months (Harcourt et al. 1980). Watts (1991) states that more recent data from Karisoke also support a period of adolescent subfecundity of about two years.

Bonobos. Thompson-Handler's (1990) survey of the captive literature gives a median period of adolescent subfecundity of 4.25 years. In the wild population at Wamba, I calculate a mean length of adolescent subfecundity of 5.0 years from Kuroda's (1989) estimates of mean age at first birth (14.2 years) minus mean age at first swelling (8.5 years) minus gestation length (255 days).

Chimpanzees. In captivity, female chimpanzees reportedly have a mean period of adolescent subfecundity of 0.9 years (Young and Yerkes 1943). In four females at Gombe where menarche (first full swelling) and first birth were observed, conception occurred on average 2.4 years later (Wallis 1997). At other study sites, where menarche and first birth have not been observed in the same individuals (owing to female transfer), the time between immigration and first conception has been called the period of adolescent subfecundity. However, values calculated in this manner should be viewed as minimums since females reach menarche and start copulating before they transfer between communities. Using this method gives a median of 2.1 years at Mahale for 13 females (subtracting a 228 day gestation period [Martin et al. 1978] from Nishida et al.'s [1990] figures). At Taï, the median was 2.2 years for seven females (Boesch and Boesch-Achermann 2000) and at Kanyawara, 1.6 years for five females (Wrangham, personal communication 2000).

Age at First Birth

Orangutans. International Orangutan Studbook data show mean age at first birth in captivity over the past 50 years as 11.2 years (Markham 1995). However, it is not known how many of these animals were housed with fertile males. Thus, Markham (1995) provides a modal range of 9–9.9 years (when 20% of first parturitions occurred) as a more indicative figure. In Tilson et al. (1993), age at first birth is reported at a median of 16 years at both Tanjung Putting and Ketambe. Details about the age determination of these females is not provided, although most or all were probably not followed from birth and therefore are estimates.

Gorillas. First birth in captive lowland gorillas (some of estimated age) occurs at a mean age of 9.3 years (extrapolated from age at first conception provided by Dixson 1981). In the wild, Harcourt et al. (1981) report a median age at first parturition of 10.0 years for five females. Watts (1991) found the same 10.0 median for eight additional females in the same population.

Bonobos. In captivity, three intervals from Kuroda (1989) and 17 intervals from Thompson-Handler (1990) indicate a median age at first birth of 10.0 years. The median age at first birth for six females at Wamba (estimated ages) was 14.0 years (Kuroda 1989). However, Kuroda notes that two females over 15 years old had not yet given birth; thus, he feels that this figure will increase.

Chimpanzees. Reports from captivity place age at first birth for chimpanzees as 10.8 years (Smith et al. 1975). Kuroda (1989) reports that the earliest age at first birth in Japanese zoos was 7 years. Age at first birth is higher at all wild chimpanzee sites, although female emigration means that most ages are only estimates. Wallis (1997) reports a mean age at first birth of 13.3 years for four females at Gombe. Sugiyama (1994) reports an age at first birth of 12–14 years at Bossou, Guinea (some estimated ages). Nishida et al. (1990) place this figure at a median of 15.0 years (all estimated ages) for chimpanzees of Mahale. At Taï, Ivory Coast, the median was 14 years (all estimated ages), which includes one unusual female who did not emigrate and who gave birth at 18.5 years (Boesch and Boesch-Achermann 2000). The median for Kanyawara chimpanzees was 15.0 years (estimated ages; Wrangham, personal communication 2000).

Interbirth Intervals

Interbirth intervals can be prematurely shortened by death or removal of the first infant before it has been weaned. Unless otherwise noted, I only report intervals where the infant was known to have remained with the mother until weaning. Some authors use a Kaplan-Meier analysis, which has the advantage of taking into account long intervals that have not been completed.

Orangutans. International Studbook records give the mean interbirth interval of captive orangutans as 3.0 years. Thirty-six percent of the interbirth intervals occurred within a modal range of 1–1.9 years (Markham 1995). Lippert (1977) also reports captive orangutan interbirth intervals as less than 3 years. However, these figures do not distinguish between mothers who were allowed to rear their infants and those that had infants taken away after birth. Markham (1990) presents data for one "natural" interbirth interval for a female who remained continuously with her infant and had access to a male. Her interbirth interval was 6.3 years. In contrast, wild orangutans gave birth after a median of 7.7 years at Tanjung Putting (computed using a Kaplan-Meier analysis on 11 censored and 12 uncensored intervals; Galdikas and Wood 1990). This figure is 8.4 years for 9 intervals at Ketambe when data from one female who had a miscarriage is excluded (Utami, personal communication 2001). At Gunung Palung, Borneo, I can estimate the length of four intervals, giving a median of 7.0 years.

Gorillas. Sievert et al. (1991) surveyed gorillas in 24 captive institutions and found the median interbirth interval for mother-reared infants was 4.0 years. The median interval between surviving births for 26 intervals in wild mountain gorillas at Karisoke was 3.9 years (Watts 1991). Sievert and colleagues (1991) attribute the similarity of captive and wild interbirth intervals primarily to problems with infertility in captive gorillas. For example, Beck and Power (1988) found that only 61% of captive female gorillas in North America had given birth to a live infant. Factors accounting for this high degree of infertility in captivity have included lack of prior social experience, environmental constraints, social stress, diet, and incompatibility with the paired male (Maple and Hoff 1982; Nadler 1977). Testicular atrophy (Dixson 1981) and early sterility of males (Beck 1982) are also common.

Bonobos. Thompson-Handler (1990) surveyed the captive bonobo population and reports a mean interbirth interval of 3.6 years. These were all females who kept their infants until the birth of their next infant and were continuously housed with a male. Harvey (1997) calculates the interbirth interval for captive bonobos as 5.1 years for females who remained with their infants, but it is not clear if all of these individuals were constantly housed with a male. In the wild, Takahata et al. (1996) report a mean interbirth interval of 4.5 years at Wamba. However, Kano (1992) argues that the mean interbirth interval will end up being over 5 years. In contrast, using a Kaplan-Meier survival analysis, Barbara Fruth (personal communication, 2000) found that the median interbirth interval between 1990 and 1998 in the Eyengo community of bonobos in Lomako, Democratic Republic of the Congo, was 9.0 years.

Chimpanzees. In captivity, chimpanzees who were allowed to rear their offspring had a mean interbirth interval of 3.8 years in the Taronga Zoo in Sydney (Courtenay 1987). Similarly, a range of 3.5–4.0 years is reported from the University of Texas Chimpanzee colony (Bloomsmith, personal communication [to Wallis] 1997). Goodall's (1986) analysis of the Gombe data shows a mean interbirth interval of 5.5 years. At Mahale, Nishida et al. (1990) report a median interbirth interval of 6.0 years. Chimpanzees at Bossou had a median interbirth interval (in mothers whose first offspring survived at least 3 years) of 5.0 years (Sugiyama 1994). In Taï, the interval was a median of 5.4 years (Boesch and Boesch-Achermann 2000). The latest calculation by Wrangham (personal communication, 2000) gives a median of 6.0 years for Kanyawara using a Kaplan-Meier analysis on 11 censored and 20 uncensored intervals. A mean of 6.2 years was obtained for just uncensored intervals.

Postpartum Amenorrhea

Postpartum amenorrhea is defined here as the time between birth and the first subsequent onset of menstrual cycling. This period has also been called lactational amenorrhea. However, because lactation may extend after cycling has resumed, the former term is preferred here. Data below are for mothers with living infants.

Orangutans. In captivity, Masters and Markham (1991) monitored a female who had been suckling an infant for 4 years and showed no signs of menstruation. Another adult female did not menstruate for 4.7 years after her infant's birth (Markham 1990). In the wild, with the lack of an estrous swelling and the difficulty of detecting menstruation, this reproductive parameter is particularly hard to assess. Thus, I report here on age at first completed mating after parturition. This period has been estimated as over 6 years in the wild (Galdikas 1980). At Gunung Palung, I found that the time from birth to the first known completed mating was 4.5 years for one female (KR). This interval followed the birth of her third known infant. Another female (MR) was first seen mating after an estimated 7 years since the birth of her last offspring. Both undeveloped and developed males had attempted to mate with this female 18 months before, and thus it is possible that an earlier mating was not observed.

Gorillas. Sievert et al. (1991) found that in captive female gorillas the median length of time until first postpartum sexual behavior was 2.4 years. They attribute this to the recognized problems with breeding gorillas in captivity. Watts (1991) reports that in 23 such intervals in wild mountain gorillas the median was 3.2 years.

Bonobos. Resumption of menses following parturition for females who kept their infants was 1.3–2.7 years in captivity (Harvey 1997). However, Harvey cautions that this does not necessarily indicate regular cycling since Vervaecke and colleagues (unpublished data cited in Harvey 1997) describe the menstruation of captive bonobos as irregular for 0.3–3.1 years after parturition. Vervaecke and colleagues (unpublished data) record that the resumption of swelling was 1 month to 0.8 years after parturition. *Full* swelling occurred 0.3–1.4 years post-parturition. Kano (1989, 1992) was not able to detect menstruation but found that females at Wamba resume genital swelling and begin to copulate within one year of parturition. He speculates, however, that these cycles are nonovulatory for 3–4 years because lactation lasts until the infant is about 4 years old (Kano 1989, 1992). Thus, sexual swellings may not indicate regular cycling and ovulation in bonobos, and more precise hormonal measurements are necessary to establish this parameter.

Chimpanzees. Courtenay's (1987) study of 11 captive chimps indicated a mean postpartum amenorrhea of 2.3 years. Wallis (1997) found that at Gombe the mean length of postpartum amenorrhea in mothers with living infants was 3.9 years. Most females were still nursing when they resumed postpartum cycling (Tutin and McGinnis 1981). This period has been reported as a median of 4.6 years at Mahale (Nishida et al. 1990), 1.9 years at Taï (Boesch and Boesch-Achermann 2000), and 4.0 years at Kanyawara (Wrangham, personal communication 2000). At Mahale, wild chimpanzees normally do not show sexual swellings while lactating (Nishida et al. 1990). However, one exceptional female resumed swellings within 7 months of parturition while continuing to lactate (Takasaki et al. 1986).

Waiting Time to Conception

Following parturition and postpartum amenorrhea, the period from the resumption of regular cycles/sexual activity to the next conception is called the waiting time to conception. Data below are for mothers with living infants.

Orangutans. Lippert (1974) reports that orangutans in captivity cycle for one or two months before conception. Markham (1990) presents data for one 36-year-old female who conceived again 10 months after weaning her ninth infant. Her cycles were on average 58 days long, and she may not be representative. Galdikas (1981) describes one wild female who consorted for two months before a possible conception. A second female was seen to mate while in the process of weaning her offspring and did not get pregnant. Then, six months later during the first cycle of another consortship she apparently conceived. A third female resumed postpartum sexual activity in 1976 and did not give birth again until 1979 (Galdikas 1980). Given an 8.1-month gestation length (Markham 1995), this individual would have had a waiting time to conception of approximately 2.3

years. At Gunung Palung, I found that one female (MR) conceived after 2.5 months of sexual activity.

Gorillas. In captive gorilla mothers who raised their infants, the median length of time between sexual behavior and conception was 2.0 months (Sievert et al. 1991). In the wild, Watts (1991) reports a median of five cycles until conception for 23 females who had a surviving infant.

Bonobos. The waiting time to conception has not been reported specifically for bonobos in either captivity or the wild. However, we can determine a maximum and minimum range by subtracting the lengths of postpartum amenorrhea from the interbirth intervals (minus a gestation length of 225 days [Kuroda 1989]) reported above to obtain a mean range of 2.4–37.2 months in captivity and 0–33.6 months for the wild at Wamba. As discussed above, because of the difficulty of determining when ovulatory cycles actually resume, the waiting time to conception in bonobos cannot be reliably determined until hormonal measurements are made.

Chimpanzees. I calculated chimpanzee waiting time to conception from Courtenay's (1987) postpartum amenorrhea and interbirth interval figures, subtracting a gestation length of 228 days (Martin et al. 1978). This gives a mean waiting time to conception in captivity of 10.5 months. In the wild, the mean time between resumption of postpartum cycles and conception was 4.7 months at Gombe (Wallis 1997). Nishida et al. (1990) found that the median period between the resumption of swelling and the next birth was 16.5 months. Subtracting 228 days of gestation gives an 8.9-month waiting time. Data from Taï (Boesch and Boesch-Achermann 2000) indicate a mean of 34.5 months from resumption of cycling to birth. Subtracting gestation length gives a waiting time of 26.9 months. At Kanyawara, the waiting time can be calculated from the median interbirth interval minus the median period of postpartum amenorrhea and the length of gestation to arrive at a figure of 18.9 months.

WHAT ACCOUNTS FOR CAPTIVE VS. WILD DIFFERENCES?

The Ecological Energetics Hypothesis

The above data show a striking contrast in reproductive parameters between captive and wild populations of chimpanzees and orangutans. The captive apes of these two species have accelerated reproductive timetables for age at menarche, adolescent subfecundity, age at first birth, interbirth interval, length of postpartum amenorrhea, and waiting time to conception relative to their wild counterparts. Where sufficient data exist at more than one study site for each species, intersite variability also exists. This difference also appears to be the case in bonobos for age at first birth, but interbirth interval differences are unresolved. Reproductive parameters do not appear to differ between captive and wild gorillas, a peculiarity that will be discussed later.

What may account for this variation in reproductive parameters? What I propose here is that the recent, extensive anthropological research into human reproduction which attempts to understand ovarian function within an adaptive, ecological context (e.g., Ellison 1990, Ellison et al. 1993) provides a guiding framework with which to approach the study of reproductive variance within the great apes. As in the apes, human populations show tremendous population variability in reproductive parameters. Some of this variance is due to cultural practices, such as differences in the duration and patterning of lactation. However, a growing body of evidence suggests that outside of lactation and age, energetic differences, caused by varying local ecologies, are the major modifiers of female reproductive function (Ellison et al. 1993). Energetics plays a role both in development and in short-term modulation of reproductive function. Humans growing up under conditions of energy deficit have slower reproductive maturation, accompanied by slower overall maturation (Ellison 1990). In the short term, female ovarian function is finely modulated to respond to environmental perturbations on a continuum ranging from luteal and follicular suppression to complete amenorrhea (Ellison 1990). For example, in normal weight women with adequate fat reserves, small degrees of weight loss cause a reduction in reproductive hormones (Schweiger et al. 1987; Lager and Ellison 1990). This ovarian responsiveness is also seen in seasonal reductions in ovarian function of nonwestern women in response to short-term nutritional stress (Ellison et al. 1986; Panter-Brick et al. 1993). These studies suggest that rather than simply nutritional status or fatness per se, it is positive or negative energy balance that affects ovarian function (Ellison 1990). Furthermore, moderate levels of exercise (Ellison and Lager 1986) and heavy workload independent of weight loss (Jasienska and Ellison 1998) can reduce ovarian function in women. This ability of ovarian function to respond to energetic conditions is interpreted as an adaptive response to time reproductive effort to occur when it has the highest probability of success (Ellison et al. 1993).

In contrast, other models of primate reproduction come from studies of seasonally breeding animals in the temperate zone. In many of these mammals it appears that conception is timed so that births occur during the period of highest food production (Bronson 1989). This may be a good strategy for a temperate zone animal that lives in a highly seasonal but *predictable* environment, where the timing of high food availability can be anticipated and conception timed accordingly. But for many long-lived, tropical animals like great apes, food availability is sufficiently unpredictable that conception cannot be timed so that birth will occur during such periods (van Schaik and van Noordwijk 1985). Instead, I would predict that, just as in humans, conception is more likely to occur during periods of positive maternal energy balance in order to begin the period of intensive reproductive investment when energy availability is sufficient.

Evidence from Orangutans

To test this hypothesis, which I refer to as the "Ecological Energetics Hypothesis," I began a study of the reproductive ecology of wild orangutans in Gunung Palung National Park. In this study I tested the hypothesis that nutritional intake, energy expenditure, and energy balance have a significant effect on orangutan ovarian function.

Based on approximately 6,000 hours of observation over 14 months I found that significant changes in fruit availability were correlated with changes in nutritional intake (Knott 1997a, 1997b, 1998, 1999). These changes in availability were assessed through monthly monitoring of 558 orangutan fruit trees. From December of 1994 through February of 1995 the forest at Gunung Palung experienced a "mast fruiting" period of high flower and fruit availability. During the three months of peak fruit abundance, orangutans spent 98–100% of their feeding time eating energy-rich seeds and pulp. In contrast, when fruit availability reached a low several months later, seeds and pulp composed only 24% of the diet. The remainder was made up of 37% bark, 23% leaves, 9% pith, and 6% insects. All foods eaten by orangutans were analyzed for metabolizable energy, revealing that caloric intake was significantly higher during the mast period than in the other periods.

Activity patterns and energy expenditure varied in accordance with fluctuations in diet and fruit availability. During periods of high fruit availability, orangutans spent significantly more time foraging, but did so within a small day range. As fruit availability decreased, average day range increased as they searched for fruit over a larger area. During severe fruit shortage, however, day range shrank as orangutans fed on low quality, but abundant, bark and leaves.

The effects of these energetic changes on orangutan physiology were assessed through a number of noninvasive techniques. More than 400 urine samples were obtained from >40 orangutans by placing plastic sheets beneath individuals during urination. Ketones, a measure of fat metabolism, were present in significantly more urine samples during the non-mast period of low fruit availability. Estrone conjugates (E1C) were measured using radioimmunoassay to assess changes in ovarian function as a result of changing energetic status. Two nonpregnant females were followed extensively during periods of high and low fruit availability, and both showed a significant decrease in E1C levels during the low fruit availability period. Comparisons of weekly mean E1C values in 12 nonpregnant females showed a significant decrease in E1C when fruit availability decreased. Several conceptions also occurred during the period of high fruit availability. The importance of E1C levels for conception was shown by Masters and Markham (1991), who found that higher peak, as well as mean, levels of estrone conjugates were associated with increased fecundity of orangutan ovarian cycles in captivity. These data from the wild suggest that changes in nutritional intake and energy balance have a significant effect on orangutan ovarian function, much as they do in humans.

Does the Model Apply to Other Apes?

Intrapopulation variability. The relationship between caloric intake and hormonal functioning has not yet been studied in other wild great apes. However, other researchers have speculated about the importance of nutrition in explanations of reproductive variance in these species (Bentley 1999; Courtenay 1987: Galdikas 1995; Markham 1995; Nishida et al. 1990; Sugiyama 1994; Tutin 1994; Wallis 1995, 1997). Here I present several lines of evidence indicating that nutrition is an important modulator of reproduction in the most studied of the great apes—chimpanzees.

First, just as in orangutans, chimpanzees have an earlier age at menarche and first birth and shorter interbirth intervals in captivity than in the wild. It seems abundantly clear that this is due to energetic differences between the two conditions. Given the ready availability of food and the lower levels of energy expenditure inherent in captivity, one can logically conclude that captive apes have a more consistent and positive energetic status than their wild counterparts.

Second, Wallis (1997) points out in her review of reproductive parameters in chimpanzees at Gombe National Park that the individuals with the shortest interbirth intervals were all descendants of one female, named Flo. These family members were the most frequent visitors to the banana feeding station, and thus Wallis speculates that they may have received better nourishment. No data were available on the relative food availability in the forest when the chimpanzees came to the feeding station, but such visitation may have been important for making up any caloric deficits.

Alternatively, it may have been that Flo and her descendants had access to better foraging areas (Pusey et al. 1997). Using 35 years of field data from Gombe, Pusey et al. (1997) found that high-ranking chimpanzee females were more reproductively successful in a number of dimensions.

They reached sexual maturity sooner (which was significantly correlated with age at first birth), they had significantly higher offspring survival, their annual production of offspring surviving to weaning age was significantly greater—indicating shorter interbirth intervals, and they tended to live longer. The daughters of high-ranking females reached sexual maturity earlier owing to their higher rates of weight gain. The authors attribute these differences primarily to the ability of high-ranking females to maintain access to the best foraging areas, which gave them higher nutritional status than subordinates.

Third, Uehara and Nishida (1987) provide evidence that periods of low fruit availability are associated with negative energy balance in chimpanzees. They weighed wild chimpanzees at Mahale and found that body weights decreased when fruit was scarce. In humans, small changes in body weight are sufficient to have measurable effects on progesterone levels (Bullen et al. 1985). Lipson and Ellison (1996) found that a relatively small increase in body weight in women was associated with higher midfollicular estradiol levels, which were correlated, in turn, with conception cycles. Thus, a decline in chimpanzee energetic status during periods of low fruit availability may likewise lower their ovarian function.

Fourth, seasonality linking food availability with a variety of reproductive parameters has been found at several wild chimpanzee field sites. Conceptions are reportedly seasonal at Gombe and Mahale, with the majority occurring during the dry season (Goodall 1983, 1986; Nishida et al. 1990; Wallis 1992, 1995). Wallis (1997) found that *all* postpartum cycles that led to conception occurred during the dry season. She also reports that "paradoxically" more births in Gombe chimpanzees occurred during the wet season, which she states is the riskier time of year owing to higher rates of deaths and other health problems (Wallis 1995). Thus, chimpanzees do not time conceptions so that births occur during the optimum period.

A number of other reproductive states also peak in the late dry season at Gombe: the first full anogenital swelling in adolescents, the appearance of anogenital swellings in lactating and pregnant females, maximal swelling in cycling females (Wallis 1995), resumption of cycling after weaning (Goodall 1986), and peak number of swellings (Tutin 1975). Cycling females were more likely to show just partial swellings during the early wet season (Wallis 1995). These partial swellings probably reflect low or insufficient levels of the ovarian hormones necessary for reproduction. This assertion is based on Emery and Whitten's (in review) work, which has shown strong correlations between the size of sexual swellings and levels of estrogen and progesterone.

A similar seasonal pattern is reported by Nishida et al. (1990) from Mahale, where first sexual swellings after postpartum amenorrhea occurred significantly more often during the late dry season (September–October). These authors point out that this is also when the food supply increases, and they suggest that the first postpartum swelling is triggered by increased food availability. Uehara and Nishida (1987) show that body weights increased between the early and late dry seasons. Births showed a significant bimodal distribution, with peaks in May and January. While the January peak is unexplained, the May birth peak suggests a late dry season conception peak in September coincident with the increased food supply (Nishida et al. 1990).

What is happening during the dry season to influence reproductive physiology? These data strongly suggest an ecological effect because of the influence of season on the timing of female swellings in all reproductive stages: cycling, lactation, pregnancy, menarche, and postpartum resumption of cycles. Reproductive events are spread throughout the year but concentrate during this time. Is there evidence that the dry season in Gombe and Mahale is associated with greater food availability? First, the dry season has larger party sizes than the wet season (Nishida 1974; Sakura 1994; Wrangham 1977). In turn, at all major chimpanzee field sites there is an observed relationship between party size and food abundance, (Boesch 1996; Chapman et al. 1995; Goodall 1986; Nishida 1974; Sakura 1994; Wrangham 1986, 2000). These larger group sizes during the dry season are also associated with the presence of females with sexual swellings (Riss and Busse 1977; Wallis and Matama 1993; Wrangham 2000). Thus, the dry season is associated with increased food abundance, larger party sizes, and a greater number of maximally swollen females.

To test this relationship in chimpanzees further, data are needed on hormonal functioning, fluctuations in preferred foods, the caloric content of those foods, and ideally, actual differences in caloric intake and energy balance. Thus, we must look to future fine-grained studies of individuals within populations that incorporate both nutritional and hormonal information to investigate this hypothesis in chimpanzees. In addition, as suggested by Nishida et al. (1990), because nutrition is important in regulating chimpanzee reproductive events, quantification of seasonal changes in food supply is needed. I have focused here primarily on nutritional intake and energy balance. Investigation of differences in energetic expenditure between and within the great apes also warrants further inquiry, although we may not find the kinds of extreme energetic expenditure found in some human populations with heavy workloads.

Interpopulation variability. Between-site comparisons are also intriguing, particularly in chimpanzees for which a good deal of data exist. Bossou, for example, has the shortest interbirth intervals and Kanyawara has the longest. Sugiyama (1994) attributes this to differences in food availability between Bossou and the other sites. Boesch and Boesch-Achermann (2000) found that Taï chimpanzee females have increased infant survivorship with longer interbirth intervals and thus speculate that different chimpanzee populations may be adapted to different infant mortality rates. Wrangham et al. (1996) speculate that the low reproductive rate of Kanyawara chimpanzees may be due to greater fruit scarcity and heavier reliance on fallback foods such as figs and terrestrial herbaceous vegetation. However, the Kanyawara chimpanzees are relatively large and do not appear to suffer from seasonal weight loss.

As more data are collected these apparent study site differences are narrowing. An initial estimate of the interbirth interval at Bossou was 4.2 years (Sugiyama 1989) whereas the most recent analysis puts it at 5.1 years (Sugiyama 1994). At the other extreme, in Kanyawara, the early estimate of interbirth intervals was 7.2 years (Wrangham et al. 1996), but with the addition of more intervals the figure has fallen to 6.0 years (Wrangham, personal communication 2000). Additionally, the length of postpartum amenorrhea and the waiting time to conception are also quite markedly variable between sites, with Taï being particularly relevant (Table 18.1). It remains to be seen whether these differences are real or just differences in definition. Clearly, detailed studies that examine hormonal levels and energetics in the wild are needed to investigate these interpopulation differences.

In bonobos, the difference in interbirth intervals between the two wild study sites is striking. As with chimpanzees, these differences may narrow with additional sampling; alternatively, they may reflect real differences between the sites. Two possibilities come to mind. First, the bonobos at Wamba are provisioned for 2 to 3 months each year (Kano 1992), which would be expected to result in improved nutritional status. Alternatively, Kano (1992) attributes the good nutritional status of Wamba bonobos to a decrease in human pressure since the initiation of the study. He argues that without the threat from humans, bonobos are now able to forage at will in preferred locations from which they were previously restricted by human presence.

Gorillas. Finally, what can we make of the interesting finding that gorillas do not appear to have faster reproductive timetables in captivity? Tutin (1994) suggests that the similarity in reproductive parameters between wild and captive gorillas indicates that they are reproducing up to their species potential in the wild. Wild mountain gorillas subsist primarily on readily available herbs and vegetation and no seasonality in births or conceptions has been discovered (Watts 1998), suggesting that wild mountain gorillas may not suffer the same intensity of food shortage found in orangutans and chimpanzees (Tutin 1994). Alternatively, the problems with captive breeding in gorillas (Beck 1982; Beck and Power 1988; Maple and Hoff 1982; Nadler 1982; Sievert et al. 1991; Watts 1990) may have resulted in a lengthening of these reproductive variables in captivity. Because captive researchers see these difficulties as a constraint on gorilla reproduction, it is difficult to know if they are really breeding at their full "captive potential." Comparable data on wild western lowland gorillas are not yet available.

Alternative Explanations

Immigration Stress Hypothesis. Several alternative hypotheses have been put forward to explain variation in great ape reproductive parameters. Nishida et al. (1990) note that the period of adolescent subfecundity is longer at Mahale than at Gombe. They tie this to the finding that female chimpanzees at Mahale are much more likely to emigrate than are Gombe females and suggest that Mahale females have longer periods of adolescent subfecundity owing to increased stress from immigration. However, even *resident* Mahale females who are no longer experiencing the stress of immigration have longer periods of postpartum amenorrhea, waiting time to conception, and interbirth intervals than do Gombe chimpanzees. The fact that these other reproductive parameters are extended in Mahale females does not support the immigration stress hypothesis. An alternative explanation is that Gombe chimpanzees that remain in their natal group have better access to and better knowledge of local food resources.

Critical Fatness Hypothesis. Tutin (1994) suggests that the critical fatness hypothesis postulated by Frisch and Revelle (1970) for humans may apply to menarche in chimpanzees. However, as Ellison (1981, 1982) has shown, menarche in humans is better predicted by increase in skeletal maturation than by attaining a certain fatness level. Both, of course, may be directly influenced by nutrition, but in humans there does not appear to be a critical level of body fat at which females either start or stop menstruating (Ellison 1990). It appears more likely that positive or negative changes in weight (energy balance), rather than a critical level of fatness, influence reproductive function.

Reproductive Synchrony Hypothesis. Wallis (1997) proposes that there may be an *indirect* influence of food availability on chimpanzee ovarian function—the effect of social contact on menstrual synchronization in females. She suggests that owing to larger feeding parties in the dry season, more females would be associating with each other and stimulating each other to cycle. However, even if females are likely to synchronize with each other (Wallis 1985, 1992), this would not necessarily influence their *levels* of ovarian hormones or the probability of conception. As suggested earlier, a more likely explanation is that larger feeding parties and the presence of females with sexual swellings are both correlated with greater food availability, the latter as a result of improved energy availability.

Phytoestrogen Hypothesis. Wallis (1997) has also suggested ingestion of plant estrogens as a possible explanation for seasonal variation in reproduction. However, no phytochemical studies have been conducted on chimpanzee (or other ape) foods. Additionally, given the strong association between food availability and reproduction in humans, orangutans, and chimpanzees, it is difficult to accept this association as a spurious correlation and argue that the ingestion of phytoestrogens is the causal agent. Radically different diets and plant species are eaten by humans and the other apes, and it is unlikely that a phytochemical in each of these diets is responsible for this relationship.

Competition Hypothesis. Watts (1990, 1991) suggests that social factors might affect reproduction since birth rates in gorillas decline with increasing group size, apparently because of competition between females for access to adult males. However, it may not be competitive stress per se that affects ovarian function but the energetic consequences of competition. For example, increased competition for mates or food may negatively impact female nutritional intake and result in lower ovarian function. Thus, it may not be competition itself, but the interaction between competition and energetics, that affects reproductive functioning.

Photoperiod Hypothesis. Photoperiod is thought to be the primary reproductive cue for many temperate zone mammals (Tamarkin et al. 1985). However, photoperiod is not a likely regulator of reproductive events in tropical apes because day length only varies slightly throughout the year in the equatorial regions where apes are found. For example, at Gombe, Tanzania, there is just a 36 minute annual variation in photoperiod (Wallis 1995). Photoperiod varies even less in sites closer to the equator. Temperate zone animals may use photoperiod as a proxy measure of upcoming changes in food availability, but this is not a predictor of food availability in tropical forests. It is thus unlikely to be a factor regulating ape reproduction.

Interspecies Comparisons

Ecological Energetics Hypothesis. I have focused primarily on what may cause variation in reproductive patterns *within* a given species. However, the Ecological Energetics Hypothesis may ultimately be important in explaining differences *among* ape species as well. The degree of predictability in the food supply may be one of the factors that led to the evolution of differences in the apes' reproductive parameters (Tutin 1994). This can be seen by comparing gorillas, on one end of the food predictabiliy spectrum, with orangutans, on the other. Although there is variability in the fruit supply eaten by gorillas (Goldsmith 1999), their more regular consumption of leaves and other herbaceous vegetation means that their diet does not fluctuate as much in quality as does the more fruit-rich diet of chimpanzees and orangutans. Owing to mast fruiting in Southeast Asia, orangutans are subject to the greatest fluctuations in fruit availability among the apes (Knott 1999). Thus, the species with the greatest variability in food resources (orangutans) has the longest interbirth interval whereas the species with the most predictable food supply (gorillas) has the shortest. Western lowland gorillas incorporate significantly more fruit in their diet than do mountain gorillas (Goldsmith 1999); it will be interesting to see how this difference affects the reproductive parameters of these western populations when such data become known.

Tutin (1994) makes the argument that the greater demands of chimpanzee infants, particularly infant carrying, help explain why they have longer interbirth intervals than gorillas. I would argue that this is consistent with the Ecological Energetics Hypothesis—that the constraints imposed by infant carrying and investment have an energetic cost that affects the interbirth interval. This may be especially true for orangutans. Orangutans, with their almost exclusive use of the canopy (particularly by females), may bear heavier energetic costs than gorillas or chimpanzees because of arboreal infant carrying. This may constrain their ranging patterns and their ability to sample more widely dispersed foods. Mountain gorilla mothers with their readily abundant, terrestrial food supply may not be as constrained by infant travel and may be able to range more easily without this encumberment. Fossey (1979) reports that once gorillas reach age two they are carried very little by their mothers. Orangutans at least occasionally carry their infants up to age 7 or older (Knott, personal observation). Similarly, Wrangham (2000) has proposed that the travel costs imposed on females by traveling with and carrying infants may be a critical factor in explaining grouping differences between bonobos and chimpanzees. Thus, since the degree of infant carrying varies among the ape species we can expect it to be a factor in maternal energetics.

While I argue that energetic factors are particularly important in determining great ape reproductive parameters, other hypothesis are discussed below.

Paternal Investment Hypothesis. Galdikas and Wood (1990) point out that the average interbirth interval in the great apes is negatively associated with paternal investment. They argue that male gorillas invest by protecting their offspring from infanticide, and chimpanzee males may occasionally share food with females and thus indirectly invest in offspring. Chimpanzee males also engage in border patrols that can help protect young from infanticidal neighbors. Orangutan juveniles, on the other hand, receive no direct or indirect paternal care. Galdikas and Wood (1990:190) thus suggest that "differences in paternal investment may have an important effect on the pace of reproduction."

Cost of Vigilance Hypothesis. Tutin (1994) argues that chimpanzee mothers, compared with gorilla mothers, must bear greater costs of vigilance against infanticide which contributes to longer interbirth intervals in chimpanzees. However, consideration of orangutans indicates that the cost of vigilance is probably not a very good explanation for differences in interbirth intervals. Orangutans have the longest interbirth intervals and yet engage in almost no vigilant behavior (Setiawan et al. 1996).

Immigration Stress Hypothesis—between ape species. Tutin (1994) argues that a version of the "Immigration Stress Hypothesis" may account for shorter interbirth intervals and earlier age at menarche and first birth in gorillas compared with chimpanzees. She argues that female immigration into a new group is more stressful for chimpanzees than it is for gorillas, thus delaying the onset of fertile cycles and causing a high rate of first pregnancy loss. When orangutans are brought into this comparison, however, this explanation falters since orangutans have longer interbirth intervals than either of these other apes and yet they do not have to face any stresses related to immigration into a new social group.

Suckling Hypothesis. Galdikas and Wood (1990) propose that the suckling period may be longer in orangutans than in the other great apes, which may account for the variance in interbirth interval between them. In humans, maternal nutritional status may modulate the length of the suckling period (Perez-Escamilla et al. 1995). Thus, if differences in suckling do exist among the apes, these differences may again relate to basic ecological differences between species. The long lactation period in orangutans may be due to negative female energetic status caused by extended periods of low fruit availability. An additional factor here is the availability of fallback foods for young apes. Fallback foods, in particular bark eaten by orangutans, may be more difficult to access and process by juveniles than the terrestrial herbaceous vegetation relied upon by chimpanzees during fruit scarcity. Thus, orangutan juveniles may need to suckle for a longer period given the inadequacy of their diet during fruit-poor periods. Mountain gorillas show very little variation in their standard herbaceous diet (Watts 1998).

Finally, there is no reason to assume that all apes should have the same reproductive timetables. Different environmental and social conditions in each species have undoubtedly selected for different reproductive potentials. Investigation of these factors is an important step in our understanding of ape evolution and will be a fruitful area for future comparative inquiry. What we now know is that apes and humans appear to have many similarities in the way reproduction responds to ecological conditions. We have just begun to investigate reproductive ecology in the apes (Bentley 1999), and future studies will reveal the extent to which these responses are shared across species and with humans. Below I discuss how knowledge of the mechanisms that regulate ape reproduction can help us understand human evolution.

IMPLICATIONS FOR HUMAN EVOLUTION

Compared with the other great apes, humans have the shortest interbirth intervals. Studies of natural fertility populations have reported median interbirth intervals of 3.4 years for the !Kung of South Africa (Howell 1979), 3.0 years for the Gainj of Papua New Guinea (Wood 1994), 2.8 years for the Matlab of Bangladesh (Wood 1994), 1.6 years for the Hutterites (a North American Anabaptist sect; Wood 1994), and approximately 3.0 years for the Hadza of Tanzania (Frank Marlowe, personal communication 2000). Depending on local ecological constraints, the optimal interbirth interval may vary among these different populations (Blurton Jones 1993), but all natural fertility human societies appear to have interbirth intervals that are shorter than those found among wild great apes.

In apes, the interbirth interval represents the period during which the offspring is nutritionally dependent on its mother. This is accomplished through lactation, which eventually tapers off as juvenile apes gradually incorporate other foods in their diet. Once nursing is over juvenile apes are, for the most part, nutritionally independent. Although there may be occasional food sharing and juveniles may continue to stay close to their mothers and learn from them, ape mothers do not directly provide nourishment to more than one offspring at a time. This is not the case with humans. Humans are characterized by having overlapping, nutritionally dependent offspring (Lancaster and Lancaster 1983). We do this by providing nutrition outside of lactation to our offspring. We can nurse an infant, have a four-year-old to whom we are providing weaning foods, and have an eight-year-old who helps to collect and prepare food but is still reliant on adults to meet some of his or her nutritional needs. We have thus broken from the anthropoid pattern of only being able to provide nutritionally for one offspring at a time.

Human children have the longest period of juvenile dependency of any of the apes, but the shortest period of lactation. Draper and Cashdan (1988) report that !Kung childhood lasts from about 5 to 15 years during which time they rarely forage and derive almost all of their food from adults. Among the Hadza of northern Tanzania, children over 8 sometimes help their mothers gather and children left in camp can sometimes forage on their own when the food supply is rich (Blurton Jones 1993), but children still rely heavily on adult assistance. Thus, if humans were to follow the great ape pattern, supplementing offspring nutrition with lactation and not conceiving again until juveniles were totally nutritionally independent, we would expect 10- to 15-year interbirth intervals—a severe constraint on human reproductive potential.

How have humans managed to have the shortest interbirth interval of any of the apes and yet the longest period of juvenile dependency? Insight derived from human and ape reproductive ecology can help us understand how early hominids may have moved from an apelike pattern to the human pattern we see today. Studies of human and ape reproductive ecology suggest that ovarian hormonal levels can be increased and interbirth interval shortened by improving female energetic status: in other words, by increasing nutritional intake, decreasing energy expenditure, or both. Any changes that ameliorated the energetic burden on human females would have had important reproductive consequences.

In addition to maternal condition, the length of the interbirth interval is also governed by the needs of dependent offspring. Suckling is very energetically costly to mothers and has a suppressive effect, at least in the initial stages, on female ovarian function. It is the primary factor influencing the length of interbirth interval (Valeggia and Ellison, chapter 4, this volume). Thus, any changes that would have shortened the period of suckling would also have had a direct effect on interbirth intervals.

Thus, I propose here that a critical suite of hominid adaptations involved finding ways to extract more energy from the environment in order to reduce female energetic burdens and shorten the period of lactational dependence of juveniles on their mothers. A number of authors have recently explored ways in which early hominids were able to overcome the nutritional constraints operating on other apes (Aiello and Wheeler 1995; Conklin-Brittain et al. in press; Leonard and Robertson 1997; Milton 1987; Wrangham et al. 1999). These arguments, however, have not focused on the consequences of increased energy efficiency on female reproductive physiology and the spacing of births.

When might this transition have occurred? Australopithecines were probably similar to great apes in many of their life history characteristics (Smith 1992); thus it is unlikely that the human pattern had emerged at that time, although it is possible that incipient changes could already have appeared. Conklin-Brittain et al. (in press) argue that the first stage in a transition to improved dietary quality occurred with the exploitation of roots, and reduced dietary fiber in australopithecines. If australopithecines exploited roots that were difficult for juveniles to access (O'Connell et al. 1999) there may have been increased food sharing between mothers and offspring. Conklin-Brittain et al. (in press) suggest that australopithecines had an improved dietary quality relative to chimpanzees that set the stage for further improvements in dietary quality with the advent of *Homo*. The emergence of *Homo*, or more specifically *Homo erectus* at 1.9 mya, has been postulated as representing a major shift in evolutionary strategy and increased dietary quality (Aiello and Wheeler 1995; Wrangham et al. 1999). The genus *Homo* is associated with increased body size, reduced sexual dimorphism, reduction in dentition (Walker and Leakey 1993), increased brain size (Holloway 1979), and the presence of flaked stone tools and cutmarked bones (Klein 1984) among other features. I would propose that a shift towards shorter interbirth intervals was part of this complex of new behaviors emerging at that time.

A suite of behaviors that can be inferred to have emerged with early *Homo* would have had a significant impact on interbirth interval: (1) exploitation of new foods; (2) development of new methods of food acquisition and processing—in particular, cooking; (3) provisioning and introduction of appropriate weaning foods; and (4) changes in social structure with an increase in non-maternal child care. These changes would have allowed hominid females to successfully shorten their interbirth intervals and would have permitted, for the first time, the occurrence of overlapping, nutritionally dependent offspring. Furthermore, I argue that rather than being just a *consequence* of changing hominid behavior, decreasing interbirth interval, increasing fertility, and increasing juvenile survivorship could themselves have been selective forces driving the changes seen in the *Homo* clade.

Exploitation of New Foods

The transition between an apelike ancestor and modern *Homo sapiens* has been punctuated by periods of environmental change in which the climate became cooler, drier, and perhaps more seasonal—thereby either forcing or enabling early hominids to shift into new habitats and exploit new dietary resources (O'Connell et al. 1999). Humans have much higher-quality diets (defined as lower in fiber) than do other apes (Conklin-Brittain et al. in press). This is associated with an overall reduction in gut size (Aiello and Wheeler 1995), an enlarged small intestine, and a shortened colon relative to apes (Milton 1999). Aiello and Wheeler (1995) propose that this shift in dietary quality allowed for more energy to be diverted to brain development. Increased energy availability may also have been important in the increase in overall body size, particularly in females, which is seen in the transition between australopithecines and *Homo erectus* (Wrangham et al. 1999). However, an as-yet-overlooked aspect of this increased energetic efficiency would have been its positive effect on maternal energy reserves and hence female ovarian function.

What dietary changes would have provided increased energy availability for females? Two food sources have been proposed as critical in this transition: meat (e.g., Dart 1953; Milton 1999; Washburn and Lancaster 1968) and tubers (O'Connell et al. 1999; Wrangham et al. 1999). Supporters of the meat-eating hypothesis draw attention to evidence of increased reliance on hunting within the *Homo* genus. The tuber argument looks to the prevalence of underground storage organs, which were a relatively unexploited and reliable food source, on the African plains (O'Connell et al. 1999; Wrangham et al. 1999). The critical feature of both foods is that they are easily digestible and could have lowered the fiber content of the diet, thus improving female energetic status.

Changes in Tool Use: Food Acquisition and Food Preparation

The ability of hominids to exploit these new foods would have been contingent upon the development of technologies to extract and process them. Indeed, the advent of *Homo* is accompanied by a huge increase in the variety and sophistication of tools found in the archaeological record (Klein 1984). In the meat-eating scenario, the development of weapons for hunting and tools for processing of animals, including those for extracting bone marrow, would have greatly opened up this food resource to hominid exploitation.

Tools would also have been extremely important in the acquisition and processing of plant foods such as tubers. O'Connell et al. (1999) argue that stone tools found after 2.5 mya would have been suitable for making digging sticks. Perhaps most important is the possible advent of cooking at this time, fully elaborated upon by Wrangham et al. (1999) and supported by O'Connell et al. (1999) as well. Cooking greatly increases the digestibility of foods and would have been a significant way that hominids were able to increase energy availability. Wrangham et al. (1999) argue that cooking increases energy intake to a greater extent than does the replacement of plants in the diet with meat.

Changes in food and feeding technologies are also evidenced in the dentition of early hominids. Several of the earliest *Homo* species have quite enlarged dentition, similar to that of the australopithecines (Walker and Leakey 1993). This gradually evolved to the reduced dentition seen in *Homo erectus*. Food processing techniques, in particular cooking, could have reduced the emphasis on oral preparation of the food and selected for this reduced dentition (Wrangham et al. 1999). Other techniques such as grinding and pounding could also have been important.

Such new methods of food acquisition and preparation would have been essential in enabling these hominids to shift to a more energy-rich diet. The effect of tools on increasing the efficiency of food processing and enhancing female energetic status is also suggested by studies of chimpanzees. For example, Bossou, one of the nutcracking sites, has the shortest interbirth intervals.

Provisioning and Introduction of Weaning Foods

All human societies provide food to dependent offspring and prepare some sort of special weaning foods. In contrast, apes rarely share food with dependent offspring and provide no special "transition" foods. The human ability to provide foods to juveniles would have allowed mothers to stop nursing sooner and thus shorten their interbirth intervals. Galdikas and Wood (1990) also suggest that supplementation may have resulted in shorter interbirth intervals in humans. O'Connell et al. (1999) propose that it was primarily the labor of grandmothers that enabled this pattern of provisioning. However, although the labor of grandmothers could have helped, I argue that it is primarily the labor reduction for mothers themselves from the use of new tools and the exploitation of new, superior foods that would have been central to shortening the interbirth interval.

Milton (1987, 1999) and others (Dart 1953; Washburn and Lancaster 1968) have argued that meat was the important new food addition with *Homo*. Meat may have been an important weaning food. Moir (1994) points out that all mammals are initially carnivorous—subsisting at first solely on mother's milk. Single plant foods are inadequate for juvenile growth because they are deficient in certain amino acids and vitamins (Moir 1994). This can be remedied through eating a diverse plant diet, but meat consumption is an even more efficient solution. Meat provides the full complement of amino acids needed by growing children. It would not be necessary for children to consume great quantities of this food, but small portions (as seen for Hadza children; Frank Marlowe, personal communication 2000) could have been an important dietary supplement. Marrow could also have served this purpose. The increased digestibility of cooked meat would have made it even more accessible to young children.

The incorporation of new foods and new food processing techniques could have been important for preparing plant foods for weanlings as well. Cooking food and thus making it more digestible would have allowed juveniles to be weaned onto adult plant foods much more quickly than if these same foods were consumed in their natural, whole state.

Study of a more recent human subsistence transition, between hunting and gathering and agriculture, provides an analogy for what might have changed in human evolution. Buikstra et al. (1986) argue that the development of large, thin-walled cooking vessels facilitated the cooking of starchy weaning foods, enabling native populations in the American Southwest to wean their children onto maize at an earlier age. This transition between hunting-gathering and agriculture has been associated with a decrease in interbirth interval (Bentley et al. 1993), thus providing a historic model for how technological change could have reduced interbirth interval during earlier hominid evolution.

O'Connell et al. (1999) propose that the trend towards a cooler/drier climate around 1.8 mya led to seasonal reductions in the plant foods easily available to juveniles, which then led to the provisioning of juveniles, particularly by grandmothers. Again, grandmothers may have assisted, but I argue that the primary focus should be on what mothers themselves did to improve their energetic status and reduce their own interbirth intervals.

One of the commonalties of the meat and tuber/plant food arguments for weaning foods is that juveniles would not have been able to obtain these foods solely by themselves. Manufacture of stone tools, hunting, and animal carcass preparation would be beyond the scope of young children. Similarly, most tubers would have required the manufacture and use of a digging stick. Cooking also requires adult involvement. O'Connell et al. (1999) point to their experiences among the Hadza, where young children require adult assistance to start a fire.

Thus the use of new foods, application of new technologies, and preparation of weaning foods were dramatic breakthroughs that enabled early hominids to (1) increase the energetic quality of the diet and thus female energetic status and (2) allow a woman to wean her offspring sooner than an ape mother normally would. These two biological consequences of changing feeding technology would have enabled a female to resume full fecundity more quickly than she would if she were more energetically stressed or had a longer period of obligate lactation. Thus, interbirth interval could have shortened at the same time as juvenile dependency increased.

Changes in Social Structure

In all the great apes, care of offspring rests primarily with females. Except for a few examples of paternal care, such as gorillas protecting offspring from infanticide, other adults do not actively assist a mother in raising her young. Ape females are unable to invest nutritionally in multiple dependent offspring. Shorter interbirth intervals and longer periods of juvenile dependency in humans would have had to be coupled with changes in group structure that would allow females to care for these closely spaced dependent offspring. The precise social structure of early hominids is unknown, but sexual dimorphism is clearly reduced between the australopithecines and later *Homo*. This implies multimale/multifemale groups rather than the single male breeding systems associated with pronounced sexual dimorphism. Wrangham et al. (1999) suggest that this is the period when the human mating system of pair bonds enmeshed within multimale, multifemale communities (Rodseth et al. 1990) first came into being. Hrdy (1999) argues that humans are "cooperative breeders" in order to meet the needs of offspring care. Regardless of the exact nature of the social structure, maternal support from a male partner, female relatives, or other group members would clearly have been essential to this adaptation.

CONCLUSION

From comparative studies of great apes we can see that energetics plays a central role in regulating reproductive parameters. Now we can project how they might have affected early hominid reproductive ecology. Ape females are more heavily constrained by the needs of dependent offspring than are humans. Our technological and social adaptations have allowed us to have phenomenal reproductive success. We have moved into almost all imaginable environments and increased our numbers at exponential rates. This could not have been accomplished if humans had retained an apelike interbirth interval and the need for one offspring to be nutritionally independent before producing the next. Once some individuals exploited new foods or processed existing foods in new ways, the resultant increase in dietary quality would have had dramatic effects on interbirth intervals. The cooking of plant foods, possibly tubers, is one likely candidate for this new resource. The consumption of some quantity of meat or marrow may have been an important weaning supplement as well.

Thus, changes in foods consumed, the development of technology for processing them, and the introduction of weaning foods would have had dramatic effects on female energetics, juvenile nutritional dependency, and the interbirth interval. First, it would have increased the energetic quality of the human diet, having a net positive effect on female energetic status. This would have improved female reproductive condition and allowed females to recoup energetic investment in offspring more quickly. Second, for the first time it would have allowed a hominoid to provision offspring outside of lactation. Third, the associated reduction in sexual dimorphism and a postulated change in social structure would have made the care of these closely spaced, dependent offspring feasible. Ultimately, I see this complex of hominid adaptations as an important driving force in human evolution through their effects on female energetics and reductions in interbirth interval.

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