Development of Ecological Competence in Sumatran Orangutans

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ABSTRACT   Data on orangutans (*Pongo pygmaeus abelii*) living in a Sumatran swamp forest yield an estimated median interbirth interval of at least 8 years, concurring with findings from other sites. This longest known mammalian interbirth interval appears due to maternal amenorrhea during the long exclusive dependence of the offspring. We describe the development of various components of offspring independence. In this arboreal ape, 3-year-olds had largely reached locomotor independence. Nest-building skills were also well-developed in 3-year-olds, but immatures shared their mother's nest until weaned at around age 7. At time of birth of the new sibling, association with the mother had begun to decline for both male and female offspring, suggesting that the immatures had mastered all the necessary skills, including basic tool use, to feed themselves. By about 11 years of age, they also ranged independently from the mother. These results show that orangutans do not develop independence more slowly than chimpanzees. Why, then, is weaning 2 years later in orangutans? In chimpanzees, mothers are often accompanied by two or even three consecutive offspring, unlike in orangutans. This contrast suggests that an orangutan mother cannot give birth until the previous offspring is ecologically competent enough to begin to range independently of her, probably due to the high energy costs of association. Thus, the exceptionally long interbirth intervals of orangutans may be a consequence of their solitary lifestyle. Am J Phys Anthropol 127:79–94, 2005.   © 2004 Wiley-Liss, Inc.

Primates differ from other mammals in their slow life history (Read and Harvey, 1989), including relatively long interbirth intervals and long periods of juvenility (Harvey and Clutton-Brock, 1985; Pereira and Fairbanks, 1993). The interbirth intervals of apes, e.g., 3–5 years for gorillas (Watts, 1991; Yamagiwa and Kahekwa, 2001) and 5–7 years for chimpanzees (reviewed in Boesch and Boesch-Achermann, 2000), are similar to the longest intervals found among mammals, i.e., in elephants and whales (Lee and Moss, 1986; Whitehead and Mann, 2000; Whitehead and Weilgart, 2000). Long-term data on wild populations of orangutans (*Pongo pygmaeus*) documented an even longer interbirth interval of approximately 8 years (Galdikas and Wood, 1990; Leighton et al., 1995; Knott, 2001). Long interbirth intervals could be due to late weaning of the infant or to long recovery periods of the mother after she has weaned her previous offspring. In apes and many other primates, conception of the next offspring tends to coincide more or less with weaning (Pusey, 1983; Graham and Nadler, 1990; Watts, 1991; Lee and Bowman, 1995). Hence, a long interbirth interval indicates late weaning, and thus slow infant development. However, it is not clear why orangutan infants are weaned later than those of other great ape species.

The slower development to nutritional independence in orangutans relative to the other great apes could simply reflect their slower life history. The latter is either due to lower adult mortality (Charnov, 1993), a greater need to learn ecological and/or social skills (e.g., Ross and Jones, 1999), or unusually large payoffs of ecological risk reduction through slow growth of the body and/or brain (Janson and van Schaik, 1993; Deaner et al., 2003). Although what these life history models explain is variation in total length of the pre-reproductive period, the latter is strongly correlated with age at weaning. Alternatively, the slower infant development of orangutans could reflect the combination of the low productivity of Southeast Asian rain forests (Terborgh and van Schaik, 1987) and the orangutan's energetically costly lifestyle as imposed by large body size and arboreality (Knott, 1998, 2001). Thus, the anomalous position of the orangutan, relative to the other great apes, could reflect its unusual life history, its unusual ecology, or both.

An important first step toward understanding life history differences between apes is to recognize that the end of lactation, i.e., weaning, may only be one of several markers of independence from the mother rather than an adequate summary of the whole process, even though it has become the defining step in our terminology (infant vs. juvenile). A broader approach (Pereira and Altmann, 1985) holds that the distinction between infants and juveniles is the ability to survive the death of the mother. Since lactation is the most obvious uniquely maternal service, weaning is often seen as the essential transition to the ability to survive. However, the mother serves multiple functions: in addition to nutrition, she provides transportation, shelter (against elements), and protection (against conspecifics and predators), and demonstrates numerous skills that the offspring can learn, including knowledge of food species (diet competence), foraging techniques (foraging competence), and efficient use of the range (ranging competence). The offspring eventually has to reach independence in all these aspects, but does not necessarily do so at the same time for all of them. In addition, some of the mother's services could be shared with a younger sibling or, in gregarious species, may also be provided by other group members. Our understanding of the life histories of different apes would be advanced if we could identify which aspects of dependence limit the mother's interbirth interval.

In this paper, we present findings on the development of immature orangutans in an attempt to document how the development of orangutans differs from that of other apes. Building on earlier work by MacKinnon (1974), Horr (1977), Rijksen (1978), and Galdikas and Briggs (1999), we collected focal data on females and independently traveling immatures, and ad libitum data on mother-offspring interactions in a wild population of orangutans in a Sumatran swamp forest. We used these data to disentangle different aspects of independence. Our analyses provide estimated ages of independence for specific aspects of competence. They suggest that orangutan infants are weaned so late because the mother and older offspring cannot afford to associate continuously while the mother cares for her next infant. Therefore, the close association between mother and offspring is terminated before the next infant makes the greatest energy demands on the mother. In contrast, in the other great apes, juveniles tend to accompany the mother for several (chimpanzees) or many (gorillas) years following the birth of a sibling, allowing for a gradual development of ranging competence after weaning, and hence earlier weaning.

METHODS

Subjects and methods

Data were collected on the orangutans (*Pongo pygmaeus abelii*) of the coastal swamp forest of Suaq Balimbing (03°04′ N, 97°26′ E), Leuser Ecosystem, South Aceh, Sumatra, Indonesia, starting in Febru-
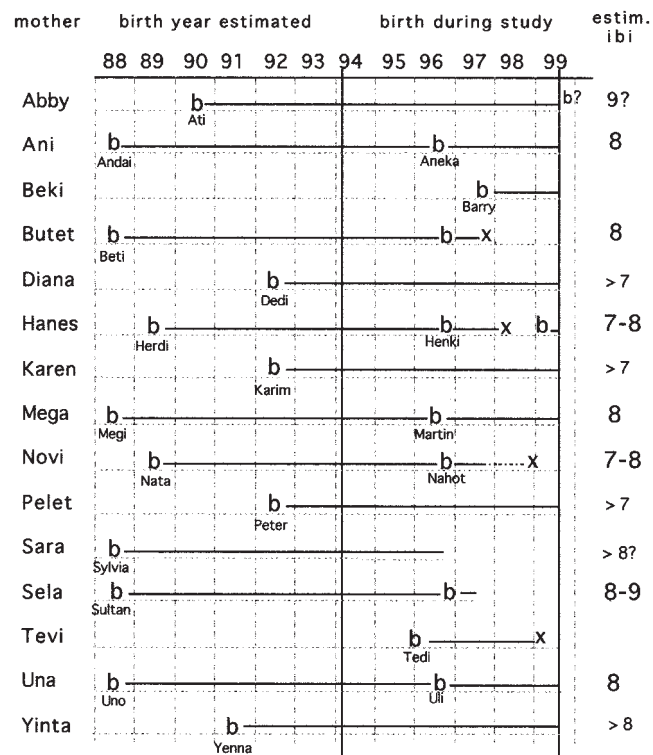

Fig. 1. Estimated and known births and estimated interbirth intervals (estim. Ibi) for focal females listed at left. b, birth; x, disappearance. Abby was probably pregnant at end of study. Sara and Sela were not encountered after 1996.

ary 1994 (see van Schaik, 1999; Singleton and van Schaik, 2001, 2002). Sustained civil unrest forced an abrupt and definitive end to data collection in September 1999.

Figure 1 names the individuals in the study, and also gives the known month and year of birth for infants born after the onset of the study in early 1994 and the estimated birth year for immatures born earlier. These age estimates reflect the consensus reached by experienced researchers: Bahlias, ElizaBeth Fox, Ibrahim bin'Mohammad, Ian Singleton, and C.P.v.S. They were subsequently checked against sizes of infants of known age born later in the study, using photographs taken earlier in the study. All estimates were finalized in the field before data analysis began. During the study, births were concentrated in one peak year. No births were apparent until late 1995, followed by eight births in 1996, one in 1997, and none in 1998. Thus, the uneven distribution of estimated ages of offspring born before 1994 probably reflects the study animals' actual reproductive synchrony (see also Fox, 2002; Singleton and van Schaik, 2002). During the study, four females lost their immature offspring (see Fig. 1). The circumstances of these losses are unknown, since none happened during weeks of frequent encounters by observers with the mothers. Nothing seemed unusual in the activity pattern or health of at least two frequently observed immatures before their disappearance (Tedi and Henki;

see below). Unfortunately, human disturbance (illegal logging) in the surroundings of the study area cannot be excluded as a cause for these disappearances.

We refer to infants, juveniles, and adolescents together as immatures. Data were collected by a team of trained observers, who frequently checked their interobserver reliability (see Fox, 1998). Throughout the study, focal samples were taken on individual orangutans encountered in the study area. Due to the difficulties of reliably locating individuals, no predetermined sampling schedule could be followed, but once an individual was found, it was followed as a focal animal for the rest of the day and often on subsequent days. A focal's activity was recorded every 2 min (for definitions, see van Schaik, 1999) during the active period of the day (after sitting up in the morning nest and before laying down on the night nest). A full account of its social interactions and the presence of other individuals within 10 m ("proximity") and within 50 m ("association") was kept. The 50-m distance was chosen to reflect the observed distance at which active coordination was maintained by individuals. Thus, immatures spending most of the day at >50 m from their mother were regarded as ranging independently for that period, most likely visiting other major food sources than their mother.

Behavioral data on immatures come from three sources. First, ad libitum notes on offspring behavior were taken during all focal samples of mothers throughout the study (February 1994–September 1999; total mother focal time, 8,835 hr). These data were used as qualitative indicators for the presence of hard-to-observe or relatively rare behavior, e.g., nipple contact, nursing conflicts, nest building, or sharing of nests. Second, mother-infant distance as well as the mother's activity at the time was recorded once every 30 min during a subset of these focal follows (March 1997–September 1999; classes used here: "on mother," 0–10 m, 10–50 m, and >50 m). Data taken within 1 year were pooled to obtain an annual sample of at least 80 distance scans per mother-offspring pair (initial analysis showed 80 scans to be the minimum for a reliable estimate; individual annual samples were between 80–549 scans, for a total of 5,239 mother-offspring distances). Third, focal animal samples (each sample with a minimum duration of 3 hr) were collected on two young infants (Aneka and Barry) for a total of 155 hr in 1999, one immature estimated to be at least 9 years old but without a younger sibling (Ati in 1999; 70 hr), and four others after their mother had given birth to a younger sibling (in total, 1,110 hr of focal samples for older siblings; in the case of Ani-Andai, sampling started during the mother's late pregnancy).

Analyses

As in most other studies of great ape development, we have low power due to relatively small numbers of individuals and the one-zero nature of some of the behavioral indices (e.g., weaning in a given year). We also have a possible lack of independence of data because comparisons contained mixed longitudinal and cross-sectional data, and because most focal samples were collected on several consecutive days followed by days or weeks without any observations of that focal, rather than in randomly allocated, widely separated days. Because samples of individuals lack natural "data points" (days, months, years?), formal statistical analysis is often impossible, especially when the only null hypothesis available is that of no change rather than specified relationships (cf., Altman, 1980). Instead, therefore, we had to rely on 1) strong consistency of time courses among individuals, 2) the fact that the confidence limits of most long-term (e.g., annual) means of individual variables, although unknown, must have been very small due to large numbers of observation hours for each of them, or 3) the fact that exceptions to the trend had a straightforward biological explanation. For some analyses, data for several individuals were pooled to a obtain a larger sample for a first indication of a trend. This was only done when there seemed to be no striking differences between individuals. Throughout, we will indicate sample sizes (numbers of individuals) on which our conclusions were based.

Statistical analysis was possible in some cases. Thus, for the analysis of the dependence of mother-offspring distance on maternal activity, we used the half-hourly mother-infant distance scans as independent points. Chi-square tests were used to test whether the frequency of body contact was equally distributed over different maternal activities. For nonparametric (censored) survival analysis (Kaplan Meier method) of interbirth intervals, we used the statistical package Minitab (version 13.1, 1999).

RESULTS

Interbirth intervals

None of the 12 females with a surviving youngest offspring gave birth twice within the 5.5-year study period (Fig. 1). Moreover, none of the three females with an infant estimated to be 1–2 years old in 1994, and surviving until the end of the study, gave birth before the forced end of the study in 1999, suggesting an interbirth interval (after a surviving offspring) of at least 7 years.

Our estimates of interbirth intervals are based on the estimated ages of offspring present at the start of the study. Thus, the median (estimated) interbirth interval in this sample was 8 years (N = 8). Survival analysis based on estimated complete intervals and uncompleted (right censored) intervals yielded a median interbirth interval (after a surviving infant) of 8.2 years (Kaplan-Meier method).

Two lines of evidence suggest that the duration of interbirth intervals is set by the length of lactational amenorrhea. First, females with surviving offspring showed very little sexual behavior until the offspring was estimated to be at least 5–6 years old,
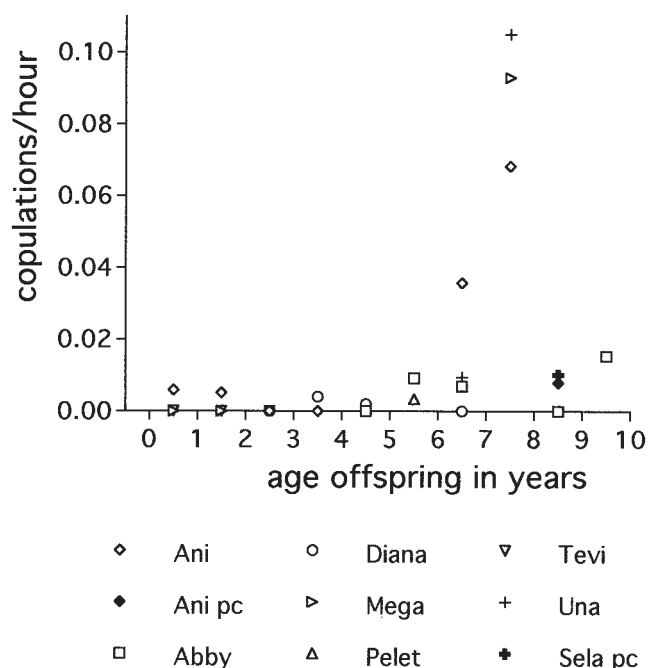
Fig. 2. Relationship between age of youngest surviving offspring and frequency of copulations by their mothers (based on copulations seen per hour of focal female sample if more than 100 hr of focal sample were available for that year). pc, postconception matings (for Ani and Sela).

with a major increase in frequency of copulations when the offspring was at least 7 years old (Fig. 2; the three points available for age 7 were the three highest by far among all 28 annual copulation rates for all females). This peak was followed by a peak in births when the previous offspring was an estimated 8 years old. Urinary hormone analyses by Fox (1998), during the early years of this study, confirmed a close relationship between the presence of ovarian cycles and sexual activity, including copulations resisted by the female (see also Fox, 2002). Thus, the extremely low copulation rates for mothers with offspring under 6 years old is probably a reflection of a lack of ovarian activity.

The second indication of long lactational amenorrhea is that females became sexually active within a relatively short period after the loss of a suckling offspring. Of the 4 females who lost their infant, at least 2 became sexually active within several months of the disappearance of the offspring (most females were not observed every month). One (Hanes) gave birth within 13 months of the loss of her 1-year-old son, and another (Tevi) was seen copulating with the dominant male within 3 months of the last sighting of her 3-year-old son, and may have been pregnant by the end of the study. The 2 other females (Butet and Novi) were encountered less often, but were at least sexually active before the end of the study (within a year after the disappearance). Thus, of the 8 females who gave birth during the study and were still seen in 1999, only the 4 who had lost their infants were sexually active again before the end of the study.

Offspring development: distance between mother and offspring

Body contact. The half-hourly distance scans during focal sampling of mothers revealed that during their first 3 months of life, infants were always in body contact with the mother (100%; N = 85 scans, pooled for all individuals). The percentage of time in body contact decreased continuously over the next 2 years: from 79% for 3–6 months (N = 806), to 48% for 6–12 months (N = 809), 40% for 12–18 months (N = 648), 25% for 18–24 months (N = 200), and 16% at 2–2.5 years of age (N = 524 scans). Only in the latter period did the distance between mother and offspring start to exceed 10 m (for about 10% of the time). At the individual level, the same pattern was apparent. During the first year of life, all 4 infants observed were in body contact with their mother most of the time, but in the second year, all 5 observed infants were already moving or sitting without contact for about half of the active period of the mother (Fig. 3a). Yet for the subsequent 6 years, immatures still spent around 10% of the day in body contact with their mother. At around the time a younger sibling was born, physical contact between mother and offspring had decreased to only an occasional touch in all four frequently observed mother-offspring pairs. Just as among adults, there was hardly any grooming between mother and offspring.

Mother-offspring body contact, as estimated by these distance scans, was not evenly distributed over the mother's activities: chi-square contingency-table analysis of 13 annual samples involving six different immatures yielded 11 samples with an uneven distribution at $P < 0.01$ (one had $P < 0.05$, and one was not significant). Hence, we examined time in body contact separately when the mother was traveling (transportation function, i.e., infant being carried or clinging onto mother during her travel; Fig. 3b), when she was feeding (Fig. 3c), when she was resting on a day nest (other functions such as suckling, reduction of heat loss, or protection; Fig. 3d), and when she was resting but not on a nest (Fig. 3e).

In the first years of life, an orangutan infant did not have the locomotor skills to travel between trees and was thus dependent on its mother for transportation. Although very young infants were temporarily out of body contact when the mother was feeding (Fig. 3c), with 1-year-olds being in contact less than half the time, contact was restored as soon as the mother started to travel. Indeed, up to 2 years of age, infants were carried by the mother more than 80% of the time she traveled (n = 5 different infants; Fig. 3b). Offspring of 3 years or older (n = 5 different individuals) were carried by their mother less than 20% of her travel time, although some were carried occasionally for several more years. In addition, mothers frequently helped 4- and 5-year-olds cross larger gaps between trees by serving as a bridge, without actually carrying their offspring, and mothers occasionally assisted even older offspring.
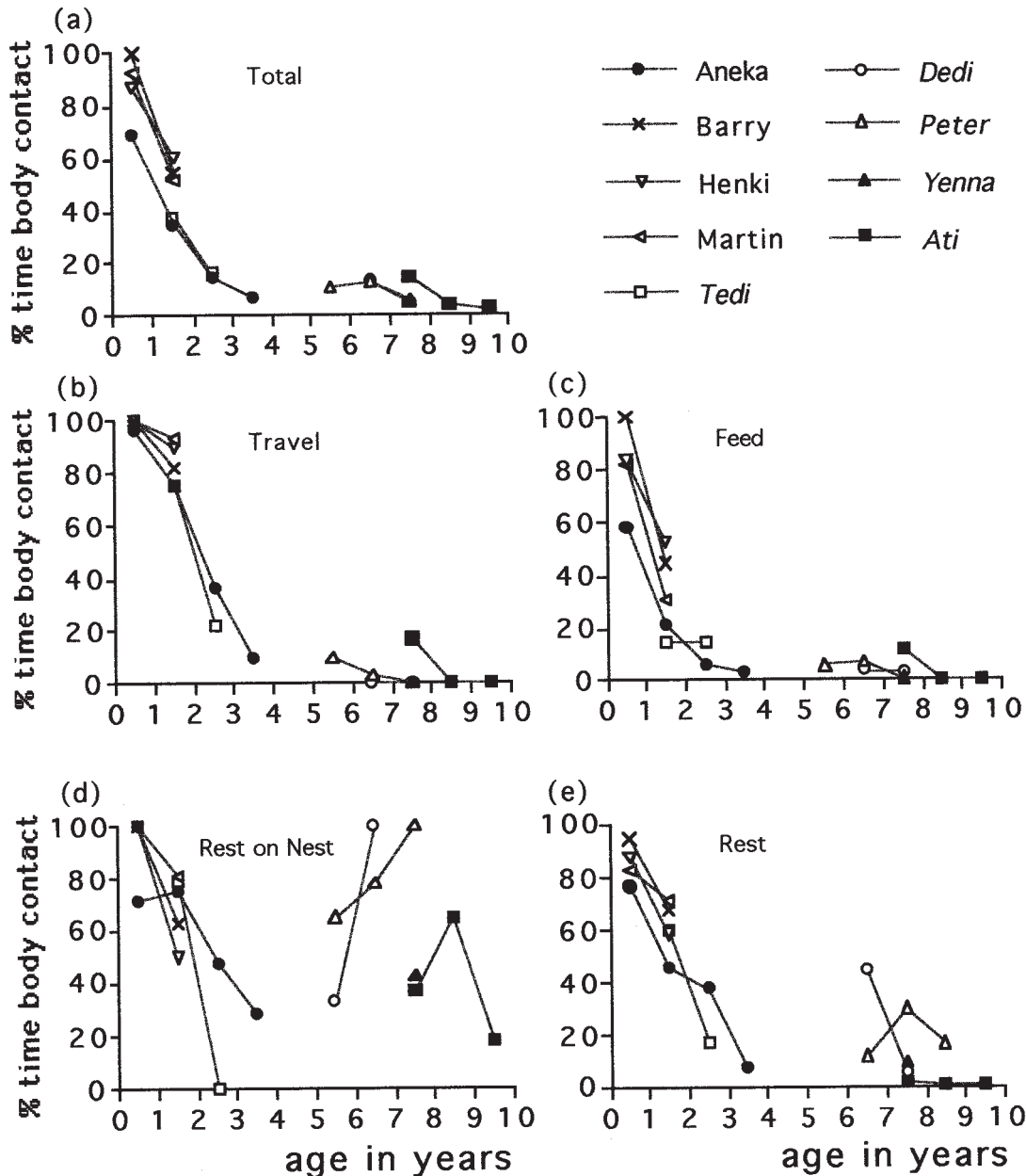
Fig. 3. Age of offspring and percentage of time that immature was in body-contact with mother. **a:** Total, i.e., regardless of mother's activity. **b:** While mother was traveling. **c:** While mother was feeding. **d:** While mother was on day-nest. **e:** While mother was resting during day, not on a nest. Solid symbols indicate females; open symbols indicate males. Italics indicate individuals with estimated age.

In contrast, when the mother was resting on a nest during the day (Fig. 3d), there was no clear pattern with age in the amount of time spent in contact. During this contact time, offspring may either have been suckling, or mother and offspring played or rested together. During the mother's other resting time (i.e., not on a nest), some of the older offspring would still be in body contact for 20% of the time or more (Fig. 3e). Thus, while 3-year-old orangutans had mostly reached locomotor independence and were mostly off the mother during feeding, they continued to be in body contact with the mother for other needs, such as nutrition, warmth, and protection, until around 8 years of age.

Distance from mother. A young infant moving away from its mother stayed in the same tree, and if it ate, did so from the same food source as its mother (a distance of less than 10 m represents staying mostly in the same tree, and often feeding on the same food as the mother; a distance between 10–50 m represents being within visual and hearing distance, but usually in a different tree and often choosing a different food source, except for large-crowned fruit trees). To show the changes with age in distance from the mother, we combined the focal data on older immatures with the distance scans of mother-offspring pairs. Figure 4a shows a consistent drop in the amount of time spent in proximity to the
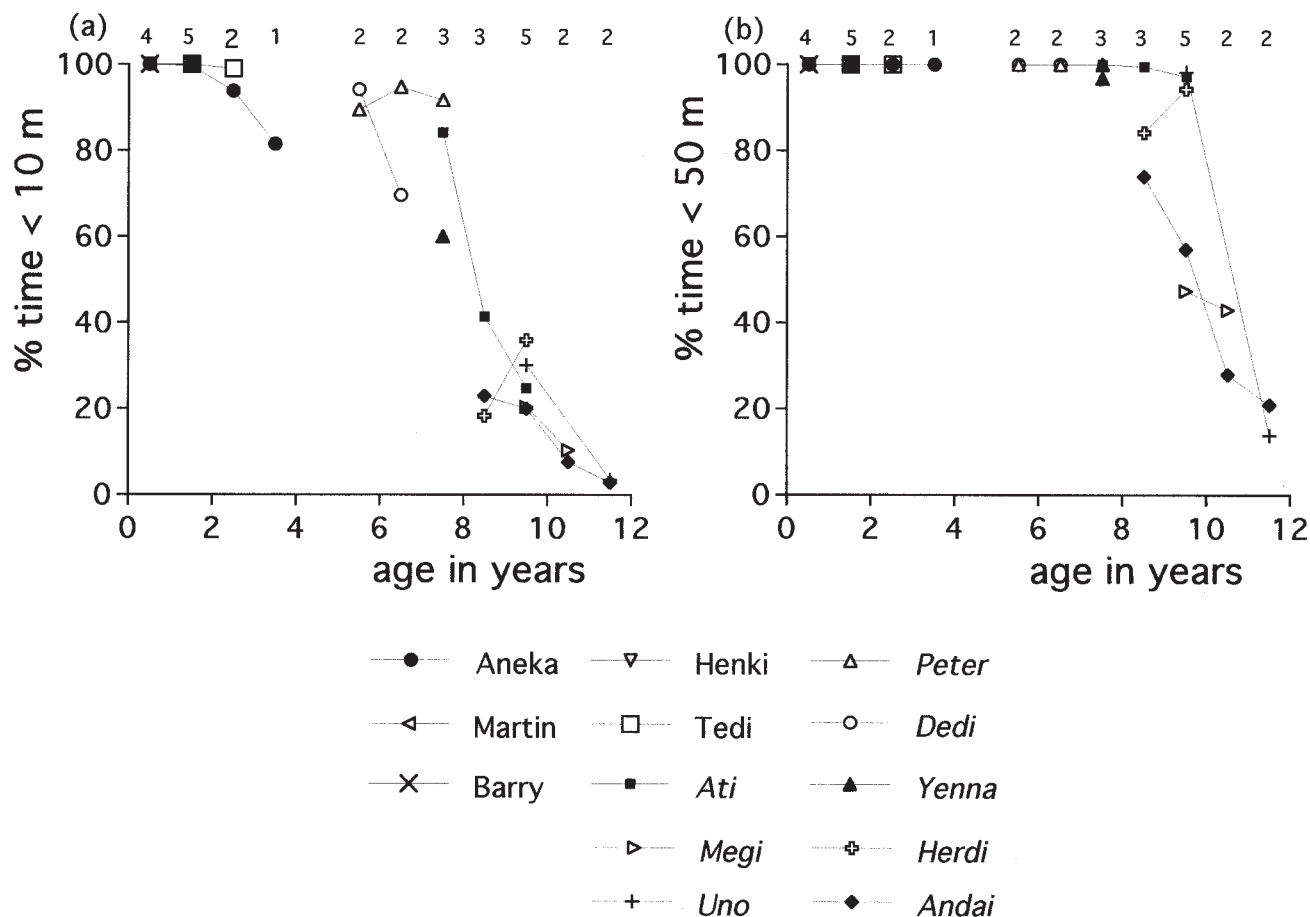
Fig. 4. Age of offspring and percentage of time mother and offspring were (**a**) less than 10 m apart ("same tree") and (**b**) less than 50 m apart (at least within hearing and usually sighting distance), based on focal samples of both mothers and immatures. Symbols and italics as in Figure 3. Numbers above graph indicate number of individuals per age.

mother (at <10 m) starting at around age 6 or 7. One of the exceptions, Peter, whose mother was in poor condition (e.g., showing signs of ringworm), showed more distress (whining) than any other immature in the sample; his proximity did not decline with age, at least not before he was 8 years old. The other exception, Herdi, returned to pre-pregnancy levels after his mother's new infant had died.

A similar but even more sudden decline was seen in the time spent in association (<50 m) with the mother beginning at age 8 (Fig. 4b; 4 out of 5 individuals showing the trend). This decline was related to the mother's subsequent pregnancy and the birth of a new sibling. Thus, one 8–9-year-old (Ati), whose mother had not yet conceived during sampling, showed only a very modest decline in association. The exception again was Herdi (see above).

We suspect that the immediate cause of the decline in proximity is not the birth of the younger sibling but a change in the relationship during the early phase of the mother's pregnancy. For the offspring with the largest sample, Andai, the birth of a younger sibling did not seem to be related to the increase in separation. In the 6 months before and the 6 months after the birth of the younger sibling, the percentage of her time at <10 m was virtually

unchanged (27.3% vs. 28.3%), whereas that at >50 m showed only a very modest increase (17.85 vs. 22.9%) during 102 and 114 hr of focal animal sampling, respectively. (We had started to follow Andai as an independent focal because of the sudden drop in association with the mother.)

Several observations suggest that when mother and offspring started to spend time out of association, their ranging did not immediately become independent. Mothers were seen to quickly respond to any signs of distress of their offspring within hearing distance, although, remarkably, when mother and offspring restored visual contact, there were no obvious greetings or reunions with body contact. Hence, mother and offspring stayed within visual and auditory contact for most of the first 8–10 years after the offspring's birth.

When immatures began to spend more time out of association with the mother at around 8 years of age (Fig. 4b), they often did so in the company of conspecifics other than the mother, but eventually all immatures in this sample spent time completely alone (see below).

Nest-sharing. Immatures continued to share their mother's night nest until they were at least 5

name	f/m	YoB	0	1	2	3	4	5	6	7	8	9	10	11
Barry	m	1997	S-	S-										
Aneka	f	1996	S-	S-	S-	S-								
Henki	m	1996	S-	S-										
Martin	m	1996	S-	S-	S-									
Tedi	m	1996	S-	S-	S-									
Uli	f	1996	S-	S-										
Dedi	m	1992			S-	S-	--		--	--				
Peter	m	1992			S-			S-	SO	S-				
Yenni	f	1991								S-	--			
Ati	f	1990					S-	S-	--	--	-O	-O		
Herdi	m	1989						--	--		-O	(S)O	-O	
Andai	f	1988							SO	SO	SO	(S)O	-O	-O
Megi	m	1988								SO	-O	-O	-O	-O
Sultan	m	1988							--	--	S-			
Uno	m	1988							SO	-O	-O	-O		-O

S = Share mother's nest
O = Own night nest
_ = S or O not observed

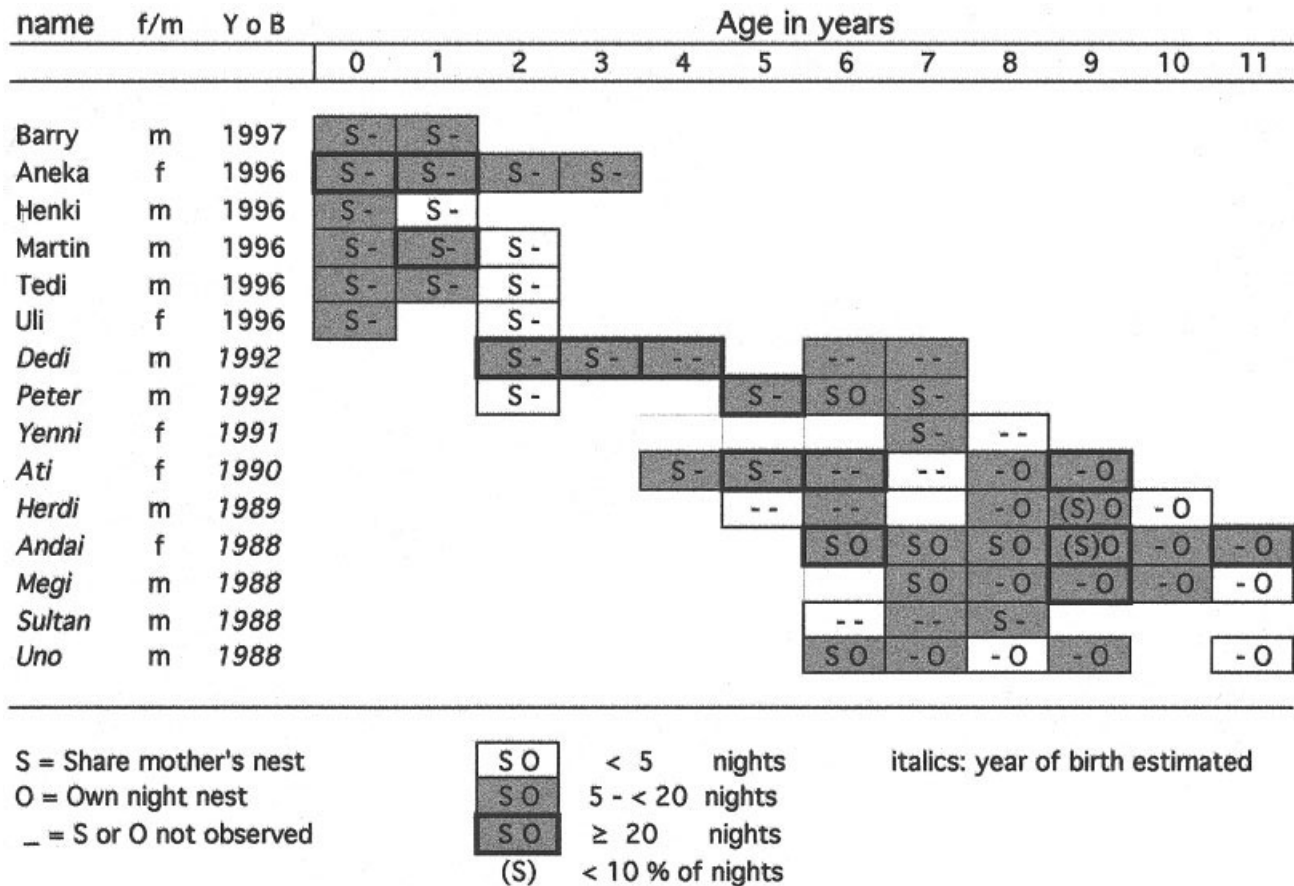|	
SO	< 5 nights
SO	5 - < 20 nights
SO	≥ 20 nights
(S)	< 10 % of nights

italics: year of birth estimated

Fig. 5. Age in years at which immatures were seen to share night nest with mother or slept in their own nest.

years old. First observed ages of independent nesting for the night were between 6–8 years (Fig. 5). Six- and 7-year-olds started to make their own night nest, but tended to move over to their mother's nest for at least part of the night. Once an immature consistently slept in its own nest from around age 7 or 8, this was usually close to their mother's, being not more than 50 m away and thus easily within earshot. Finally, by 8 or 9 years of age, immatures rarely spent the night in their mother's nest. Whereas immatures stopped nesting with their mothers before the birth of a younger sibling (n= 4), one of them, a 9-year-old son (Herdi), reverted to sleeping in his mother's nest a few times after the disappearance of his 1-year-old sibling. Although immatures occasionally shared a nest for rest and play during the day, they were never seen to share a nest with each other for the night, nor with any adult other than the mother.

Associations

From the focal animal samples of the older immatures, we calculated the total time spent in association with the mother (with and without others) and with others than the mother, as well as time alone. Since for most individuals the samples were smaller than 100 hr per year, we pooled four immatures by age to get a first indication of the changes with age (Fig. 6a). Among adults, the percentage of time spent alone varied both between years and individuals. During the sampling period, the mothers of the sampled immatures spent between 40–70% of their time alone (i.e., only accompanied by their youngest unweaned offspring; not shown). Eight-year-olds still spent half the time with their mother, and when they were away from the mother they were in the vicinity of others most of the time. However, 10–11-year-olds had reached "adult" levels of gregariousness (Fig. 6a). The drop to zero time with mother for 11-year-olds (n = 3, pooled) in Figure 6a is probably due to small sample size. In the larger sample, including the distance scans during the mothers' focal follows (Fig. 4b), these three 11-year-old immatures spent up to 20% of the active day within 50 m of the mother. Thus, even though 11-year-old immatures are not full-grown and not yet sexually mature, they spent little time with a close relative and were without companions within easy hearing distance for about half the time.

Associations at night

Figure 6b shows the total percentage of nights that 8–11-year-old immatures spent with their mother or with others within a 50-m distance of their nest. Small sample sizes (and samples consisting of clusters of consecutive nights) preclude a
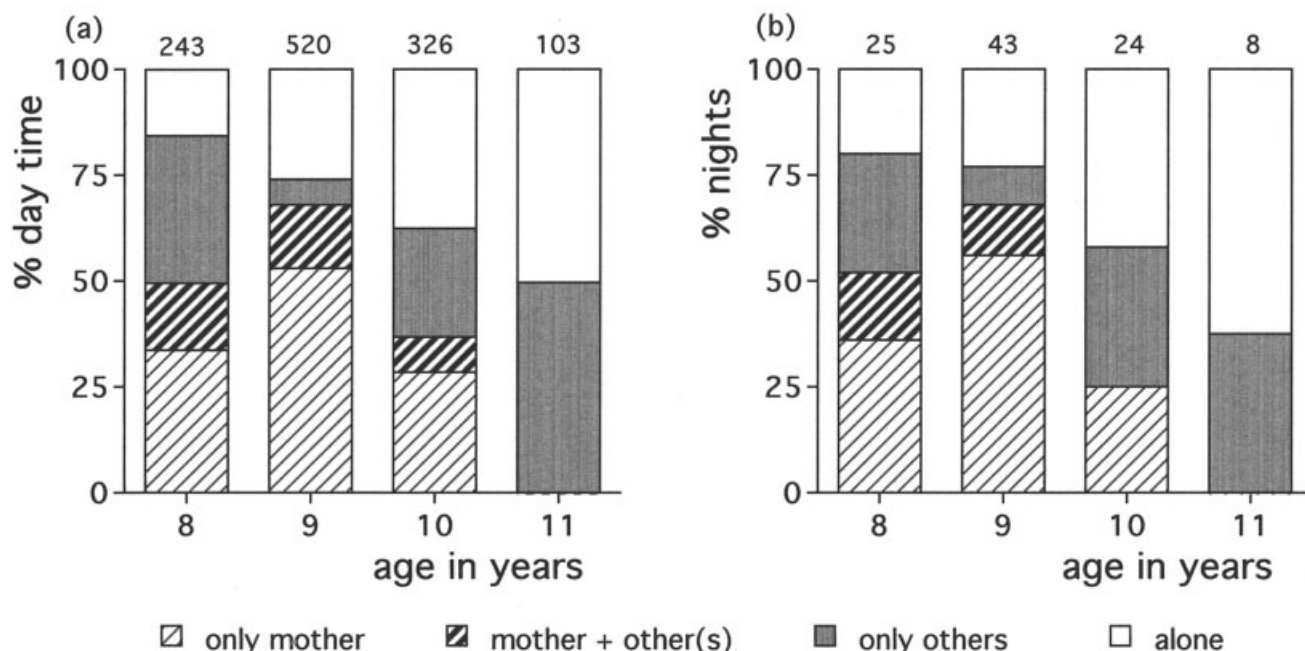
Fig. 6. Percentage of daytime (**a**) and percentage of nights (**b**) spent by immatures within 50 m of conspecifics, in various social contexts. Numbers above bars are total number of focal observation hours (daytime) and total number of nights, pooled for immatures. Based on immature focal samples only (unlike Fig. 4; hence slight discrepancy).

meaningful statistical comparison between individual immatures. Until about 9 years of age, immatures (n = 4, pooled) spent at least half their nights associated with their mothers, but this decreased rapidly from age 10 onward, when daytime associations also became very low. In this small sample, the three 11-year-olds had reached adult levels of association both during the day and at night.

Activities

The ad libitum notes taken during the focal observations of mothers can be used as a positive confirmation of the occurrence of a behavior at a certain age, but not as reliable estimates of their frequency. Nonetheless, we found clear patterns in development of independence based on 2–9 individuals per year class for several major developmental markers.

Time budget. The focal samples of two young immatures suggest that, although offspring started to eat solid food when they were about 1 year old, their activity budgets differed dramatically from their mothers' (Fig. 7a,b) these differences were found consistently on a daily basis for feed and play. Thus, until at least 3 years of age, infants spent less than half as much time feeding on solid food as their mothers. At the same time, they spent more than half of the daytime on energy-demanding activities not involved in foraging, such as play (both solitary and social) and "moving around." We have no data on activities during intermediate ages, but by 8 years of age, Andai's activity budget closely resembled that of her mother (Ani), and was not clearly affected by the birth of her younger sibling (Fig. 7c,d).

Nursing and weaning. Due to the orangutan's arboreal lifestyle, observers on the ground were unable to determine whether an offspring was being nursed, and often even whether there was nipple contact. Orangutan mothers nurse their infants inconspicuously throughout the day, often while feeding or even traveling themselves, as well as on the night nest. Older infants, who rarely clung to their mother outside the nest (Fig. 3), frequently returned to their mother for short bouts of suckling that lasted only a few minutes. The youngest infants whose mothers began to reject "suckling" visits were around 5 years old (Fig. 8), but the mothers often allowed suckling at another moment the same day. Offspring often responded to these rejections with screaming and sometimes with tantrums. Nevertheless, weaning seemed to be a very gradual process, since at least 7 of the 9 different 7-year-olds were seen to visit their mother for an occasional short bout of nipple contact, but none of 7 different 8-year-olds were seen to do so, irrespective of the birth of a younger sibling. Thus, the median age for the last observed "suckling visit" was 7 years (n = 9; range, 6–8). Although it could not be seen whether offspring were nursed on the nest, the age of last suckling more or less coincided with the age when the night nest was last shared with the mother (Figs. 5, 8). Thus, weaning and independent nesting appeared to coincide.

Play. Mothers occasionally played with their offspring, either on or off a nest. Around the time of weaning, mothers sometimes appeared to distract the immature from seeking contact with her nipple by initiating play (cf. chimpanzees: Goodall, 1986, p.
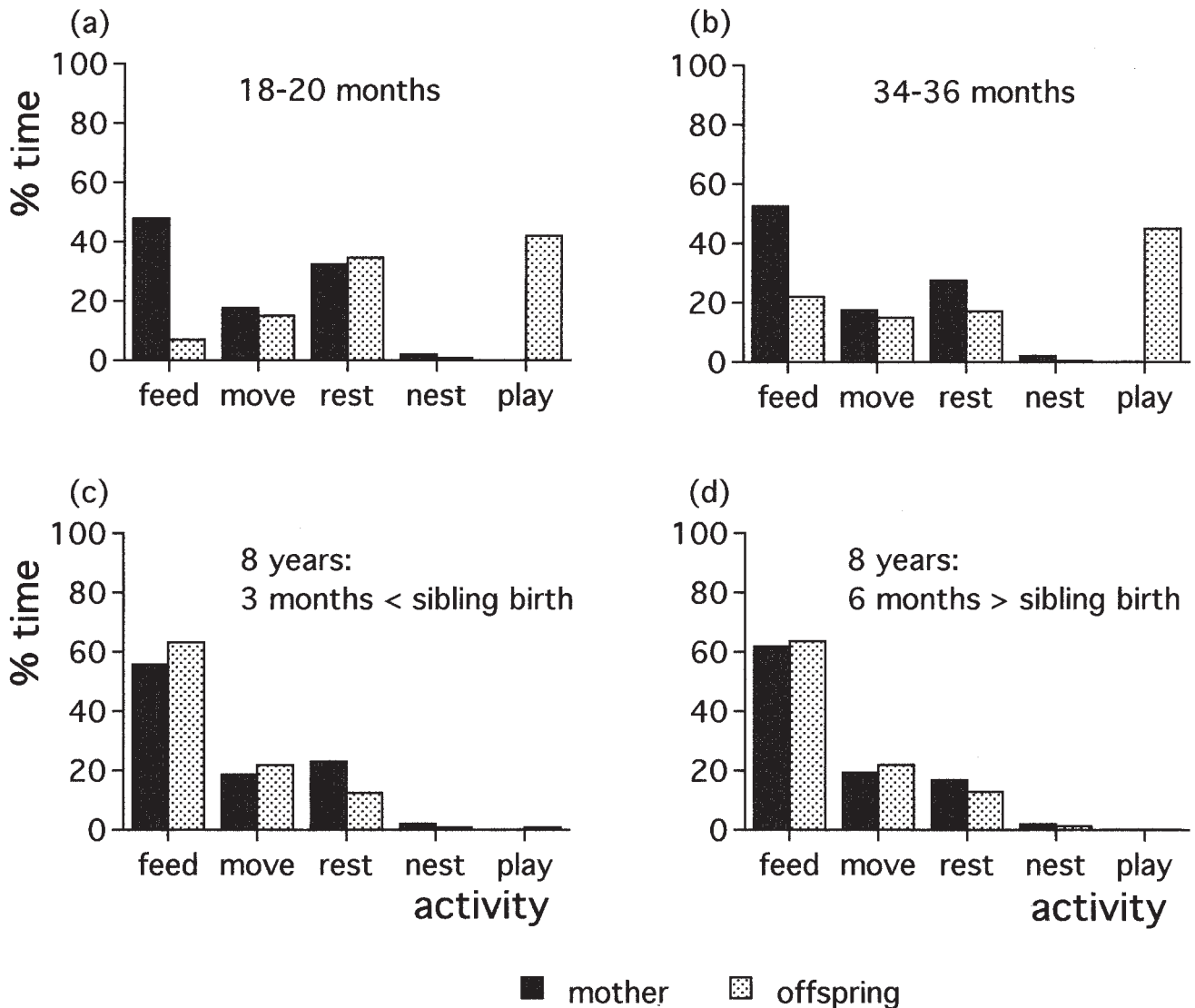
Fig. 7. Comparison of time spent per activity for mothers and offspring sampled in same period. **a:** Mother Beki (62.3 hr) with son Barry (65 hr), data collected when 18–20 months old. **b:** Mother Ani (61.4 hr) with daughter Aneka (50.7 hr), when 34–36 months old. **c:** Mother Ani (191.7 hr) with daughter Andai (99.8 hr), during 3 months preceding birth of younger sibling. **d:** Mother Ani (168.1 hr) with daughter Andai (114.1 hr), during 6 months following birth of younger sibling.

572). Although at least three mothers were seen to play with their 7-year-old offspring, no play was seen between any offspring older than 7 years and its mother (N = 8 possible pairs; 2,984 hr of focal observations on mothers, and 1,222 hr on offspring). Thus, the end of mother-offspring play more or less coincided with complete weaning. From an early age, infants frequently played with peers and continued to do so after weaning.

In general, mothers remained tolerant of their independent offspring. They usually allowed them to eat in the same tree and occasionally allowed them to take turns at the same food item (e.g., liana, honey from tree hole). However, whereas unweaned offspring were only rarely denied access to already picked and/or processed food items, weaned ones (7 years and older) were sometimes chased away when they tried to feed on the same branch in a fruiting

tree. Although such interactions were rare, they may have contributed to the increased spacing between mothers and offspring.

Technological skills

Orangutans construct nests in trees for the night and for rest or play during the day. They also make "rain hats" out of large-leafed twigs, covers for their nests (especially when it rains or is about to rain), and "bee-swatters" to cover their face while opening bees' nests (van Schaik et al., 2003). In addition, the Suaq Balimbing population of orangutans is known for unique local tool-use traditions (van Schaik et al., 1996; Fox et al., 1999; van Schaik and Knott, 2001). All frequently observed individuals in this population use stick tools to harvest insects and their products, and they use small sticks to extract the nutritious seeds of *Neesia* fruits from among
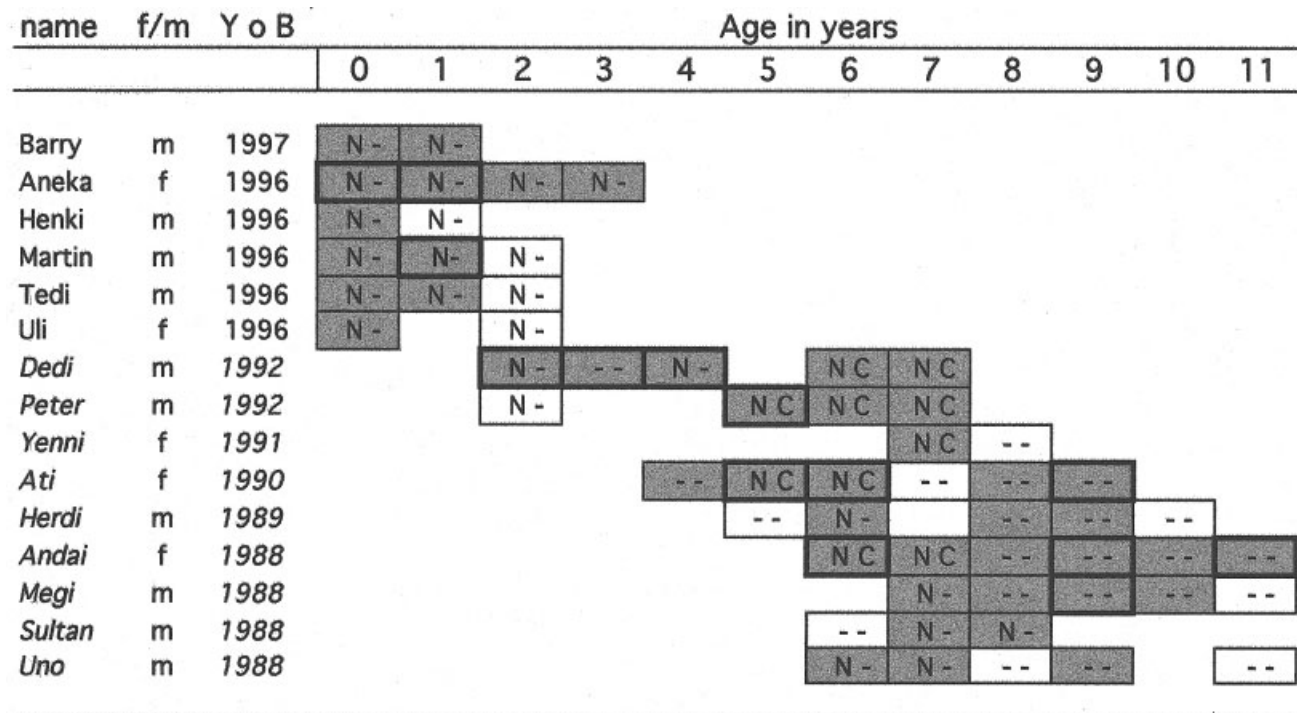
Fig. 8. Age in years at which immatures were seen to have nipple contact with their mother and when nursing conflicts were observed. Shading indicates number of focal observation hours.

stinging hairs. These skills need to be learned by a combination of socially biased, probably observational learning (van Schaik, 2003) and individual practice.

At what age do immatures master these important skills? Although not systematically collected, the available data give at least a qualitative indication of the age at which immatures are able to perform these skills.

Nest building. All immatures commonly closely watched their mothers making a nest. Infants as young as 1 year of age (n= 6) frequently made their own little nests during the day within a few meters of their feeding or resting mother, and sometimes added some twigs to their mother's nest while she was building. At age 3, immatures were capable of building a nest good enough for a daytime nap or as a platform on which to play.

Head cover. Two-year-old infants were seen covering their head with large leaves in the rain even when their mothers did not, indicating that they were not copying their mother's current behavior. Four- and 5-year-olds made their own covers over a day nest, even when their mothers ignored the rain and kept feeding.

Tree-hole tools. Infants tended to pay close attention to what their mothers were eating, often copy-

ing them. Four-to-6-year-olds started using tools in insect holes, sometimes using a tool left or discarded by their mother. At 6–7 years of age, immatures made their own tools and sometimes used them independently of their mother's activity.

Neesia tools. Young immatures were not seen to use and manufacture tools to reach the nutritious seeds of *Neesia* sp. Instead, up to about 5 years of age, they begged seeds from their mother. However, at least several 7-year-olds were seen to be competent tool users, successfully exploiting this rich resource.

Thus, many skills seem to be learned, or at least practiced and perfected, during the second half of lactation. By the time an offspring was weaned, it was able to protect itself against the elements and recognize opportunities for tool use.

Establishing a range

It has been inferred that female orangutans establish a home range or core area adjacent to, or in a part of, their mother's range, whereas sons move away (Galdikas, 1995; Singleton and van Schaik, 2002). We compared the location of sightings for known mother-offspring pairs in this population to test the expected pattern.

This study had to end before the known immatures had reached the age of sexual maturity. Four

young males, known since they were estimated to be 5 and 6 years old (and still permanently associated with their mothers), still spent at least some time in the study area when they were 10 years (Herdi and Nata) and 11 years old (Megi and Uno). Although at this age they were only occasionally seen with their mothers and rarely made a night nest within 50 m of her (Figs. 4, 6), all sightings of them were within the known ranges of their mothers (even though researchers were active outside these ranges). On the other hand, previously unknown young males, estimated to be somewhat older than these "local" immatures, were occasionally seen in the study area throughout the years.

The only known daughter reaching independence, Andai, was still in the area when she was 11 years old, and still spent some time in association with her mother and younger sibling. She frequently ranged alone in the same area as her mother, but was also seen in the southwest corner of her mother's normal range, whereas the latter was more often seen to range in the northeastern part of her range than in the years before.

Thus, for the first few years of independent ranging, both sons and daughters appeared to stay (mostly) within their natal range. Ranging data from the same population suggest that sons later expand their range to 2–3 times that of adult females, but whether this can include (part of) their natal range is not yet known (Singleton and van Schaik, 2002).

DISCUSSION

Orangutan development

The density of orangutans at Suaq Balimbing is higher than at any other known site (van Schaik, 1999), suggesting favorable living conditions. This idea is supported by their having the highest proportion of fruit in their diet and the largest average party size (van Schaik et al., 1999; Fox et al., in press). Yet estimated interbirth intervals at Suaq (8.2 years) are at least as long as in other populations of either Sumatran or Bornean orangutans (Knott, 2001). In captivity, where food is abundant and of high energy density, orangutan immatures separated from their mothers are known to grow and mature faster than in the wild (Fooden and Izor, 1983). However, when infants are left to be nursed by their mother, weaning is almost as late as in the wild (Brandes, 1939; Markham, 1990). Thus, the pattern of late weaning and long interbirth intervals appears to be consistent over a variety of conditions.

This study showed the following pattern in infant development of wild orangutans. Around age 3, infants approach locomotor competence (although they still need help to cross major gaps), can build nests and protect themselves against rain, and begin to spend time in another tree than that of their mother. The next major change occurs at time of weaning, around age 7, when mothers stop playing with their offspring and occasionally become less tolerant around food, the youngsters sleep in their own night nest, and proximity (<10 m) begins a precipitous decline. At this age, the weanling has already achieved an adult-like activity budget, and, by definition, foraging competence. Around the time the next infant is born, association time (<50 m) declines steeply to reach adult levels at around age 10 or 11, indicating that immatures at that age have also achieved ranging competence. Thus, consecutive infants overlap only briefly in their association with the mother. Data on immatures at Ketambe (Sumatra: van Adrichem, 2000; S.A. Wich, personal communication) and qualitative descriptions from Tanjung Puting (Borneo: Galdikas and Briggs, 1999) generally concur with this summary. Hence, orangutan development is indeed characterized by an exceptionally long period of nursing.

Comparison with other apes

Gorillas and chimpanzees have a shorter period of nursing and shorter interbirth intervals than orangutans. Gorilla mothers wean their offspring when the latter are 3–4 years old (Watts and Pusey, 1993), have interbirth intervals of 3–5 years (Watts, 1991), and are known to grow and mature faster than the other apes (Leigh, 1996). Chimpanzees are weaned completely when they are around 5 years old (Watts and Pusey, 1993; Boesch and Boesch-Achermann, 2000), more or less coinciding with the timing of their mother's next conception (Pusey, 1983). However, these shorter periods of lactational support as compared to orangutans do not necessarily correspond to a faster pace of development. Figure 9 summarizes the ages at which different components of independence from the mother are achieved by different apes.

Locomotion. Gorilla infants have reached complete locomotor independence at 3–4 years of age, when their locomotor patterns have become largely adult-like (Doran, 1997). Chimpanzee infants start to follow their mothers during travel when they are about 3 years old, but are still carried occasionally until the birth of a sibling (Hiraiwa-Hasegawa, 1990a; Tutin, 1994). Their locomotor patterns are not fully mature until 6 years of age (Doran, 1997), i.e., around the time that their younger sibling is born. Although we do not have similarly detailed data on the ontogeny of locomotor patterns in orangutans, the current data suggest that they reach locomotory independence at around 3 years of age, with some continued support to cross gaps in the canopy until they are at least 5 years old. In the absence of such support, individuals could in virtually all cases choose alternative routes that would not require descent to the ground.

Nest building and sharing. In gorillas, chimpanzees, and orangutans alike, sharing the mother's nest at night tends to end around the time of weaning (Hiraiwa-Hasegawa, 1989). Certainly, chimpanzees and orangutans are capable of building their
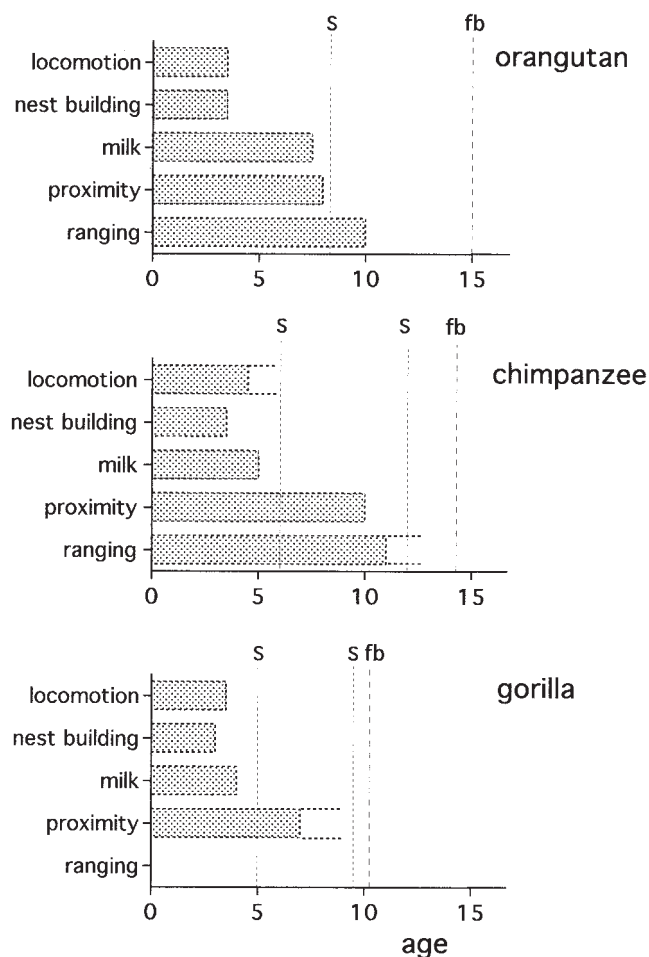
Fig. 9. Comparison of age of independence for developmental markers for three great ape species. Independence in locomotion: orangutan carried by mother during travel <10% of time; chimpanzee and gorilla "only rarely carried;" nest building: able to build a nest for daytime sleep and play (but in all three species, immatures tend to sleep with mother at night until weaned); proximity: less than 50% of time at <10 m for orangutans, <15 m for chimpanzees, and <5 m for gorillas (references in text). s, birth of a sibling; fb, age at first birth for females.

own nest long before they stop sleeping in their mothers' nests. After weaning, gorilla immatures are known to spend the night occasionally with another conspecific, most notably the group's silverback male, especially after the death or emigration of the mother (Stewart, 2001; Yamagiwa and Kahekwa, 2001). Although chimpanzee orphans were seen to share the nest with a sibling, nest-sharing with others than the mother appears rare (Goodall, 1986).

Association. After weaning, immature gorillas stay in the same social group as the mother and, at least while feeding, still spend about half of the time within 5 m of her when they are 7 years old (Watts and Pusey, 1993). As long as immatures stay in the same group, they receive agonistic support from their relatives, even in the absence of the mother. Chimpanzees are less gregarious, but nonetheless the association between mother and offspring, and

therefore the opportunity for socially learning ecological and social skills, continues for many years. The postweaning association between mother and offspring lasts at least as long as the preweaning period: immatures stay within 15 m of the mother most of the time until they are around 10 years old (Pusey, 1983, 1990). Although offspring, especially sons, may occasionally spend a night with others away from the mother, most only start to range independently when they become sexually active at about 10 years of age (Pusey, 1983, 1990; Goodall, 1986). Thus, despite their earlier weaning, chimpanzees seem to become independent in their ranging behavior at about the same age as orangutans, if not later.

Feeding behavior. Weaned gorillas eat about the same diet as adults and spend a similar proportion of time feeding, although their intake is lower because they eat more slowly (Watts and Pusey, 1993). Nevertheless, some complex leaf-gathering techniques may not be fully mastered until about 9 years of age (Byrne and Byrne, 1993). Similarly, chimpanzee infants eat fewer mature leaves than their mothers, but have acquired an adult food repertoire by the time of weaning (Hiraiwa-Hasegawa, 1990b, c). Special skills needed to process "difficult" foods may require years of practice: some are mastered around the time of weaning (e.g., *Saba* fruits; Corp and Byrne, 2002), but others are not refined to the level of adult competence until the immature is 8–10 years old, e.g., stone hammers for extraction of nuts (Matsuzawa, 1994). (Because participation by males in hunting starts at later ages, some aspects of hunting may be mastered even later; Boesch and Boesch-Achermann, 2000). Thus, offspring seem to have mastered most complicated feeding techniques at around age 10, i.e., before they start to range independently from the mother. The orangutans of Suaq Balimbing were also able to use the two kinds of tools of the local repertoire by the time they were weaned at about 7 years of age, although subsequent improvements may have occurred. The diet of recently independent immatures is similar to that of their mothers (unpublished findings).

This comparison of developmental landmarks indicates that Sumatran orangutans are not markedly slower in acquiring and achieving locomotor, foraging, and technological competence than chimpanzees, whereas both are slower than gorillas. Gorilla females can give birth to their first offspring when they are around 11 years old, chimpanzees at around 14 years old, and orangutans around 15 years of age (Knott, 2001). Both orangutans and chimpanzees are in the near-constant company of their mother during most of their development. Ranging independence (Fig. 9) is attained perhaps even earlier in orangutans than in chimpanzees, and is followed in both species by several years of further growth before age of first reproduction is reached. In order to range independently, the individual must be both ecologically independent, in

being able to plan and execute its own resource exploitation schedule, and socially independent, in no longer needing the social protection of its mother. At present, we lack the data needed for both species to evaluate which of the two prevents earlier independence.

Explaining late weaning in orangutans

This study suggests that there is no evidence that orangutans develop more slowly than chimpanzees. However, there are two major differences in the immature stage of the life histories of chimpanzees and orangutans. First, weaning is about 2 years earlier in the chimpanzee, and hence interbirth intervals (after surviving offspring) about 2 years shorter. Second, immature chimpanzees continue to stay in close proximity to the mother about 2 years longer than immature orangutans.

If orangutans do not develop more slowly than chimpanzees, then why are they weaned so late? In general, weaning occurs when the mother gains more from starting to invest in the next offspring than she loses due to termination of energetic investment in the current offspring (and thus its fitness prospects; Trivers, 1974). Thus, late weaning is thought to be a consequence of a slow life history. However, adult female body weight, age of first reproduction, and maximum life span (in captivity) of chimpanzees and orangutans are very similar. Thus, a general difference in life history is unlikely to explain the difference in weaning age.

We suggest instead that the late weaning in orangutans is related to their solitary lifestyle, enforced by ecological conditions. Southeast Asian forests are known for their low mean productivity and huge interannual variation in productivity (Terborgh and van Schaik, 1987; van Schaik and Pfannes, in press), probably even more dramatic in Bornean than in Sumatran forests (Delgado and van Schaik, 2000). When food is scarce, orangutans need to forage alone (Sugardjito et al., 1987; Knott, 1998; van Schaik, 1999). Orangutan females range and forage on average 60–90% of the time without associates other than their youngest offspring (Galdikas, 1985, 1995; Wich et al., 1999; van Schaik, 1999).

Due to these apparent ecological constraints, an orangutan mother could not do what a chimpanzee female does: wean her infant, but allow it to stay in close association for some 6 more years. Yet the data indicate that prolonged association with the mother is required, for ecological or social reasons, before the immature can range independently, as indicated by the late age at which range-use independence is attained (at 10–11 years of age). The only option available for an orangutan female, therefore, is not to wean her offspring before it approaches the point at which it is capable of independent foraging and ranging. By timing weaning closer to the age of complete independence, an orangutan mother is ensured that she can forage alone when needed to support her subsequent offspring, without endangering the survival of the weaned one.

The difference between orangutans and chimpanzees suggests that the opportunity for continued association in chimpanzees allows earlier weaning without jeopardizing the immature's continuing development toward complete independence. As in group-living primates, the prolonged mother-offspring association, as well as possible close association with other conspecifics, gives immatures ample opportunity to grow and perfect their skills while the mother is able to care for her subsequent offspring at the same time. Such prolonged association allows for continued maternal investment after the end of lactation (cf. Fairbanks, 2000) for much longer in chimpanzees than in orangutans. Thus, in slowly developing organisms such as primates, shorter interbirth intervals are a benefit of gregariousness.

The solitary lifestyle hypothesis is supported by field data. Figure 10 illustrates the solitary tendency of mothers in relation to the age of their youngest offspring. Singleton and van Schaik (2002) showed that there were two distinct clusters of females in the Suaq Balimbing population with different social profiles. The females with core home range areas in the northern part of the study area had a smaller average party size than the females with core home range areas in the central part. Therefore, we analyzed the data on these clusters separately. There was a consistent tendency for each mother in either cluster to be most often without associates (Fig. 10a,c) and to have on average fewer associates (Fig. 10b,d) when an offspring was 2–3 years old (although the data were collected over several years and several females were pooled for this graph, the trends showed consistency within females as well). As an infant matures, its energetic needs increase. Thus the mother's energetic contribution is expected to peak when the infant expends much energy, needs to be carried frequently, and is yet incapable of providing for its own energy needs. This burden may peak between 3–4 years of age, just around the time the infant was found to begin to travel (i.e., no longer be carried by the mother: Fig. 3), but did not yet do much feeding (Fig. 7). Before this moment arrived, however, the association between the mother and her previous offspring had declined, in part because the mother had become less tolerant toward her older offspring (see above). The mother's frequency of association with others increased again by the time the offspring approached weaning age (around 6–7 years of age), and thus coincided with an increase in the probability of the mother's return to fertility. The latter increase in association was caused by the sexual interest of subadult and adult males (Fig. 10b,d).

Other support for the solitary lifestyle hypothesis comes from studies on Bornean orangutans. Here, mothers spend even less time in association than their Sumatran counterparts (only 10% on average: Galdikas, 1995). Unlike Sumatran adolescent females who are as gregarious as their mothers (van Schaik, 1999), Bornean adolescent females go
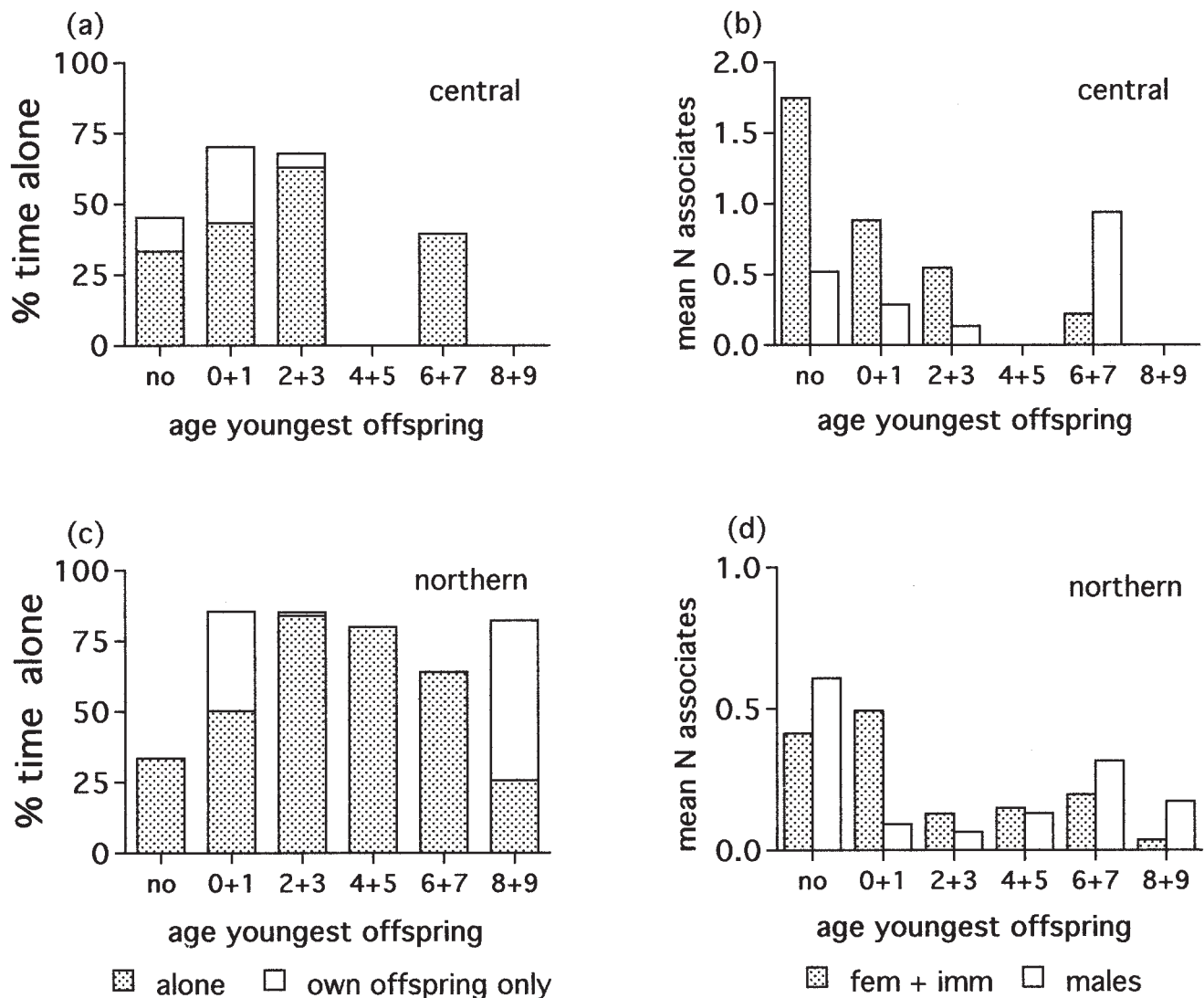
Fig. 10. Age of youngest surviving offspring in relation to percentage of focal time mothers spent alone (i.e., with only youngest offspring) or only associated with their own weaned offspring (**a** and **c**) and average frequency of associates, either (subadult and adult) males or females and immatures (**b** and **c**). fem + imm, female and immature. For central females (**a** and **b**), total focal time, 3,879 hr; for northern females (**c** and **d**), total focal time, 3,690 hr. no, females without a youngest surviving offspring under 10 years old; for "central" females, data represent females who had lost their youngest offspring; for "northern" females, data come from one female before birth of her first offspring (total, 324 hr).

through a phase of increased gregariousness. However, after the birth of their first offspring, they become less tolerant toward their former close (nulliparous female) associates (Galdikas, 1985), suggesting that the energetic burden of reproduction cannot be combined with a high level of gregariousness.

Although it was argued that mother-offspring units of Sumatran orangutans and chimpanzees are equally solitary (Wich et al., 1999), it should be noted that such units in chimpanzees usually contain one or two additional weaned offspring (Pusey, 1983; Goodall, 1986). In contrast, orangutan mothers with 2–3-year-olds had dramatically reduced association time with their previous offspring. Hence, even Sumatran orangutan females are still far below the gregariousness threshold that would allow *continuous* association with weaned offspring.

CONCLUSIONS

The orangutan's timing of weaning and a mother's return to fertility were found to be late compared to those in chimpanzees, despite great similarity in the ages at which other developmental markers such as independence in locomotion, feeding skills, and range use are reached. Although orangutans do not need more time than chimpanzees to grow into competent (sub)adults, it seems that constraints on orangutan gregariousness prevent constant association of weaned offspring with their mother.

Gregariousness thus provides a generally hidden benefit in that it allows weaning of infants before full ecological competence is reached. Thus, the infant can be weaned once locomotor and nutritional competence (food processing and digestion) is attained, but (long) before social and/or ranging com-

petence is reached. In this way, gregarious species can afford to have shorter interbirth intervals.

What remains to be determined is whether the onset of independent range use in orangutans and chimpanzees is determined by late acquisition of ranging competence or by a prolonged need for social protection of the young. Future work on orangutans should distinguish between these possibilities. If late range-use independence is governed by slow acquisition of ranging competence, this would support the hypothesis that the slowdown of human life history (e.g., long pre-reproductive period) is due to prolonged ecological incompetence as a result of the complexity of the human foraging niche (Kaplan et al., 2000; Byrne, 1997).

ACKNOWLEDGMENTS

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