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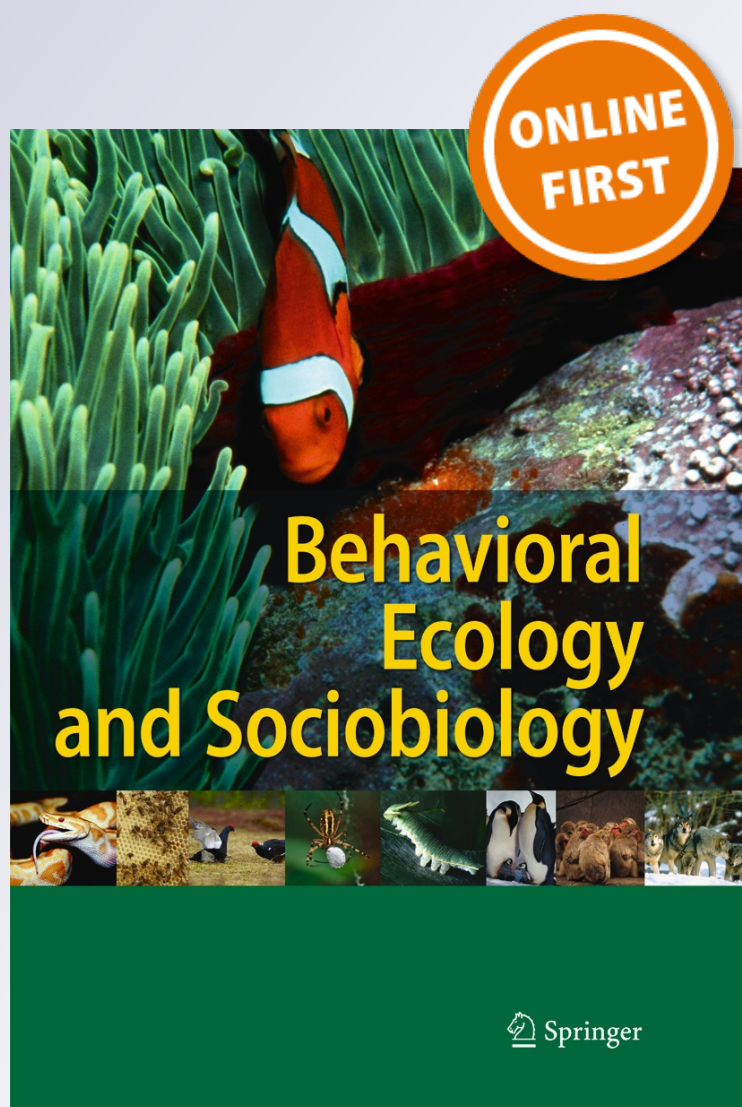
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Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*)

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Abstract In most mammals, females pay for reproduction by dramatically increasing net energy intake from conception to mid- or late lactation. To do this, they time their reproductive events in relation to environmental cycles so that periods of peak food availability coincide with peak demand or are used to build energy stores. This timing is not possible in species with slow development in which lactation is prolonged over a multi-year period with fluctuating food availability. Here, mothers are expected to sustain a stable but generally lower level of nutrient transfer. In a sample of over 1,050 complete follow days of eight mother–infant pairs collected over 7 years, we document maternal effort for wild Bornean orangutans (*Pongo pygmaeus wurmbii*) over their average 6.5-year lactation period. As predicted, maternal feeding time was independent of the age of her growing offspring, indicating a stable sustained “plateau” effort of $\leq 25\%$ above baseline level, instead of a short peak lactation as seen in seasonal breeders. Infant orangutans started to regularly supplement milk with self-harvested food when they were 1–1.5 years old, indicating milk intake was insufficient from this age onwards, even though maternal effort did not decrease. We expect the same regulation of sustained maternal effort in

other large and large-brained mammals with slow infant development. We also predict that mother–infant conflict over suckling may show another peak at the onset of the milk+solid food phase, in addition to the well-known conflict around the endpoint of lactation (weaning), which is reached after a long and gradual increase in solid food intake by the infant.

Keywords Great apes · Maternal investment · Parent–offspring conflict · Sustained lactation · Weaning

Introduction

To nourish her offspring through lactation, a mammalian mother must increase her own food intake, use previously stored reserves, sacrifice her own body tissues, or reduce her own activity level (Prentice and Whitehead 1987; Gittleman and Thompson 1988; Dufour and Sauter 2002). Mammals living in an environment with predictable fluctuations in food availability can time their reproduction, and thus their peak nutritional requirements, to take advantage of peaks in food availability (enabling higher feeding efficiency). This leads to seasonality in reproductive activity, in which females either use previously stored reserves (capital breeding: Stearns 1992), time the period of highest energy transfer to coincide with increased food abundance and increase their food intake accordingly (income breeding), or use some combination of strategies at different stages during the nutritional dependence of the offspring (Brockman and van Schaik 2005).

Many mammal species manage to complete their reproductive cycle within the period of the environmental cycle, usually a year. Capital breeders elevate their food intake before or during gestation, whereas in income breeders, which are the majority of non-aquatic mammals, mothers increase their intake, sometimes two to four times (Speakman 2008), in

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accordance with the increasing needs of their offspring. In income breeders, maternal energy intake thus shows a characteristic inverted-U-shaped curve, rising to a peak during mid- to late lactation before returning to baseline levels following weaning and gradually rising again during the next pregnancy (e.g., Clutton-Brock et al. 1982; König and Markl 1987; Dunbar and Dunbar 1988; Tarnaud 2006).

This option of adjusting energy needs to food abundance, and thus the period with highest feeding efficiency, is not available to species with multi-year lactation. In such species, infants do not develop fast enough to be able to utilize a single peak in food abundance to reach nutritional independence from their mother. Accordingly, a mother needs to sustain lactation over an extended period that covers multiple seasons of high and low food availability, protecting her offspring against starvation during its development. It is unlikely that she could support all her offspring's needs throughout the entire multi-year lactation period by storing enough reserves in advance, by increasing her food intake according to increasing needs, or by sacrificing her own body tissue or minimizing her own activity as can be done by faster species (Prentice and Whitehead 1987; Clutton-Brock 1991; Speakman 2008).

Multi-year lactation should therefore have two major consequences. First, energy intake to sustain lactation probably needs to be set at a level that is both rather stable and conservative throughout the lactation period rather than showing the steep rise followed by a more or less rapid fall seen in species with shorter lactation. Second, this conservative but stable level of maternal investment almost inevitably also implies that infants must begin to feed independently to supplement the maternal contribution to their increasing requirements well before the end of lactation.

Multi-year lactation is found in very large species (e.g., giraffes: Pellow 1984; odontocete whales: Whitehead and Mann 2000; elephants: Lee and Moss 2011) or smaller-bodied species with unusually large relative brain size (e.g., great and lesser apes: Alvarez 2000, other large-bodied primates, e.g., spider monkeys: Di Fiore and Campbell 2007). Humans have unusually large brains and wean infants around age 2.5 years (among foragers: Alvarez 2000; Sellen 2001) and thus also belong in this group of species. Nonetheless, the implications of multi-year lactation have received little attention thus far.

Consideration of multi-year lactation requires that we clarify the meaning of weaning. Normally, the weaning phase is thought to begin with the onset of solid food intake by the offspring, because this point also marks the beginning of the progressive decline in milk transfer from mother to offspring (e.g., Martin 1984; Lee 1997; Langer 2008). However, in slowly developing species we expect that lactation would be rather stable and at a modest level, implying

that the onset of solid food consumption by the infant does not coincide with a decrease of the mother's investment in milk. Therefore, we use the term "weaning" here only to refer to the decrease in lactation, rather than to indicate the entire period in which infants supplement their milk diet with solid food.

Here, we present data, collected over 7 years, on the energy budgets of lactating Bornean orangutans (*Pongo pygmaeus wurmbii*), which have the longest lactation period of any land mammal other than the even slower Sumatran orangutan (*P. abelii*: Wich et al. 2004; van Noordwijk and van Schaik 2005). The study population inhabits a swamp forest with highly fluctuating food availability including major variation between successive years. The average measured interbirth interval is close to 7 years (unpublished data). Because the majority of females conceive again before their previous offspring is fully weaned, the females in this population seem to have an energy balance allowing them to reproduce without long periods of recovery between successive offspring despite the unpredictability of the food supply. The infant mortality rate is also extremely low (unpublished data; cf. Wich et al. 2004).

The main questions we address are (1) whether mothers show a stable level of intake over time, rather than the inverted-U-shaped curve found in studies of smaller mammals with seasonal reproduction, and (2) how mothers manage to support the ever-increasing needs of their growing offspring over such a long period of nutritional dependence.

Methods

Data collection

Behavioral observations used here were collected from July 2003 to July 2010 on a natural population of Bornean orangutans in the Tuanan Orangutan Research Area, Mawas Reserve, Kalimantan Tengah, Indonesia (2° 09' S; 114° 26' E). Focal animal follows on well-habituated individuals were conducted following standard field methods (<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>), recording activity of mother and offspring every 2 min.

Ages of infants born before the start of the study were estimated (cf. Wich et al. 2004). These estimates were updated in comparison with subsequently born infants using extensive photographic records (e.g., Fig. S1). Omitting the three infants with estimated ages did not affect the results. Unlike in other orangutan populations (e.g., Knott et al. 2009), conceptions and births of the sampled immatures were regularly spread across years, and during each calendar year immatures of different ages were sampled. None of the known immatures died during the study period (or is known

to have died thereafter). However, one mother died, probably due to a clouded leopard attack, and her 4-year-old offspring was transported to a rescue center by the local authorities.

Monthly values in the current analyses are based on at least five full days within a calendar month of nest-to-nest follows per female/offspring (Table 1). On average, the nest-to-nest active period lasted 655 min. Thus, in total, the dataset covers over 11,500 h of focal observation by an experienced team.

Since orangutans are arboreal and often nurse on the nest (both during the day and at night), or during other maternal activities, it was not possible to get an accurate estimate of time spent drinking milk by the infant, let alone of milk intake. Only qualitative data on the occurrence of nipple contact at different ages could be obtained. A clear indication of completed weaning is that the immature sleeps in its own night nest, whereas unweaned offspring always share the nest with their mother (van Noordwijk and van Schaik 2005).

Since females in this population devote on average ca. 70 % of their feeding time on fruits and seeds (unpublished data, cf. Morrogh Bernard et al. 2009; Russon et al. 2009), around 1,500 trees in a phenology plot were checked each month for the presence of fruit, to estimate food availability. The monthly fruit abundance index, measured as the percentage of trees bearing fruit, is often used as an indication of overall food availability, which is also positively correlated with orangutan density (Marshall et al. 2009). In addition to fruit, orangutans in Tuanan feed on (young) leaves, insects (mostly termites, ants), flowers, the inner bark of several tree species and various other parts of plants (trees, lianas, epiphytes).

Table 1 Overview of focal mothers, their offspring and observation time

Mother	Immature	known/(estimated) year of birth	Age in years (range)	# follow days ^a	# monthly samples ^{b,c}
Jinak	Jerry	2003	0–7	286	34
Juni	Jip	2006	0–4	134	17
Mindy	Milo	(2001)	2–8	221	21 (+7)
Mindy	Mawas	2008	0–2	54	7
Kerry	Kondor	(1999)	4–8	118	10 (+6)
Kerry	Kino	2007	0–3	82	12
Sidony	Streisel	(2002)	6–8	12	2 (+1)
Sidony	Sony	2010	0	8	1
Sumi	Susi	2003	0–4	138	19

^a Only complete days from nest to nest

^b At least five follow days within a calendar month

^c Within parentheses the number of days after the birth of a younger offspring while older offspring was but still in permanent association with the mother

Estimating the energetic burden of offspring

Our approach in this analysis was to estimate the total caloric burden represented by the offspring (basal metabolism+activity+energetic costs to the mother of carrying). Maternal metabolism (milk) was assumed to provide all this energy until the infant started to supplement its diet by consistently feeding on solid food. To estimate the energy requirements of a growing orangutan, the percentages that are derived from mother (milk) versus solid food, as well as how these change with infant age, we had to make some assumptions. Results are presented for our best estimate, with an upper and lower estimate to assess the possible impact of error in the various variables estimated (see supplementary material).

Even though maternal weight is expected to vary among adult females, and since we did not have weights on the individual animals in this study, we assumed an average maternal weight of 38 kg (range 34–42 kg, based on Leigh and Shea [1995], Smith and Jungers [1997], and Plavcan and van Schaik [1997]) and a birth weight of 1.6 kg (range 1.3–1.9 kg: Robson et al. [2006]). Likewise, we had to estimate weight at the age at nutritional independence (fully weaned), which occurs at a mean age of 6.5 years in this population (unpublished data). We estimated weaning weight as 17 kg (range 12–22 kg), similar to the median of 15–20 kg (Leigh and Shea 1995) in captivity, even though there weaning is completed 2–3 years earlier than in the wild. These assumed weights agree well with known weights of wild-caught infants, of which age estimates are based on dentition, brought into nearby rehabilitation centers (A. Nurcahyo and S.J. Husson pers. comm.) and with visual estimates made in the field (based on photographs of the relative size of weanlings vs. their mothers). For simplicity, we also assumed an approximately linear rate of increase in weight between the age of birth and independence (Leigh and Shea 1995). Even though growth is accelerated shortly after birth, the absolute metabolic impact of this should be limited. Because orangutans grow extremely slowly, we assumed that the cost of growth itself was negligible (e.g., Butte 2005, Wells and Davies 1998). We also assumed no sex difference in requirements (cf. Grund et al. 2000), since there was no evidence for a sex difference in interbirth interval, weaning age, or developmental trajectory in our small sample (unpublished data; van Noordwijk et al. 2009), and because growth rates of males and females in captivity do not diverge until after weaning (Leigh and Shea 1995).

We estimated BMR at all ages based upon the assumption that caloric expenditure follows the general relationship for mammals according to Kleiber's law: BMR [in megajoule per day]= $4.1 \times \text{weight} [\text{in kilogram}]^{0.751}$ (Peters 1983). In a study of captive but free ranging animals, Pontzer et al. (2010) suggested that orangutan BMR is 36 % below estimates based on Kleiber's law. However, comparative work has shown that,

among the apes, orangutans are especially prone to excess fat deposition in captivity (Leigh and Shea 1995), which reduces mass-specific BMR. We therefore derived our estimates under the assumption that the wild animals in our study were leaner than the captive ones investigated by Pontzer et al. (2010) and thus closer to our Kleiber-based estimate. However, our conclusions are not substantively affected by the actual value of BMR used because we used the ratio of energy costs of mother+offspring relative to the mother's baseline for our analyses. For example, a 20 % lower estimate of BMR for mother and offspring increases the relative cost of the offspring by a maximum of 0.29 % when the offspring is 30 months old; and at 36 % lower BMR the maximum relative cost would be only 0.51 % higher.

We based estimated daily energy expenditure (DEE) on observed individual time budgets and estimated values of the metabolic equivalents (METs, with basal metabolic rate=1.0) of common activities in humans (Ainsworth et al. 2000). We assumed resting to be 1.05 METs, feeding 2.2 METs, locomotion 3.0 METs and play at 4.0 METs (See Table S1 for details). Using the actual time budget data for the sampled orangutan females yielded an average DEE for mothers of $1.5 \times \text{BMR}$. As expected, the average estimates for food-stressed, wild animals are somewhat higher than found for two captive females, where Pontzer et al. (2010) measured an average DEE value of $1.36 \times \text{BMR}$ ($N=2$) based on doubly labeled water measurements.

The cost of carrying offspring was only calculated for the time mothers carried an infant during their own locomotion, and was estimated by assuming that weight carried contributes isometrically to her energetic costs of locomotion (Schmidt-Nielsen 1984). Thus carrying cost is the percentage of the mother's locomotion cost due to the added weight of the infant (cf. Altmann and Samuels 1992; Kramer 1998). Ignored in this estimate is the time the infant sits on the mother while the mother is stationary. Costs of total offspring energetic needs were estimated based on offspring's BMR (generated from its weight) and offspring activity budget using the same METs as for the mothers. The total energetic cost of maintaining the dyad (mother+offspring) would equal the cost to the mother if the infant did not contribute any energy to its own maintenance until weaning. It thus provides the upper boundary of the potential cost to the mother.

The cost of lactation could not be measured directly. We used the food to milk conversion efficiency of 80–85 % for humans (Prentice and Prentice 1988) to estimate how much energy was transferred to the infant based on the increase in feeding effort by lactating mothers.

Statistical analyses

To assess the effect of offspring age and fruit availability on maternal investment, expressed as the mother's monthly

average time spent feeding and her day journey length, we constructed linear mixed effects models in which the identity of the offspring was included as a nested random factor within the identity of its mother. The same analyses were applied to the amount of time spent feeding on fruit, insects, flowers, leaves, bark and other vegetative parts. Model significance and the significance of fixed factors in the model were calculated using likelihood ratio tests (LRT), following Johnson and Omland (2004). In addition, we investigated the influence of offspring age and food availability on the offspring's own monthly averaged feeding time, taking the same linear mixed effects modeling approach as outlined above. All analyses were conducted using the "lme4" package for R 2.12.1 (R Development Core Team 2010).

Results

Lactation and weaning

Focal immatures in the study population were fully weaned at an average age of ca. 6.5 years (range 5.75–7.5; $N=6$; including demographic data up to January 2012; both the youngest and oldest weaning age were individuals with known age, the others based on estimated ages). At least four immatures were weaned after the mother had conceived again, and only one of six females conceived well after weaning her previous offspring. Final weaning from suckling tends to be not very dramatic in orangutans, and immatures whose mothers had conceived again seemed to lose interest in nipple contact during their mother's gestation. Thus, because the subsequent gestation generally overlapped with the end of lactation, mothers were effectively in a perpetual state of reproduction and did not appear to require a "recuperation" period between successive bouts of reproduction.

Fruit availability

Fruit availability varied between months and years. The percentage of trees bearing fruit during the sampling period fluctuated between 0.2 and 14.0 % (Fig. 1). Maximum fruit abundance in some years was lower than the minimum in other years. Thus, fruit availability was rather unpredictable, and was sometimes low for extended periods (>1 year). Every mother–offspring dyad in our sample was therefore exposed to multiple periods of high, intermediate and very low food availability during their 6–7 year lactation period.

Maternal time budget

In an income-breeding scenario one would expect an increase over the course of lactation in maternal feeding efforts driven by the increasing energy requirements of the

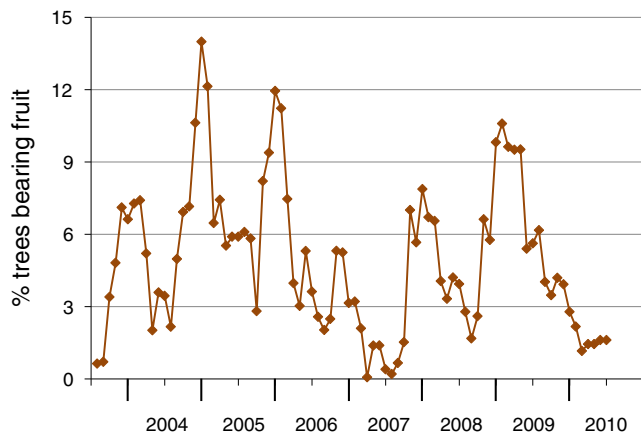


Fig. 1 Fruit availability July 2003–July 2010: percentage of ca 1,500 trees bearing fruit in a plot in the central part of the study area Tuanan

growing offspring. However, although the identity of the mother and the offspring explained a small proportion of the variation in time budgets, maternal feeding time was not affected by the age of her current dependent offspring within mother–offspring dyads ($\chi^2_{LRT}=1.15$, $P=0.28$; Table 2; Fig. 2), whereas it decreased during months in which more food was available ($\chi^2_{LRT}=11.26$, $P<0.001$). Likewise, diet composition was significantly affected by fruit availability,

but not by offspring age (Table S2). Similarly, the distance a female traveled per day was unaffected by offspring age ($\chi^2_{LRT}=1.49$, $P=0.22$), yet was longer during months characterized by a higher fruit availability index ($\chi^2_{LRT}=22.60$, $P<0.0001$), reflecting feeding in dispersed preferred fruit trees rather than foraging on less dispersed fallback food.

Infant time budget

In contrast to their mothers' constant feeding effort, the amount of time the offspring themselves spent feeding each month increased as a function of age, as expected ($\chi^2_{LRT}=164.34$, $P<0.0001$; Table 2; Fig. 3a). Even though infants under a year old show some interest in what their mothers eat and sometimes obtain morsels from their mother, they only start to consistently spend more than a few percent of their time feeding on solid food when they are around 1–1.5 years old (Fig. 3a). From then on, feeding time steadily increased (age immature 19–84 months: $\chi^2_{LRT}=66.18$, $P<0.0001$; Table 2), and around the age of full weaning, at 6–7 years, reached a value similar to the average feeding time of the mothers. The feeding time of immatures (19–84 months) was inversely related to fruit availability ($\chi^2_{LRT}=14.53$, $P<0.0005$), like that of their mothers.

Table 2 Results of linear mixed effects models to assess the effect of offspring age (in months) and % fruit availability on maternal and offspring feeding time and travel distance

	β	SE	t	χ^2_{LRT}	P	
Feeding time mother^a						
Intercept	370.174	16.87	21.94			
Age offspring	0.462	0.27	1.74	2.69	0.1010	
Fruit availability	-1.553	1.71	-0.91	10.87	0.0010	***
Day journey length^b						
Intercept	617.483	77.07	8.01			
Age offspring	1.665	1.27	1.32	1.81	0.1784	
Fruit availability	26.051	8.72	2.99	22.75	<0.0001	***
Feeding time immature 0–84 months^c						
Intercept	-0.115	12.97	-0.01			
Age offspring	5.345	0.23	23.03	164.34	<0.0001	***
Fruit availability	-2.321	1.76	-1.32	14.62	<0.0005	***
Feeding time immature 19–84 months^d						
Intercept	36.031	25.12	1.44			
Age offspring	4.727	0.43	11.03	66.18	<0.0001	***
Fruit availability	-3.501	2.34	-1.50	14.53	<0.0005	***

^a $\Delta AIC_{null\ model}=9.49$, $\chi^2_{LRT}=13.84$, $P<0.001$ ***. $N=121$ monthly averages of maternal feeding time of six females with nine different dependent immatures. Variance explained by ID mother 9.49 %; by ID offspring (within mother) 10.05 %

^b $\Delta AIC_{null\ model}=19.5$, $\chi^2_{LRT}=23.53$, $P<0.0001$ ***. $N=116$ monthly averages of six females with nine different infants. Variance explained by ID mother 7.24 %; by ID offspring (within mother) 2.38 %

^c $\Delta AIC_{null\ model}=174.3$, $\chi^2_{LRT}=178.29$, $P<0.001$. $N=123$ monthly averages of nine immatures from six different mothers. Variance explained by ID mother 4.54 %; by ID offspring (within mother) 0.0 %

^d $\Delta AIC_{null\ model}=80.02$, $\chi^2_{LRT}=84.02$, $P<0.001$ ***. $N=84$ monthly averages of eight immatures from six different mothers. Variance explained by ID mother 0.0 %; by ID offspring (within mother) 6.47 %

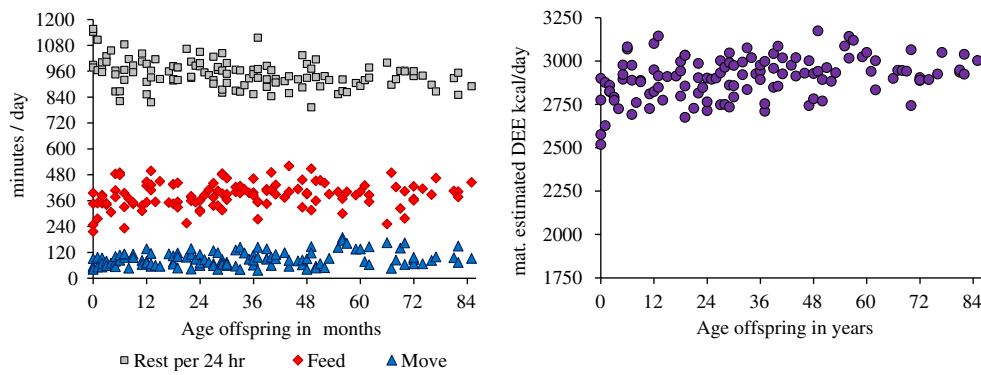


Fig. 2 Feeding time and energy expenditure in relation to offspring age in months. **a** Average number of minutes per full follow day that mothers spent feeding. **b** Estimated Daily Energy Expenditure for mothers, based on their actual activity budget, and a BMR based on

a maternal weight of 38 kg (see methods). Note that every point in these graphs represents the average of at least 5 complete nest-to-nest follow days within a calendar month

Maternal contribution to offspring energy requirements

To estimate the energy costs of lactation, the maintenance budgets of non-pregnant, non-lactating females would be required as a baseline. However, because all females were typically pregnant, lactating or both, it was not possible to obtain sufficient data for a such a baseline. Moreover, too few samples were available for pregnant females, and these few were taken under conditions that were too varied for a meaningful comparison. Instead, we took two other approaches to estimate these costs. First, we compared the time budgets of females at different stages of lactation (0–84 months after birth; see above). Despite the absence of a significant effect of offspring age on maternal time budget, feeding time did significantly increase during the first 6 months following giving birth ($\chi^2_{LRT}=14.09, P<0.001$; Table S3), although no significant age effect was found over the entire first year (Table S3). This suggests a rapid increase in feeding time in the first few months stabilizing before or around 6 months. Since the analyses consider within-female trends, the number of samples per female over the first year, which covered variation in fruit availability, was probably too small to detect

a significant effect. Feeding time samples taken during the first month following birth were ca. 15 % below the average throughout the offspring’s 6–7-year dependent period.

Second, we estimated the mother’s contribution to fulfill her offspring’s energy needs by estimating the mother’s feeding effort right around the age at which the offspring starts to contribute to its needs by consuming measurable quantities of solid food. We assume this coincides with the time when energy from milk alone does not cover its needs. At this age, 1–1.5 years old for the infants in our sample, the mother–offspring dyad is estimated to require ca. 22 % (18–25 %) more energy for their combined DEE than the mother would require for herself (calculations are based on weight-specific BMR and actual activity budgets: Fig. 3b; see also Fig. S2 for values based on other weights). Since mothers do not spend significantly more or less time feeding around this age than at any other stage of lactation, we conclude that they consistently provide up to ca. 22 % more energy than needed for their own maintenance. Taking food to milk conversion loss into account, we estimate that mothers feed at most ca. 25 % more than females would need when not reproducing, or recuperating from or storing reserves for reproduction.

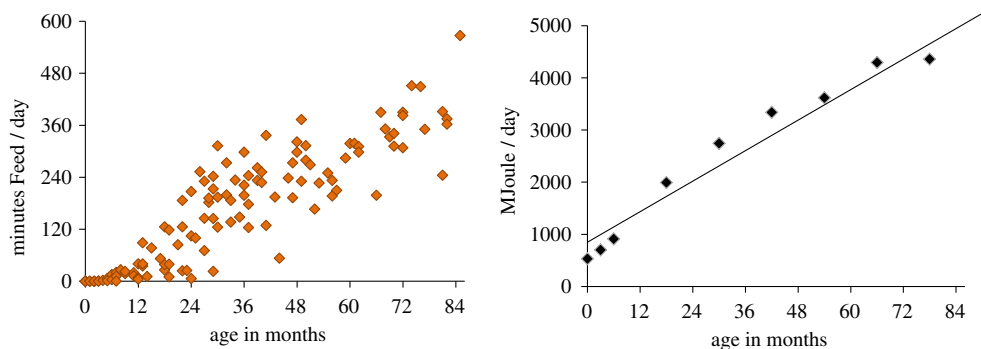


Fig. 3 Feeding time and energy requirements of immatures in relation to age in months. **a** Average number of minutes per full follow day that immatures spent feeding on solid food. **b** Estimated Daily Energy

Requirement of immatures, based on their estimated weight, derived BMR and their measured activity budgets (for alternative weight estimates at birth and weaning see Fig. S2)

Discussion

Orangutans

The Bornean orangutans in this study showed no systematic increase in maternal feeding time with offspring age during the long lactation period of ca. 6.5 years, apart from a moderate increase during the first few months after giving birth. Thus mothers seemed to have a remarkably stable level of feeding effort despite systematic variation in the level of offspring demand for resources. This constancy was not due to methodological issues or lack of resolution, for three reasons. First, we did find the expected changes in activity budgets in the immatures. Second, we found that feeding time of both mothers and infants was reduced during times of high fruit abundance, along with increased travel effort and a change in diet composition (indicative of greater selectivity: Vogel et al. 2012). Finally, we found consistent differences in the time budgets of individual females (Table 1), probably reflecting differences in their size, or quality of their home range.

In orangutans, with their arboreal lifestyle, body fat storage options are limited and females cannot sustain negative protein or energy balance for long (Knott 1998; Vogel et al. 2012), nor can lactation demand be met by increased food intake during times of scarcity. In addition, travel time or distance, and thus costs were not consistently affected by offspring age, only by food availability. However, the relatively modest daily energy cost of lactation, maximally 25 % above baseline, may give females flexibility in using different solutions to meet the energy demands, including a mix of increased food intake, mobilization of reserves or reduced activity level adjusted on a daily basis, just as is seen in humans (Piperata 2009).

Despite the extended maternal effort to raise an offspring to independence, most immatures in our sample were fully weaned only after their mother had conceived her next offspring, implying the absence in mothers of a distinct recovery period to compensate for lost condition or to build up reserves. Thus, the pattern of reproductive expenditure in female Bornean orangutan can be characterized by near-constancy across the adult reproductive lifespan. However, since no changes in feeding time were detected towards or shortly after weaning of the offspring, females may use the period of relatively low energy needs during the postweaning phase to build up some reserves while they are pregnant and during the first year of lactation of the next offspring. Similarly, they may be storing energy at any moment throughout lactation whenever it is not directly needed, which may be used to buffer future periods of negative energy balance (Knott 2005).

We found that maternal feeding effort in Bornean orangutans was only moderately increased relative to their non-reproductive baseline. It is possible that the low productivity

of Southeast Asian forests (Terborgh and van Schaik 1987) and the resulting metabolic adaptations in orangutans (Pontzer et al. 2010) have exaggerated the conservative nature of orangutan lactation. However, we expect the basic pattern of lactation to be similar in other species with a slow life history and a multi-year lactation pattern, because they all face the same basic problem. They cannot predictably time their period of highest need to coincide with peak food availability, but experience (multiple) fluctuations in food availability during lactation and for such long periods that neither storing reserves nor entering negative energy or protein balance are viable options (cf. Oftedal 2000). Indeed, some estimates of the cost of the milk-only-phase of lactation on humans and captive baboons are within the same range of requiring a 10–30 % increase in food intake (Butte et al. 2001; Rosetta et al. 2011).

It appears that mothers already achieve their stable level of energy intake many months before the infant would need it, as estimated based on the linear growth assumption. For example, at birth, the infant's needs were estimated to add ca 7 % to the mother's own energy needs, and when the infant is 6 months old this is increased to ca 12 % and at 18 months to 25 % (Fig. S2). Yet, only mothers of newborns less than 6 months old were distinguishable in their feeding time allocation from mothers of all older infants, suggesting that they are either storing reserves during the first year of lactation, transferring more energy than "needed" when the infant is still very small, or both. The postpartum dip in maternal feeding may also indicate that females move around less easily when they still have to physically support a young infant. Most likely, orangutan newborns experience relatively rapid growth as is known for human neonates (Eveleth and Tanner 1976). Thus the mother's excess capacity in the early months is probably used at least in part for a postnatal growth spurt, and perhaps it is also used to store reserves to be used to offset the greater needs of the infant at later ages (cf. Kuzawa 1998).

As a consequence of the mother's stable feeding effort, the infant orangutan itself has to provide the additionally required energy by independent feeding on self-provisioned food once it has grown to a size at which its energy needs exceed the mother's lactation effort. Importantly, as shown in Fig. 4, an orangutan mother does not decrease her lactation effort at the time her infant starts to supplement milk intake with solid food (as in most other mammals: Langer 2008), but she continues her effort at a stable level, which was reached previously (thus, there is a "plateau" rather than "peak" lactation).

In the current study, independent feeding started when the infant was around 1.25 years old, thus after less than a quarter of the total lactation period. Similarly, independent feeding started long before locomotory independence (van Noordwijk et al. 2009; Phillips et al. unpublished data) This is not surprising, because young infants can collect and feed on fruit while clinging to their mother or while clambering

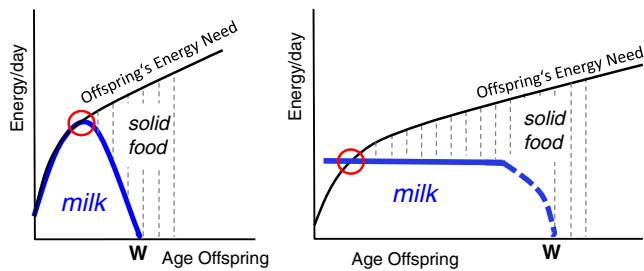


Fig. 4 Offspring's postnatal energetic needs supplied by the mother (milk) and by the offspring through independent feeding on solid food. **a** Classic scenario for seasonal breeders, where offspring develop during a period of predictable food abundance. **b** Scenario for species with slowly developing offspring with an extended dependent period covering multiple seasons or years. *W* indicates final cessation of milk supply by mother

around in close proximity to her. Thus, small and dependent infants are already able to supplement their diet with self-collected solid food, which we suggest typically starts to contribute a non-trivial fraction of caloric intake sometime early in the second year of life. In general, strong selection is expected to ensure that the infant has acquired sufficient maturity in digestive ability and food acquisition and processing skills at the age at which milk alone generally becomes insufficient. Thus, the mother's level of maximum sustained lactation should be at a level that matches the timing of sufficient digestive maturation when the infant very slowly takes over responsibility for its own energy supply during a very long "transitional" phase with continued milk consumption at a rather stable level.

Multi-year lactation and its consequences

Extrapolating from the orangutan data we expect a similar pattern of maternal investment in other species with slow life history and multi-year lactation. Here, we develop five predictions and examine preliminary evidence from the literature. First, when lactation is protracted over an extended period we expect maternal effort to be rather constant. Unlike species with shorter seasonal breeding, among which increasing offspring needs are met by parallel increases in maternal effort, studies of baboons with a lactation of just over a year found a more limited increase in maternal feeding effort than anticipated (Altmann 1980; Barrett et al. 2006). Similarly, the feeding effort of giraffe mothers, during their 1–1.5-year lactation period, was reported to be remarkably constant and unaffected by offspring age (Pellew 1984). The fact that detailed studies of chimpanzee maternal time budgets did not differentiate by age of the infant (Murray et al. 2009) suggests a similar constant effort in this great ape as well.

Second, maternal increase in food intake is expected to be rather modest compared to a baseline non-reproductive state. Indeed several authors have noted only a modest increase in maternal feeding effort during lactation compared to other

states. For example, in a small sample of wild siamang females (Lappan 2009) the maximum difference between early (0–4 months) and later lactation in feeding time was found to be 25–50 %, but some females showed their peak effort during mid-lactation (5–9 months) and others closer to weaning (10–15 months), suggesting some interfering effect of food availability. In chimpanzees, with a lactation period of ca. 4 years, lactating females increased their feeding time less than 10 % relative to pregnant females and spent less time feeding than non-pregnant-non-lactating females (Murray et al. 2009).

Third, once the physiology of lactation is no longer dependent on predictable seasonality, the timing of a female's next reproductive event is also expected to be less restricted. Thus, females can be in a permanent reproductive state, being either pregnant, lactating, or both, without needing "recovery" periods. Consistently, like orangutans, female giraffes (Pellew 1984), elephants (Lee and Moss 2011) and gorillas (Nowell and Flotscher 2008) often conceive their next offspring while still nursing the previous one without a "recuperation" period. Nevertheless, elephant interbirth intervals and offspring survival are affected by extreme fluctuations in food availability (Lee et al. 2011).

Fourth, the suggested "milk insufficiency point" (MIP hereafter) and the accompanying infant's start of independent feeding are expected to be reached early relative to weaning, whereas, in contrast to faster species, the mother does not respond to this by changing her feeding effort. Accordingly, a protracted period of self-provisioning that overlaps with continued suckling is found in baboons (Lycett et al. 1998), chimpanzees (Hiraiwa-Hasegawa 1990), gorillas (Nowell and Flotscher 2008) and elephants (Lee and Moss 2011). At least in baboons, mothers also sustain a stable level effort during most of this period (Barrett et al. 2006), whereas no published data indicating an effect of offspring age were found for the other species.

Fifth, mother–offspring conflict over the level of maternal investment is expected around the time MIP is reached. This may well be more pronounced than the classic conflict over the timing of "final weaning", the complete cessation of milk transfer, (Trivers 1974), since in species with multi-year lactation final weaning happens when the immature is already responsible for meeting most of its needs. Indeed, Barrett and Henzi (2000) found that baboon mothers in a population with relatively late weaning, most often rejected their infants' attempts to make nipple contact just around the time they started to feed independently, rather than around the age of final weaning. Similarly, Lee and Moss (2011) report a peak in conflict between elephant mothers and (female) calves around the age the calves started to feed independently, long before final weaning. In addition, weaning is reported to be rather gradual and uneventful for several larger primates (e.g., baboons: Lycett et al. 1998; chimpanzees: Goodall 1986;

Sumatran orangutans: van Noordwijk and van Schaik 2005). A slowdown of growth around the timing of MIP would support the presence of such a conflict over the level of investment. Unfortunately, accurate growth data are hardly available for species with slow life history under natural conditions.

In conclusion, it appears that multi-year lactation among mammals, as illustrated here by Bornean orangutans, leads to many differences in the mother's feeding effort and mother–infant relations relative to seasonally breeding mammals. Recognition of the common features of multi-year lactation in species with slow life histories allows us to identify which features of the human lactation pattern are ancestral and which can be considered derived and linked to distinct features of the human lifestyle, e.g., allomaternal care and active provisioning of pre-processed food (van Noordwijk et al. unpublished).

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Ethical standards The observations on wild orangutans were conducted in accordance with the local regulations.

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