



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
Main Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2013

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

van Noordwijk, Maria A ; Willems, Erik P ; Utami Atmoko, Sri Suci ; Kuzawa, Christopher W ; van Schaik, Carel P

DOI: <https://doi.org/10.1007/s00265-013-1504-y>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-84511>

Journal Article

Accepted Version

Originally published at:

van Noordwijk, Maria A; Willems, Erik P; Utami Atmoko, Sri Suci; Kuzawa, Christopher W; van Schaik, Carel P (2013). Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behavioral Ecology and Sociobiology*, 67(5):805-814.

DOI: <https://doi.org/10.1007/s00265-013-1504-y>

1 Multi-year lactation and its consequences in Bornean orangutans

2 (*Pongo pygmaeus wurmbii*)

3 

4

5 Maria A. van Noordwijk^{*a}, Erik P. Willems^a, Sri Suci Utami Atmoko^b, Christopher W. Kuzawa^c, and Carel P.

6 van Schaik^a

7

8 ^aAnthropological Institute and Museum, University of Zurich, Zurich, Switzerland

9 ^bFakultas Biologi, Universitas Nasional, Jakarta, Indonesia

10 ^cDepartment of Anthropology and Institute for Policy Research, Northwestern University, Evanston, IL 60208,

11 USA

12

13 * Corresponding author: vnoord@aim.uzh.ch

14

15 Running headline: Multi-year lactation in orangutans

16

17

18 Accepted for publication in Behavioral Ecology and Sociobiology

19 2013

20

21 Abstract

22 In most mammals, females pay for reproduction by dramatically increasing net energy intake from conception to
23 mid-or late lactation. To do this they time their reproductive events in relation to environmental cycles so that
24 periods of peak food availability coincide with peak demand or are used to build energy stores. This timing is not
25 possible in species with slow development in which lactation is prolonged over a multi-year period with
26 fluctuating food availability. Here mothers are expected to sustain a stable but generally lower level of nutrient
27 transfer. In a sample of over 1050 complete follow days of eight mother-infant pairs collected over seven years,
28 we document maternal effort for wild Bornean orangutans (*Pongo pygmaeus wurmbii*) over their average 6.5-
29 year lactation period. As predicted, maternal feeding time was independent of the age of her growing offspring,
30 indicating a stable sustained 'plateau' effort of $\leq 25\%$ above baseline level, instead of a short peak lactation as
31 seen in seasonal breeders. Infant orangutans started to regularly supplement milk with self-harvested food when
32 they were 1-1.5 years old, indicating milk intake was insufficient from this age onwards, even though maternal
33 effort did not decrease. We expect the same regulation of sustained maternal effort in other large and large-
34 brained mammals with slow infant development. We also predict that mother-infant conflict over suckling may
35 show another peak at the onset of the milk+solid food phase, in addition to the well-known conflict around the
36 endpoint of lactation (weaning), which is reached after a long and gradual increase in solid food intake by the
37 infant.

38

39 Key-words:

40 Great Apes, maternal investment, parent-offspring conflict, sustained lactation, weaning

41 **Introduction**

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

51 Many mammal species manage to complete their reproductive cycle within the period of the
52 environmental cycle, usually a year. Capital breeders elevate their food intake before or during gestation,
53 whereas in income breeders, which are the majority of non-aquatic mammals, mothers increase their intake,
54 sometimes 2-4 times (Speakman 2008), in accordance with the increasing needs of their offspring. In income
55 breeders, maternal energy intake thus shows a characteristic inverted U-shaped curve, rising to a peak during
56 mid- to late lactation before returning to baseline levels following weaning and gradually rising again during the
57 next pregnancy (e.g. Clutton-Brock et al. 1982; König and Markl 1987; Dunbar and Dunbar 1988; Tarnaud
58 2006).

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

68 Multi-year lactation should therefore have two major consequences. First, energy intake to sustain
69 lactation probably needs to be set at a level that is both rather stable and conservative throughout the lactation
70 period rather than showing the steep rise followed by a more or less rapid fall seen in species with shorter
71 lactation. Second, this conservative but stable level of maternal investment almost inevitably also implies that

72 infants must begin to feed independently to supplement the maternal contribution to their increasing
73 requirements well before the end of lactation.

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

80 Consideration of multi-year lactation requires that we clarify the meaning of weaning. Normally, the
81 weaning phase is thought to begin with the onset of solid food intake by the offspring, because this point also
82 marks the beginning of the progressive decline in milk transfer from mother to offspring (e.g. Martin 1984; Lee
83 1997; Langer 2008). However, in slowly developing species we expect that lactation would be rather stable and
84 at a modest level, implying that the onset of solid food consumption by the infant does not coincide with a
85 decrease of the mother's investment in milk. Therefore, we use the term 'weaning' here only to refer to the
86 decrease in lactation, rather than to indicate the entire period in which infants supplement their milk diet with
87 solid food.

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

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

101

102 **Methods**

103 *Data collection*

104 Behavioral observations used here were collected from July 2003 to July 2010 on a natural population of
105 Bornean orangutans in the Tuanan Orangutan Research Area, Mawas Reserve, Kalimantan Tengah, Indonesia
106 (2° 09' S; 114° 26' E). Focal animal follows on well-habituated individuals were conducted following standard
107 field methods (<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>), recording activity of
108 mother and offspring every 2 minutes.

109 Ages of infants born before the start of the study were estimated (cf. Wich et al. 2004). These estimates
110 were updated in comparison with subsequently born infants using extensive photographic records (e.g. Fig. S1).
111 Omitting the 3 infants with estimated ages did not affect the results. Unlike in other orangutan populations (e.g.
112 Knott et al. 2009), conceptions and births of the sampled immatures were regularly spread across years, and
113 during each calendar year immatures of different ages were sampled. None of the known immatures died during
114 the study period (or is known to have died thereafter). However, one mother died, probably due to a clouded
115 leopard attack, and her 4-year-old offspring was transported to a rescue center by the local authorities.

116 Monthly values in the current analyses are based on at least 5 full days within a calendar month of nest-
117 to-nest follows per female/offspring (Table 1). On average, the nest-to-nest active period lasted 655 min. Thus,
118 in total the dataset covers over 11,500 hours of focal observation by an experienced team.

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

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

131 *Estimating the energetic burden of offspring*

132 Our approach in this analysis was to estimate the total caloric burden represented by the offspring (basal
133 metabolism + activity + energetic costs to the mother of carrying). Maternal metabolism (milk) was assumed to

134 provide all this energy until the infant started to supplement its diet by consistently feeding on solid food. To
135 estimate the energy requirements of a growing orangutan, the percentages that are derived from mother (milk)
136 versus solid food, as well as how these change with infant age, we had to make some assumptions. Results are
137 presented for our best estimate, with an upper and lower estimate to assess the possible impact of error in the
138 various variables estimated (see supplementary material).

139 Even though maternal weight is expected to vary among adult females, and since we did not have
140 weights on the individual animals in this study, we assumed an average maternal weight of 38 kg (*range 34 – 42*
141 *kg*, based on Leigh and Shea [1995], Smith and Jungers [1997], and Plavcan and van Schaik [1997]) and a birth
142 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
143 nutritional independence (fully weaned), which occurs at a mean age of 6.5 years in this population (unpublished
144 data). We estimated weaning weight as 17 kg (*range 12-22 kg*), similar to the median of 15-20 kg (Leigh and
145 Shea 1995) in captivity, even though there weaning is completed 2-3 years earlier than in the wild. These
146 assumed weights agree well with known weights of wild-caught infants, of which age estimates are based on
147 dentition, brought into nearby rehabilitation centres (A. Nurcahyo and S.J. Husson pers. comm.) and with visual
148 estimates made in the field (based on photographs of the relative size of weanlings vs. their mothers). For
149 simplicity, we also assumed an approximately linear rate of increase in weight between the age of birth and
150 independence (Leigh and Shea 1995). Even though growth is accelerated shortly after birth, the absolute
151 metabolic impact of this should be limited. Because orangutans grow extremely slowly, we assumed that the cost
152 of growth itself was negligible (*e.g.* Butte 2005, Wells and Davies 1998). We also assumed no sex difference in
153 requirements (*cf.* Grund et al. 2000), since there was no evidence for a sex difference in interbirth interval,
154 weaning age, or developmental trajectory in our small sample (unpublished data; van Noordwijk et al. 2009), and
155 because growth rates of males and females in captivity do not diverge until after weaning (Leigh and Shea 1995).

156 We estimated BMR at all ages based upon the assumption that caloric expenditure follows the general
157 relationship for mammals according to Kleiber's law: $BMR [MJoule/day] = 4.1 * weight [kg]^{0.751}$ (Peters 1983).
158 In a study of captive but free ranging animals, Pontzer et al. (2010) suggested that orangutan BMR is 36% below
159 estimates based on Kleiber's law. However, comparative work has shown that, among the apes, orangutans are
160 especially prone to excess fat deposition in captivity (Leigh and Shea 1995), which reduces mass-specific BMR.
161 We therefore derived our estimates under the assumption that the wild animals in our study were leaner than the
162 captive ones investigated by Pontzer et al. (2010) and thus closer to our Kleiber-based estimate. However, our
163 conclusions are not substantively affected by the actual value of BMR used because we used the ratio of energy
164 costs of mother + offspring relative to the mother's baseline for our analyses. For example, a 20% lower estimate

165 of BMR for mother and offspring increases the relative cost of the offspring by a maximum of 0.29% when the
166 offspring is 30 months old; and at 36% lower BMR the maximum relative cost would be only 0.51 % higher.

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

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

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

186 *Statistical analyses*

187 To assess the effect of offspring age and fruit availability on maternal investment, expressed as the
188 mother's monthly average time spent feeding and her day journey length, we constructed linear mixed effects
189 models in which the identity of the offspring was included as a nested random factor within the identity of its
190 mother. The same analyses were applied to the amount of time spent feeding on fruit, insects, flowers, leaves,
191 bark and other vegetative parts. Model significance and the significance of fixed factors in the model were
192 calculated using Likelihood Ratio Tests (LRT), following Johnson and Omland (2004). In addition, we
193 investigated the influence of offspring age and food availability on the offspring's own monthly averaged
194 feeding time, taking the same linear mixed effects modelling approach as outlined above. All analyses were
195 conducted using the "lme4" package for R 2.12.1 (R Development Core Team 2010).

196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226

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 4 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 growing offspring. However, although the mother' and the offspring' identity 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 ($\chi^2_{\text{LRT}} = 1.15$, $P = 0.28$; Table 2; Fig. 2), whereas it decreased during months in which more food was available ($\chi^2_{\text{LRT}} = 11.26$, $P < 0.001$). Likewise, diet composition was significantly affected by fruit availability, but not by offspring age (Table S2). Similarly, the distance a female travelled per day was unaffected by offspring age ($\chi^2_{\text{LRT}} = 1.49$, $P = 0.22$), yet was longer during months characterized by a higher fruit availability index ($\chi^2_{\text{LRT}} = 22.60$, $P < 0.0001$), reflecting feeding in dispersed preferred fruit trees rather than foraging on less dispersed fallback food.

227 *Infant time budget*

228 In contrast to their mothers' constant feeding effort, the amount of time the offspring themselves spent
 229 feeding each month increased as a function of age, as expected ($\chi^2_{\text{LRT}} = 164.34$, $P < 0.0001$; Table 2; Fig. 3a).
 230 Even though infants under a year old show some interest in what their mothers eat and sometimes obtain morsels
 231 from their mother, they only start to consistently spend more than a few percent of their time feeding on solid
 232 food when they are around 1-1.5 years old (Fig. 3a). From then on feeding time steadily increased (age immature
 233 19-84 months: $\chi^2_{\text{LRT}} = 66.18$, $P < 0.0001$; Table 2), and around the age of full weaning, at 6-7 yr, reached a value
 234 similar to the average feeding time of the mothers. The feeding time of immatures (19-84 mo) was inversely
 235 related to fruit availability ($\chi^2_{\text{LRT}} = 14.53$, $P < 0.0005$), like that of their mothers.

236

237 *Maternal contribution to offspring energy requirements*

238 To estimate the energy costs of lactation, the maintenance budgets of non-pregnant, non-lactating
 239 females would be required as a baseline. However, because all females were typically pregnant, lactating or
 240 both, it was not possible to obtain sufficient data for a such a baseline. Moreover, too few samples were available
 241 for pregnant females, and these few were taken under conditions that were too varied for a meaningful
 242 comparison. Instead, we took two other approaches to estimate these costs. First, we compared the time budgets
 243 of females at different stages of lactation (0 - 84 months after birth; see above). Despite the absence of a
 244 significant effect of offspring age on maternal time budget, feeding time did significantly increase during the
 245 first 6 months following giving birth ($\chi^2_{\text{LRT}} = 14.09$, $P < 0.001$; Table S3), although no significant age effect was
 246 found over the entire first year (Table S3). This suggests a rapid increase in feeding time in the first few months
 247 stabilizing before or around 6 months. Since the analyses consider within-female trends, the number of samples
 248 per female over the first year, which covered variation in fruit availability, was probably too small to detect a
 249 significant effect. Feeding time samples taken during the first month following birth were ca. 15% below the
 250 average throughout the offspring's 6-7 year dependent period.

251 Second, we estimated the mother's contribution to fulfil her offspring's energy needs by estimating the
 252 mother's feeding effort right around the age at which the offspring starts to contribute to its needs by consuming
 253 measurable quantities of solid food. We assume this coincides with the time when energy from milk alone does
 254 not cover its needs. At this age, 1-1.5 years old for the infants in our sample, the mother-offspring dyad is
 255 estimated to require ca. 22% (18-25%) more energy for their combined DEE than the mother would require for
 256 herself (calculations are based on weight-specific BMR and actual activity budgets: Fig. 3b; see also Fig. S2 for
 257 values based on other weights). Since mothers do not spend significantly more or less time feeding around this

258 age than at any other stage of lactation, we conclude that they consistently provide up to ca. 22 % more energy
259 than needed for their own maintenance. Taking food to milk conversion loss into account, we estimate that
260 mothers feed at most ca. 25 % more than females would need when not reproducing, or recuperating from or
261 storing reserves for reproduction.

262

263 **Discussion**

264 *Orangutans*

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

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

281 Despite the extended maternal effort to raise an offspring to independence, most immatures in our
282 sample were fully weaned only after their mother had conceived her next offspring, implying the absence in
283 mothers of a distinct recovery period to compensate for lost condition or to build up reserves. Thus, the pattern
284 of reproductive expenditure in female Bornean orangutan can be characterized by near-constancy across the
285 adult reproductive lifespan. However, since no changes in feeding time were detected towards or shortly after
286 weaning of the offspring, females may use the period of relatively low energy needs during the post-weaning
287 phase to build up some reserves while they are pregnant and during the first year of lactation of the next

288 offspring. Similarly, they may be storing energy at any moment throughout lactation whenever it is not directly
289 needed, which may be used to buffer future periods of negative energy balance (Knott 2005).

290 We found that maternal feeding effort in Bornean orangutans was only moderately increased relative to
291 their non-reproductive baseline. It is possible that the low productivity of Southeast Asian forests (Terborgh and
292 van Schaik 1987) and the resulting metabolic adaptations in orangutans (Pontzer et al. 2010) have exaggerated
293 the conservative nature of orangutan lactation. However, we expect the basic pattern of lactation to be similar in
294 other species with a slow life history and a multi-year lactation pattern, because they all face the same basic
295 problem. They cannot predictably time their period of highest need to coincide with peak food availability, but
296 experience (multiple) fluctuations in food availability during lactation and for such long periods that neither
297 storing reserves nor entering negative energy or protein balance are viable options (cf. Oftedal 2000). Indeed,
298 some estimates of the cost of the milk-only-phase of lactation on humans and captive baboons are within the
299 same range of requiring a 10-30 % increase in food intake (Butte et al. 2001; Rosetta et al. 2011).

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

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

317 In the current study, independent feeding started when the infant was around 1.25 years old, thus after
318 less than a quarter of the total lactation period. Similarly, independent feeding started long before locomotory

319 independence (van Noordwijk et al. 2009; A. Phillips et al. unpublished data) This is not surprising, because
320 young infants can collect and feed on fruit while clinging to their mother or while clambering around in close
321 proximity to her. Thus small and dependent infants are already able to supplement their diet with self-collected
322 solid food, which we suggest typically starts to contribute a non-trivial fraction of caloric intake sometime early
323 in the second year of life. In general, strong selection is expected to ensure that the infant has acquired sufficient
324 maturity in digestive ability and food acquisition and processing skills at the age at which milk alone generally
325 becomes insufficient. Thus the mother's level of maximum sustained lactation should be at a level that matches
326 the timing of sufficient digestive maturation when the infant very slowly takes over responsibility for its own
327 energy supply during a very long 'transitional' phase with continued milk consumption at a rather stable level.

328

329 *Multi-year lactation and its consequences*

330 Extrapolating from the orangutan data we expect a similar pattern of maternal investment in other
331 species with slow life history and multi-year lactation. Here we develop 5 predictions and examine preliminary
332 evidence from the literature. First, when lactation is protracted over an extended period we expect maternal
333 effort to be rather constant. Unlike species with shorter seasonal breeding, among which increasing offspring
334 needs are met by parallel increases in maternal effort, studies of baboons with a lactation of just over a year
335 found a more limited increase in maternal feeding effort than anticipated (Altmann 1980; Barrett et al. 2006).
336 Similarly, the feeding effort of giraffe mothers, during their 1-1.5 year lactation period, was reported to be
337 remarkably constant and unaffected by offspring age (Pellew 1984). The fact that detailed studies of chimpanzee
338 maternal time budgets did not differentiate by age of the infant (Murray et al. 2009) suggests a similar constant
339 effort in this great ape as well.

340 Second, maternal increase in food intake is expected to be rather modest compared to a baseline non-
341 reproductive state. Indeed several authors have noted only a modest increase in maternal feeding effort during
342 lactation compared to other states. For example in a small sample of wild siamang females (Lappan 2009) the
343 maximum difference between early (0-4 months) and later lactation in feeding time was found to be 25-50%, but
344 some females showed their peak effort during mid-lactation (5-9 months) and others closer to weaning (10-15
345 months), suggesting some interfering effect of food availability. In chimpanzees, with a lactation period of ca. 4
346 years, lactating females increased their feeding time less than 10% relative to pregnant females and spent less
347 time feeding than non-pregnant-non-lactating females (Murray et al. 2009).

348 Third, once the physiology of lactation is no longer dependent on predictable seasonality, the timing of
349 a female's next reproductive event is also expected to be less restricted. Thus, females can be in a permanent

350 reproductive state, being either pregnant, lactating, or both, without needing ‘recovery’ periods. Consistently,
351 like orangutans, female giraffes (Pellew 1984), elephants (Lee and Moss 2011) and gorillas (Nowell and
352 Fletscher 2008) often conceive their next offspring while still nursing the previous one without a ‘recuperation’
353 period. Nevertheless, elephant inter-birth intervals and offspring survival are affected by extreme fluctuations in
354 food availability (Lee et al. 2011).

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

362 Fifth, mother-offspring conflict over the level of maternal investment is expected around the time MIP
363 is reached. This may well be more pronounced than the classic conflict over the timing of ‘final weaning’, the
364 complete cessation of milk transfer, (Trivers 1974), since in species with multi-year lactation final weaning
365 happens when the immature is already responsible for meeting most of its needs. Indeed, Barrett and Henzi
366 (2000) found that baboon mothers in a population with relatively late weaning, most often rejected their infants’
367 attempts to make nipple contact just around the time they started to feed independently, rather than around the
368 age of final weaning. Similarly, Lee and Moss (2011) report a peak in conflict between elephant mothers and
369 (female) calves around the age the calves started to feed independently, long before final weaning. In addition,
370 weaning is reported to be rather gradual and uneventful for several larger primates (e.g. baboons: Lycett et al.
371 1998; chimpanzees: Goodall 1986; Sumatran orangutans: van Noordwijk and van Schaik 2005). A slowdown of
372 growth around the timing of MIP would support the presence of such a conflict over the level of investment.
373 Unfortunately, accurate growth data are hardly available for species with slow life history under natural
374 conditions.

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

381

382

383 **Acknowledgements**

384 We are indebted to the Tuanan team of assistants and students over many years for their efforts in data
 385 collection. We thank Tatang Mitra Setia MSc and the students of the Fakultas Biologi Universitas Nasional
 386 (UNAS) in Jakarta, and in particular Rahmalia N. Amda and Neneng Mardianah, for their collaboration and
 387 support for the Tuanan project. We gratefully acknowledge the Indonesian Institute of Science (LIPI), and the
 388 Indonesian State Ministry for Research and Technology (RisTek), the Director General Departemen Kehutanan
 389 (PHKA), Departamen Dalam Negeri, the local government in Central Kalimantan, the BKSDA Palangkaraya, the
 390 Bornean Orangutan Survival Foundation (BOSF) and MAWAS in Palangkaraya for their permission and support
 391 to the project. For major financial support we thank the University of Zurich, and the A.H. Schultz Stiftung. We
 392 appreciate the constructive comments by the anonymous reviewers.

393

394 **Ethical standards**

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

396

397 **References**

- 398 Ainsworth BE, Haskell WT, Whitt MC, Irwin ML, Swartz AM, Strath SJ, O'Brien WL, Bassett DRJ, Schmitz
 399 KH, Emplancourt PO, Jacobs DRJ, Leon AS (2000) Compendium of physical activities: an update of
 400 activity codes and MET intensities. *Med Sci Sports Exerc* S498-S516
- 401 Altmann J (1980) Baboon mothers and infants. Harvard University, Cambridge, MA
- 402 Altmann J, Samuels A (1992) Costs of maternal care: infant-carrying in baboons. *Behav Ecol Sociobiol* 29:391-
 403 398
- 404 Alvarez HP (2000) Grandmother hypothesis and primate life histories. *Am J Phys Anthropol* 113:435-450
- 405 Barrett L, Halliday J, Henzi SP (2006) The ecology of motherhood, the structuring of lactation costs by chacma
 406 baboons. *J Anim Ecol* 75:875-886
- 407 Barrett L, Henzi SP (2000) Are baboon infants Sir Phillip Sydney's offspring? *Ethology* 106:645-658
- 408 Brockman DK, van Schaik CP (2005) Seasonality and reproductive function. In: Brockman DK, van Schaik CP
 409 (eds) *Seasonality in primates: Studies of living and extinct human and non-human primates*. Cambridge
 410 University Press, Cambridge, pp 269-305

- 411 Butte NF (2005) Energy requirements of infants. *Publ Health Nutr* 8:953–967
- 412 Butte NF, Wong WW, Hopkinson JM (2001) Energy requirements of lactating women derived from doubly
413 labeled water and milk energy output. *J Nutr* 131:53-58
- 414 Clutton-Brock T (1991) *The evolution of parental care*. Princeton University Press, Princeton
- 415 Clutton-Brock TH, Guinness FE, Albon SD (1982) *Red deer: behavior and ecology of two sexes*. The University
416 of Chicago Press, Chicago
- 417 Di Fiore A, Campbell CJ (2007) *The Atelines. Variation in ecology, behavior, and social organization*. In:
418 Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) *Primates in perspective*. Oxford
419 University Press, Oxford, pp 155-185
- 420 Dufour DL, Sauter ML (2002) Comparative and evolutionary dimensions of the energetics of human pregnancy
421 and lactation. *Am J Hum Biol* 14:584-602
- 422 Dunbar RIM, Dunbar P (1988) Maternal time budgets of gelada baboons. *Anim Behav* 36:970-980
- 423 Emery Thompson M, Muller MN, Wrangham RW 2012 The energetics of lactation and the return to fecundity in
424 wild chimpanzees. *Behav Ecol* 23:1234-1241
- 425 Eveleth PB, Tanner JM (1976) *Worldwide Variation in Human Growth*. Cambridge University Press, Cambridge
- 426 Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. *Am Zool* 28:863-875
- 427 Goodall J (1986) *The chimpanzees of Gombe*. Harvard University Press, Cambridge, MA
- 428 Grund A, Vollbrecht H, Frandsen W, Krause H, Siewers M, Rieckert H, Müller MJ (2000) No effect of gender
429 on different components of daily energy expenditure in free living prepubertal children. *Int J Obes* 24:299-
430 305
- 431 Hiraiwa-Hasegawa M (1990) A note on the ontogeny of feeding. In: Nishida T (ed) *The chimpanzees of the*
432 *Mahale Mountains. Sexual and life history strategies*. University of Tokyo Press, Tokyo, pp 277-283
- 433 Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101-108
- 434 Knott CD (1998) Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating
435 fruit availability. *Int J Primatol* 19:1061-1079
- 436 Knott CD (2005) *Energetic responses to food availability in the great apes: implications for hominin evolution*.
437 In: Brockman DK, van Schaik CP (eds) *Seasonality in primates: Studies of living and extinct human and*
438 *non-human primates*. Cambridge University Press, Cambridge, pp 351—378
- 439 Knott CD, Emery Thompson M, Wich SA (2009) The ecology of female reproduction in wild orangutans. In:
440 Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) *Orangutans: Geographic variation in*
441 *behavioral ecology and conservation*. Oxford University Press, Oxford, pp 171-188

- 442 König B, Markl H (1987) Maternal care in house mice: I. The weaning strategy as a means for parental
443 manipulation of offspring quality. *Behav Ecol Sociobiol* 20:1-9
- 444 Kramer PA (1998) The costs of human locomotion: maternal investment in child transport. *Am J Phys*
445 *Anthropol* 107:71-85
- 446 Kuzawa CW (1998) Adipose tissue in human infancy and childhood: An evolutionary perspective. *Yearb Phys*
447 *Anthropol* 41:177-209
- 448 Langer P (2008) The phases of maternal investment in eutherian mammals. *Zoology* 111:148-162
- 449 Lappan S (2009) The effects of lactation and infant care on adult energy budgets in wild siamangs
450 (*Symphalangus syndactylus*). *Am J Phys Anthropol* 140:290-301
- 451 Lee PC (1996) The meanings of weaning: growth, lactation, and life history. *Evol Anthropol* 5:87-96
- 452 Lee PC, Lindsay WK, Moss CJ (2011) Ecological patterns of variability in demographic rates. In: Moss CJ,
453 Croze H, Lee PC (eds) *The Amboseli elephants. Long-term perspective on a long-lived mammal.*
454 University of Chicago Press, Chicago, pp 74-88
- 455 Lee PC, Moss CJ (2011) Calf development and maternal rearing strategies. In: Moss CJ, Croze H, Lee PC (eds)
456 *The Amboseli elephants. Long-term perspective on a long-lived mammal.* University of Chicago Press,
457 Chicago, pp 224-237
- 458 Leigh SR, Shea BT (1995) Ontogeny and the evolution of adult body size dimorphism in apes. *Am J Primatol*
459 36:37-60
- 460 Lycett JE, Henzi SP, Barrett L (1998) Maternal investment in mountain baboons and the hypothesis of reduced
461 care. *Behav Ecol Sociobiol* 42:49-56
- 462 Marshall AJ, Ancrenaz M, Brearley FQ, Frederiksson GB, Ghaffar N, Heydon M, Husson SJ, Leighton M,
463 McConkey KR, Morrogh-Bernard HC, Proctor J, van Schaik CP, Yeager CP, Wich SA (2009) The effects
464 of forest phenology and floristics on populations of Bornean and Sumatran orangutans. In: Wich SA, Utami
465 Atmoko SS, Mitra Setia T, van Schaik CP (eds) *Orangutans: Geographic variation in behavioral ecology*
466 *and conservation.* Oxford University Press, Oxford, pp 97-117
- 467 Martin PS (1984) The meaning of weaning. *Anim Behav* 32:1257-59
- 468 Morrogh-Bernard HC, Husson SJ, Knott CD, Wich SA, van Schaik CP, van Noordwijk MA, Lackman-Ancrenaz
469 I, Marshall AJ, Kanamori T, Kuze N, bin Sakong R (2009) Orangutan activity budgets and diet. In: Wich
470 SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) *Orangutans: Geographic variation in behavioral*
471 *ecology and conservation.* Oxford University Press, Oxford, pp 119-133
- 472 Murray CM, Lonsdorf EV, Eberly LE, Pusey AE (2009) Reproductive energetics in free-living female

- 473 chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol 20:1211-1216
- 474 Nowell AA, Fletcher AW (2008) The development of feeding behaviour in wild western lowland gorillas
475 (*Gorilla gorilla gorilla*). Behaviour 145:171-193
- 476 Oftedal OT (2000) Use of maternal reserves as a lactation strategy in large mammals. Proc Nutr Soc 59:99-106
- 477 Pellew RA (1984) Food consumption and energy budgets of the giraffe. J Appl Ecol 21:141-159
- 478 Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- 479 Piperata BA (2009) Variation in maternal strategies during lactation: The role of the biosocial context. Am J
480 Hum Biol 21:817-827
- 481 Plavcan JM, van Schaik CP (1997) Intrasexual competition and body weight dimorphism in anthropoid primates.
482 Am J Phys Anthropol 103:37-68.
- 483 Pontzer H, Raichlen DA, Shumaker RW, Ocobock C, Wich SA (2010) Metabolic adaptation for low energy
484 throughput in orangutans. P Natl Acad Sci USA 107:14048-14052
- 485 Prentice AM, Prentice AM (1988) Energy cost of lactation. Annu Rev Nutr 8:63-79
- 486 Prentice AM, Whitehead RG (1987) The energetics of human reproduction. Symp Zool Soc Lond 57:275-304
- 487 R-Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for
488 Statistical Computing, Vienna, Austria
- 489 Robson SL, van Schaik CP, Hawkes K (2006) The derived features of human life history. In: Hawkes K, Paine
490 RR (eds) The evolution of human life history. School of American Research Press, Santa Fe NM, pp 17-44
- 491 Rosetta L, Lee PC, Garcia C (2011) Energetics during reproduction: A double labeled water study of lactating
492 baboons. Am J Phys Anthropol 144:661-668
- 493 Russon AE, Wich SA, Ancrenaz M, Kanamori T, Knott CD, Kuze N, Morrogh-Bernard HC, Pratje P, Ramlee H,
494 Rodman P, Sawang A, Sidiyasa K, Singleton I, van Schaik CP (2009) Geographic variation in orangutan
495 diets. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (eds) Orangutans: Geographic
496 variation in behavioral ecology and conservation. Oxford University Press, Oxford, pp 135-156
- 497 Schmidt-Nielsen K (1984) Scaling. Cambridge University Press, Cambridge
- 498 Sellen DW (2001) Comparison of infant feeding patterns reported for nonindustrial populations with current
499 recommendations. J Nutr 131:2707-2715
- 500 Smith RJ, Jungers WL (1997) Body mass in comparative primatology. J Hum Evol 32:523-559
- 501 Speakman JR (2008) The physiological costs of reproduction in small mammals. Philos T Roy Soc B 363:375-
502 398
- 503 Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

- 504 Tarnaud L (2006) Feeding behavior of lactating brown lemur females (*Eulemur fulvus*) in Mayotte: influence of
505 infant age and plant phenology. *Am J Primatol* 68:966-977
- 506 Terborgh J, van Schaik CP (1987) Convergence vs. non-convergence in primate communities. In: Gee JHR,
507 Giller PS (eds) *Organization of communities: Past and present*. Blackwell Scientific Publications, Oxford,
508 pp 205-226
- 509 Trivers RL (1974) Parent-offspring conflict. *Am Zool* 14:249-264
- 510 van Noordwijk MA, Sauren SEB, Nuzuar, Abulani A, Morrogh-Bernard HC, Utami Atmoko SS, van Schaik CP
511 (2009) Development of independence Sumatran and Bornean orangutans compared. In: Wich SA, Utami
512 Atmoko SS, Mitra Setia T, van Schaik CP (eds) *Orangutans: Geographic variation in behavioral ecology*
513 and conservation. Oxford University Press, pp 189-203
- 514 van Noordwijk MA, van Schaik CP (2005) Development of ecological competence in Sumatran orangutans. *Am*
515 *J Phys Anthropol* 127:79-94
- 516 Vogel ER, Knott CD, Crowley BE, Blakely MD, Larsen MD, Dominy NJ (2012) Bornean orangutans on the
517 brink of protein bankruptcy. *Biol Lett* 8:333-336
- 518 Wells JCK, Davies PSW (1998) Estimation of the energy cost of physical activity in infancy. *Arch Dis*
519 *Childhood* 78:131-136
- 520 Whitehead H, Mann J (2000) Female reproductive strategies of Cetaceans: Life histories and calf care. In: Mann
521 J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean Societies*. Field studies of dolphins and whales.
522 University of Chicago Press, Chicago, pp 219-246
- 523 Wich SA, Utami-Atmoko SS, Mitra Setia T, Rijksen HD, Schurmann C, van Hooff JARAM, van Schaik CP
524 (2004) Life history of wild Sumatran orangutans (*Pongo abelii*). *J Hum Evol* 47:385-398
525

526 Table 1

527 Overview of focal mothers, their offspring and observation time

528

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

Notes: a) *only complete days from nest to nest*; b) *at least 5 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*

529

530

531 Table 2

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

534

Feeding time mother	β	SE	t	χ^2_{LRT}	P	
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	***

$\Delta AIC_{null\ model} = 9.49, \chi^2_{LRT} = 13.84, P < 0.001^{***}$

535 N= 121 monthly averages of maternal feeding time of 6 females with 9 different dependent
 536 immatures. Variance explained by ID mother 9.49 %; by ID offspring (within mother) 10.05 %
 537

Day journey length	β	SE	t	χ^2_{LRT}	P	
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	***

$\Delta AIC_{null\ model} = 19.5, \chi^2_{LRT} = 23.53, P < 0.0001^{***}$

538 N= 116 monthly averages of 6 females with 9 different infants. Variance explained by ID mother 7.24
 539 %; by ID offspring (within mother) 2.38%
 540

Feeding time immature 0-84 months	β	SE	t	χ^2_{LRT}	P	
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	***

$\Delta AIC_{null\ model} = 174.3, \chi^2_{LRT} = 178.29, P < 0.001$

541 N=123 monthly averages of 9 immatures from 6 different mothers. Variance explained by ID mother
 542 4.54%; by ID offspring (within mother) 0.0%
 543

Feeding time immature 19-84 months	β	SE	t	χ^2_{LRT}	P	
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	***

$\Delta AIC_{null\ model} = 80.02, \chi^2_{LRT} = 84.02, P < 0.001^{***}$

544 N=84 monthly averages of 8 immatures from 6 different mothers. Variance explained by ID mother
 545 0.0%; by ID offspring (within mother) 6.47%

546 Figure legends

547

548 Fig. 1

549 Fruit availability July 2003-July 2010: Percentage of ca 1500 trees bearing fruit in a plot in the central part of the
550 study area Tuanan

551

552 Fig. 2

553 Feeding time and energy expenditure in relation to offspring age in months. a) Average number of minutes per
554 full follow day that mothers spent feeding. b) Estimated Daily Energy Expenditure for mothers, based on their
555 actual activity budget, and a BMR based on a maternal weight of 38 kg (see methods). Note that every point in
556 these graphs represents the average of at least 5 complete nest-to-nest follow days within a calendar month

557

558 Fig. 3

559 Feeding time and energy requirements of immatures in relation to age in months. a) Average number of minutes
560 per full follow day that immatures spent feeding on solid food. b) Estimated Daily Energy Requirement of
561 immatures, based on their estimated weight, derived BMR and their measured activity budgets (for alternative
562 weight estimates at birth and weaning see Fig. S2)

563

564 Fig. 4

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

Fig. 2

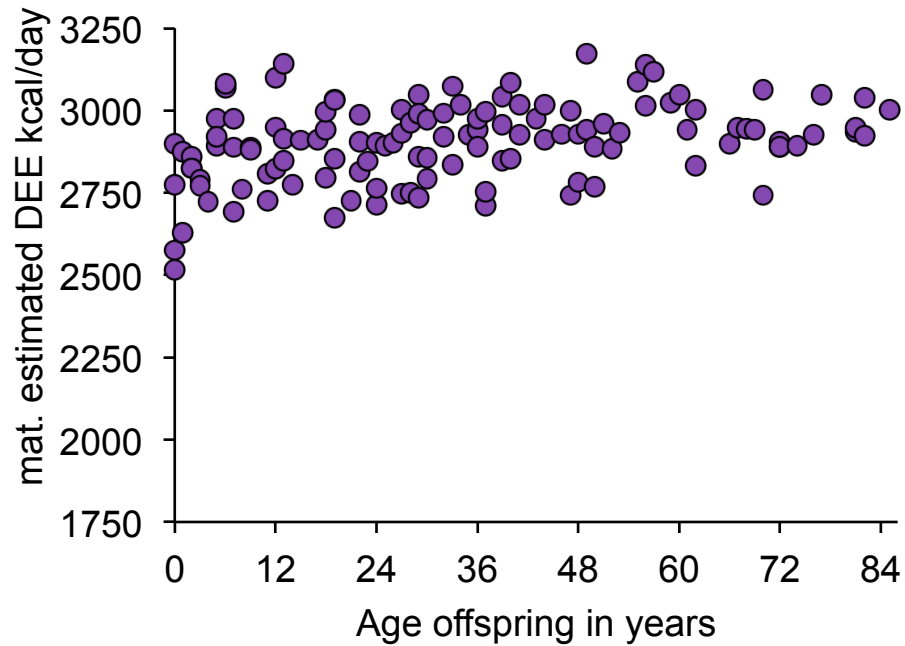
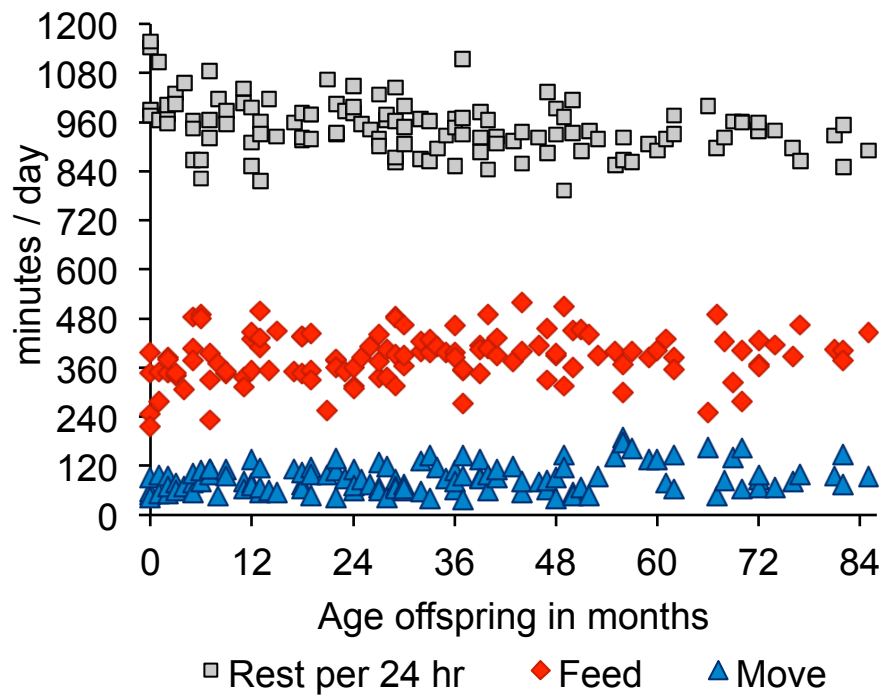


Fig. 3a,b

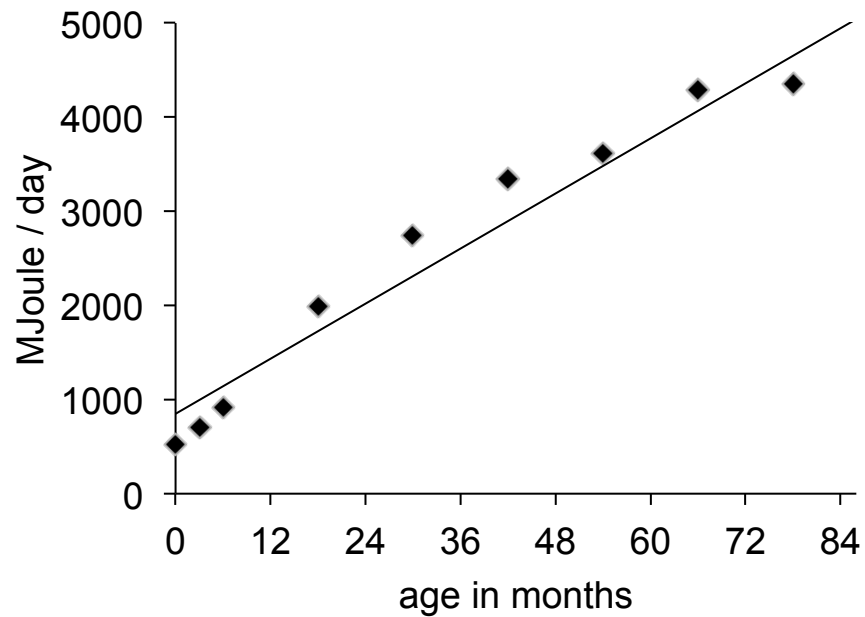
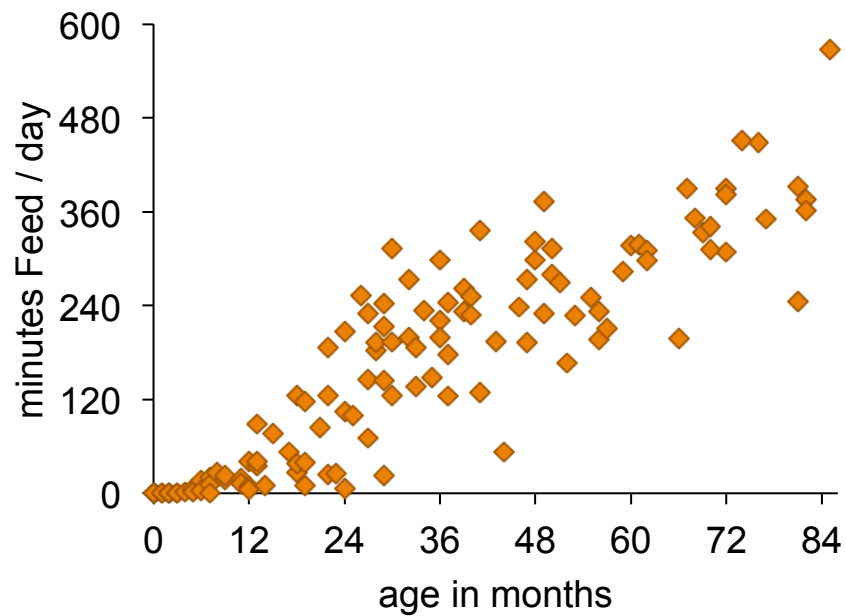
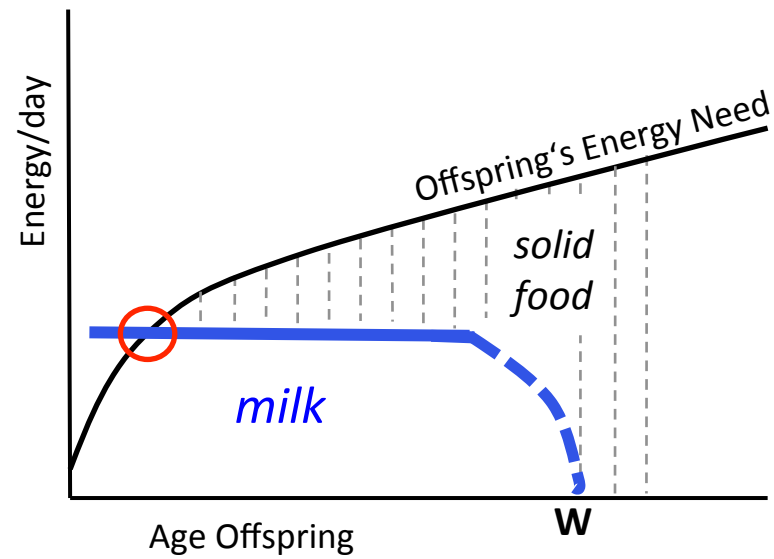
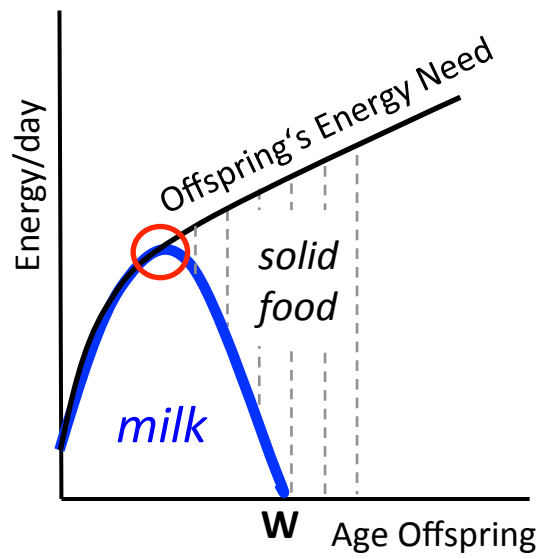


Fig. 4



Supplementary Tables

Table S1

Metabolic equivalents of orangutan activities based on human METs (Ainsworth et al. 2000)

COD E	MET S	Human example	Orangutan activity	OU MET
07011	1.0	Lying quietly doing nothing	Rest in nest	1.0
07021	1.0	Sitting quietly, watching movie	Rest	1.05
07040	1.2	Standing quietly		
09100	1.5	Sitting, relaxing, eating	Feed	2.2
09110	2.5	Camping, standing, walking, sitting		
08427	3.0	Picking flowers, vegetables, fruit, walking/standing		
11791	2.0	Walking slowly	Locomotion	3.0
11795	3.0	Walking, carrying light objects		
11800	4.0	Walking moderately, carrying light objects		
05175	4.0	Walk/run moderately, play with children/animals	Social Play & Solitary play	4.0

Table S2.

Maternal feeding time (minutes per day) on different diet components in relation to offspring age (in months) and % fruit availability. N= 121 monthly averages of 6 mothers with 9 different infants. Significance levels were adjusted to 0.0083 after Bonferroni correction

Fruit	β	SE	t	χ^2_{LRT}	P	
Intercept	146.434	19.65	7.45			
Age offspring	0.625	0.38	1.66	2.78	0.0953	
Fruit availability	15.000	2.76	5.43	38.21	<0.0001	***
$\Delta AIC_{null\ model}=36.80, \chi^2_{LRT}=40.77, P< 0.0001$ ***						
Variance explained by ID mother 0.0 %; by ID offspring (within mother) 0.0%						
Insects	β	SE	t	χ^2_{LRT}	P	
Intercept	9.133	7.59	1.20			
Age offspring	0.062	0.11	0.156	0.28	0.5937	
Fruit availability	1.205	0.75	1.61	11.10	<0.0005	***
$\Delta AIC_{null\ model}=6.90, \chi^2_{LRT}=10.89, P< 0.005$ *						
Variance explained by ID mother 17.69 %; by ID offspring (within mother) 3.52%						
Bark	β	SE	t	χ^2_{LRT}	P	
Intercept	33.382	4.32	7.72			
Age offspring	-0.095	0.08	-.79	1.36	0.243	
Fruit availability	-3.890	0.61	-6.40	44.71	<0.0001	***
$\Delta AIC_{null\ model}=41.7, \chi^2_{LRT}=45.68, P< 0.0001$ ***						
Variance explained by ID mother 0.0 %; by ID offspring (within mother) 0.0%						
Young leaves	β	SE	t	χ^2_{LRT}	P	
Intercept	72.881	7.58	9.62			
Age offspring	-0.078	0.15	-0.54	0.30	0.5857	
Fruit availability	-5.015	1.07	-4.71	30.00	<0.0001	***
$\Delta AIC_{null\ model}=26.3, \chi^2_{LRT}=30.33, P< 0.0001$ ***						
Variance explained by ID mother 0.0 %; by ID offspring (within mother) 0.0%						
Other veg. matter	β	SE	t	χ^2_{LRT}	P	
Intercept	55.715	10.04	5.65			
Age offspring	-0.055	0.15	-0.38	0.00	1.000	
Fruit availability	-4.651	0.99	-4.69	29.54	<0.0001	***
$\Delta AIC_{null\ model}=25.6, \chi^2_{LRT}=29.61, P< 0.001$ **						
Variance explained by ID mother 17.83 %; by ID offspring (within mother) 3.40%						
Flowers	β	SE	t	χ^2_{LRT}	P	
Intercept	56.575	13.57	4.17			
Age offspring	-0.060	0.26	-0.23	0.05	0.8171	
Fruit availability	-4.755	1.91	-2.49	16.64	<0.0001	***
$\Delta AIC_{null\ model}=12.8, \chi^2_{LRT}=16.73, P< 0.0005$ ***						
Variance explained by ID mother 0.0 %; by ID offspring (within mother) 0.0%						

Table S3

Results of linear mixed effects models to assess the effect of offspring age and fruit availability (FAI) on maternal feeding time during the first 6 month (N= 17 monthly samples for 5 mothers with 5 infants) and the first 12 months after giving birth (N= 28 monthly samples for 6 mothers with 6 infants)

Feeding time mother (first 6 months)

	β	SE	t	χ^2_{LRT}	P
Intercept	309.192	24.96	12.39		
Age offspring	26.986	6.36	4.24	14.05	<0.001 **
FAI	-5.542	5.16	-1.07	1.35	0.2459

$\Delta AIC_{null model} = 10.1, \chi^2_{LRT} = 14.09, P < 0.001^{**}$

Feeding time mother (first 12 months)

	β	SE	t	χ^2_{LRT}	P
Intercept	335.942	26.05	12.90		
Age offspring	5.071	3.49	1.45	2.27	0.1321
FAI	-0.867	5.20	-0.17	0.03	0.8598

$\Delta AIC_{null model} = -1.62, \chi^2_{LRT} = 2.39, P = 0.3035$

Supplementary Figures

Figure Legends

Fig. S1

Examples of yearly snapshots of known immatures, used to estimate ages of immatures not known from birth. In addition to facial changes size and body proportions relative to their mothers were used to assign estimated ages

Fig. S2

The calculations of BMR and DEE were based on our 'best estimate' of a maternal weight of 38 kg, infant weight of 1.6 kg and weaning weight of 17kg. The figure shows the calculations for lower and higher weight scenarios: maternal weight 34 and 42 kg, infant weight 1.3 and 1.9 kg and weaning weight 12 and 22 kg in addition to the standard scenario. The extreme scenarios of a 34kg mother with 1.9 kg newborn (and 22 kg weaning weight) would result in a DEE increase at offspring age of 1 year of 22 % and at 1.5 year of 32%, whereas for a 42kg mother with a 1.3 kg newborn (and 12 kg at weaning) the increase at 1 year would be 11% and at 1.5 year 20% relative to the mother's own DEE

Figure S1

	0 - 1 yr	1 - 2 yr	2 - 3 yr	3 - 4 yr	4 - 5 yr	5 - 6 yr	6 - 7 yr	7 - 8 yr
Kondor ♀ (Kerry) II 1999								
Milo ♀ (Mindy) II 2001								
Jerry ♂ (Jinak) May 2003								
Jip ♂ (Juni) Feb 2006								
Kino ♂ (Kerry) Jan 2007								

Figure S2

