

# Cost of reproduction in female non-human primates: an anthropological perspective

## Coût de la reproduction chez les femelles primates non-humains : une perspective anthropologique

C. Garcia

Received: 16 April 2013; Accepted: 3 March 2014  
© Société d'anthropologie de Paris et Springer-Verlag France 2014

**Abstract** Our research aims to further knowledge on the adaptive significance of reproductive processes in female primates, using a comparative approach. Our studies in semi-free ranging olive baboons (*Papio anubis*) show that sampled baboon mothers resume cycling and reconceive when their infants reach a relatively constant threshold mass, as predicted from interspecies life history theory. We suggest that the duration of maternal investment acted as a facultative adjustment to infant growth rates, and depends on the maternal physical and social characteristics (e.g. body mass and social rank). Energetic costs associated with reproduction are surprisingly low in our sample. Energy intake and energy expenditure do not closely predict the time to resumption of cycling. We also find a positive correlation between maternal energy expenditure and infant growth rates. Using the baboon model, this study places these results on infant growth and reproductive energetics into a broader perspective on primate life history, and explores the question of how costly non-human primate infants are. We have divided these expenditures into time and energy costs, investigating each of these during the early phase of growth.

**Keywords** Lactation · Postpartum amenorrhea · Postnatal growth · Maternal investment · Energy balance · Baboon model

**Résumé** Notre recherche a pour objectif de permettre, grâce à une démarche comparative, une meilleure compréhension de la signification adaptative des processus reproductifs chez les femelles primates. Nos études chez le

babouin olive (*Papio anubis*) en semi-liberté montrent que les femelles babouins de notre échantillon reprennent une cyclicité ovarienne et conçoivent à nouveau quand leurs bébés atteignent un poids seuil relativement constant, tel que celui prédit par la théorie d'histoire de vie interspécifique. Nous suggérons que la durée d'investissement maternel agit comme un ajustement facultatif aux taux de croissance du jeune, et dépend des caractéristiques physiques et sociales de la mère (e.g. masse corporelle et rang social). Les coûts énergétiques associés à la reproduction sont étonnamment faibles dans notre échantillon. Les apports alimentaires et la dépense énergétique des femelles ne prédisent pas précisément la durée de blocage de la fonction ovarienne. La dépense énergétique de la mère et les taux de croissance du jeune sont positivement corrélés. En utilisant le modèle babouin, nous replacerons ces résultats sur la croissance du jeune et l'énergétique de la reproduction dans une perspective plus large d'histoire de vie des primates, et nous explorerons la question du coût (temps et énergie) d'un jeune primate non-humain au cours de la phase précoce de croissance.

**Mots clés** Lactation · Aménorrhée du postpartum · Croissance post-natale · Investissement maternel · Bilan énergétique · Modèle babouin

## Introduction

Is reproduction energetically costly, and do these energy costs underlie variations in fertility? In primates with dilute milk and long lactations with regard to body size [1], the interaction of energetics and reproductive rates has remained a subject of considerable debate as to mechanisms, controls and costs [2]. Despite the long-held view that reproduction is a costly activity, there have been only a few studies to date

C. Garcia (✉)  
UPR 2147, CNRS, 44, rue de l'Amiral Mouchez,  
75014 Paris, France  
e-mail : cecile.garcia@cnrs.fr

(i.e. unconstrained primates living in social groups) [3,4]. Anthropologists have long viewed humans and other primates as organisms with particularly high costs allocated to reproduction, due to their large brain size, long periods of infant and juvenile dependence and socially mediated learning. This combination of energy costs (growth to weaning) and time costs (such as the prolonged period to reach first reproduction), has confounded the assessment of reproductive effort in primates.

This paper presents the main results of our studies in semi-free ranging female baboons (i.e. captive but living in social groups) and places those results into a broader perspective on primate life history. As in other organisms, primate life histories can be formalized as strategies for optimizing reproductive effort, or the allocation of resources to reproduction. Necessary constraints on the allocation of resources generate unavoidable trade-offs between the mother's investment in herself and in her offspring, and between finer categories of allocation. Thus, optimization of the reproductive effort can be viewed as the cornerstone of successful life history strategies.

This review explores the question of how costly non-human primate infants are, and aims to highlight the links between energetics and reproduction in female primates, using a comparative approach. Physiological regulation of the reproductive effort is manifested primarily in the allocation of metabolic energy to reproduction. Both the amount of energy allocated and the temporal pattern of allocation have profound consequences for ultimate reproductive success. Baboons are excellent animal models to help understand the energetics of human reproduction: humans and baboons share many female reproductive characteristics such as long ovarian cycles, spontaneous ovulation, extended receptivity and mating periods, long gestation periods, intensive maternal behaviour, suckling "on demand", slow postnatal growth rates and a long period of lactational dependence [1]. The aims of our project were to compare energetics parameters (energy intake, energy expenditure and energy availability) in normally lactating female olive baboons between early lactation and after the resumption of ovarian functions. The key questions addressed here were: a) How costly is lactation among primates? b) What is the role of energy in primate fertility, i.e. the capacity to conceive, gestate, and lactate? c) How do female primates minimise these costs? To answer these questions, we explored the effects of maternal rank, maternal mass, infant growth rates and infant sex on energetic measurements in each period (early lactation vs. resumption of fertility) and on reproductive outcomes. This paper presents a concise review of progress in our understanding of postnatal maternal investment patterns in primates, with the ultimate goal of achieving a better understanding of the evolution of human patterns of maternal investment.

## Material and Methods

### Study subjects and activity budgets

Twenty-three multiparous adult female olive baboons (*Papio anubis*) contributed to the study ( $16.9 \pm 2.0$  kg mass and  $13.9 \pm 2.8$  years of age). These subjects belonged to two social groups housed in semi-free ranging conditions at the CNRS Primatology Station (UPS 846) in France.

Observational data were collected over 2 years (2003-2004) from these twenty-three female baboons. All females with an infant under the age of three months at the beginning of the study were selected as focal subjects, and all females giving birth from January 2003 to July 2003 were subsequently included in the sample. Females and infants were excluded from the study at the second parturition.

The social and demographic histories of these females had been documented since 2001, including reproductive cycles (daily monitoring of the colour and size of sexual swellings) and social interactions. The monitoring data included dates of birth, death and conception, as well as data on maternal age and dominance status (see also [5] for further details). In order to assess the time costs of raising offspring, we examined three different time variables: timing of the resumption of cycling (duration of postpartum amenorrhea, PPA), delay to subsequent conception and the absolute length in days of the interbirth interval (IBI).

Behavioural sampling consisted of focal animal samples of mother-infant dyads [6]. To obtain a representative longitudinal sample across seasons and reproductive stages, all the focal animals were sampled for 1-2 hours in every month of the study. Overall, the data used in the analyses are based on 465 hours of focal animal sampling. During each focal sample (15 min), the mother's activity was recorded by instantaneous point sampling at 1 minute intervals (categories of activity: foraging, moving, resting, grooming, and social interactions).

### Anthropometric measurements

Size and condition: mothers and infants were captured for measurement at two specific points in time: peak lactation ( $78.4 \pm 3.3$  days postpartum on average, range = 74 – 88 days) and after resumption of cycling ( $29.9 \pm 4.3$  days after the end of postpartum amenorrhea, range = 21 – 38 days). In addition, the animals were also measured opportunistically throughout and after the study. As a result, we have longitudinal mass and size data for up to 800 days in age for some subjects.

Overall pattern of growth: infants were weighed and measured at varying ages according to the timing of their mothers's resumption of cycling. All data were initially used to describe growth, with body mass (BM) and crown-

rump length (CRL) as the dependent variables and age as the independent variable (see [7] for further details). Growth rates were calculated from BM and CRL curves as the gain in mass and length between successive ages, and expressed in grams/day and cm/day.

### Energy intake assessment and energy expenditure measurements

We followed a sub-sample of eight females for this purpose. Females were assessed twice: at the end of the first month postpartum ( $43.0 \pm 8.1$  days postpartum), and at the end of lactational amenorrhea during the second menstrual cycle ( $59.0 \pm 18.0$  days after resumption of cycling).

**Energy intake:** major energy intake of the female subjects was monitored via focal animal samples. For each doubly labelled water experiment (see below), each female was observed during feeding time and to determine their activity budgets during each 24 hour period of energy assessment. Food consumption was based on one day of observation per female and per period. Energy intake (EI) calculated from counts of pellets and fruit or vegetable intake were used with digestibility and caloric values and extrapolated to represent energy intake over a 24-hour period (MJ/day).

**Energy expenditure measurement by the isotopic method:** 24-hour total energy expenditure (TEE) was determined over a 4-day period by the two-point doubly labelled water (DLW) method described by Schoeller et al. [8] (see [9] for further details). The samples were analyzed for hydrogen ( $^2\text{H}/^1\text{H}$ ) and oxygen isotope ratios ( $^{18}\text{O}/^{16}\text{O}$ ) by isotope ratio mass spectrometry at the *Centre d'Ecologie et de Physiologie Energétiques* (Strasbourg, France). TEE is presented as MJ/day. EI minus TEE represented Energy Availability (EA). We compared our measurements of TEE with measurements of the resting metabolic rate (RMR) using Leonard and Robertson's [10] anthropoid-interspecies equation for determining RMR. We also explored the difference between measured TEE and the daily energy expenditure (DEE) as predicted by Leonard and Robertson's [10] interspecies equation. DEE approximates mass-specific, non-reproductive energy expenditure over that of resting, and the ratio of TEE to DEE is used as potentially indicative of the costs of reproduction over and above those due to average activities.

## Results and discussion

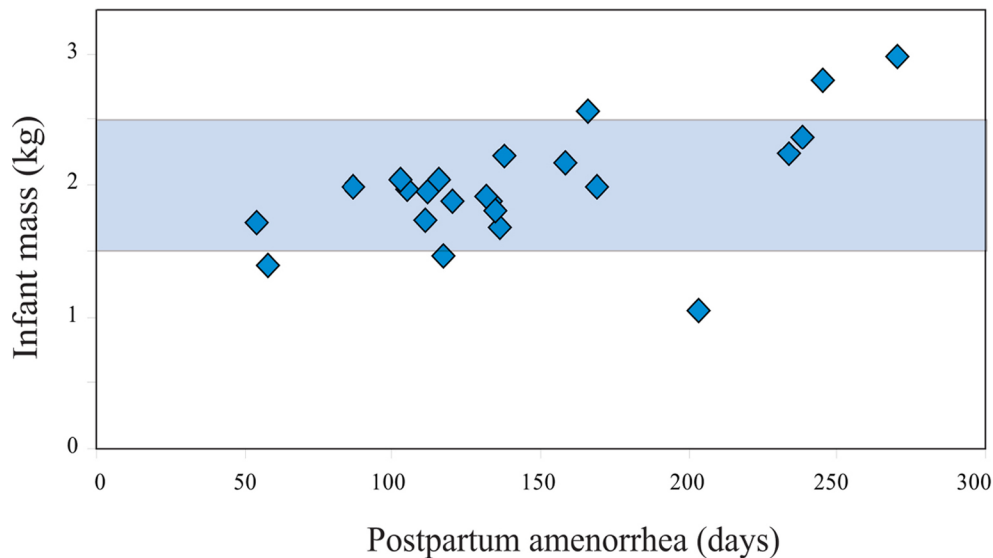
### Time costs

We found that female dominance rank was related to several reproductive parameters (i.e. waiting time to conception, gestation length and total interbirth interval), with high-ranking females having shorter reproductive intervals and

higher fertility [5,11]. Rank was also associated to some degree with the duration of postpartum amenorrhea and cycling phase duration, as seen in many captive and wild primates [12,13]. This could be due to the fact that high-ranking females have more energy available to invest in their infants' growth or protection, or that they are more embedded in a social network, as suggested by Silk et al. [14], which then provides them with helpers. Maternal rank had more influence on investment strategies than the sex of offspring, and this rank interacted with infant sex. Low-ranking females rearing a daughter had the longest duration of postpartum amenorrhea, suggesting that it was more difficult for subordinate mothers to sustain a daughter's growth to the threshold that allowed the resumption of cycling.

We also found that the duration of postpartum amenorrhea was variable (range = 54–270 days), but that infant mass at weaning (i.e. after the end of PPA) seems to be constrained. For both sexes, mothers resumed cycling when their infants weighed close to 2 kg, and 3 kg for subsequent conception. The similarity between infant mass, regardless of sex and maternal characteristics, both at the end of PPA and at conception, suggested that infants either needed to attain a threshold mass (Fig. 1) or some ratio of maternal mass. Studies on a range of primate and non-primate species suggest that infants need to reach a threshold weight of around 3–4 times their birth weight before they can be weaned, or for maternal fertility to resume, regardless of the time needed to reach this mass [15,16]. In our study, infant body mass at subsequent conception (3 kg) represents the expected increase of 3–4 times the average mass of newborn baboons, of around 0.8 kg [17], as previously reported in captive rhesus macaques [16]. While a threshold mass was apparent, the time taken to reach this threshold varied four-fold (from 110 to 475 days). Therefore, prolonging the investment period appeared to be mainly a compensatory mechanism to reach this threshold mass.

Overall, we showed that IBI was strongly associated with infant growth to PPA and with maternal rank and infant sex (see [7]). Slower infant growth up to the end of PPA was associated with a longer IBI, and low-ranking females had a longer IBI for the same infant growth rates. We also found that male infants had a faster growth rate for a similar IBI and that mothers of sons of all ranks had a longer IBI than did mothers of daughters. Low-ranking mothers of sons had the longest investment period overall. Sons thus seemed to cost more in terms of total time invested and in terms of growth rate during a reproductive event. The only consistent pattern that emerges from our data and from other studies on fertility rates [18,19] is that a high maternal dominance rank positively impacts fitness components, regardless of the sex of the previous infant. However, the question of how mothers partition their investment between sons and daughters remains open.



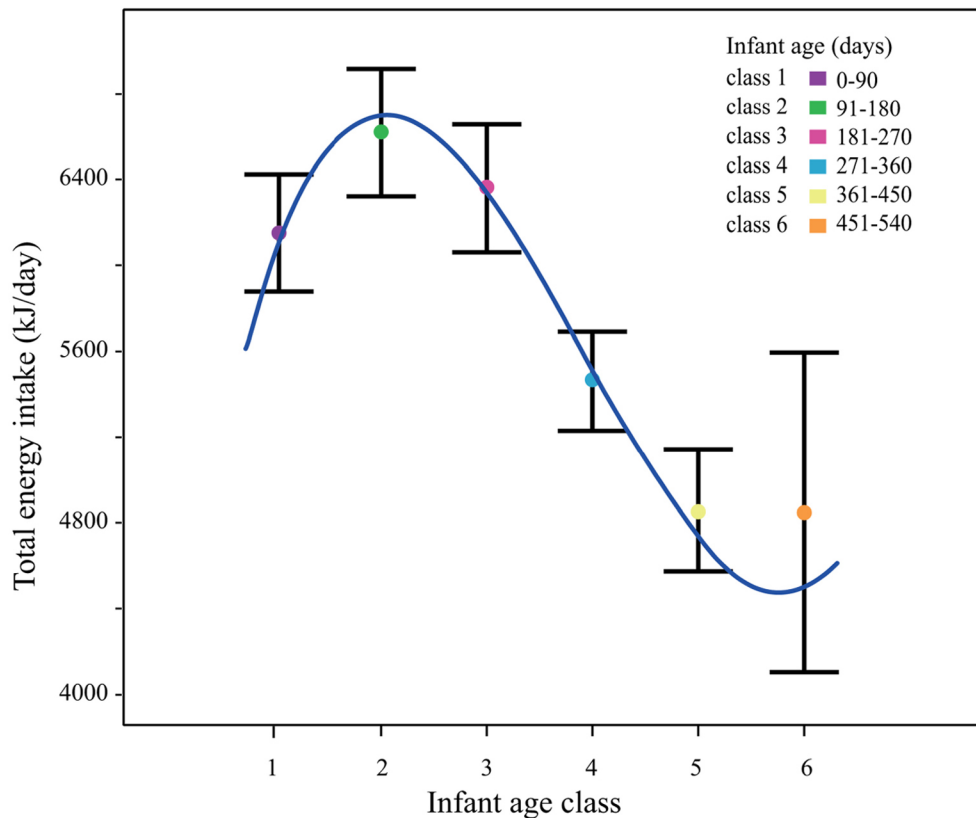
**Fig. 1** Infant mass at the end of postpartum amenorrhea in female olive baboons. The threshold mass of ca. 2.0 kg (range = 1.5 - 2.5 kg) is indicated by the coloured area. Adapted from Garcia et al. [5] / *Masse du bébé à la fin de l'aménorrhée du post-partum chez des femelles babouins olive. La masse seuil de ca. 2.0 kg (dispersion = 1.5 - 2.5 kg) est indiquée par l'aire colorée. Adapté de Garcia et al. [5]*

### Energy costs

Besides time costs, infant primates also have a cost in terms of energy, both direct (carrying, lactation, protection) and indirect ("teaching", social maintenance, route learning, etc.). The energy cost of lactation is assumed to be above and beyond the needs of the non-reproductive state. We showed that the energetic costs of early lactation obtained by doubly labelled water techniques for female baboons represent 1.2 times the normal active daily energy requirements or 1.5 times the resting metabolic requirements [9], which is very similar to the costs of early lactation reported in humans [20]. Our captive female baboons therefore had relatively low energy costs associated with peak lactation. Mothers cope with reproductive costs, and especially lactational costs, through flexible behavioural strategies, for example through changes in the time spent foraging, in physical activity levels and possibly in time spent socializing. Detailed measurements of energy intakes during early to peak lactation (up to 270 days) showed that female baboons increased their energy intake and met the small (30-50% increase) additional energy costs of infant care through subtle adjustments in intake (Fig. 2). These findings are similar to those recently reported in other studies that estimated maternal feeding time in orangutans, and thus average mean intake, at only 20%-25% higher than for an adult female with no dependent offspring [21]; the values for baboons vary from 0% to 57% depending on methods and habitat or living conditions [see 21]. Human lactation requires an increase in food intake of only ca. 15%-30%, varying among indivi-

duals and populations [22], partly due to differences in the activity level of mothers and their chronic nutritional status. These increases are quite modest compared to other mammals, which can increase their intake by 2-4 times during the period of maximum lactation [23]. We also showed that mothers did not move significantly less during early lactation to save energy, but seemed instead to change the time spent in social interactions [24]. Therefore, it appears that both human and non-human primates tend to increase their overall energy intake to meet part of the cost of lactation, but use other strategies like relying on tissue stores, reducing their physical activity and/or changing their time budget to meet the remainder of the costs. Nevertheless, the potential for female primates and women to change their level of activity is dependent on their environmental context, with some females being able to do so and others not. It is also clear from the data available for primates that females in different populations may use a different combination of strategies to meet the costs of lactation, and that the way humans and non-human primates meet the energy costs of lactation varies to some degree between populations and between individuals within the same population [25].

We also found that energy intake during early lactation was negatively correlated with interbirth intervals (i.e. females with a higher energy intake were those with the shortest interbirth interval), but was unrelated to the number of cycles until conception once cycling had resumed. Similarly, despite our prediction that energy expenditure would relate to fertility, in baboon mothers it did not closely predict the time to resumption of cycling. We found a positive



**Fig. 2** Non-linear relationship between maternal energy intake (kJ/day) and infant age / *Relation non-linéaire entre les apports énergétiques maternels et l'âge du bébé*

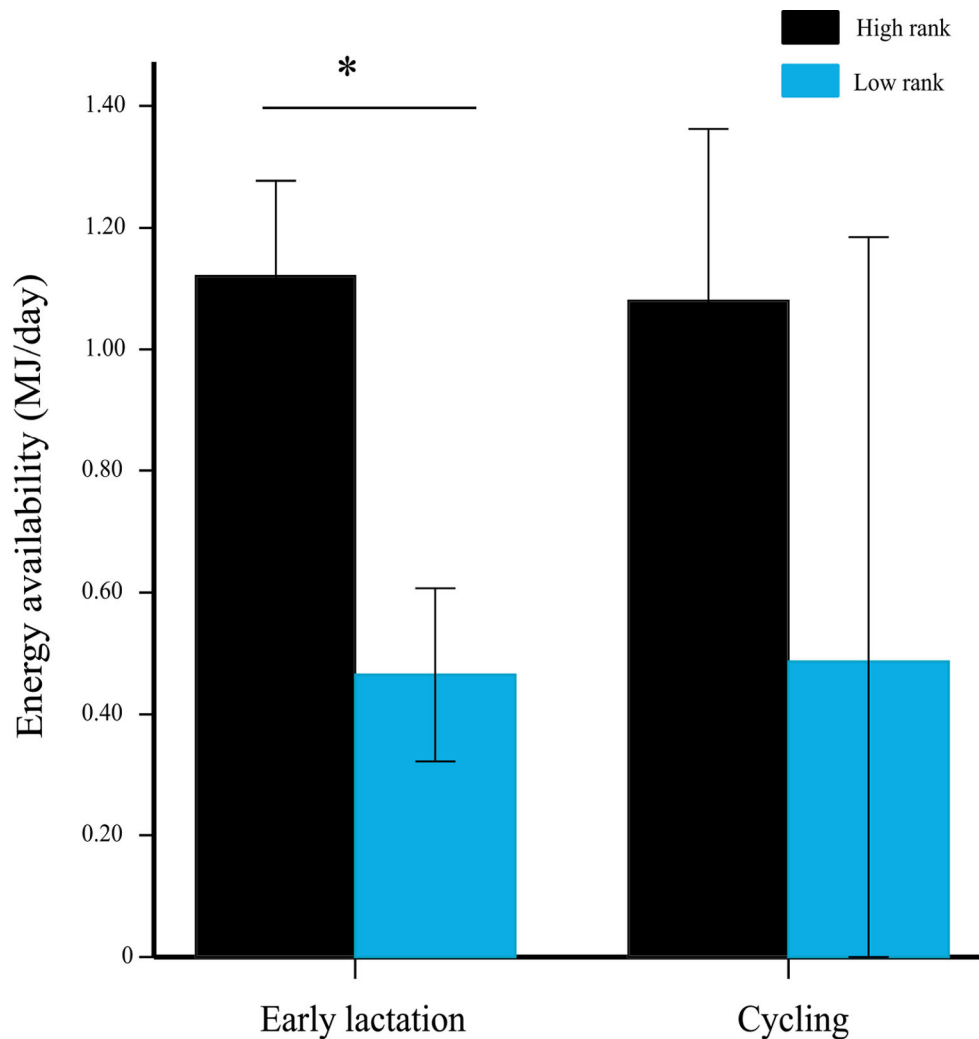
relationship between maternal energy expenditure and infant growth rates, i.e. mothers with rapidly growing babies had a higher energy expenditure than did those with slowly growing babies. Energy availability (intake minus expenditure) varied by dominance rank during early lactation (Fig. 3), with dominant females having greater energy availability than subordinates. As a consequence of their lower energy availability, low-ranking females in our captive context experienced a longer duration of postpartum amenorrhea even though energy expenditure after resumption of cycling did not differ between dominant and subordinate females. These results concur with previous studies in humans and non-human primates showing that postpartum resumption of the ovarian function appears to be determined by the availability of metabolic energy to support the allocation of effort to a new pregnancy. This availability is in turn determined both by the level of allocation to milk production and by the energy condition of the mother [26].

As in humans [27], energy availability in baboons can be modelled as a non-linear relationship interacting with social status, infant growth, lactation stage and fertility (see also Rosetta et al's model [9] based on Valeggia and Ellison's original model for humans [27]). There is a drop in the energy balance during the period of early to peak lactation,

and an increase in the energy balance and body condition associated with resumption of cycling. Whether there is a threshold duration for maintaining a positive energy balance prior to resumption of cycling in large mammals such as baboons remains to be empirically determined, but managing the energy balance appears to be fundamental to the regulation of primate fertility.

## Conclusions

For primates in general, and especially large-bodied primates including humans, the estimated daily cost of lactation is relatively low because postnatal growth is comparatively prolonged and breast milk is relatively dilute in composition. This suggests that primates have more flexibility in meeting the energy costs of lactation than other mammals of similar size. Physiological, behavioural and social mechanisms influence the reproductive function in primates, suggesting that unless females are at the extremes of their capacity for energy intake, various alternatives can compensate for the costs of infant care. It seems that primates, including humans, have optimized a strategy of fine-tuning their care-giving behaviour within a social and supportive context



**Fig. 3** Relationship between energy availability (MJ/day) and social rank during early lactation and at resumption of cycling. Bars show the mean and standard error of the mean. (High rank,  $N = 4$ ; low rank,  $N = 4$ ). Adapted from Rosetta et al. [9] / *Relation entre la disponibilité énergétique (MJ/jour) et le rang social en début de lactation et à la reprise de la cyclicité ovarienne. Les barres montrent la moyenne et l'erreur standard de la moyenne. (Haut rang,  $N = 4$ ; bas rang,  $N = 4$ ). Adapté de Rosetta et al. [9]*

as an evolved life history strategy, rather than simply trading off time and energy with respect to reproductive output. More research on non-human primates, especially in the wild, is nevertheless needed to place human reproductive energetics in a comparative light, and more emphasis is required on the scope and importance of inter-individual variability in meeting the energy costs of reproduction.

**Acknowledgments** I would like to thank Gilles Berillon and Guillaume Daver for the organization of the Symposium on “Primates non-humains : bilan des recherches et perspectives anthropobiologiques”, 1838 èmes Journées de la Société d’Anthropologie de Paris. Thanks to our collaborators Phyllis C. Lee and Lyliane Rosetta, to Guy Dubreuil (Director) and to the staff of the Primatology Station at Rousset-sur-Arc

(France) for their technical assistance, and to the Department of Ecology, Physiology and Ethology of the Hubert Curien Multidisciplinary Institute, (Strasbourg, France) for the isotope analyses. Funding: CNRS grant to Lyliane Rosetta (GDR 2655).

## References

1. Martin RD (2007) The evolution of human reproduction: A primate perspective. *Am J Phys Anthropol* 134(S45):59–84
2. Key C, Ross C (1999) Sex differences in energy expenditure in non-human primates. *Proc R Soc Lond B* 266:2479–85
3. Emery Thompson M, Wrangham RW (2008) Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *Am J Phys Anthropol* 135(2):171–81

4. Simmen B, Bayart F, Rasamimanana H, et al (2010) Total energy expenditure and body composition in two free-living sympatric lemurs. *PLoS One* 5:e9860
5. Garcia C, Lee PC, Rosetta L (2006) Dominance and reproductive rates in captive female olive baboons (*Papio anubis*). *Am J Phys Anthropol* 131(1):64–72
6. Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–67
7. Garcia C, Lee PC, Rosetta L (2009) Growth in colony living anubis baboon infants and its relationship with maternal energetics and reproductive status. *Am J Phys Anthropol* 138(2):123–35
8. Schoeller DA, Ravussin E, Schutz Y, et al (1986) Energy expenditure by doubly labeled water: validation in humans and proposed calculation. *Am J Physiol* 250:R823–30
9. Rosetta L, Lee PC, Garcia C (2011) Energetics during reproduction: a doubly labeled water study of lactating baboons. *Am J Phys Anthropol* 144:661–8
10. Leonard WR, Robertson ML (1997) Comparative primate energetics and hominid evolution. *Am J Phys Anthropol* 102:265–81
11. Garcia C, Lee PC, Rosetta L (2008) Impact of social environment on variation in menstrual cycle length in captive female olive baboons (*Papio anubis*). *Reproduction* 135:89–97
12. Wasser SK, Norton GW, Rhine RJ, et al (1998) Ageing and social rank effects on the reproductive system of free-ranging yellow baboons (*Papio cynocephalus*) at Mikumi National Park, Tanzania. *Hum Reprod Update* 4:430–38
13. Setchell JM, Wickings EJ (2004) Social and seasonal influences on the reproductive cycle in female mandrills (*Mandrillus sphinx*). *Am J Phys Anthropol* 125:73–84
14. Silk JB, Beehner JC, Bergman TJ, et al (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc Biol Sci* 276:3099–104
15. Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. *J Zool (Lond)* 225:99–114
16. Bowman JE, Lee PC (1995) Growth and threshold weaning weights among captive rhesus macaques. *Am J Phys Anthropol* 96:159–75
17. Lee PC (1999) Comparative ecology of postnatal growth and weaning among haplorhine primates. In: Lee PC (ed) *Comparative primate socioecology*. Cambridge University Press, Cambridge, pp 111–36
18. Wasser SK, Norton GW, Kleindorfer S, et al (2004) Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons (*Papio cynocephalus*). *Behav Ecol Sociobiol* 56:338–45
19. Cheney DL, Seyfarth RM, Fischer J, et al (2006) Reproduction, mortality and female reproductive success in Chacma baboons of the Okavango Delta, Botswana. In: Swedell L, Leigh SR (eds) *Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives*. Springer, New York, pp 147–76
20. Rosetta L, Kurpad A, Mascie-Taylor CGN, et al (2005) Total energy expenditure ( $H_2^{18}O$ ), physical activity level, and milk output of lactating rural Bangladeshi tea workers and non-tea workers. *Eur J Clin Nutr* 59:632–8
21. van Noordwijk MA, Kuzawa C, van Schaik CP (2013) The evolution of the patterning of human lactation: a comparative perspective. *Evol Anthropol* 22:202–12
22. Butte NF, King JC (2005) Energy requirements during pregnancy and lactation. *Public Health Nutr* 8:1010–27
23. Speakman JR (2008) The physiological costs of reproduction in small mammals. *Philos Trans R Soc* 363:375–98
24. Garcia C (2005) *Energétique et régulation de la fonction de reproduction chez des femelles captives babouins olive (Papio anubis)*. Ph.D. dissertation, Université d'Aix-Marseille II, France.
25. Dufour DL, Sauter ML (2002) Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *Am J Hum Biol* 14:584–602
26. Ellison PT (2003) Energetics and reproductive effort. *Am J Hum Biol* 15:342–51
27. Valeggia C, Ellison PT (2004) Lactational amenorrhoea in well-nourished Toba women of Formosa, Argentina. *J Biosoc Sci* 36:573–95