CHAPTER 11

The ecology of female reproduction in wild orangutans

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11.1 Introduction to reproductive ecology

Energetics has shaped the life histories and behavior of apes. Orangutans, in particular, display adaptations that indicate a need to manage energy availability, such as a large body with enhanced storage of body fat (Wheatley 1982), a dispersed social system with frequent solitary foraging (Rijksen 1978), and the use of tools to access high-fat fruits (van Schaik and Knott 2001). Reproduction appears to be particularly energetically costly in orangutans, which give birth in the wild, on average, only once every 7–9 years—the longest interbirth interval of any mammal (Galdikas and Wood 1990; Wich *et al.* 2004b). However, as reflected in this volume, geographic separation and resulting genetic divergence between the two orangutan species have produced genetic, morphological, and behavioral differences (Groves *et al.* 1992; Xu and Arnason 1996; Uchida 1998a; Groves 2001; Warren *et al.* 2001) that may relate to the differing ecologies of orangutan habitats on Borneo and Sumatra.

In this chapter, we review the role of energy availability in the reproduction of apes, including humans. Then, we specifically examine the case of orangutans, detailing available evidence on how reproduction is influenced by the ecology and life history of these two species. Within this context we explore the mechanisms by which energetics might influence reproduction. We make recommendations for future research that will allow more thorough investigation of orangutan reproductive ecology and suggest several new hypotheses for investigation. Our review will focus on the models and mechanisms of energetic influence on reproduction in apes, with attention to the type of data that is needed to examine this phenomenon effectively in orangutans. Because data from orangutans are very limited in this area, one of our aims is to explain the theoretical background and provide research findings from other apes and humans to help guide future studies of orangutan reproductive ecology.

11.1.1 Overview of energetics and reproduction

Reproductive success depends on the appropriate allocation of energy among the burdens of somatic growth, maintenance, and reproduction (Gadgil and Bossert 1970). This trade-off is particularly exaggerated in mammalian species that face a long period of obligate lactation to ensure infant survival. As a general rule, energy is limited, and food resources are subject to substantial competition. Thus, strategies that allow mammalian females to reproduce successfully in the face of limited energetic resources are key products of natural selection. However, there are a variety of ways for animals to cope with the energetic demands of reproduction in changing environments. Selection of a low-quality, consistent food resource, such as leaves or piths, is one means of avoiding this problem (cf, mountain gorillas). Other animals may translate energy availability into adjustments in the size and number of offspring in their litters (e.g., *Leontopithecus rosalia*, Dietz *et al.* 1994). Some species, particularly those in which mating opportunities are limited, sustain a high rate of preterm abortion when nutritional status is low (e.g., *Eumetopius jubatus*, Pitcher *et al.* 1998). Commonly, when ecological conditions become very poor, females cease reproductive cycles entirely (Schneider and Wade 2000); delaying reproduction in such a manner can ultimately increase reproductive success by reducing the energy invested in failed reproductive efforts and subsequently investing in reproduction when conditions are once again favorable (Wasser and Barash 1983).

Many primates deal with periodic energy shortages by reproducing seasonally. Seasonal breeding may be most appropriate for relatively low investment species that are capable of completing the cycle from conception to weaning within a year (Lindburg 1987). Seasonal breeding should be most likely to occur if food abundance is highly variable, as is usually the case for species that rely on high quality resources. For example, in a seasonal rainforest in Brazil, frugivorous muriquis (*Brachyteles arachnoids hypoxanthus*) have strong birth seasonality while sympatric, folivorous brown howler monkeys (*Alouatta fusca clamitans*), who experience fewer fluctuations in their food supply, do not (Strier *et al.* 2001). Seasonal breeding is feasible in an environment with predictable periods of food abundance (van Schaik and van Noordwijk 1985a). Thus, the onset of the breeding season in primates often cues not to energy intake itself but to correlates of annual food availability, such as photoperiod, temperature, or rainfall (Daly and Wilson 1983; Lindburg 1987; Ganzhorn *et al.* 2003). Generally, however, mating seasons are timed so that the most expensive or fragile phases of the reproductive process—lactation and/or weaning—occur during periods of high food availability (Nash 1983; Lindburg 1987). For example, patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) in the same habitat give birth in different seasons, though each is timed so that births occur during the time of highest energy availability for that species (Nakagawa 2000).

Some primate species, those facing relatively long reproductive efforts and unpredictable availability of high-quality foods, show a contrasting pattern: they conceive during periods of peak food availability and maternal condition. This appears to be the case for muriquis (Strier 1996; Strier *et al.* 2003), Hanuman langurs (*Presbytis entellus*, Koenig *et al.* 1997), and long-tailed macaques (*Macaca fascicularis*, van Schaik and van Noordwijk 1985a). As we review in the next section, the concordance of conception with periods of high food availability is particularly characteristic of the apes (Knott 1999a, 2001; Emery Thompson 2005a; Anderson *et al.* 2006; Emery Thompson and Wrangham 2008) including humans (Ellison 1990, 1991, 2003; Ellison *et al.* 1993).

11.1.2 The ecology of reproduction in the great apes

The great apes are long-lived species with long-term, often lifetime, investment in their offspring. These species evolved in the tropics where food availability often fluctuates in unpredictable ways. Thus timing birth to correspond to a period of high food availability may not be possible in these non-seasonal breeders. Maternal condition seems to be more important in determining the probability of conception during a given period. Effects of energetic condition on reproduction can be seen within and between populations, as well as across species.

Several studies of apes support the role of variation in energy availability as a key determinant of reproductive timing. Populations of both orangutans and chimpanzees have been shown to have increased ovarian function and to be more likely to conceive during, or just after, seasons of high fruit abundance (Knott 1999a, 2001; Emery Thompson 2005; Emery Thompson and Wrangham 2008). Although chimpanzees are not seasonal breeders, the number of sexually receptive females (i.e., females with sexual swellings) varies with the availability of high-quality foods in both Eastern and Western subspecies of chimpanzee (Emery Thompson 2005; Anderson *et al.* 2006; Emery Thompson and Wrangham 2008). Additionally, in chimpanzees, competitive access to preferred foods is a significant predictor of reproduction across individuals. At Gombe National Park, high-ranking females have increased reproductive success, including higher birth rates and faster-maturing daughters (Pusey *et al.* 1997). This may be mediated by preferential access to fruit-rich core areas (Williams *et al.* 2002), as has been demonstrated for females in Kanyawara, where females ranging in higher-quality areas have increased ovarian function, shorter interbirth intervals, and improved infant survivorship (Emery Thompson *et al.* 2007).

Population comparisons illustrate that energetics predict reproductive rates in many ape populations. Captive apes, with consistent availability of high-quality food and relatively low energy expenditure, typically mature earlier and reproduce at substantially faster rates than semi-free ranging or wild members of the same species (Tutin 1994; Knott 2001; Brewer-Marsden *et al.* 2006; Anderson *et al.* 2008; Table 11.1). Wild orangutans (Knott 1999a) and chimpanzees (Emery Thompson 2005) produce significantly lower levels of ovarian hormones during their menstrual cycles than do their captive counterparts. Populations of chimpanzees with more consistent fruit availability have comparatively higher ovarian function and shorter interbirth intervals (Emery Thompson 2005; Emery Thompson *et al.* 2006).

Cross-species comparisons of ape energetics are particularly important for understanding the evolutionary heritage of human reproductive ecology (Knott 2001, 2005). Among great apes in the wild, mountain gorillas have short interbirth intervals (approximately 4 years), while chimpanzees and orangutans have the longest interbirth intervals (approximately 6 years and 6–9 years, respectively) (Knott 2001; Wich *et al.* 2004b; Table 12.1). This reflects the constraints of their feeding ecology: while

Table 11.1 Reproductive parameters of wild and captive orangutans. Means are given, followed by medians in parentheses. Ranges and sample sizes, when available, are provided in parentheses below (*n* is the number of samples or intervals and *f* is the number of females)

Site	Age at menarche (years)	First sexual behavior (years)	First mating (years)	Adolescent subfecundity (years)	Age at first birth (years)	Interbirth interval (years)	Postpartum amenorrhoea (years)	Waiting time to conception (months)
Captive								
–Bornean	–	–	–	–	15.5[2] (n = 246)	6.3 (5.3)[2,d] (n = 135)	–	–
–Sumatran	–	–	–	–	16.4[2] (n = 284)	5.8 (4.4)[2,d] (n = 149)	–	–
Captive Overall	7.7 (7.6)[3,11,12,a,d] (4.5–11.1, n = 8)	5.5–9[3,10]		0.8 (0.6)[3,11,a,b] (0.6–1.2, n = 3)	15.9	6.0	4.7[11] (n = 1)	1–10[9, 11] (n = 2)
Borneo								
–Tanjung Puting		10–11[6,f] (n = 1)	–	1?–4[6,c,f] (n = 2)	15.7 (16.0)[15] (15–16, n = 3)	7.7 (7.7)[7,3,d] (5.2–10.4, n = 23, f = 11)	6+[4]	10.3 (2)[4,5,d] (1–28, n = 3, f = 3)
–Gunung Palung	–	12.5[8,f] (n = 1)	13.9[8,f] (n = 1)	1.3[8,c,f] (n = 1)	14.5[8,f] (n = 1)	7.2 (7.1)[8,d] (7.1–7.4, n = 8, f = 6)	4.6 (4.5)[8,g] (3.0–6.3, n = 3, f = 3)	1.7 (2.4)[8,h] (1.0–2.4, n = 2, f = 2)
–Kinabatangan	–	–	–	–	–	6.5[1]	–	–
–Kutai	–	–	–	–	–	6.1[14]	–	–
–Borneo overall	–	11.5	13.9	1.7	15.1	6.9	5.3	6.0
Sumatra								
–Ketambe	–	–	–	5[13,c] (n = 1)	15.4[16,f] (13–18, n = 7)	9.3[16,d] (6.4 – 11.6, n = 19, f = 7)	–	–
–Suaq	–	–	–	–	–	(8.2)[17,d,e,f] (7–9, n = 15, f = 15)	5–6[17,g] (n = 7, f = 7)	3.9[17, h] (n = 7, f = 7)
–Sumatra overall	–	–	–	5	15.4	8.8	5–6	3.9
Wild overall	–	11.5	13.9	2.8	15.2	7.5	5.4	5.3

[1] Ancrenaz, unpublished data in Chapter 5; [2] Anderson *et al.* 2008; [3] Asano 1967; [4] Galdikas 1980; [5] Galdikas 1981; [6] Galdikas 1995; [7] Galdikas and Wood 1990; [8] Knott data; [9] Lippert 1974; [10] Lippert 1977; [11] Markham 1990; [12] Markham, 1995; [13] Schürmann and van Hooff 1986; [14] Suzuki, unpublished data in Wich *et al.* 2004b and Chapter 5 this volume; [15] Tilson *et al.* 1993; [16] Wich *et al.* 2004b; [17] van Noordwijk and van Schaik 2005;

[a] The mean and median were calculated by pooling all the original raw data from multiple studies; [b] period between first menstruation and conception; [c] period between first copulation and conception; [d] computed using a Kaplan–Meier analysis from censored and completed intervals; [e] no complete intervals; [f] some or all of data based on estimated ages; [g] period between birth and resumption of regular mating activity; [h] period between resumption of regular mating activity and conception.

mountain gorillas primarily consume low quality but consistently and abundantly available foods like terrestrial herbaceous vegetation, chimpanzees and orangutans rely on higher-quality fruit that is sporadically available. Similarly, the longer interbirth intervals of orangutans compared to chimpanzees may be related to more highly variable nutritional intake in orangutans as compared to chimpanzees (Conklin-Brittain *et al.* 2006). Bonobos, whose feeding ecology is intermediate between gorillas and chimpanzees—that is, they consume fruits when available but supplement their diet with abundant vegetation—also have birth intervals that are intermediate (approximately 5 years) (Knott 2001, 2005; de Lathouwers and van Elsacker 2005). These differences in feeding ecology may impact the species response to changes in energy availability. For instance, while orangutans and chimpanzees experience a significant decrease in interbirth interval under captive conditions (Knott 2001; Anderson *et al.* in 2008), bonobos and gorillas do not, suggesting that they reproduce near their physiological capacity in the wild (Tutin 1994; de Lathouwers and van Elsacker 2005).

11.1.3 The ecology of reproduction in humans

Reproductive ecology is perhaps best studied and understood in humans. A wide range of natural and controlled experiments by human reproductive ecologists have demonstrated the effects of energy intake and energy expenditure on reproductive function in women. These studies have focused on the assessment of ovarian hormone production during the menstrual cycle. Relative production of estrogen and/or progesterone is correlated with ovarian follicle size (Eissa *et al.* 1986), probability of fertilization (Yoshimura and Wallach 1987), and success of implantation (Lenton *et al.* 1988; Akman *et al.* 2002), with increased ovarian function (i.e., higher hormonal indices) being strongly associated with conception success (Lipson and Ellison 1996; Lu *et al.* 1999).

Ellison (1990, 1991; Fig. 11.1) has shown conceptually how the relationship between energetic stress and ovarian hormones is best viewed as a continuum rather than an 'on/off' switch. At one end are fully functional and fecundable cycles associated with low energetic stress and high hormonal levels. At the other end is the cessation of reproductive functioning, associated with high energetic stress and low ovarian hormone production. In between are graded levels of ovarian responsiveness to a continuous scale of variation in energetics. Detailed studies of humans, both in controlled studies and in natural settings, have shown how various types of energetic stress result in this ovarian responsiveness.

Both energy intake and energetic expenditure have been recognized as important influences on

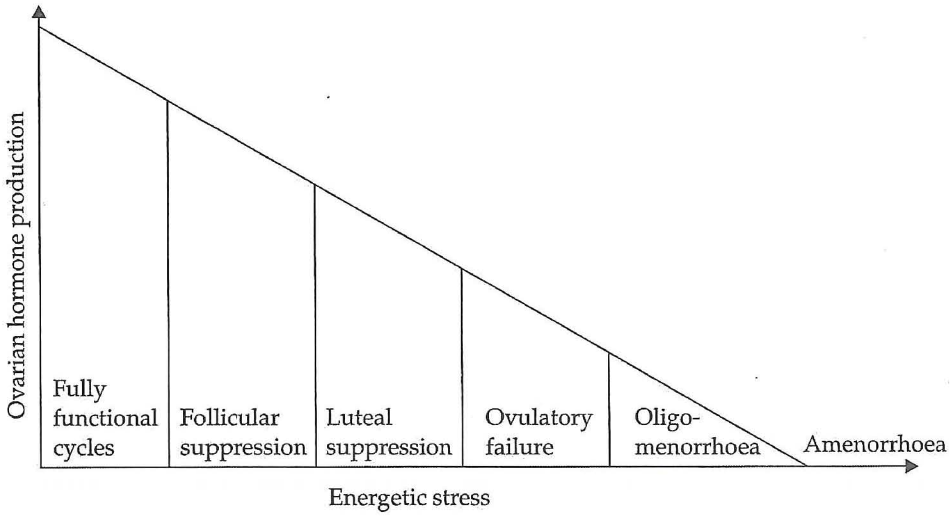

Figure 11.1 The continuum of ovarian function, as proposed by Ellison (1990, 1991).

ovarian function. For example, in a groundbreaking study of the effects of exercise on reproduction, Bullen *et al.* (1985) subjected university students to a rigorous running and exercise regime for 5 weeks, feeding half of the subjects sufficient calories for weight maintenance and allowing the others to lose approximately 2 kilograms. Subjects in both treatments experienced decreased ovarian function, although effects were exacerbated in the weight loss group. Most significantly, many of the subjects experienced luteal phase deficiencies and absence of the mid-cycle surge in luteinizing hormone (essential for ovulation), although they did not exhibit clinically recognized menstrual disturbance, defined as absence of menses. This study (Bullen *et al.* 1985) suggested that both negative energy balance and high energy expenditure, independent of weight loss, could alter human ovarian function. Researchers later demonstrated that declines in progesterone could be observed in recreational runners experiencing more moderate levels of energy expenditure (Ellison and Lager 1986; de Souza *et al.* 2003).

Similar effects have been demonstrated by studies of women living under natural conditions of periodic energy shortages and subsistence workloads. Women in developing populations produce less progesterone than American women (Ellison *et al.* 1989, 1993). Within a population of Lese horticulturalists in Zaire, progesterone levels were reduced even more during periods of seasonal weight loss and in women of the lowest nutritional status (Ellison *et al.* 1989). Similarly, Nepalese women who lost weight during the heavy work period of the monsoon experienced a decrease in progesterone levels (Panter-Brick *et al.* 1993; Panter-Brick 1997). In addition, a study of Polish women found that high workload alone, even without weight loss, could lower ovarian function (Jasienska and Ellison 1998, 2004).

Most studies of energetics and reproduction in humans have focused on cycling women. However, there is strong evidence that energy availability has a significant influence on other aspects of reproduction, such as the timing of menarche (Ellison 1981; Hill and Hurtado 1996), duration of lactational amenorrhea (Valeggia and Ellison 2001, 2004), the timing of parturition (Ellison 2001), and even the later health of the child (Ellison and Barrett 2004; Ellison 2005).

11.2 Interpopulation comparison of orangutan reproductive ecology

11.2.1 Ovarian cycles

Hormonal levels in cycling females show a strong link to energy balance in at least one of the orangutan species, *Pongo pygmaeus*, as illustrated in a comprehensive study of energetics and reproductive function in the Bornean orangutans at Gunung Palung National Park (Knott 1998a, 1999a, 2001). This study period encompassed a masting event in which a large percentage of orangutan fruit trees simultaneously fruited over a 3-month period; this boom in energy availability occurs rarely, approximately once every 2–10 years, and can be followed by intense fruit scarcity (van Schaik 1986; Ashton *et al.* 1988). During the mast, the orangutan diet consisted of nearly 100% fruit and the caloric intake of male and female orangutans was more than doubled in comparison with the non-mast period (Knott 1998a). This change in energy availability resulted in a profound effect on reproduction. During the period of positive energy balance females produced significantly higher levels of estrogens (Knott 1999a). Following the mast, hormone levels declined significantly, and, despite lower activity levels, orangutans excreted urinary ketones, indicating that their accumulated fat reserves were being burned to compensate for lower energy availability in the environment (Knott 1998a). Ovarian hormone production has not been studied in other wild populations of orangutans.

11.2.2 Timing of conception

At Gunung Palung, high orangutan food availability and positive energy balance were also correlated with higher conception rates (Knott 1999a), leading to birth clusters in 1995 and again in 2002. Similarly, data from Suaq Balimbing in Sumatra shows significant birth peaks with 8 of 10 births occurring in 1996 and 6 of 13 juveniles estimated to have been born in 1988 (Singleton and van Schaik 2002; van Noordwijk and van Schaik 2005). These data strongly suggest synchrony of reproduction with ecology, although this has not been tested directly. In contrast, a study of *P. abelii* in Ketambe found that conception timing was not correlated to phenological measures of fruit availability (Wich *et al.* 2006b). As we will discuss in the next section, there are a number of possible interpretations for this latter finding. First, it is possible that the increased sensitivity of the reproductive system to fluctuations in energy quality is a derived feature of Bornean orangutans, while the genetically distinct Sumatran orangutans have not faced sufficient evolutionary pressures for such an adaptation, although the finding from Suaq would argue against this. Second, it is feasible that such a system is common to the two species, but that energy fluctuations in Ketambe are not substantive enough to produce significant reproductive variation over time. Third, overall forest fruit production in Ketambe may not be tightly correlated with individual energy intake, thus a possible relationship between energetics and reproduction may be obscured.

11.2.3 Interbirth intervals

As discussed above, variation in the length of the interbirth interval has also been shown to be linked to energetic variation in other hominoids and is thus a variable of interest for orangutan reproductive ecology (Table 11.1). The Bornean population, with the most extensive data set, Tanjung Puting, (12 complete and 11 incomplete intervals from 11 females) reports a mean inter-birth interval of 7.7 years (Galdikas and Wood 1990), whereas the Sumatran population with the most data, Ketambe, (16 complete and 7 incomplete intervals from 9 females) reports a mean interbirth interval (IBI) of 9.3 years (Wich *et al.* 2004b). Smaller data sets exist for the other sites, but tend in the same direction of longer interbirth intervals in Sumatra. Suaq Balimbing in Sumatra reports an IBI of 8.2 years (Singleton and van Schaik 2002). Eight interbirth intervals from Gunung Palung suggest a preliminary IBI of about 7.2 years (Kaplan–Meier analysis of 2 complete and 6 censored intervals). Very small samples from populations in Eastern Borneo suggest they may have the shortest IBIs: 6.1 years at Kutai (Suzuki *et al.*, Chapter 5) and 6.5 years at Kinabatangan (Ancrenaz in Wich *et al.*, Chapter 5). Life history datasets from wild orangutans are very limited, making it difficult to assess whether these differences are biologically significant, as well as whether population or species is a better predictor of IBI.

There is also preliminary empirical support for a habitat difference between key study sites on each island. Sumatran orangutans spend more time consuming fruit and insects, while Bornean orangutans spend more time consuming low-quality foods like the cambium bark layer (Delgado and van Schaik 2000; Fox *et al.* 2004, see also Chapter 8). Sumatran orangutans at Ketambe experience fewer fluctuations in fruit availability over time than is reported for Bornean orangutans (Wich *et al.* 2006a, b); this seems to result in fewer periods of negative energy balance, as evidenced by the relative lack of ketone-positive urine detected in the Sumatran population at Ketambe (Wich *et al.* 2006a) versus the Bornean population at Gunung Palung (Knott 1998a). Finally, female Sumatran orangutans are more gregarious than the mostly solitary Bornean orangutans, fitting the socio-ecological prediction that when food resources are more abundant or distributed in larger patches orangutans should become more social (Delgado and van Schaik 2000). These factors suggest that energy is more readily available on the island of Sumatra, a finding consistent with the rich volcanic soils found on this island (Delgado and van Schaik 2000).

This ecological comparison coupled with what we know about ape reproductive ecology predicts shorter interbirth intervals in Sumatran orangutans because their more productive habitat should lead to increased reproductive output. As reviewed above, this Ecological Energetics Hypothesis (Knott 2001, 2005) is in line with studies of other apes that show that within populations, and apparently between closely related species, increasing energy availability increases reproductive rates. Thus, the data showing longer interbirth intervals for orangutans in Sumatra than in Borneo is puzzling and presents an intriguing paradox.

Wich *et al.* (2004b) have proposed the Ecological Life History hypothesis to explain this paradox. They propose that more consistent energy availability and lower mortality on the island of Sumatra has led to a decrease in the pace of the life history of the orangutans who live there. This hypothesis follows the general logic of life history differences between apes and other primates, or between primates and other mammals (Charnov 1991; Charnov and Berrigan 1993). Given low extrinsic mortality pressure, animals can grow slower and larger and reproduce at a slower rate. The slower rate of reproduction might at first seem maladaptive, but it allows for more intensive investment in each offspring (the so-called offspring quality–quantity trade-off), perhaps the best means of ensuring success in such an environment.

Figure 11.2 compares these two models and shows the contrasting long- and short-term strategies for energy allocation. While our focus here is on reproductive rates, other life history variables, such as age of maturity, age of first birth, and longevity, should show correlated responses for each model.

11.2.4 Other reproductive parameters

Other reproductive parameters that may be influenced by energetics include age at menarche, age at first sexual behavior, age at first mating, the length of adolescent subfecundity, age at first birth, the length of postpartum amenorrhea, and the waiting time to conception (Table 11.1). These data (Table 11.1) are extremely limited in the wild, and sample sizes are too small to test for any species differences. Most female ages are only estimates and uneven and inconsistent sampling of individuals likely leads to missing data. However, the much richer dataset on captive orangutans do show significantly earlier ages at puberty and first birth compared to their wild counterparts (Knott 2001). This is in concordance with the general pattern we see in other animals of an increase in reproductive output with the increased food availability/ decreased energy expenditure experienced in captivity.

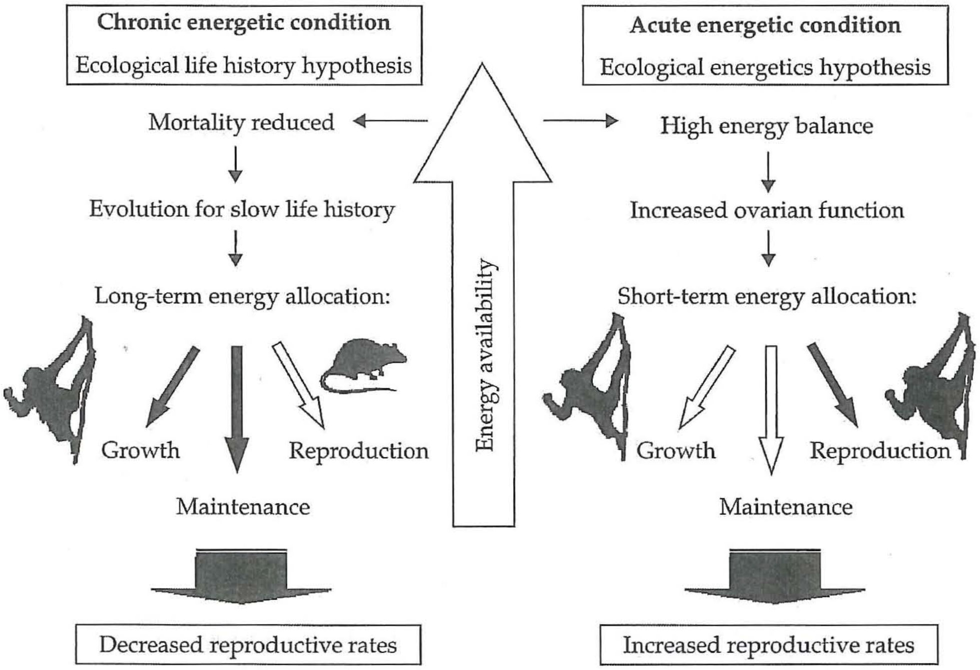

Figure 11.2 Two potential energy allocation models for predicting species variation in reproductive life history in orangutans. In the long term, species with chronically higher energetic condition are selected for 'slow' life histories, in which energy allocation to somatic growth and maintenance take precedence over reproductive output (cf. the Ecological Life History hypothesis, Wich *et al.* [2004b]). The alternative model proposes that over an individual's lifespan, surplus energy is utilized to increase reproductive output (cf. the Ecological Energetics hypothesis, Knott [2001]).

One potential test of the Ecological Life History Model can be conducted by comparing captive Bornean and Sumatran orangutans. This comparison would suggest whether there are differences in life history features that are independent of the proximate influence on energetics. An examination of this evidence (Anderson *et al.* 2008; see Chapter 5) shows no consistent difference in life history between these two orangutan species in captivity, suggesting that there may not be genetic life history differences. However, it should be noted that the reproduction of captive animals is manipulated by their handlers, thus variables such as the age at menarche and age at first sexual behavior may be more accurate indicators of unmanipulated ovarian activity. Therefore, the ideal test would come from a detailed comparative study of reproductive ecology in wild orangutan populations experiencing different ecological conditions. Below we suggest further data and hypotheses that may help to resolve this dilemma.

11.3 Refining our measures of orangutan reproductive ecology: suggestions for future research and new hypotheses

Despite the ample data to connect energetic condition with reproductive function in apes, proximate mechanisms for this relationship are not well understood in any species. What energetic signal is most highly correlated with ovarian function in orangutans? The data on comparative orangutan reproductive ecology is limited at this stage. In this section we describe ways that reproduction, especially ovarian function, may be influenced by energetics in orangutans and other hominoids, and suggest how future research programs may incorporate these elements to more fully elucidate the interaction between reproduction and local ecology in this and other species.

The results of any study of *reproductive ecology* are largely dependent on how precisely these two variables—reproductive functioning and ecology—are measured, as well as the way in which the interaction between the two is assessed. Exploratory studies of the relationship between ecology and reproduction typically employ correlations, for instance between monthly fruit availability and conception rates. For a number of reasons, such correlational studies often fail to reveal these relationships. Below we discuss how using precise methods of data collection and transformation will allow us to more thoroughly examine the relationships between reproductive functioning and ecology.

11.4 Measuring reproductive function

11.4.1 Ovarian function

What is the most precise way to measure the *reproductive* part of reproductive ecology? As reviewed earlier, ovarian function has proven to be a useful predictor of fecundability (the probability of conception in a particular cycle) in orangutans and other species. This sensitive measure can allow us to assess the influence of energetics on orangutan fecundity along a gradient from fully fecund cycles that have a high probability of being fertilizable to complete amenorrhea. Thus, where possible, hormonal monitoring can assess ovarian function to give a fine-grained measure of reproductive function, in addition to allowing diagnosis of conception and pregnancy loss and more accurate determination of the reproductive variables presented in Table 11.1.

An example of the value of ovarian hormone measurement is in determining when orangutan females are cycling. There is no reliable behavioral measure of the resumption of ovarian activity following birth. Although nursing mothers copulate rarely, copulations can occur as early as 6 months postpartum (van Noordwijk and van Schaik 2005), thus resumption of any mating activity is likely not a reliable indicator of resumption of ovarian activity. Van Noordwijk and van Schaik (2005) use 'a major increase in the frequency of copulations' as an indicator that ovarian activity has returned following a birth. Clearly, hormonal data could more accurately pinpoint the resumption of ovarian activity as many mating events are likely to be missed.

Regular monitoring of ovarian function across orangutan sites may help us answer key questions: how long do females cycle before they conceive?

How does this vary? In periods of low food availability, is reproduction fully suppressed, or is there lowered production of hormones in line with the continuum of ovarian function described by Ellison (2003)? Are females conceiving more than we recognize but having early pregnancy losses? How do female energetics and fecundity influence mating patterns? Regular hormonal monitoring will allow us to answer these questions. This is particularly important in orangutans, which do not have the visible indicator of cycle quality provided by the sexual swellings of *Pan* (Emery and Whitten 2003; Deschner *et al.* 2004).

11.4.2 Conception

In the absence of hormonal data, the likely date of conception can be calculated from known birth dates and then correlated with environmental variables to test for a relationship between reproductive functioning and ecology. However, the rarity of births in wild orangutans means that very few events are spread over long periods of fluctuating food usage. The data require precise knowledge of when an infant is born, which is often not possible in orangutan studies where individuals may not be followed for months at a time; for the same reason, pregnancies and even births may not be observed. Thus, determining the day or even month of conception necessarily involves some uncertainty. Without knowledge of the number and reproductive condition of all females in a population, it is difficult to make comparisons of ecology between conception periods and months in which researchers are unaware of a conception.

11.4.3 Lactational amenorrhea and the lengths of inter-birth intervals

Orangutans lactate throughout all or most of their long interbirth intervals. Presumably during much of this period they are in a state of lactational amenorrhea. However, the relationship between suckling frequency, maternal energetic status, and ovarian function in orangutans is not understood. Recent work suggests that maternal energetic status, in addition to suckling frequency, is an important predictor of the resumption of ovarian function during lactation in humans (Valeggia and Ellison 2001, 2004). Observations in the field (Knott, personal observation) suggest this may be true in orangutans as well because mothers often do not appear to be cycling despite low rates of suckling in older offspring. Regular hormonal monitoring in conjunction with records of lactation frequency and duration will help us address this question. It may be that variability in the length of lactation is a key determinant of differences in interbirth intervals found between orangutan populations. If so, we must ask what ecological correlates, such as weaning foods, lead to variation in nursing intensity?

An additional consideration for such an analysis is that the long period of lactational amenorrhea in orangutans limits the number of females who could conceive during a period of food abundance. An appropriate analysis of ecological effects on reproduction would evaluate the proportion of non-lactating females that conceived during a good fruiting period.

The long interbirth interval should also be considered when we evaluate reproductive data from relatively short study periods. Stochastic ecological variation and impacts of habitat disturbance could lead to spurious comparisons. For example, mast fruiting events occur at unpredictable intervals (Ashton 1988). Birth interval data from a population that had recently experienced short intermasting intervals might be expected to differ from those in a population which recently experienced long intermasting intervals, leading to interbirth interval differences that would not be borne out by more extensive long-term data.

Further, because birth intervals are so long, it is difficult to obtain adequate sample sizes of complete intervals. For example, in computing Suaq interbirth intervals, van Noordwijk and van Schaik (2005) used estimated ages for six of the juveniles that formed one end of an interbirth interval, and no complete intervals occurred during the study. Additionally, many individuals in orangutan study populations may be absent for months at a time, confounding our ability to accurately assess whether a birth and subsequent infant death occurred during the period of absence.

11.5 Measuring ecology

11.5.1 Energy intake

Ecology refers to the interaction between an organism and its environment. In reproductive ecology we are referring to the energetic condition of the animal—a condition which is largely derived from its ecological context. The energetic condition of an animal includes both positive inputs to the system (energy intake) as well as outputs (energy expenditure, Fig. 11.3). The sum of these two variables is energy balance, which can be increasing (gaining weight), decreasing (losing weight), or neutral (weight maintenance). In some species, humans in particular, changes in body weight can be easily measured by simply using a scale. However, in most species of wild primates measurement of body weight is difficult to impossible and typically involves artificial manipulation of energy balance (i.e., provisioning). Even in captive situations assessment of body weight is usually only done when the animal is anesthetized, although more sophisticated set-ups to weigh alert animals do exist.

11.5.2 Food availability

One of the most commonly used proxy measures of energy intake is food availability, with the assumption being that these two variables should be correlated. Food availability is usually assessed through phenological surveys which are also important for understanding general habitat fluctuations as well as food preferences in relation to availability. However, such surveys may not reflect the *actual* energy intake of the individuals being studied. This is due to several methodological problems.

First, phenology is typically assessed once, or perhaps twice, per month but is used as an indicator of fruit availability across the entire month. Dramatic shifts in fruit availability may occur on a much shorter timeframe and thus monthly assessments may not be reflective of the actual food availability at the time an individual animal was followed. The calendar month is, of course, an artificial timeframe and it may be more appropriate in some cases to analyse data in terms of the fruiting season. In chimpanzees, where feeding may be predominantly on one fruit during certain seasons,

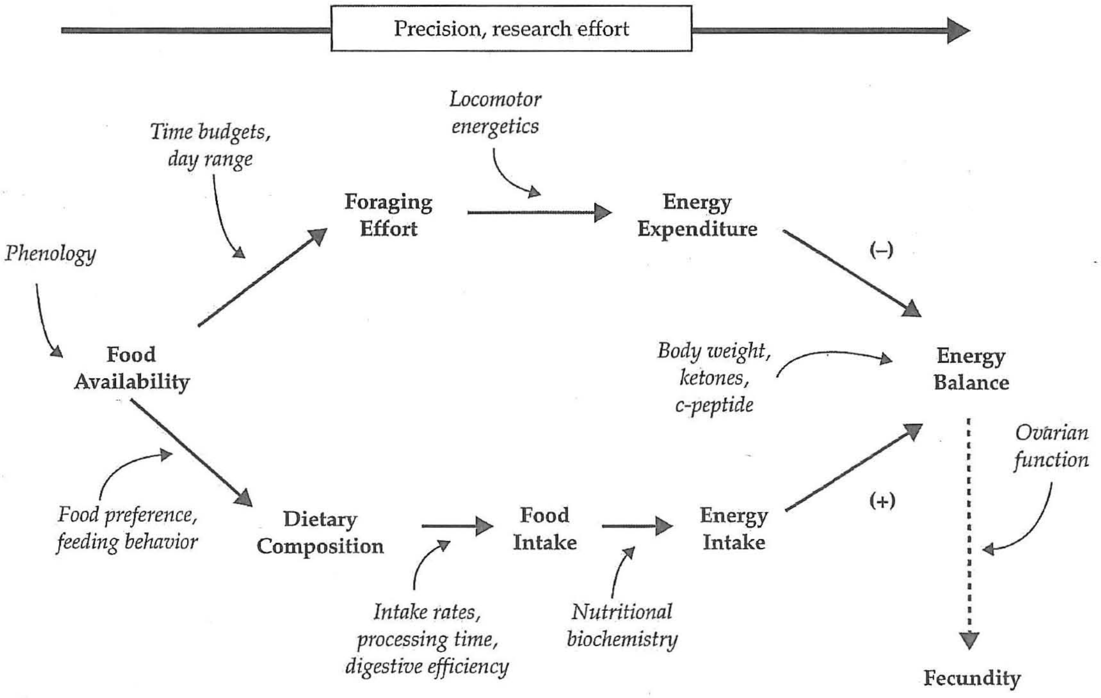

Figure 11.3 Methods (italics) for assessment of energetic variables (bold) on fecundity (the probability of conception) used in reproductive ecology. Increasing research effort leads to greater precision.

this has been done effectively (Emery Thompson and Wrangham 2008; Gilby and Wrangham 2007). This also avoids the problem of pseudoreplication where contiguous months of high food availability are incorrectly treated as independent units.

Second, what is the proper unit of analysis? Is it overall fruit production—a measure which may include many species that orangutans do not eat—or is it just the availability of fruits actually eaten by orangutans, or the availability of just preferred orangutan fruits? Each of these measures may produce different results, yet phenological trails are typically set up with broad goals of monitoring general habitat fluctuations. We would argue that if phenological measurements are to be relied on, they should as closely as possible reflect the availability of the foods that orangutans actually eat.

Third, while fruit availability may be correlated with intake, it often only explains a small part of the variation in dietary intake. For example, the first available data comparing habitat fluctuations to reproductive events in Sumatran orangutans was derived from long-term data for Ketambe (Wich *et al.* 2006b). In this dataset, forest-wide phenological data were continuously available from 1980. The authors found that forest fruit productivity in this habitat was not significantly linked to reproductive events, nor to variation in party sizes (Wich *et al.* 2006b). However, during periods of intensive study, researchers also collected continuous data on the feeding behavior of focal animals. From these data, we can derive estimates of dietary composition for comparison to phenology. Ripe fruit availability was a significant predictor of ripe fruit consumption, suggesting that phenology is a good predictor of orangutan diet. However, the phenological measure explained only a small fraction of the variation in ripe fruit in the orangutan diet ($r^2 = 0.080$, df = 93, $p = 0.006$). Future studies at Ketambe are planned to include more intensive dietary examination to confirm or reject the hypothesis for variation in energetic responsiveness between orangutan species.

At Gunung Palung, Knott (1998a, 1999a) also found a strong correlation between availability of orangutan fruits, energetics, and ovarian function. However, the relationship did not always hold. For example, during an extended period of low fruit availability orangutans experienced one month of high energy intake, despite the overall low availability of orangutan foods, because they were eating *Neesia* seeds—a very high-energy food (Knott 1998a; van Schaik and Knott, 2001). Thus, knowledge of the nutritional quality of the foods ingested may help us understand deviations from the expected relationships.

11.5.3 Dietary composition

Dietary composition, separated out by plant type, often provides a closer approximation of energy intake than does food availability. Generally, fruit is higher in calories and preferred by apes, while lower-quality bark and leaves serve as fallback foods (Knott 2005; Marshall and Wrangham 2007). Thus, minutes spent eating fruit versus other food categories can provide a rough indication of diet quality, particularly where fruits are available sporadically. Knott (1999a) has shown a strong positive relationship between orangutan fruit consumption and food availability and a strong negative relationship between food availability and bark and leaf consumption.

However, we also must recognize that fruit species vary considerably in nutritional content, as well as processing time and ease of digestion—variables that may create additional variance in our assessments of energetic condition. One simple comparison is the distinction between fig and non-fig (typically, drupe) fruits. Figs are not technically fruits but packages of tiny flowers; they are typically lower in caloric value than are true fruits (Conklin and Wrangham 1994). Apes, including orangutans, are heavily reliant on figs in many habitats (Wrangham *et al.* 1993; O'Brien *et al.* 1998). Fig trees are common in mature secondary forest growth, fruit more regularly than many drupe species, and can be incredibly productive, which makes them a desirable intermediate fallback for apes in many habitats (Marshall and Wrangham 2007). For instance, in the Kanyawara range in Kibale National Park (Uganda), chimpanzees have access to figs during the majority of the year, although they prefer to eat seasonal drupe fruits when available (Wrangham *et al.* 1996; Emery Thompson and Wrangham 2008). Thus, chimpanzee ovarian function in this population increases significantly during periods of high drupe fruit consumption but not during periods of high fig consumption (Emery Thompson 2005; Emery Thompson and Wrangham 2008).

Fruit type might also be important in understanding differences in orangutan feeding preferences and reproductive ecology between populations. For instance, the Ketambe orangutan site is generally considered to be a habitat with stable fruit availability, although orangutans here still show a strong preference for non-fig fruits, as illustrated by the strong inverse correlation between fig and non-fig fruit consumption (Spearman's $r = -0.838$, $n = 136$, $p < 0.001$).

11.5.4 Nutrient and caloric intake

These broad considerations of diet variability bring us closer to understanding the energy intake of apes, although there may still be considerable variability in the quality of non-fig fruits. For example, Knott (1998a) has shown that during the mast period in Gunung Palung fruits eaten by orangutans were not only more abundant but were significantly more calorically dense than the fruits available during non-mast periods. Thus, during two periods an orangutan may have the same percentage of non-fig fruit in the diet, but during one period their energy intake may be significantly higher because the fruits available then are higher in calories.

Ideally, energy intake should be measured as kilocalories (kcals) or kilojoules consumed. This can be calculated for each feeding bout by multiplying data on intake rate (food items/minute), mean grams/food item, mean kcals/gram of the food item, and the percentage of each food item eaten (i.e., animals may only eat a portion of each fruit they feed on) (Knott 1998a; Conklin-Brittain *et al.* 2006). This produces a measure of kcals consumed/feeding bout. These feeding bout measures are then summed over the day to produce an estimate of kcals consumed/day. Data on full days are preferred as using a partial day measure, such as the rate of energy intake/hour, may not accurately reflect total energy intake because total time spent feeding per day can vary dramatically between food availability periods (Knott 1998a).

Clearly, the precision of data on energy intake depends on the conditions of the field site and the amount of research effort that can be devoted to this task, which can be considerable. We would ideally have continuous data on food availability, representative nutritional and morphometric analyses of orangutan fruits, and detailed behavioral analyses of intake rates and processing times, in order to understand the variance of energy availability for orangutans. Collaborative studies are being conducted to accomplish this labour-intensive task (Vogel *et al.* personal communication). In the absence of such detailed information, we suggest careful collection of data (continuous or point sampling) on dietary composition and calculation of percentage fruit and non-fig fruit constituents of the monthly diet.

11.5.5 Energy expenditure

The opposite side of the energetic equation is energy expenditure. This can be computed in a variety of ways. The most common method is to use time allocation profiles, i.e. examining the percentage of the day, or the total minutes, a group or an individual spends in different activities. Another more detailed method is to combine these time allocation profiles with estimates of the kilocalories expended for each activity to estimate total energy expenditure (Coelho 1976; van Schaik and van Noordwijk 1985a; Coelho 1986; Altmann and Samuels 1992; Nakagawa 2000). Time spent locomoting has been shown to have the greatest impact on variance in energy expenditure in orangutans and other apes (Knott 1999a; Pontzer and Wrangham 2004) and thus this measure alone may provide a fairly precise measure of changes in the level of energy expenditure.

Obtaining some measure of energy expenditure can be quite important, as the relationships between energy intake and expenditure are not always consistent. For example, in most ape populations time spent traveling actually increases during periods of high food availability (Knott 2005); however, this is not the case when the period of high energy intake is due to geographically restricted species such as lipid-rich nuts, e.g., Taï chimpanzees (Doran 1997; Boesch and Boesch-Achermann 2000) or large fig crops, e.g., orangutans (Sugardjito *et al.* 1987; Utami *et al.* 1997). Additionally, body size and reproductive status (i.e. pregnant, lactating or cycling) are extremely important contributors to energy expenditure, potentially resulting in large variation between individuals, and thus must be taken into consideration.

11.5.6 Energy balance

Energy balance is the integrated signal from the environment reflecting whether the animal is gaining weight (intake exceeds expenditure), losing weight (expenditure exceeds intake) or maintaining weight. In the wild, where weighing individuals is not possible, energy balance can be computed from detailed measurements like those described above. Knott (1999a), for example, combined detailed data on energy intake (kcals of intake/day) with computed estimates of energy expenditure (kcals expended/day) to calculate energy balance. These data showed that orangutans at Gunung Palung experienced periods of positive and negative energy balance which were well correlated with fruit availability, intake, and hormonal levels.

Another means to evaluate energetic deficit is to use urinalysis strips to assess ketone bodies in urine. Ketones are produced as a byproduct of fatty acid metabolism, and their excretion in urine is diagnostic of extreme carbohydrate shortage. Knott (1998a) showed that during a period of extreme negative energy balance, orangutans at Gunung Palung excreted ketones in their urine. Urinalysis strips can be used to detect a period of extreme energy depletion but they do not appear to be very sensitive to mid-range variation in energy balance (Kelly *et al.* 2004; Emery Thompson 2005) and are only indicative of *negative* energy balance.

A promising new advance is the non-invasive measurement of C-peptide—an indicator of insulin levels. Insulin, a hormonal product of the pancreas, is chiefly responsible for regulating energy metabolism and is hypothesized to be the key hormone involved in transmitting information about energy balance to the ovaries (Ellison 2001). The presence of insulin in the blood is generally indicative of energy available for short- or long-term storage. *In vitro*, large doses of insulin have been shown to enhance aromatase activity, allowing greater oestradiol production (Garzo and Dorrington 1984). Physiological levels of insulin augment estrogen and progesterone production by normal ovarian cells *in vitro* both directly and by enhancing the stimulatory effect of leutenizing hormone (LH) (Greisen *et al.* 1996; Willis *et al.* 1996). In a natural experiment that demonstrates the interrelationships of insulin, energetics, and ovarian function, recreational runners who experienced luteal phase deficiencies were found to have significantly lower insulin levels than those who did not; insulin levels did not differ significantly between sedentary women and runners with normal cycles (de Souza *et al.* 2003).

During the production of insulin in the pancreas, a protein called connecting-peptide (or C-peptide) is cleaved from the pro-insulin molecule. Unlike insulin itself, C-peptide does not undergo additional metabolism or transformation but is excreted into the urine, providing a more accurate measure of the amount of insulin produced by the pancreas (Polonksy *et al.* 1986). Thus, non-invasively collected urine samples may be used for the assessment of energy balance in addition to ovarian hormone levels. In a validating study of human females, increases in urinary C-peptide levels (representing increases in surplus energy) were closely tied to the resumption of cycling in women after birth and lactational amenorrhea (Valeggia and Ellison 2004). Preliminary examinations with apes indicated that serum C-peptide correlates well with urinary C-peptide and broad shifts in dietary quality were reflected in C-peptide levels (Sherry and Ellison 2007). Our data from wild orangutans suggest that C-peptide is well-correlated with behavioral measures of caloric consumption in orangutans at Gunung Palung (Fig. 11.4, Emery Thompson and Knott 2008). This is thus a promising new tool for the assessment of energy balance in wild orangutans and other animals.

11.5.7 Energy flux

In addition to energy balance, energy flux has been identified as an important influence on ovarian

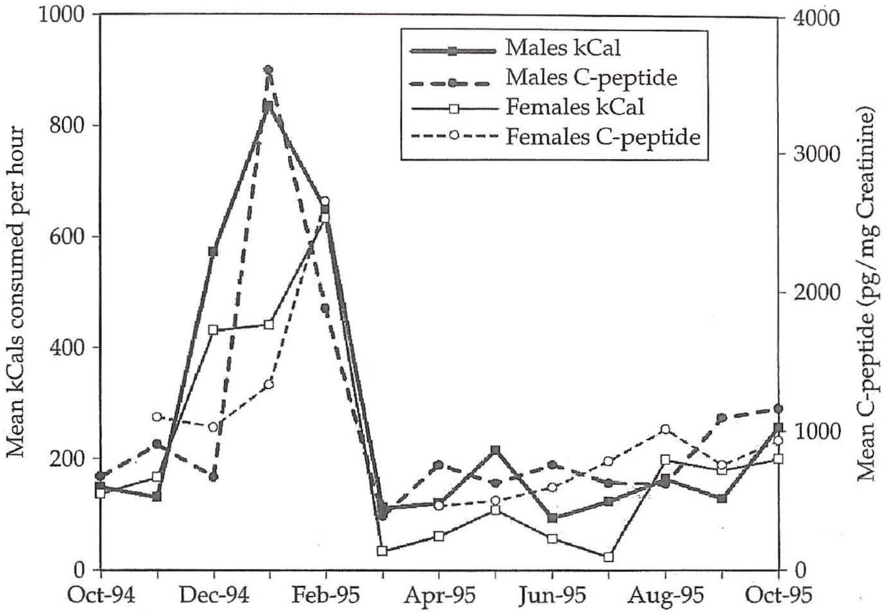

Figure 11.4 Energy intake determinations for Gunung Palung orangutans (Knott 1999a) compared with urinary C-peptide concentrations.

function in humans (Jasienska and Ellison 1993, 1998; Jasienska 2003). Energy flux is the rate of flow of energy through the system—or the magnitude of energy fluctuations during the day. A sedentary individual who consumes 1500 kcal/day and expends 1500 kcal/day would be in neutral energy balance but low energy flux. By contrast, a Tour de France racer who consumes 8000 calories/day and expends 8000 calories a day would be in neutral energy balance but high energy flux. Although energy balance and energy flux are frequently linked, where they can be distinguished, high flux (independent of energy balance) has a negative effect on ovarian function in humans (Jasienska and Ellison 1993, 1998; Jasienska 2003). The relative importance of energy flux versus energy balance in orangutans is unknown but could be assessed using the above methods.

11.6 Interactions between reproduction and energetics

11.6.1 Acute vs cumulative effects of energy on ovarian function

The final component in studying the reproductive ecology of any species is determining, based on theoretical and empirical reasoning, how to test for relationships between reproduction and energetics. For example, we must consider *why* it is hypothesized that apes have evolved reproductive adaptations to ecology. This hypothesis is based on the prediction that females will reproduce not just when they achieve positive energy balance, but when energy intake and/or storage are sufficiently high to make it feasible to invest in a reproductive effort. Thus, we might expect conceptions to occur as the result of *successive* months of high energy availability.

Indeed, in humans, the impact of energy deficit on ovarian function is rapid but not immediate; ovarian function is typically impacted in the subsequent menstrual cycle after weight loss (Bullen *et al.* 1985). Similarly, in chimpanzees, conceptions occur in the months that *follow* the months of highest fruit availability (Emery Thompson 2005; Emery Thompson and Wrangham 2008). In chimpanzees from two ecologically divergent populations, Emery Thompson (2005b) and Emery Thompson and Wrangham (2008) found that the length of the period from cycle resumption to conception was significantly reduced when mean dietary quality over that period was high; this cumulative effect explained considerably more of the variance in conception timing than immediate energy availability.

Functionally, this may mean that the menstrual cycle's trajectory is largely set out from the beginning—indeed, in chimpanzees (Emery and Whitten 2003) and humans (Lipson and Ellison 1996) we see strong correlations between early cycle parameters and the development of the entire menstrual cycle. In practice, this means that we must carefully consider that the energetic and hormonal milieu of mating, the hallmark by which wild primate cycles are typically defined, may be influenced by events occurring several weeks earlier.

11.6.2 Magnitude of the shift in energy intake

Many orangutan populations experience mast fruiting events that are novel features to consider in understanding the energetics of reproduction. In some habitats, these masting events create rather dramatic feast-or-famine conditions that may affect the metabolic–reproductive signaling systems, even in contradiction to the smoothing cumulative effects described in the previous section. When we use energy intake rates and nutritional biochemistry to examine and compare energetic fluctuations in Bornean orangutans at Gunung Palung National Park to those of chimpanzees at Kibale National Park (considered a relatively seasonal chimpanzee habitat) we see a markedly different pattern of energy shifts (Fig. 11.5, Conklin-Brittain *et al.* 2000). The Bornean masts create dramatic shifts in caloric consumption that dwarf the energy fluctuations experienced by chimpanzees. Thus, we might hypothesize that orangutan populations that habitually experience these types of fluctuations may have adapted to respond quickly to large-scale shifts in energy intake (a trigger rather than a valve). These energetic fluctuations experienced by orangutans may be similar to the feast-or-famine conditions experienced by some human populations (typically demonstrated by changes in body weight) (Prentice and Prentice 1988).

The fruit abundance of the masting period lasts approximately 3 months and is very likely to be immediately followed by habitat-wide fruit scarcity lasting 6 months or longer (Knott 1999a), thus the optimal reproductive strategy would incorporate a means of hedging against such a poor period. If a female conceived at the beginning of a masting event, she would theoretically have the opportunity to store additional energy during the

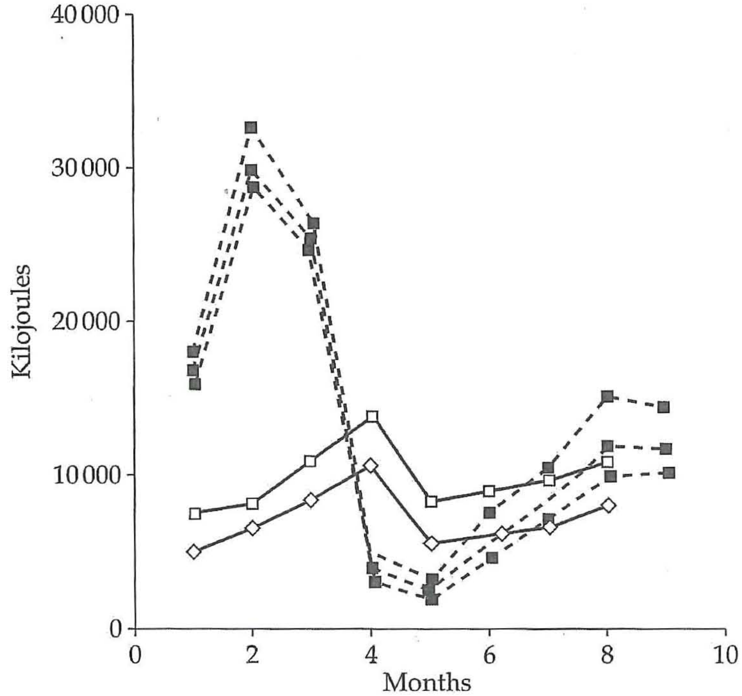

Figure 11.5 Range of energy intake of female orangutans (*/Pongo pygmaeus/*, dotted lines) at Gunung Palung National Park compared to female chimpanzees (*/Pan troglodytes schweinfurthii/*, solid lines) at Kibale National Park over successive study months based on nutritional and behavioral analyses. Multiple lines indicate estimates based on a range of digestibility values (0–6.7 kJ/g) for fibre. Modified from Conklin-Brittain *et al.* (2004).

early part of pregnancy. This stored energy could be used during the predicted crash in fruit availability, after the pregnancy had been established but before the more pressing energetic demands of lactation.

Thus, the condition of orangutans being exposed to periods of dramatic differences in energy availability raises the possibility of another energetic axis to consider: the magnitude or swiftness of the change between high and low energy periods. Switching between a relatively low to high period of energy intake/energy balance may be a potent catalyst for increased ovarian function. This has not been directly studied in orangutans (or any other species) but Knott's (1999a) study indicated that conceptions may, in fact, have occurred toward the beginning of the period of increasing energy intake rather than at the peak.

This hypothesis presents a means of distinguishing orangutan species, as well. Phenological evidence suggests that mast fruitings are rarer and of less magnitude in Sumatra compared to Borneo (Wich and van Schaik 2000) and indeed the peat-swamp forests, where many orangutans now live, are typically non-masting. If the magnitude of the shift in energy intake is an important trigger of ovarian function this may account for some of the population differences in features such as the interbirth interval. These differences could be genetic, or all populations of orangutans may have this capacity, but those that live in non-masting forests may not experience this trigger.

11.6.3 Developmental effects

Emerging evidence in humans suggests that early developmental effects may cause profound effects later in life (Barker 1998). One surprising finding is that the condition of gestation may actually predict later ovarian function. Jasienska *et al.* (2006) found that newborns with a high ponderal index (an index, similar to body mass index, indicating relative fatness) had higher estrogen levels as adult women. Furthermore, their estrogen levels were more buffered to energetic expenditure than the estrogen levels of girls with a low ponderal index. Thus women with a high ponderal index needed to have high levels of energy expenditure to reduce their estrogen levels, whereas women with a low ponderal index needed only moderate levels of expenditure to reduce their estrogen levels. Similarly, studies of the relationship between age at menarche and later reproductive function in girls suggest that those girls who had earlier age at menarche also had more ovulatory cycles five years after they started ovulating than did girls who started menarche later (Apter and Vihko 1983). Studies such as these suggest that the effects of early development may set females on a lifelong reproductive trajectory.

These effects have not been studied in orangutans or other apes, but theoretically, they might apply as well. Because orangutans can experience dramatic fluctuations in energy availability, individual infant orangutans may be gestated or nursed under very different conditions and/or experience dramatic differences during their early developmental years. These effects may carry over to determine their levels of ovarian function later in life and impact reproductive milestones such as the age of menarche and age at first birth, as well as timeframes for adolescent subfecundity and the lengths of interbirth intervals. Such possible effects may also be important determinants of population and species-level differences in reproductive parameters. One prediction would be that where there is more variance in energy intake, such as in some orangutan populations on Borneo, we should find greater variability in reproductive parameters than we do in populations where energy intake fluctuates less. Only with continued long-term studies of orangutans that include data on hormonal levels, energetics, and individual life histories can such hypotheses be investigated.

In this chapter, we detailed the field of reproductive ecology as it applies to the study of orangutans. Clearly, the ecology of organisms is critical to shaping both short- and long-term reproductive responses, yet as a field we are as yet unsure how these models might apply to closely related species such as Bornean and Sumatran orangutans. Understanding population diversity in ecology and life history is critical to evaluating the nature of genetic divergence between these two species. In light of this, we suggest a number of approaches toward fine-tuning our understanding of energetic condition and reproductive function. Though labor-intensive, these methods have yielded critical new insights into the reproductive ecology of orangutans and other apes and continued studies that include additional populations will help further elucidate the ways in which reproductive physiology and ecology interact.

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