CHAPTER 8

Orangutan activity budgets and diet

A comparison between species, populations and habitats

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8.1 Introduction

Recent studies on interpopulation comparisons in African great apes, particularly gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) have

shown interesting variation in diet, behavioral ecology and culture (McGrew 1992a, 1998; Boesch and Boesch-Achermann 2000; Doran *et al.* 2002a, b; Goldsmith 2003; Rogers *et al.* 2004; Lehmann *et al.* 2007). One of the first orangutan studies to compare

populations was John MacKinnon's (1974) study of a population in Sabah, Borneo (Ulu Segama) and one in Sumatra (Ranun). Several basic reviews of diet, activity budget and behavioral ecology have been published since then using data from the literature for their comparisons or summaries (Rodman 1988; Knott 1999b; Rijksen and Meijaard 1999; Delgado and van Schaik 2000; Fox *et al.* 2004; Wich *et al.* 2006a). In addition, in recent years there have been several comparisons that have focused on cultural traits (van Schaik and Knott 2001; van Schaik *et al.* 2003a, 2006a), morphology (Taylor 2006a) and life history (Wich *et al.* 2004b). Overall those studies indicate that orangutans, like the African apes, show interpopulation variation (MacKinnon 1974; Rijksen 1978; Galdikas 1988; Rodman 1988; Mitani 1989; Knott 1998a; Delgado and van Schaik 2000; Wich *et al.* 2004b; van Noordwijk and van Schaik 2005; Wich *et al.* 2006a; Taylor 2006a and Chapter 2 this volume). Interestingly, a pattern arises from these comparisons that indicates differences between populations on Sumatra and Borneo in their morphology (Groves 2001; Taylor 2006a), population density (van Schaik *et al.* 1995; Russon *et al.* 2001; Morrogh-Bernard *et al.* 2003; Johnson *et al.* 2005b; Ancrenaz *et al.* 2005; Chapter 6 behavior (e.g. tool use), reproductive strategies and life history (Delgado and van Schaik, 2000; van Schaik *et al.* 2003a; Wich *et al.* 2004b, Utami and van Hooff 2004; Goossens *et al.* 2006b).

This chapter aims to add to the current literature on interpopulation variation by comparing orangutan activity budgets and diet across sites using a standardized method. We hypothesize that the orangutans may allocate their time differently depending on the habitat they inhabit: good habitat vs poor habitat; logged vs un-logged; masting forests vs non-masting forests. Thus, we address the question of what strategies orangutans employ to cope with the environmental conditions they live under by investigating both the activity budget and diet.

An animal's main daily activities consist of feeding, resting, traveling and socializing (Williams and Dunbar 1999). The percentage of time taken up by each activity forms the overall *activity budget.* These activities take place during the *active period*, defined for orangutans as starting when they sit up in their nest in the morning, and ending when they lie down in their nest at night. There are many variables that can influence active period length (within and between sites), ranging from environmental conditions to social organization (Chivers 1974, 1980; Ahsan 2001; Lodwick *et al.* 2004). Lodwick *et al.* (2004) found that the active period length in individual female chimpanzees (*Pan troglodytes schweinfurthii)* varied according to their reproductive status and dominance ranking. In the hoolock gibbon (*Hylobates hoolock*), Ahsan (2001) found that the start and end of the active day was highly correlated with sunrise and sunset, but was also influenced by the weather. Hoolocks delayed their start until late dawn in winter due to fog, but began earlier in the summer when it was warm. Similar results have been found for the siamang (*Hylobates syndactylus*) and lar gibbon (*Hylobates lar*: Chivers 1974, 1980). In addition, Chivers (1974, 1980) reported that the day ended earlier for siamangs and lar gibbons when food availability decreased. In this chapter we conduct the first standardized comparison of activity budgets between orangutan populations, in an attempt to identify where differences lie and to explain the possible sources of interpopulation variation.

We draw on both published and unpublished behavioral data from ten orangutan research sites to compare activity budgets between orangutan populations (Box 8.1, Table 8.1).

Two habitat types dominated the research sites surveyed: non-masting forests, where the habitat was predominantly peat-swamp forest; and masting forests, where the habitat was predominantly mixed-dipterocarp forest (Chapter 7). We standardized these data sets in order to achieve an unbiased assessment of the extent of variation in activity budgets between sites, differences that may have been obscured or inflated had we used non-standardized data. We used a 12 hour day for all activity budgets, and corrected active period start times for local time of sunrise (See Box 8.1). We compared orangutan activity budgets, start-time and length of active period between age–sex classes, populations and species/subspecies with regard to variations in habitat type, logging disturbance, food availability and diet.

Box 8.1

Data were collected from:

• Gunung Palung National Park (1°13′ S, 110° 07′ E), West Kalimantan, Borneo.
• Sabangau (2° 19′ S, 114° 00′ E), NLSPSF (Natural Laboratory for the Study of Peat Swamp Forest) Central Kalimantan, Borneo.
• Tuanan (2° 09′ S, 114° 26′ E), Mawas Reserve, Central Kalimantan, Borneo.
• Kinabatangan Wildlife Sanctuary (5° 32′ N, 118° 17′ E), Sabah, Borneo.
• Danum Valley (5° 01′ N, 117° 48′ E), Sabah, Borneo.
• Suaq Balimbing (3° 04′ N, 97° 26′ E), Gunung Leuser National Park, Sumatra.
• Ketambe (3° 41′ N, 97° 39′ E), Gunung Leuser National Park, Sumatra.

Only published data were available from Ulu Segama, Sabah, Borneo; Mentoko, Kutai National Park, East Kalimantan, Borneo and Tanjung Puting National Park, Central Kalimantan, Borneo. All sites are located in Indonesia with the exception of Kinabatangan, Ulu Segama and Danum Valley which are in Malaysia. See Table 8.1 for descriptions of each site and the dates and number of hours of data collection.

Data

Data used in the analysis were standardized as much as possible. At most sites, including all sites providing raw data, standard focal-animal sampling techniques using standardized definitions of behavior were used (www.aim.unizh.ch/orangutannetwork.html). Data were collected either instantaneously at intervals from 1–5 minutes or continuously over the period of daily activity. Data from non-habituated individuals and from all follows less than 3 hours long, were excluded. The three main activities of feeding, resting and traveling were recorded, which represent the bulk of the active period in orangutans. All other activities including mating, have been grouped as *Other*. We calculated orangutan active period length when they sat up in the previous-night's nest to when they lay down in their night-nest. The length of time taken up by each activity is typically presented as a percentage of this active period. In order to standardize activity patterns between sites, we present all figures here as minutes of a 12-hour day. To convert activity budgets presented as percentages of active period length into minutes per day, we multiplied the percentage of time spent conducting each activity by the mean active period length of the age–sex class under investigation. As mean active period lengths

were all less than 12 hours, the difference was added to the total time resting (sleeping). For inter-site comparisons we used annual means of age–sex classes as independent data points, whereas monthly means were used for intra-site comparisons (for which all months with less than 15 hours of data/month were excluded). Overall figures are means of the respective figures of the four age–sex classes.

Fruit availability was recorded monthly as percentage of large trees bearing fruit (all tree species >15cm dbh (diameter at breast height), which excludes most strangling figs and woody climbers) for Tuanan, Sabangau and Ketambe. Additionally, an indicator of whether fruit availability was high or low was recorded for Sabangau, Gunung Palung and Ketambe. This was assessed in different ways at each site; Sabangau used percentage of trees fruiting (<10% = low fruit, >10% = high fruit); Gunung Palung used kilocalories of mature and ripe orangutan fruit available/hectare (combining data on percentage of orangutan trees fruiting, density, crop size, and energy content of the fruit) and then classified months as low, medium and high (for this analysis low = low fruit, and only high fruit levels were used for high fruit); For Ketambe data, Wich *et al.* 2006 describe four levels of fruit availability. For this comparison levels 1 and 2 are low fruit and levels 3 and 4 high fruit. Fig density was recorded as individuals/hectare >10cm dbh for Ketambe and Kinabatangan, and >5cm dbh for Gunung Palung. The percentage of each food type in the diet was taken from published data except for Gunung Palung and Sabangau, where raw data were available.

Four age–sex classes were used:

1. Unflanged males (UFM) – includes both unflanged adult males and independent, non-sexually active males
2. Non-sexually active females (NSAF) – includes adolescent females and nulliparous adult females
3. Sexually active females (SAF) – females with dependent infants
4. Flanged males (FM) – fully mature males with developed cheekpads.

All correlations are Pearson's. For ANOVAs with significant results we used Tukey post-hoc comparisons to determine significant pairwise differences. Where data did not conform to the normal distribution, or where Levene's Test for Homogeneity of Variance produced a significant result, we used Kruskal–Wallis tests instead of ANOVAs, followed by Siegel and Castallan (1988), post-hoc test with the significance levels set at a 5% level. All p-values were presented as either $p = <0.05$, $p = <0.01$, or $p = <0.001$.

Table 8.1 Site description

Site	Research dates	No. of hours	Species	Habitat type	Disturbance
Suaq Balimbing	1994–1999	17084	*P. abelii*	Peat swamp	Unlogged
Ketambe	1976–2002	17109	*P. abelii*	Mixed dipterocarp	Unlogged
Sabangau	2003–2005	5502	*P. p. wurmbii*	Peat swamp	Logged
Tuanan	2003–2005	8300	*P. p. wurmbii*	Peat swamp	Logged
Tanjung Puting [1]	1971–1975	6804	*P. p. wurmbii*	Peat swamp (main)/mixed dipterocarp	Unlogged
Gunung Palung	1994–1996	5615	*P. p. wurmbii*	Mixed dipterocarp (main)/peat swamp	Unlogged
Mentoko [2]	1981–1983	3900	*P. p. morio*	Mixed dipterocarp	Unlogged
Danum Valley	2004–2006	977	*P. p. morio*	Mixed dipterocarp	Unlogged
Ulu Segama [3]	1968–1979	–	*P. p. morio*	Mixed dipterocarp	Unlogged
Kinabatangan	1998–2006	–	*P. p. morio*	Mixed dipterocarp (main)/freshwater swamp	Logged

[1] Galdikas (1988); [2] Mitani (1989); [3] MacKinnon (1974)

8.2 Results

8.2.1 Activity budgets and diet

8.2.1.1 Geographical variation

The overall activity budgets from nine sites are shown in Fig. 8.1. In this figure, the sites have been ordered by the amount of time spent feeding, the thick vertical line divides these sites into those where orangutans fed for more than 50% of a 12-hour activity budget and those where orangutans fed for less than 50%. The same line is also the divide between sites where feeding time exceeds resting time and those where resting exceeds feeding. All of the sites where orangutans fed for less than 50% are predominantly mixed-dipterocarp forests where masting occurs, and all sites where orangutans fed for more than 50% of the time are predominantly peat swamp forests where masting events do not occur. The only exception here is Ketambe, a mixed-dipterocarp forest, where feeding is >50%.

We found significant differences between sites in time spent feeding (ANOVA, $F_{4,98} = 25.52$, p <0.01), traveling (ANOVA, $F_{4,96} = 20.39$, p <0.01) and resting (Kruskal–Wallis as Leven's test was significant, $\chi^2_{(4)} = 57.87$, p <0.01). Tukey post-hoc analyses revealed that orangutans from peat-swamp forest (Sabangau and Tuanan) spent more time feeding and traveled for longer periods than orangutans from most mixed-dipterocarp forest (Gunung Palung and Kinabatangan). However, orangutans

in Ketambe, a mixed-dipterocarp forest, exhibited similar activity patterns to orangutans in peat swamp forest, although they did rest significantly more than orangutans from Sabangau (Dunns' post-hoc test). This may be due to differences in the fruiting patterns and/or productivity between these habitat types (Chapter 7).

Although it was not possible to evaluate geographical variation in diet statistically, Table 8.2 provides an overview of orangutan diet for nine populations. Orangutans in all populations clearly spend most time feeding on fruit, then on leaves and then bark or invertebrates. There are several interesting patterns that indicate geographical variation in diet. Orangutan populations in Sumatra show less variation in the time feeding on fruits than the sites on Borneo (cf. Wich *et al*. 2006a). In Borneo orangutans can have months were fruit is a minor part of the diet, whereas in the Sumatran populations fruit is always the major part of the diet. As with fruit, the variation in time spend feeding on leaves is also larger on Borneo than Sumatra. In addition, the time spent feeding on bark is higher and more variable on Borneo than on Sumatra. All these indicate differences between the two islands. Interestingly, the two large peat swamp populations in this study that are in Borneo spend more time feeding on invertebrates than bark, which is similar to the two Sumatran populations. This indicates that forest type might also be of influence on feeding time variation.
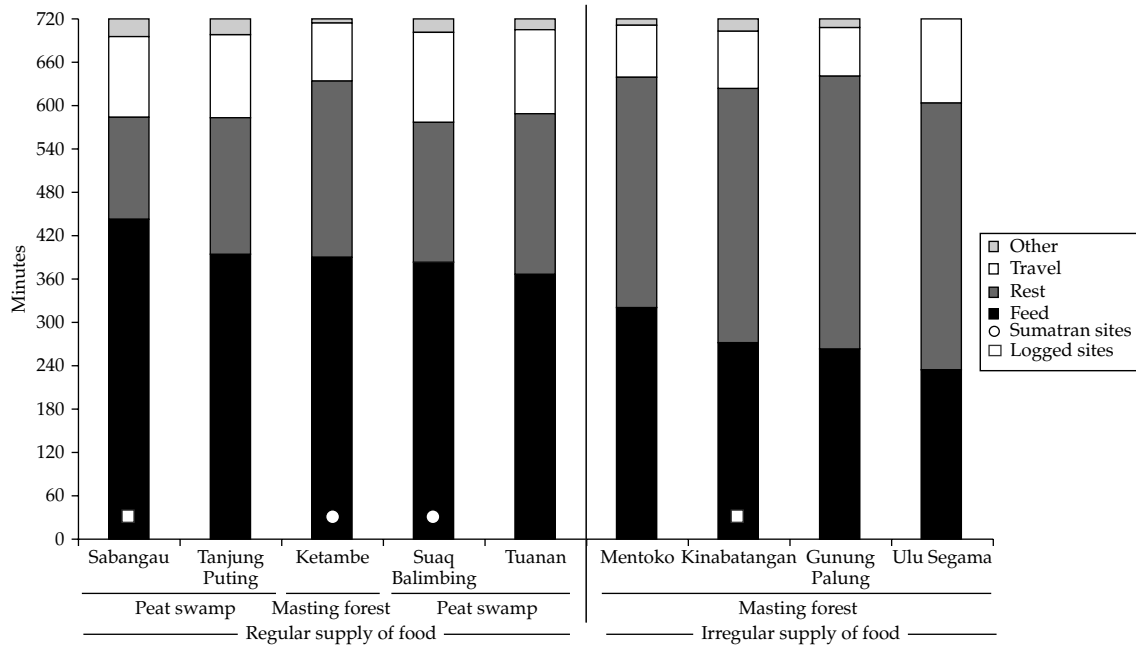
Figure 8.1 Activity budgets from nine different sites (Data expressed as minutes of a 12-hour day used for all sites.)

Figure 8.2 compares diet composition, as measured by percentage of total feeding time, from an irregular (Ulu Segama mixed-dipterocarp forest) and a regular (Sabangau peat-swamp forest) fruiting habitat. It appears that in Sabangau (peat-swamp forest) orangutans have a higher proportion of fruits in their diet year round compared to Ulu Segama (mixed-dipterocarp forest). A similar high proportion of fruit in the diet has been found for Ketambe, which Wich *et al.* (2006a) attributed to the high density of large strangling fig trees at Ketambe.

We thus examined strangler-fig density as a potentially important indicator of forest productivity differences between the sites, particularly in mixed-dipterocarp habitats. We found that strangler-fig density in the mixed-dipterocarp forest of Ketambe, Sumatra (2.7 ind./ha – all stems >10cm dbh) was much higher than that found in a mixed-dipterocarp forest in Borneo (Kinabatangan – 0.33 ind./ha – all stems >10cm dbh) (see Chapter 7). Thus, regularity in fruiting pattern, and not forest type, may explain the differences found in activity budget between these sites, with orangutans

inhabiting forest with a more regular fruit supply feeding longer and resting less.

8.2.1.2 Variation among age–sex class
The proportion of time allocated to feeding, resting and traveling for each age–sex class at the nine research sites was compared (Table 8.3).

There is a general trend across sites that non-sexually active females fed the longest and rested the least, flanged males rested the longest and fed/traveled the least and unflanged males traveled the longest. Although this trend held for most sites, it was not always statistically significant (Table 8.4). These differences were also found in a more detailed comparison at one site, Suaq Balimbing (see Chapter 18 this volume).

8.2.2 Start of active period

Orangutans at most sites were found to start their day around sunrise and end their day about an hour before sunset (Table 8.5). In contrast to this general pattern, orangutans in north-eastern Borneo (Ulu Segama, Danum Valley and Kinabatangan in

Table 8.2 Orangutan diet at eight sites, expressed as percentage of total feeding time

Site and range	Fruits	Flowers	Leaves	Bark	Invertebrates	Other
Suaq Balimbing[1]						
Mean	66.2	–	15.5	1.1	13.4	3.8 (inc. fl)
Monthly range						
Trimester range						
Low fruit–high fruit	62.7–69.6	–	18.3–12.7	0.8–1.4	14.6–12.2	3.6–4.1
Ketambe[2]						
Mean	67.5	3.5	16.4	2.7	8.8	1.3
Monthly range	57.5–71.5	–	10.6–20.1	2.2–3.3	5.7–11.7	–
Trimester range						
Low fruit–high fruit	64.2–70.7	5.6–1.5	17.5–15.2	3.0–2.5	8.7–8.8	1.1–1.5
Sabangau						
Mean	73.8	9.0	5.1	1.5	8.6	2.0
Monthly range	24.4–91.9	0.0–60.2	0.3–17.4	0.0–9.1	0.7–28.0	0.1–4.9
Trimester range	56.0–88.2	0.07–23.8	2.0–11.1	0.1–7.4	1.6–16.1	0.3–3.6
Low fruit–high fruit	70.7–78.1	10.7–6.6	5.1–5.0	2.2–0.5	9.2–7.7	2.0–2.1
Tuanan						
Mean	68.6	5.9	17.2	1.0	6.3	0.6
Monthly range	26.3–88.0	0.0–5.1	4.5–49.5	0.0–5.9	0.3–24.1	0.0–2.5
Trimester range						
Low fruit–high fruit						
Tanjung Puting[3,4]						
Mean	60.9	3.9	14.7	11.4	4.3	4.0
Monthly range	16.4–96.1	0.0–41.1	0.0–39.6	0.0–47.2	0.0–27.2	0.0–21
Trimester range						
Low fruit–high fruit						
Gunung Palung						
Mean	70.0	5.1	13.4	4.9	3.7	2.9
Monthly range	25.8–99.0	0.0–49.6	0.1–41.1	0.0–30.9	0.0–14.0	0.0–9.2
Trimester range	53.2–98.3	0.10–24.2	0.3–27.7	0.0–16.2	0.5–6.1	0.3–5.0
Low fruit–high fruit	60.7–98.3	4.3–5.9	9.8–7.5	8.2–1.9	3.7–3.7	3.4–2.3
Kinabatangan						
Mean	68.0	1.3	22.9	6.7	1.2	–
Monthly range						
Trimester range	20.2–97.2	0.0–7.2	2.8–76.8	0.0–40.0	0.0–4.8	–
Low fruit–high fruit						
Mentoko[4]						
Mean	53.8	–	29.0	14.2	0.8	2.2 (inc. fl)
Monthly range	25.7–89.0	–	5.3–55.6	0.0–66.6	0.0–11.1	0.0–2.5
Trimester range						
Low fruit–high fruit						
Ulu Segama[5]						
Mean	51.5	–	35.6 (inc. fl)	11.2	2.1	–
Monthly range	10.0–90.0	–	8.3–75.0	0.0–36.7	0.0–8.3	–
Trimester range	17.2–78.3	–	20.3–52.2	0.0–29.4	1.1–3.1	–
Low fruit–high fruit	26.9–75.3	–	49.3–21.9	21.0–1.4	2.8–1.4	–

Both an overall figure and the mean are presented. As different studies use different methods for calculating means, we presented ranges in three different ways: (1) monthly ranges are the highest and lowest monthly values recorded; (2) trimester ranges are the highest and lowest values for 3-month periods; (3) Values for low fruit are the mean value of all months classed as low fruit, ditto for high fruit. Monthly ranges were larger than trimester ranges in all cases. Three studies have combined flowers with other categories, marked as (inc. fl) in the table.

[1]Fox *et al.* (2004); [2]Wich *et al.* (2006a); [3]Galdikas (1988); [4]Rodman, (1988); [5]estimated from Fig. 19 in MacKinnon (1974).

Monthly diet at Ulu Segama. Table adapted from Mackinnon (1974) Figure 19

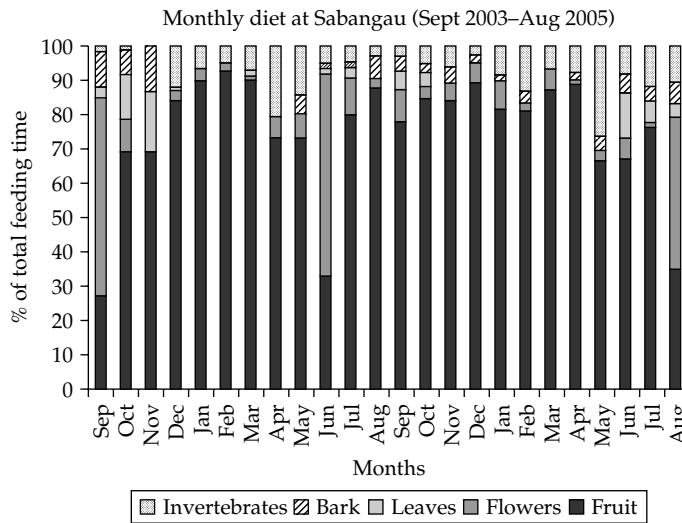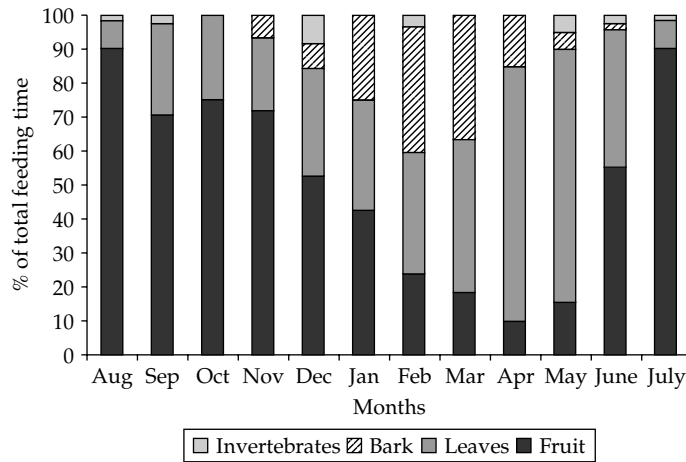Monthly diet at Sabangau (Sept 2003–Aug 2005)

Figure 8.2 Diet from a regular and an irregular fruiting forest.

Sabah), rose 0.5–1.5 hours after sunrise. We therefore investigated whether orangutan start time was influenced by sunrise (i.e. later sunrise would mean the orangutans would start their day later) or fruit availability (i.e. lower fruit availability would mean they spent longer in their night nest resting).

At Ketambe and Sabangau we had data to compare sunrise and fruit availability against start time. In Sabangau, no significant linear correlation was found between start time and either sunrise or fruit availability (sunrise: $r^2 = 0.0025$, n = 23, NS; fruit: $r^2 = 0.0025$, n = 23, NS). At Ketambe, by contrast, there was a significant positive correlation with sunrise ($r^2 = 0.07$, n = 60, p <0.05) and negative correlation with fruit availability ($r^2 = 0.15$, n = 60, p <0.01), but a multiple regression showed that fruit availability was the most important predictor of start time (sunrise: z-score = 0.174, t-test = 1.399, p = 0.17; fruit availability: z-score = –0.347, t-test = –2.797, p <0.01). Thus, at Ketambe orangutans started the day earlier when fruit availability was high (see Table 8.2 on orangutan diets). A similar

Table 8.3 Activity budgets for each age–sex class at each site

Site	Unflanged males			Flanged males			Sexually active Females			Non-sexually active females		
	F	R	T	F	R	T	F	R	T	F	R	T
Suaq Balimbing	53.6	25.7	17.9	<u>48.0</u>	**34.9**	<u>14.9</u>	54.9	25.9	16.9	**55.7**	<u>22.1</u>	19.6
Ketambe	52.6	33.5	**13.0**	<u>48.3</u>	**41.9**	<u>9.2</u>	55.4	32.0	12.1	59.3	<u>28.7</u>	11.8
Sabangau	<u>57.7</u>	<u>18.3</u>	**19.5**	63.8	21.9	<u>12.2</u>	61.6	20.2	14.1	61.9	18.2	17.6
Tuanan	49.8	28.5	**20.1**	<u>45.9</u>	**38.0**	14.8	50.1	34.6	<u>13.7</u>	56.6	<u>22.6</u>	18.6
Tanjung Puting[1]	58.0	23.7	16.4	<u>45.4</u>	**34.5**	16.3	55.5	26.9	<u>15.7</u>	**64.6**	<u>17.0</u>	**17.0**
Gunung Palung	34.3	53.2	**11.1**	<u>33.6</u>	**57.0**	<u>7.8</u>	35.2	53.7	9.8	41.3	<u>47.2</u>	10.7
Mentoko[2]	50.1	37.2	10.2	35.2	55.6	8.4	47.2	41.0	11.5	–	–	–
Ulu Segama[3]	–	–	–	32.7	52.2	15.1	31.9	50.6	17.6	–	–	–
Kinabatangan	32.5	55.3	9.6	33.5	56.7	8.9	36.4	48.8	12.3	–	–	–

F, feeding; R, resting; T, traveling.

For each activity class the highest value is in bold and the lowest is underlined between all age–sex classes for each site. All data is presented as a percentage of a 12-hour period that covers the entire active period.

[1]Galdikas (1988); [2]Mitani (1989); [3]MacKinnon (1974).

Table 8.4 Intra-site differences in activity budgets

Site	Activity	Kruskal–Wallis	ANOVA	Post-hoc
Sabangau	F		$F = 1.56$, p >0.05	No significant differences
	T	$\chi^2 = 11.55$, p <0.01		FM travel <NSAF
	R	$\chi^2 = 1.49$, p >0.05		No significant differences
Tuanan	F	$\chi^2 = 9.67$, p <0.05		NSAF feed >UFM
	T	$\chi^2 = 26.51$, p <0.01		FM travel <UFM; SAF travel <UFM and NSAF
	R	$\chi^2 = 17.65$, p <0.01		NSAF rest <SAF, FM and UFM
Gunung Palung	F		$F = 0.34$, p >0.05	No significant differences
	T	$\chi^2 = 12.56$, p <0.01		FM travel <NSAF
	R		$F = 0.54$, p >0.05	No significant differences
Ketambe	F	$\chi^2 = 31.98$, p <0.01		NSAF feed >SAF, FM and UFM
	T	$\chi^2 = 34.90$, p <0.01		FM travel <SAF, NSAF and UFM
	R	$\chi^2 = 39.17$, p <0.01		FM and UFM rest >SAF and NSAF
Suaq Balimbing[1]	F			SAF feed >FM and UFM
	T			FM travel <SAF and UFM
	R			No significant differences
Mentoko[2]	F			FM feed <SAF and UFM
	T			FM travel <SAF and UFM
	R			FM rest >SAF and UFM
Tanjung Puting[3]	All			No significant differences

All differences significant at 5% level.

F, feeding; R, resting; T, traveling; NSAF, non-sexually active female; SAF, sexually active female; FM, flanged male; UFM, unflanged male.

[1]Fox *et al.* (2004); [2]Mitani (1989); [3]Galdikas (1988).

Table 8.5 Mean start and end times at each site, and corrected start and end times relative to sunrise and sunset

Site	Species	Mean start time	Minutes after sunrise (range of monthly means)	Mean end time	Minutes before sunset (range of monthly means)
Suaq Balimbing	*P. abelii*	06:28	+ 2 (−5 to +19)	17:38	55 (44 to 68)
Ketambe	*P. abelii*	06:31	+ 6 (−5 to +23)	17:30	62 (42 to 82)
Sabangau	*P. p. wurmbii*	05:20	+ 1 (−17 to +29)	16:35	53 (29 to 94)
Tuanan	*P. p. wurmbii*	05:24	+ 6 (−9 to +16)	16:20	65 (41 to 77)
Gunung Palung	*P. p. wurmbii*	05:57	+ 14 (−30 to +107)	16:37	64 (−16 to 101)
Danum Valley	*P. p. morio*	06:31	+ 31 (−16 to +62)	17:41	33 (5 to 72)
Ulu Segama[1]	*P. p. morio*	06:30	+ 26 (mean only)	17:46	30 (mean only)
Kinabatangan	*P. p. morio*	07:45	+ 101 (54 to 158)	18:08	1 (−7 to 9)

[1]MacKinnon (1974).

Table 8.6 Mean length of active period (AP) in minutes at each site, overall and by age–sex class

Site	Mean length of AP (min)	UFM		FM		SAF		NSAF	
Suaq Balimbing	673	682	(1)	655	(4)	674	(3)	679	(2)
Ketambe	664	684	(1)	637	(4)	673	(3)	660	(2)
Sabangau	678	706	(1)	661	(4)	672	(3)	674	(2)
Tuanan	661	686	(1)	642	(4)	647	(3)	669	(2)
Tanjung Puting[1]	640	647	(2)	598	(4)	643	(3)	671	(1)
Gunung Palung	656	675	(1)	641	(3)	639	(4)	670	(2)
Mentoko[2]	684	–		–		–		–	
Danum Valley	676	–		–		–		–	
Ulu Segama[3]	676	–		–		–		–	
Kinabatangan	630	648	(1)	611	(4)	628	(3)	634	(2)

Numbers in brackets are ranking from longest (1) to shortest (4).

NSAF, non-sexually active female; SAF, sexually active female; FM, flanged male; UFM, unflanged male.

[1]Galdikas (1988); [2]Mitani (1989); [3]MacKinnon (1974).

pattern has also been observed by Knott (1999b) for the orangutans at Gunung Palung.

8.2.3 Length of active period

The mean active period length (Table 8.6) ranged from 630 minutes in Kinabatangan to 684 minutes in Mentoko. At most sites, generally, unflanged males were active the longest, followed by non-sexually active females, sexually active females and flanged males.

The few exceptions were non-sexually active females at Tanjung Puting, who had a longer active period than unflanged males; and sexually active females and flanged males who had similar active period lengths at Gunung Palung, and sexually active females in Ketambe who had a longer active period than non-sexually active females (Table 8.6). Data were analyzed statistically from Sabangau where we found that unflanged males' active periods were significantly longer than those of both flanged males and sexually active females

(Anova with Tukey post hoc: F_{3260} = 2.901, p <0.05; unflanged males vs flanged males and unflanged males vs sexually active females, p <0.05).

To determine whether fruit availability influenced active period length, we analyzed data from Sabangau and Ketambe (only sites with data available). At Sabangau, no significant correlation between active period length and fruit availability was found (r^2 <0.01, n = 265, NS), but at Ketambe active period length was positively correlated with fruit availability (r^2 = 0.07, n = 477, p <0.001: consistent with significantly earlier start time attributed to higher fruit availability, as described above). This correlation was found for adult females (r^2 = 0.04, n = 296, p <0.001) and for flanged males (r^2 = 0.06, n = 156, p <0.01), but not for unflanged males (r^2 = 0.06, n = 25, NS). However, these relationships are relatively weak (i.e. very low r^2 values), thus fruit availability explains little of the variance in active period length. Thus we tested if there was an increase in any of the main activity categories with increased fruit availability at Ketambe. The length of time spent feeding (r^2 = 0.03, n = 133, NS), resting (r^2 = 0.0324, n = 133, NS), and socializing (r^2 = 0.0196, n = 133, NS) did not change significantly, but traveling (r^2 = 0.110, n = 133, p <0.01) did. Traveling was found to be positively correlated with fruit availability. Thus, the observed increase in active period was due to a larger amount of time spent traveling.

We then investigated whether being social influenced active period length. Results from Sabangau showed that an individual orangutan's daily active period was significantly longer on days when they had social contact with another individual (Wilcoxon matched pairs: not social mean = 658, sd = 28.2, social mean = 688, sd = 28.3, W = 0.004, p <0.01). At Ketambe, the duration of the active period was found to correlate positively with minutes spent socializing (r^2 = 0.08, n = 108, p <0.01). Thus, being social increased the active period length at both sites.

8.3 Discussion

8.3.1 Methods

For this study we have tried to standardize between sites, but this was not always possible due to accessibility of data and different methods used when collecting and analysing data (e.g. duration of research period, number of individuals and age–sex classes represented) which could affect the results when broken down into smaller data sets. The general trend for active period between sites, however, is likely robust as this is based on thousands of hours of observation at most sites. The variable most likely to differ between sites in this comparison is the measure of fruit availability, as no standardized method has been used. Most sites use percentage of fruiting trees within their phenology plots, but this is not used by all sites, and size of plots varies. A more standard currency would ease inter-site comparisons. One promising alternative is to express orangutan fruit availability as kilocalories of orangutan fruit available/hectare (Knott 2005). This method incorporates data on both the quality and quantity of food available to orangutans and thus we would like to suggest this method be used for future comparative studies. As study length increases, the number of species orangutans are seen to feed on also increases (Chapter 9 this volume); thus this method cannot be used until the orangutan diet at a site is adequately characterized. Additionally, the set of orangutan fruits used to determine fruit availability should be based on those species that comprise the majority of the diet or on a preference index using a smaller dataset. It is also preferable to use a direct measure of energy intake, such as calories, rather than time spent feeding when possible. Obtaining these measures is more time intensive, but would likely give us new insights into the allocation of time budgeting in orangutans.

8.3.2 Activity budget and diet

8.3.2.1 Geographical variations
The overall activity and diet profile from the nine sites shows considerable variation. This variation seems to be influenced mainly by habitat type and the degree of fluctuation in the fruit supply. All the sites where orangutans fed for less than 50% of their active period were all masting forests (predominantly mixed-dipterocarp forest), and all sites where orangutans fed for more than 50% of their active period were all non-masting forest (predominantly swamp forests), with the exception of

Ketambe, where orangutans exhibited similar activity patterns to orangutans in peat swamp forest.

Fruit production in mixed-dipterocarp forest is highly seasonal compared to peat-swamp forest. South East Asian mixed-dipterocarp forests are known for their supra-annual masting events, during which a majority of trees will fruit in synchrony for short intervals, followed by extended periods of low fruit availability (van Schaik 1986; Ashton *et al.* 1988; Knott 1998a, Wich and van Schaik 2000). This means that fruit availability is very irregular throughout the year compared to peat-swamp forests, which have a more regular supply of fruit. Orangutans in peat-swamp forest have a high proportion of fruits in their diet year-round, unlike the mixed-dipterocarp forest. They also rest less and travel more than orangutans from mixed-dipterocarp forests. Optimality models, which consider trade-offs between cost and benefits in foraging decisions (Dunbar 2002), suggest that orangutans will respond to reduced food availability, either by expanding their diet to include lesser-quality foods or by traveling further to include more preferred foods. Thus it appears that different foraging strategies are being adopted, depending on whether the habitat has regular or irregular fruiting patterns.

The reason why orangutans in Ketambe, a mixed-dipterocarp forest, have an activity pattern more similar to orangutans in peat swamp forest may be due to the high presence of strangler figs. Strangler figs are a common genus, representing 3.1% of all tree species (Rijksen 1978). Strangler figs produce fruit year-round, and thus are fed on by orangutans constantly throughout the year, compared to non-fig fruits which have more circumscribed fruiting periods (Sugardijito *et al*. 1987). Figs, however, are normally considered a fallback food that can be relied on when non-fig fruits are low (Wich *et al*. 2006a). They are not preferred because they are generally high in fibre, and lower in energy compared to other fruits (Leighton 1993). Wich *et al*. (2006a) found no evidence of ketones, a product of fat metabolism, in the Ketambe orangutans indicating that they are able to maintain a positive or neutral energy balance year-round despite relying on figs for a large part of their diet. Thus, in order to maintain a positive energy balance, orangutans in Ketambe may be increasing the length of their feeding bouts or their feeding rates when eating figs, as their overall feeding time was not affected by fruit availability. The large strangler figs in Ketambe have large crop sizes, so orangutans can also minimize energy-expenditure and maximize energy-intake by sitting in one large tree and eating figs for long periods of time (Sugardijito 1986), when non-fig fruits are rare. However, when non-fig fruits are plentiful orangutans at Ketambe may travel more to find these preferred fruits. This could explain the positive correlation between travel time and fruit availability at this site. In comparison, strangler-fig density in Borneo is much lower, and the size of these figs are smaller (Wich and Marshall unpublisdhed data), so traveling in search of these trees at Gunung Palung and Kinabatangan, may not be energetically worthwhile. Thus, orangutans at these sites may not use figs as a fallback food to the extent they do at Ketambe. The lack of such fallback fruit on Borneo might be one of the main factors that has led to the much larger variation in time spend feeding on fruit on Borneo than Sumatra (Table 8.2).

In a clear example of this effect, Knott (1998a) found that orangutans in Gunung Palung spent up to 100% of their feeding time eating fruit during masting months, and as little as 26% eating fruit during low-fruit months. Their diet during fruit-poor periods was mainly less nutrient-rich foods, such as inner bark (cambium) and leaves, and, as a result, they lost weight as ketones were detected in their urine (Knott 1998a). The time spent feeding in fruit-rich compared to fruit-poor periods remained similar, even though the nutrient value of the foods was vastly different: 376 kcal/100g for *Dipterocarpus sublamellatus,* a commonly eaten food during the mast, compared to 110 kcal/100g for *Polyalthia sumatrana* and under 200 kcal/100g for bark and leaves, commonly eaten non-masting foods (Knott 1998a). Additionally, because of the high fibre content of the diet during fruit-poor periods, orangutans subsisting on such a diet may need significantly more time for the added cost of digestion of these nutrient-poor foods. Such a feeding pattern as observed in Gunung Palung seems to be more general for masting forests in Borneo than Sumatra (Table 8.2), and likely related to lower and less stable fruit availability in Borneo that Sumatra (Chapter 7; Wich *et al*. in review).

There is also evidence that orangutans at Gunung Palung consume *c*. 10,000 kcal/day in the mast, thereby enabling them to store fat reserves for the fruit-poor period (Knott 1998a). Wheatley (1982) estimated that orangutans have about twice the fat storage capacity in percentage of body weight than a macaque (*Macaca fascicularis*), indicating that they are very efficient at storing adipose tissue, due to their large body mass and ability to subsist on low-quality foods (Wheatley 1982; Knott 2005). The diets at Kinabatangan, Ulu Segama and Mentoko are similar to Gunung Palung (all mixed-dipterocarp forests), with very high leaf and bark-eating in some months (Table 8.2) and thus a similar pattern is predicted, i.e. orangutans with a low quantity of fruits in their diet conserve energy by increasing their resting time.

In contrast, in peat-swamp forests, compared to mixed-dipterocarp forests, it appears that orangutans spend more time feeding and traveling (between food sources) in order to meet their metabolic needs. Although there is less temporal and spatial variation in fruit availability, compared to mixed-dipterocarp forests, the nutrient content of fruits in peat-swamp forest is likely to be lower than masting species, which have large oil-rich seeds (comparative research on the energy content of foods at a number of sites is underway), and, consequently, orangutans need to eat large quantities of food to meet their metabolic requirements. The poorer the foraging quality, the further an individual would have to forage and the more time they would need to spend feeding to ingest the same quantity of nutrients (Bean 1999; Williams and Dunbar 1999). So orangutans in peat swamp forest can keep looking for fruits, as there is a higher likely hood that they will find them.

Orangutans in Ketambe (mixed-dipterocarp forest) have a similar activity budget to those in peat swamp forest, with long feeding periods and short resting periods. The high density of strangler figs means they can maintain a high percentage of fruit in their diet year-round, but must feed for long periods of time owing to the low-energy value of figs. Home ranges in Ketambe are relatively large (Chapter 13this volume), as orangutans have been found to commute in poor-fruit months to areas where there is food (Buij *et al*. 2002), similar to findings from Suaq Balimbing (Singleton 2000). At Ketambe, it appears worthwhile to spend energy searching since the reward may likely be a big strangler full of figs, as opposed to Gunung Palung (a mixed-dipterocarp forest) where no such reward is expected, and thus orangutans opt to stay put and eat suboptimal food.

These data thus indicate that there are two foraging strategies in orangutans, depending on the habitat in which they live:

1. *Sit and wait*—conserve energy by resting (and digesting low quality food) as much as possible during periods of low fruit and waiting for times of high fruit. This strategy applies to orangutans in seasonal dipterocarp forests in Borneo e.g. Gunung Palung.
2. *Search and find*—continuously feed and move in search of food, in order to maintain daily metabolic requirements. This strategy applies to orangutans who live in forest where fruit availability is more regular but of lower quality, e.g. peat-swamp forest in Sabangau and Suaq Balimbing.

8.3.2.2 Comparison with other species

These two strategies have also been reported for other species. Western gorillas (*Gorilla gorilla gorilla* and *Gorilla g. diehli*) were found to adopt a low-energy strategy by decreasing day range and feeding on more low-quality foods (herbs and fibrous fruits), when fruit abundance was low (Doran *et al*. 2002a; Rogers *et al*. 2004), but when fruit was available, they would travel further to add fruit to their diet, rather than subsist on a lower-quality diet (Doran *et al*. 2002a). Dasilva (1992) describes colobus monkeys (*Colobus polykomos*) as time minimizers who rest more and travel less when high-energy foods are not available. Howler monkeys (*alouatta* sp.) have been described as time-minimizing folivores, due to the high percentage of leaves in their diet (Milton 1980). Similar finding were also found in the siamang when high-energy foods were not available (Chivers 1974).

8.3.2.3 Variation between age–sex class

Age–sex class differences in activity budgets (feeding, resting traveling) were found to be similar between sites. In general, non-sexually active females fed the longest and rested the least,

unflanged males traveled the longest and flanged males rested the longest. The only age–sex class to be significantly different from others in most sites was flanged males, who always traveled significantly less than most age–sex classes (Chapter 18 this volume). The reason for this may be due to their large body size compared to the other age–sex classes, and their larger daily energetic costs compared to females (Bean 1999). In Kinabatangan and Ketambe flanged males had shorter day ranges compared to sexually-active females and unflanged males (Rijksen 1978; Lackman-Ancrenaz and Ancrenaz 2005), but this was not true at all sites. At Tanjung Puting, where travel time of sexually active females and flanged males was very similar, Galdikas (1988) found that flanged males traveled much further than adult females, because their travel speed was faster. This may be because flanged males routinely traveled on the ground at this site. By adopting this mode of travel they can travel faster and further than if traveling through the trees. In Sumatra where tigers are present, orangutans rarely come to the ground, so ground travel is rarely used. Alternatively, because orangutan females only conceive once every 5–12 years (Galdikas and Wood 1990; Knott 2001; Wich *et al*. 2004b; Chapter 5 this volume), male travel patterns are likely highly influenced by the availability of cycling females. Thus, the availability of females that happen to have been cycling during the sampling period may have significantly influenced reported inter-site differences in time spent traveling by flanged males.

8.3.3 Start of active period

Habitat and diet differences may be important in determining when orangutans start their day. Orangutan start times were found to be influenced more by fruit availability (higher fruit availability led to earlier rise) than sunrise at Ketambe. However, at Sabangau, time of rising was not related to fruit availability or to sunrise. In Kinabatangan a heavily logged and fragmented forest, where 100% of the emergent trees and 80% of the original canopy have been destroyed (Ancrenaz *et al*. 2004a; Lackman-Ancrenaz and Ancrenaz 2005), orangutans arose >1.5 hours after

sunrise, suggesting that forest disturbance (and the resulting changes in fruit availability) is also influencing start time, as their diet is composed of a high proportion of leaves and inner bark compared to fruit (see trimester ranges in Table 8.2). Orangutans from Danum Valley and Ulu Segama, also in East Kalimantan (*P. p. morio*), got up late as well. However, these are unlogged sites, suggesting that in Kinabantangan logging effects may contribute to late start times rather than being the cause. Why these differences exist is unclear, but dietary content may be important. For example, van Schaik (personal observsation) recorded in Sumatra that orangutans nested earlier if they had fed extensively on leaves on that day. The increased fibrous component of the diet may lead to longer digestion times which may be facilitated by increasing the time spent resting. Similarly, Dasilva (1992) found that in colobus monkeys a diet containing a substantial proportion of leaves was related to low activity levels. It is thus important to determine whether the diet of *P. p. morio* indeed differs from the other (sub)species. Although formal statistical evaluations need to be conducted, Table 8.2 indicates that *P. p. morio* diet contains more extreme high values for leaves and bark than the other (sub)species. These preliminary differences are supported by differences in jaw morphology that indicate that *P. p. morio* has jaws that are better adapted than those of the other (sub)species to feeding on tough items such as leaves and bark (Taylor 2006a and Chapter 2 this volume).

8.3.4 Length of active period

The length of the active period can be influenced by age–sex class, food availability, and time spent socializing. In orangutans there is a general trend that unflanged males are active the longest, followed by non-sexually active females, sexually active females and flanged males. Several factors may contribute to the longer active days of unflanged males. First, they spend more time traveling in an apparent effort to search for females (MacKinnon 1974; Rijksen 1978; Singleton and van Schaik 2002). Second, they are more social and they spend more time interacting with other age–sex classes (except for flanged males) (Wich *et al*.

2006b; Morrogh-Bernard unpublished data). Third, they are subordinate to flanged males, whom they actively avoid (Utami *et al.* 1997). This avoidance sometimes takes the form of waiting until a flanged male leaves a feeding tree before entering (Utami *et al.* 1997; Knott personal observstion). These factors may lead to less than optimal foraging return rates and necessitate more hours spent feeding and traveling.

The length of the active period was similar at all sites, although, intriguingly, the shortest active period was found at Kinabatangan, the most heavily logged site. Differences in the length of the active period were compared explicitly between Sabangau and Ketambe. We found no variation in active period length in Sabangau, but a difference was found in Ketambe. In Ketambe, orangutans seem to be increasing their active period by getting up early and traveling more during periods of high fruit availability. This is likely due to differences in the degree of fluctuation in food availability between the sites. Orangutans in Ketambe live in a masting forest, which despite relatively little change in overall fruit availability, does show seasonal fluctuations in non-fig fruit availability (Wich and van Schaik 2000; Wich *et al.* 2006a).

Surprisingly, the longer active period during times of high fruit at Ketambe may *not* be due to more time spent feeding. Data reported here as well as in Wich *et al.* (2006a) show that at Ketambe the length of time spent feeding did not change significantly when fruit availability increased. The same was found in Sabangau, Gunung Palung (Knott 1998a) and Suaq Balimbing (Fox *et al.* 2004). However, although orangutans may not increase their feeding time during periods of high fruit availability, caloric intake may increase substantially (Knott 1998a). Instead of feeding more, orangutans at Ketambe seem to be traveling more during high fruit periods. The same was found for orangutans at Gunung Palung (Knott 1998a). This could be a result of increased foraging effort due to visiting more food sources or traveling further in search of the most preferred foods. However, these possibilities remain to be tested.

Another reason orangutans may increase their active period during high fruit periods is because of an increase in social interactions, as has been found at Ketambe, Sabangau Tanjung Puting (Galdikas 1988) and Gunung Palung (Knott 1999b). MacKinnon (1974) and Horr (1975) hypothesized that group-living orangutans would need to travel longer distances and visit more food sources daily than lone individuals. Likewise, Mitani (1989) found that a flanged male increased his travel time when in association with adult females compared to when traveling alone, and Galdikas (1988) found that day range and resting time increased when orangutans were social, whilst their foraging time decreased. This may also explain why flanged males have the shortest active period, as they are the least social of all the age–sex classes, usually only socializing with cycling adult females. These results support the socio-ecological hypothesis that suggests that various time budget components increase with group size (Dunbar 2002). Thus, if orangutans are more social, their active period could increase. However, at some sites the increase in food availability could offset the increased cost of foraging while being social. This relative cost of sociality may vary between sites and time periods, leading to some of the inter-site differences observed.

Considering that time spent socializing, which in orangutans is equivalent to time spent in groups larger than one (plus possible offspring), was a strong predictor of active period, it is important to understand the factors that influence orangutan sociality. At some sites, the most important predictor of party size seems to be food availability. Knott (1998b) found that mating in Gunung Palung only took place during high fruit periods, whereas during the low fruit periods animals were primarily solitary. However, at Ketambe and Suaq Balimbing, mean party size was found not to change with increased fruit availability (van Schaik 1999; Wich *et al.* 2006b). This may again be explained by overall higher year-round fruit availability at these sites. Wich *et al.* (2006b) suggested that the presence of a relatively high density of large fig trees in Sumatra, could explain the reason why Sumatran orangutans maintain a high mean party size throughout the year, without their time budget changing much. In chimpanzees (*Pan troglodytes*), party size is regulated by food availability (Doran *et al.* 2002b). Eastern chimpanzees

(*Pan. t. schweinfurthii*) live in habitats where fruits fluctuate more compared to western chimpanzees (*Pan. t. verus*), and Eastern chimpanzees are generally less social (Doran *et al.* 2002b). Similarly, it is likely that productivity in Sumatra is much higher than in Borneo (Wich *et al.* in review; Chapter 7 this volume), so Sumatran orangutans can afford to socialize more (MacKinnon 1974; Sugardjito *et al.* 1987; Delgado and van Schaik 2000).

8.4 Conclusion

Our major finding from this comparative examination of activity budgets and diet is that there are two distinct foraging strategies associated with different conditions of food availability: (1) Sit and wait, where orangutans limit their energy expenditure during low fruit periods; (2) Search and find, where orangutans are constantly feeding or moving in search of food. The determining factor for which strategy is adopted appears to be the temporal availability of fruit, rather than the taxonomic group. In those sites where high-quality fruit are only available for a limited period of time, the first strategy is adopted. This is characteristic of orangutans living in mixed-dipterocarp forests that exhibit high fruiting seasonality and mast-fruiting and where peaks of high-quality fruit production are followed by extended periods of low fruit availability. During low fruit periods orangutans in those habitats feed mainly on low quality food and partly subsist off fat reserves. By contrast, orangutans living in sites where a regular supply of fruit is present follow the second strategy. This is typical of orangutans living in peat swamp forests where fruit availability is more regular, together with orangutans from forests which have a high density of strangling figs, which provide a year-round supply of fruit. Overall, the availability, quality and quantity of food seem to be the major influences on orangutan activity budgets. Habitat and food availability differences are also important for determining the length of the active period and the time of rising. Finally, age–sex class and the degree of sociality are important secondary factors for determining orangutan activity patterns and time budgets.

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