REPRODUCTIVE, PHYSIOLOGICAL AND BEHAVIORAL RESPONSES OF ORANGUTANS IN BORNEO TO FLUCTUATIONS IN FOOD AVAILABILITY

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Cheryl Denise Knott

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THESIS ACCEPTANCE CERTIFICATE

The undersigned, appointed by the

Division

Department of Anthropology

Committee

have examined a thesis entitled

Reproductive, Physiological and Behavioral Responses of Orangutans in Borneo to Fluctuations in Food Availability

presented by Cheryl D. Knott

candidate for the degree of Doctor of Philosophy and hereby certify that it is worthy of acceptance.

Signature .....

Typed name Peter T. Ellison

Signature .....

Typed name Richard W. Wrangham

Signature .....

Typed name Mark Leighton

Signature .....

Carel van Schaik

Date May 26, 1999

ABSTRACT

This research on wild orangutans (*Pongo pygmaeus pygmaeus*) in Gunung Palung National Park, West Kalimantan, Indonesia, on the island of Borneo, investigated how fluctuations in fruit availability affect orangutan nutritional intake, energetics and ultimately reproductive functioning. During this 15 month study, a high fruiting "mast" period occurred and was followed by a period of severe fruit shortage. Data from 693 daily orangutan follows totaling 5989 observation hours indicate that during periods of highest fruit availability, fruit made up almost 100% of the diet. During fruit-poor periods orangutans relied on leaves, bark, pith and insects as fall-back foods. The nutrient composition of 93 orangutan foods was analyzed and combined with detailed data from 2441 feeding bouts to calculate total caloric and nutrient intake. Orangutans maximized caloric intake through consumption of carbohydrate-rich fruits during the high fruit period and maintained a positive energy balance, allowing them to build fat reserves. During the low fruit period, orangutans reduced energy expenditure by traveling less but still endured protracted negative energy balance. Ketones present in urine samples during the low fruit period indicated that orangutans were metabolizing fat reserves to make up for insufficient intake. New methods developed to collect urine and to elute samples stored on filter paper were used to study estrone conjugates (E_1C) using radioimmunoasay. When fruit availability decreased, wild female orangutans showed significant decreases in E_1C levels. Well fed captive female orangutans had significantly higher E_1C values than did wild females. Energetics thus appears to influence orangutan ovarian function. This conclusion was further supported by the observation that in the wild, all matings and conceptions occurred during the months of highest fruit availability. The finding that energetics influences orangutan ovarian function and that orangutans appear to store fat as an adaptation to their highly variable environment has parallels with modern humans and helps us understand how early hominids may have adapted to a changing environment.

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• CHAPTER 1 •

INTRODUCTION AND BACKGROUND

INTRODUCTION

This study is based on the premise that the reproduction of any species can be better understood by placing it within its ecological context. The research is designed to ultimately test the hypothesis that reproduction in orangutans, specifically female ovarian function, is modulated by environmental conditions. The study investigates whether in female orangutans relative fecundity, defined as the biological capacity to bear offspring and measured here by ovarian hormonal levels, is responsive to intermediate energetic variables. These intermediate variables of nutritional intake, energetic expenditure, and energy balance (the difference between intake and expenditure) are hypothesized to ultimately reflect the orangutan's response to fluctuations in food availability. Behavioral responses associated with changing nutritional status, energy expenditure and hormonal levels are also explored as well as differences between males and females in the way that they respond to forest fruit production.

In the first section of this chapter I present an overview of the data and chapters that are included in this thesis. In the next section I review the basic theoretical underpinnings that form the foundation for this research. In the final section I summarize our current understanding of orangutan biology.

THESIS OVERVIEW

The data presented in this thesis consist of measures of ovarian function that are compared to data gathered simultaneously on estimates of nutritional intake, energetic expenditure, energy balance and food availability. The responsiveness of orangutan ovarian function, as well as other aspects of their behavior and physiology, to these environmentally mediated variables is examined.

Chapter Two presents an overview of the establishment of this study and a description of the study population. Results of my phenological monitoring of orangutan fruit availability form the basis of Chapter Three. This chapter establishes the pattern of fruit variability experienced by orangutans during the study period and provides general background information on fruiting patterns and their effects on vertebrates in Southeast Asia.

Chapter Four demonstrates how orangutan nutritional intake varied in response to these fluctuations in fruit availability. New data on total caloric and nutrient intake are presented here. Chapter Five presents data on how orangutan energetic and activity patterns changed in response to these fluctuations in fruit availability and nutritional intake. Data on the time spent in these activities are used to estimate total caloric expenditure. Chapter Six compares the data from the previous two chapters to calculate changes in net energy balance based on estimates of nutritional intake and energy expenditure. A new, independent measure of assessing energy balance in wild primates, ketone analysis, is presented here.

Chapter Seven details the methods I developed for collecting orangutan urine samples and processing them through drying on filter paper. It also details the procedure and validation of a new method for analysis of urinary hormones stored on filter paper through methanol elution and radioimmunoassay. Chapter Eight presents data on changing hormonal and mating patterns in wild female orangutans that are associated with these changes in food availability, nutrition, energy expenditure and energy balance. Finally, Chapter 9 summarizes the data from the previous chapters and explores the broader implications of my findings for orangutan and human evolution.

An additional objective throughout these chapters is to advance our understanding of orangutan behavioral ecology through the new data presented here as well as to compare ways in which males and females differ in their ecological responses.

GREAT APE INTERBIRTH INTERVALS

Previous Hypotheses

The physiological modulation of reproduction and interbirth interval in wild great apes has traditionally received little attention. This is in large part due to the scant information available on completed interbirth intervals in these long lived species (Tutin 1994). Studies of reproduction have primarily focused instead on variation in mating effort. In contrast, studies of other old world primates, such as baboons, macaques and vervets *have* looked at causes of variation in interbirth intervals. However, although the modulation of reproduction in these primates may be somewhat informative, because these are seasonal breeders they may not provide the most appropriate model for great apes.

Until recently, interbirth intervals in great apes have been reported as means for the species, with little focus on variance. After 20-30 years of great ape field studies in the wild, the data are now emerging to suggest a fairly wide range of interbirth intervals both within and between species. Several hypotheses have been put forward to explain this variation. Tutin (1994) suggests that social factors may account for shorter interbirth intervals and earlier age at menarche in gorillas compared to chimpanzees. She argues that female immigration into a new group is more stressful for chimpanzees than it is in gorillas, delaying the onset of fertile cycles. Tutin (1994) also mentions that nutritional factors may be involved, but she does not suggest a mechanism for how this may occur, and favors a

social stress explanation for explaining variance in interbirth intervals. When orangutans are brought into this comparison, however, this explanation falls apart since orangutans have longer interbirth intervals than either of these other apes and they do not have to face any stresses of immigration into a new social group.

Wallis (1997) finds both variance and seasonality in chimpanzee conception rates and interbirth intervals at Gombe National Park. She suggests that photo-period, nutrition, social contact and estrogens in plants could account for these findings, but does not have direct evidence to evaluate these different hypotheses. Galdikas and Wood (1990) propose that suckling frequencies may be longer in orangutans compared to the other great apes and suggest this may account for the variance.

The Ecological Energetics Hypothesis

What I propose here is that the recent, extensive anthropological research into human reproduction which attempts to understand ovarian function within an adaptive, ecological context (e.g. Ellison 1990 and colleagues 1993) can provide a guiding framework with which to approach the study of variance in reproductive parameters within the great apes and other primates. By examining whether the robust findings from human reproductive ecology also apply to our closest relatives, it can not only help us understand reproduction in other apes, but tell us whether or not the reproductive modulation seen in humans has a shared origin with other primates. Although interbirth interval cannot be studied directly we can look at the modulation of ovarian function to see what is causing this variation. Thus, in this study I examine three of the robust findings from studies of human reproductive ecology (Ellison 1990): that nutritional intake, energy expenditure and energy balance have a significant effect on ovarian function during the "waiting time to conception" (the period from the end of lactation to the next conception). I test the hypothesis that these

energetic variables, which are modulated by food availability, have a significant effect on orangutan ovarian function.

This study is thus inspired by research on the ecological context of human ovarian function as well as recent revelations about inter-population variability in great ape reproductive parameters. I hypothesize that these pieces of information are related — that the same ecological variables that are regulating reproduction in humans (Ellison *et al.* 1993) might also be influencing great apes and may help us make sense of this inter-population, and perhaps to some extent between-species, variability. If great ape and human reproductive physiology share similar adaptive responses to the environment it allows us to develop more accurate models for human, as well as great ape, evolution.

Orangutans have a number of unique features that make them an ideal species in which to examine the effects of energetics on fecundity. First, they have been reported to have an average completed interbirth interval of 8 years—the longest of any primate and indeed one of the longest in any mammal (Galdikas and Wood 1990; Tilson *et al.* 1993) —encompassing a range between births of 5.9-10.4 years at the site where they have been studied the longest (Galdikas and Wood 1990). The length of this birth interval and its high variability implies that there may be a long period after lactation, the waiting time to conception, in which females are sub-fecund. Additionally, this variability implies that female reproductive functioning may be responsive to other factors such as the local environment and maternal condition, as is proposed here. Second, the slow movement of orangutans facilitates collection of detailed data on nutritional intake and energetic expenditure (Mitani 1989), information difficult to obtain on a continuous basis in many other primates. Third, orangutans live in the Southeast Asian rain forest, characterized by substantial supra-annual fluctuations in fruit availability (Leighton and Leighton 1983; van

Schaik and van Noordwijk 1985). If ovarian function responds to fluctuating fruiting patterns, this is the habitat where such a relationship is likely to be expressed.

INTERMEDIATE DETERMINANTS OF FECUNDITY

In energy-limited environments we expect animals to try to maintain positive energy balance by negotiating a tradeoff between maximizing nutritional intake and minimizing the energetic effort of foraging. This may be especially important for females because of the high energy drain placed on them by obligatory parental investment. Indeed in most female mammals access to food resources appears to be the primary limitation on reproductive success (Trivers 1972; Wrangham 1979). In long-lived animals with substantial parental investment, such as orangutans, an important way food may limit female reproductive success is through its effect on fecundity.

In multiparous animals the time between births constitutes a trade-off between investment in an existing offspring and future reproduction (Trivers 1974). Thus, interbirth interval is governed by the needs of dependent offspring and maternal condition allowing for future reproduction. This study focuses on this second component of birth interval, the effect of maternal condition on fecundity.

The regulation of maternal fecundity is perhaps best understood in humans where lactation, age, nutritional intake, energetic expenditure and changes in energy balance have been found to be intermediate variables linking the environment and behavior to ovarian function (Ellison 1990). These relationships are not well understood in wild primates in part because of the difficulty in measuring ovarian function in the field. This study addresses this gap by using precise measures of ovarian function to examine maternal fecundity in

wild orangutans as well as collecting detailed data on the intermediate variables of nutrition, energy expenditure and energy balance.

Nutritional Intake

Nutrition has been shown to be a key factor regulating the variance in reproductive success in primates through its effect on birth season, age at menarche, and number of live births (Sadleier 1969; Gaulin and Konner 1977; Strum and Western 1982; Whitten 1982; Altmann *et al.* 1978; Altmann 1980, 1983, 1984; Van Schaik and Van Noordwijk 1985; Cheney *et al.* 1986; Dunbar 1987, 1988; Lee 1987). The effect of nutrition has been demonstrated in captive and provisioned primates who have earlier menarche, shorter interbirth intervals, and longer breeding seasons (Altmann 1986; Lee 1987; Mori 1979; Silk 1987; Sugiyama and Ohasawa 1982) than free-living conspecifics. For example, in provisioned macaques menarche is similar to that reported in captivity and is delayed when provisioning is terminated (Fa 1986, Mori 1979, Sugiyama and Ohsawa 1982). Mean birth rate and maternal body weight have also been shown to fall significantly after provisioning stops (Mori 1979). In the wild, Whitten (1982) found that the vervet birth season was longer in habitats with higher quality and more abundant food, implying that conception took place within a broader period.

In humans, reproductive ecologists have focused closely on the effect of nutritional intake on female reproduction (Frisch and Revele 1970; Pirke *et al.* 1988; Lager and Ellison 1990; Leslie *et al.* 1993). In normal dieting women hormonal functioning is suppressed in concordance with the degree of weight loss (Warren *et al.* 1975; Bates *et al.* 1982; Lager and Ellison 1990) and low body weight has been shown to affect the ability to get pregnant (Green *et al.* 1988). Lipson and Ellison (1996) showed that women were more likely to

conceive during cycles in which their ovarian hormone production was higher and that small increases in body weight were associated with higher hormonal profiles.

In orangutans, specifically, low body weight has been associated with amenorrhea and weight gain has been shown to increase urinary hormonal levels (Masters and Markham 1991). This study proposes that one primary way in which maternal nutrition affects reproduction in orangutans is through its effect on ovarian function and ultimately the probability of conception.

Energetic Expenditure

Although measurements of activity patterns such as day range and foraging patterns have been a common component of primate field studies, their relationship to fecundity has not been previously examined. This relationship has been well studied in humans where exercise can suppress ovarian function in female athletes (Shangold *et al.* 1979; Cumming 1989; Rosetta 1993; Bullen *et al.* 1985) as well as in moderate recreational runners (Ellison and Lager 1985, 1986). In a more traditional society, Bentley (1985) showed that workload for !Kung foragers was a significant factor contributing to long interbirth intervals. Among agro-pastoralist women of Nepal, Panter-Brick *et al.* (1993) report low levels of ovarian function, especially at the height of the agricultural season when workload is highest. Recently, Jasienska and Ellison (1998) have shown that in well-nourished rural Polish women, heavy workloads have a significant effect on ovarian function independent of nutrition. The current study investigates whether energetic expenditure has a similar effect on orangutan ovarian function.

Energy Balance

The combined effect of nutritional intake and energetic expenditure determines whether an animal is in positive or negative energy balance (Coelho 1986). The importance of being in positive energy balance for female reproductive functioning is pointed out by Crockett and Rudran (1987a, 1987b) who conclude from an examination of howler monkey birth data that females tend to conceive and bring infants to term only when maternal condition is adequate to rear them successfully. Another indication of the importance of energy balance comes from studies examining the effect of rank on reproduction in female monkeys. For example, Whitten (1982) found that in vervets low-ranking females tended to conceive later during the mating season than high-ranking females. These lower ranking animals fed on less-preferred food items and had higher energetic expenditure. Thus, lower nutritional intake and greater energetic expenditure may have been causative factors in the observed decrease in fecundity.

In humans, lower indices of ovarian function have been found in women on calorie-restricted diets even though their actual weight is within the normal range of comparable controls (Lager and Ellison 1990). This relationship implies that ovarian function responds to a *decrease* in net energy balance even when weight is normal (Ellison 1990). The net result of energy intake and expenditure is examined here in regard to orangutans.

Food Availability

Ultimately, it is the availability of food, and in the case of the largely frugivorous orangutan, fruit, that is the key factor that affects these energetic variables. The effect of food seasonality on diet selectivity and activity patterns in primates has received a fair amount of study. In baboons, Whiten *et al.* (1991) found significant seasonal changes in

dietary selection criteria and Altmann and Muruthi (1988) report a reduction in physical activity with increased food availability. Orangutans have been found to respond to fluctuations in food availability by modifying time spent feeding (Rodman 1977; MacKinnon 1974; Mitani 1989), food choice (Leighton 1993) and travel patterns (MacKinnon 1974; Galdikas 1988; Mitani 1989).

Studies of humans have linked seasonal reductions in fecundity to decreased nutritional status (Becker *et al.* 1986; Hurtado and Hill 1990; Leslie and Fry 1989), conception (Panter-Brick *et al.* 1993) and suppressed ovarian function (Ellison *et al.* 1986, 1989; Peacock and Ellison 1984; Bailey *et al.* 1992) when food availability is poor. This ovarian suppression often occurs just *after* the peak in food shortage demonstrating a lag-time response. The effect of food availability on fecundity could be especially important in orangutans because of the high variability in fruiting patterns in the Bornean and Sumatran rain forests in which they live (Leighton and Leighton 1983; van Schaik and van Noordwijk 1985). Gunung Palung National Park, where this study was conducted, exemplifies this pattern of fluctuating food availability.

Interbirth Interval

How do these intermediate variables come together to affect interbirth interval and ultimately reproductive success? We know from studies of other primates and of humans that changes in nutrition and energy balance can have an effect on the interbirth interval. For example, Lee (1987) found in vervet monkeys of Amboseli that groups with access to the lowest quality diet had longer interbirth intervals compared to those with higher quality diets. Bercovitch (1987) found that female olive baboons (*Papio anubis*) that weighed more had shorter interbirth intervals than lighter females. In another study of baboons,

Strum and Western (1982) showed that decreases in access to food led to an increase in interbirth interval.

Among humans, studies in the Gambia as well as in Guatemala suggest that women who have supplemented diets have shorter interbirth intervals than those who do not receive supplementation (Prentice *et al.* 1986; Delgado *et al.* 1978). In Bangladesh, women who were heavier at the time of parturition had a shorter period of postpartum amenorrhea (Ford *et al.* 1989). A similar result was found among Mopan Mayan women of Belize, where the time to next conception was shorter in women who had a higher "fat body weight" (Fink *et al.* 1992).

Timing of Conception

Most of our models of mammalian reproduction come from studies of seasonally breeding animals in the temperate zone. In many of these mammals it appears that conception is timed so that births occur during the period of highest food production (Bronson 1989). This may be a good strategy for a temperate zone animal that lives in a highly seasonal but *predictable* environment where the timing of high food availability can be predicted and conception timed accordingly. But for many long-lived, non-seasonally breeding, tropical animals like great apes food availability is sufficiently unpredictable and fluctuating that conception cannot be time to occur during such periods. Instead, I would predict that, just as in humans, conception is more likely to occur during periods of positive energy balance in order to begin the period of intensive reproductive investment when energy availability is adequate.

The hypothesis that food availability is the ultimate factor affecting conception rates is supported by data on the pattern of female cyclicity. When food supply declines the

number of cycling females declines in free-living baboons (Hall 1963) and macaques (Loy 1970). In howlers, Crockett and Rudran (1987b) found that flower and leaf availability is positively related to conception. Whitten (1982) reports that the onset of the mating season coincided with peak food availability in vervets. In the long-tailed macaque, Van Schaik and Van Noordswijk (1985) discovered that female menstrual cycles were highly seasonal, with conception being much more likely during food-rich periods. Wallis (1997) reports that "paradoxically" more births in chimpanzees of Gombe National Park occurred during the wet season which she states is the riskier time of year due to higher rates of deaths and other health problems. Conceptions occurred more often during the dry season when food availability may have been higher, although this was not measured directly.

BACKGROUND ON ORANGUTAN BIOLOGY AND BEHAVIOR

Orangutans have intrigued scientists from the days of nineteenth century explorers like Alfred Russell Wallace. However, as recently as 1965 George Schaller wrote, in a review of the subject, "there have been no field studies of the orangutan." This situation has changed dramatically over the intervening 35 years with many long- and short-term studies on orangutan behavior and ecology having been conducted in the wild. Through these investigations we have found that orangutans are extreme or unusual among primates in a number of fascinating ways. They are the most solitary diurnal primate, have the longest interbirth intervals, display an unusually high degree of forced copulation, and adult males may possibly come in two different morphological types. However, orangutans still remain difficult to study due to their predominantly solitary nature and the often difficult to access habitats where they are found. Much still remains unknown or unexplained.

In the following sections I review some of the background information about orangutan biology, reproduction, sex differences and socio-sexual behavior that is necessary to understand the context of the information presented in this thesis.

Taxonomy and Distribution

Orangutan literally means "person of the forest" in the Malaysian and Indonesian languages—spoken in the countries where orangutans are found. Currently, orangutans are restricted to the islands of Borneo and Sumatra, although during the Pleistocene they were more widespread across Southeast Asia (MacKinnon 1971). Orangutans from the two islands are normally divided into two separate subspecies, *Pongo pygmaeus pygmaeus* from Borneo and *Pongo pygmaeus abelii* from Sumatra. Bornean and Sumatran orangutans are quite behaviorally and morphologically similar, but there is a higher degree

of genetic difference between them than is found within other great ape species (Ferris *et al.* 1981; Cacoone and Powell 1989; Ruvolo *et al.* 1994; Lu *et al.* 1996; Uchida 1996). This genetic difference has led some to suggest that the two subspecies should be separated into two species (Janczewski *et al.* 1990; Ryder and Chemnick 1993). However, there is a lack of general agreement about the degree of genetic difference that justifies a species level distinction (Jolly *et al.* 1995), and in captivity, Bornean and Sumatran orangutans can easily interbreed and produce fertile offspring (Muir *et al.* 1995).

Environment

Orangutans live in rain forest habitats ranging from sea-level swamp forests up to mountain slopes, rarely exceeding 1200 m (Djojosudharmo and van Schaik 1992). These forests are true wet, rain forests with average rainfall ranging from slightly over 2000 mm per year (Galdikas 1988) to 4500 mm per year (Lawrence and Leighton 1996) depending on the site and year sampled. One of the principal orangutan habitats is forest dominated by the large trees of the *Dipterocarpaceae* family. This type of forest is characterized by "mast fruitings," a phenomenon that occurs approximately every two to ten years (Ashton *et al.* 1988) in which up to 90% of rain forest tree species may fruit in synchrony (Medway 1972; Appanah 1985; van Schaik 1986). This fruiting pattern is unique to the rain forests of southeast Asia (Janzen 1974). Some orangutan habitats, such as peat swamp forests, do not exhibit mast fruiting, but fruit production is still highly variable (Galdikas 1988).

General Description

Orangutans are the largest of all canopy animals with wild adult males weighing 86.3 kg on average and females 38.5 kg (Markham and Groves 1990). Such large animals move through the canopy by quadrumanual clambering (using all four hands and feet to grasp

and pull themselves along) and occasional brachiation (particularly by smaller individuals). They also effectively use their body weight to bend and sway small trees, using the stored momentum in the tree as a spring to propel themselves across a gap until they can grasp an adjacent branch.

Compared to humans and other great apes, the orangutan's arms, hands and feet are extremely long (Fleagle 1988). Their shallow hip joint permits them to extend their legs by more than 90° (MacLatchy 1996), allowing them to hang suspended by any hand-foot combination. These features help them contort their bodies into unusual positions in order to reach hard to access fruit and to negotiate their way through the rain forest canopy where they spend almost their entire lives. Orangutans rarely descend to the ground, although adult males do so more often than do females (Rodman and Mitani 1987). This sex difference in ground locomotion may be due to constraints posed by canopy travel on adult males (Rodman and Mitani 1987), or, alternatively, females with offspring may be more vulnerable to the occasional ground predator (Rodman and Mitani 1987; Setiawan, Knott and Budhi 1996).

Sex Differences

Female orangutans are less than half the size (approximately 45%) of developed adult males (Markham and Groves 1990). This is one of the highest degrees of sexual dimorphism seen in primates. The causes of this sexual dimorphism have been attributed to male-male competition (Rodman and Mitani 1987), female choice (Fox 1998) and sexual coercion (Smuts and Smuts 1993). All may have been important in the evolution of large male body size in orangutans. Female orangutans are considered to be the "ecological" sex, that is to exhibit a body size that is primarily constrained by nutritional factors rather than competition (Demment 1983; Rodman and Mitani 1987).

Fully adult males are striking for other secondary sexual characteristics such as the production of the long call and their protruding cheek "pads." Experiments indicate that the loud, bellowing long calls seem to function primarily to mediate spacing between males (Mitani 1985a), and the production of and response to long calls varies depending on dominance (Mitani 1985a; Utami and Setia 1995). Further studies of receptive females are needed to adequately test whether females also respond to male long calls (Mitani 1985a). The jutting cheek pads or flanges of adult males are composed of fibrous fatty tissue (Winkler 1989) and are one of the most unusual features of the orangutan's appearance. Their function has been speculated to help locate (Galdikas 1983) or concentrate the sound of a long call (Rodman and Mitani 1987). However, I suggest that an alternative explanation may be that these cheek flanges have evolved because they help increase the male's apparent size. There appears to have been strong selection for large body size in adult male orangutans, but males may not have been able to evolve beyond their current size and still maintain their primarily arboreal lifestyle. Selection may instead have operated to increase the width of the face and thus the apparent overall size of the male orangutan (Knott 1998d).

Intriguingly, it has been proposed that there may be two types of fully "adult" males (Kingsley 1982, 1988; Schürmann and van Hooff, 1986; Graham and Nadler 1990; te Boekhorst *et al.* 1990; Maggioncalda 1995a, 1995b) with one type, which I will call "developed" males exhibiting the large male body size and secondary sexual characteristics described above and the other, "undeveloped" males, retaining a smaller, "sub-adult" size morphology. Some of these small males may just be in transition before full maturation. Other males seem to remain longer in an undeveloped stage. Males have been reported to still be "sub-adults" at an estimated age of 20 years in the wild (Schürmann and van Hooff, 1986) and up to 18 years in captivity (Jones 1968; Kingsley 1988). Study of orangutan skulls show that there is continued skeletal development after the eruption of the permanent

dentition, normally the indicator of maturation (Uchida 1996). Thus, it appears that the timing of development of secondary sexual characteristics may occur within a broad age range in orangutan males, anywhere between 10-20 years of age, and that males may remain undeveloped for 10 years or longer (Kingsley 1988; Schürmann and van Hooff 1986). All males, however, do eventually develop secondary sexual characteristics as there are no known individuals from zoos or captivity that have remained undeveloped beyond 20 years.

Males who remain undeveloped for an extended period have significantly lower levels of testosterone (Kingsley 1982; Maggioncalda 1995b) and growth hormones (Maggioncalda 1995a) than do males who are in the process of developing. However, these undeveloped males appear to have adequate production of testosterone and are fully capable of fathering offspring (Kingsley 1982, 1988). Interestingly, testosterone levels are significantly higher in undeveloped males than adult males in the wild (Knott 1997b).

What triggers the timing of full development in males? It has been proposed that the presence of a developed adult male may "suppress" maturation in undeveloped males (Kingsley 1982; Schürmann and van Hoof 1986; Maggioncalda 1995a, 1995b). This is based on inferences from captivity in which an undeveloped male matures soon after he is separated from his developed cage-mate. These correlations, however, do not rule out the possibility that such males would have matured at that time regardless of the presence of a developed male. Males are also seen to develop cheek flanges while still in the presence of an already developed male (Kingsley 1982). It is also difficult to imagine how such a mechanism could operate in the wild where orangutan males are rarely within visual or olfactory contact. Maggioncalda (1995b) suggests that undeveloped males may use long calls to monitor the density of developed males as a cue for when to initiate full maturation. However, not all developed males regularly produce long calls (Utami and Setia 1995;

Knott, pers. obs.), thus this may not be an accurate indicator of density, and such an auditory mechanism has yet to be demonstrated in orangutans. Alternatively, I would suggest that rather than a facultative response to adult male density, differing ages of maturation in adult males may result from changes in energetic status brought about by fluctuating nutrition or males may simply vary genetically in their developmental timetables.

Reproduction

The orangutan menstrual cycle has a mean length of 28 days (Nadler 1988) and is particularly noteworthy because of the lack of an estrus swelling (Graham-Jones and Hill 1962; Schultz 1938). Females have been reported to reach sexual maturity at 7 to 9 years in captivity (Asano 1967; Lippert 1977; Masters and Markham 1991) and 7 (Horr 1977) to 15 years in the wild (Galdikas 1981). The duration of adolescent subfecundity has ranged from 7 months in captivity (Asano 1967) to possibly 5 years in the wild (calculated from Schurmann and van Hoof 1986). The length of lactational amenorrhea varies, often depending on how long the infant was allowed to stay with the mother. Reports from captivity range from 5 months (Lasley *et al.* 1980) to 6.5 years (van der Werff ten Bosch 1982) to over 6 years in the wild (Galdikas 1980). Galdikas (1980) describes a female who came back into estrus in 1976 and did not give birth again until 1979. Given an 8 month gestation length (Martin 1981), this individual would have had a waiting time to conception of approximately 2.4 years. This stands in contrast to Lippert (1974) who reports that orangutans in captivity experience only 1 to 2 menstrual cycles before conception. Correspondingly, birth interval length has ranged from under 3 years in some captive animals (Lippert 1977) to over 10 years in the wild (Galdikas and Wood 1990; Tilson *et al.* 1993). This study helps illuminate some of the source of this wide variability in reproductive parameters by demonstrating how energetics affects female reproduction.

Socio-Sexual Behavior

A surprisingly large percentage of orangutan matings have been characterized as forced copulations (MacKinnon 1974; Rijksen 1978; Galdikas 1981, 1985; Mitani 1985b). In the wild, undeveloped males appear to engage in more forced copulations than do fully-developed adult males (Rodman and Mitani 1987). Mitani (1985b) found that male rank and size appeared to affect whether females struggled during copulation. Whether females *choose* to mate with fully-developed males or whether they cooperate due to threat of injury from these large males is not well understood. Mitani suggests that the pattern of forced and unforced copulations may depend on the female hormonal cycle. Nadler (1977) looked at the relationship between the female hormonal cycle and mating in captive orangutans and found that when male access to the female was not limited, copulations occurred on a nearly daily basis. However, during the midcycle period female resistance to males was lower and multiple copulations occurred more frequently. In later experiments when females were allowed to *choose* when to enter a male's cage, mating was limited to midcycle (Nadler 1988).

Activity Patterns

The time orangutans spend in different activities varies depending on the availability of food, social conditions and reproductive status. Averaging across 3 studies (MacKinnon 1974; Rodman 1979; Mitani 1989), orangutans spend approximately 44% of their time resting, 41% feeding, 13% traveling, 2% nest building, and <1% engaging in other activities such as fighting, mating and socializing. These percentages, however, may vary tremendously. Because orangutans are primarily solitary their activity patterns may be very individualistic and each animal may react in a different ways to the same environmental

conditions. An individual's condition, reproductive status and habitat quality may influence these decisions.

Feeding Ecology

The orangutan diet varies dramatically depending on what foods are available. Fruit, both pulp and seeds, is the preferred food of orangutans (e.g. Sugardjito *et al.* 1987; Galdikas 1988; Leighton 1993). Orangutans prefer to feed in trees with large patches of fruit if available (Leighton 1993). Sugardjito (1986) found that adult males have longer feeding bouts than do adult females and Rodman (1979) noted that males tend to feed in fewer food patches per day than do females.

Orangutans have been seen to eat meat only on rare occasions. In Sumatra, three adult females have been observed on 7 occasions to hunt and eat slow lorises (*Nycticebus coucang*) (Utami 1997) and one female was observed to eat a gibbon (Sugardjito and Nurhada 1981). At Gunung Palung, in Borneo, I've witnessed a juvenile female orangutan catch and eat a tree rat (Knott 1998b). Thus, the ability to capture other mammalian prey may be a relatively ancient ability in hominoids since it is also observed in chimpanzees (e.g. Goodall 1963; Teleki 1973; Boesch and Boesch 1989; Stanford *et al.* 1994), bonobos (Ihobe 1992) and possibly gorillas (Fossey 1983).

Social System and Ranging Patterns

The orangutan social system has been difficult to characterize because these animals seem to range over extensive areas and their residence in a given study area may vary widely across time. Mounting evidence suggests that females stay in their natal area, whereas males disperse, (Rodman 1973; Rijksen 1978; Galdikas 1988; Knott pers. obs.). Horr

(1975) and Rodman (1973), saw little overlap in female ranges, but longer term studies (Galdikas 1988; van Schaik and van Hoof 1996; Knott 1998a) have found that female ranges can overlap considerably.

Developed adult males can have overlapping ranges, with the number of developed males using a given area at the same time ranging from one (Rodman 1973) to as many as six (Knott 1998a). Some males may stay resident in an area, whereas others appear to be more transient. However, this may be a false distinction (van Schaik and van Hoof 1996) as the researcher's perception of residence patterns may depend on the length of the time period sampled and the inability to know where individuals are when they are not in the researcher's core study area. At Gunung Palung, these differences in male ranging patterns seem to be tied to fluctuations in fruit availability, with more males using the study area during periods of high fruit availability (Knott 1998a).

Thus, developed males appear to have large and widely overlapping ranges within which they search for receptive females. This evidence suggests that the orangutan social system can best be characterized as "roving male promiscuity" in which "males cannot defend access to female ranges and females do not congregate at particular areas" (van Schaik and van Hoof 1996). Small, undeveloped males, however, are often seen to travel in groups and corral females for mating. This is similar, in some respects, to the "male-bonded promiscuity" seen in chimpanzees except there is no evidence that these males can defend the ranges of several females. Thus, I would propose that "roving male-bonded promiscuity" may be a more appropriate description of the strategy employed by undeveloped males. Further information is needed, though, on whether these associations between undeveloped males are true cooperative bonds or just temporary associations with each other. Genetic data may help us resolve some of the long-standing questions

regarding relatedness between individuals within an orangutan population as well as the relative paternity success of developed versus undeveloped males.

Social Behavior

Why do orangutans differ so much from the gregarious nature of most other primates? Why don't adult males bond together to defend female home ranges from other males as is the case with chimpanzees? The answer may lie in the comparison between the ecology of orangutans living in Asian rain forests and the ecology of the more convivial African apes. It has been suggested that orangutan fruit trees are more widely dispersed compared to African fruit trees (Fleming *et al.* 1987). However, no systematic studies have been done comparing ecological differences between these different rain forests as they might relate to great apes. It appears, though, that fruit trees preferred by orangutans in Asian rain forests are significantly smaller in diameter compared to those used by chimpanzees and bonobos (Knott unpublished data). Thus, the scarcity of large patches of fruit may limit the ability of orangutans to forage together as a group.

This is supported by examining the occasions when orangutans *are* social. Aggregations of orangutans have been found in large fig trees (Rijksen 1978; MacKinnon 1974; Sugardjito *et al.* 1987; Utami 1997), in large dipterocarp trees that only fruit during mast fruitings (Knott 1998a), and other times when closely packed trees, such as *Palaquium* are fruiting (Knott 1998a). These aggregations are primarily composed of mothers with offspring, undeveloped males, and an occasional lone developed male. During periods of increased sociality, orangutans may modify their time spent feeding (Rodman 1977; MacKinnon 1974; Mitani 1989; Galdikas 1988; Utami 1997), traveling (Galdikas 1988; Mitani 1989; Knott 1998a) and/or resting (Mitani 1989). These costs of grouping may constrain group travel of orangutans except during exceptional periods when the nature and distribution of

fruit resources permits it. Increased sociality (Knott 1998a) and density (te Boekhorst *et al.* 1990) have been found to be strongly correlated with periods of high fruit availability. Furthermore, some orangutan populations may not be as solitary as was once thought. In Suaq Balimbing forest in Sumatra, van Schaik and Fox (pers. comm.) have found that orangutans are much more social than has previously been described at other sites.

Another cause of grouping, risk of predation, appears to be not very important for orangutans given their large body size (Sugardjito 1983; Setiawan, Knott and Budhi 1996). Because individuals rarely form groups, threats by groups of orangutans directed at lone individuals has not been observed except in the case of forced matings. Lethal aggression does occur in orangutans, particularly between developed adult males (Knott 1998b), but this threat does not lead to the formation of bonds between developed males. Undeveloped males, however, may form bonds as a response to threats from developed males and as a way to gain group access to cycling females.

• CHAPTER 2 •

INITIATION AND DESIGN OF STUDY

CHAPTER SUMMARY

In 1994 I initiated this study of the reproductive, physiological and behavioral responses of orangutans to fluctuations in fruit availability. The study was established at the Cabang Panti Research Station located in Gunung Palung National Park in West Kalimantan, Indonesia, on the island of Borneo. The study area encompasses seven distinct habitats and orangutans were followed most extensively in the peat swamp, freshwater swamp, alluvial bench and lowland sandstone forests and less extensively in lowland granite forests. Most follows took place between 0 and 300 m elevation. The study site was expanded over the past four years to increase the effective area for orangutan follows from 650 to 1200 ha. During the pilot study, orangutan data and urine collection methods were validated and a photographic and descriptive database of the individual orangutans was established.

To enable multiple follows of individual orangutans, a large staff of Indonesian and Western assistants were trained in the data collection methods. Target animals were found opportunistically, although females who were thought to be cycling were given the highest priority for long-term follows. Once contacted, focal animals were followed until they made a night nest and were re-contacted at the nest before dawn the next morning. Animals were normally followed by two people working in shifts or by one person following the entire day. Follow durations during the first year ranged form less than 1 day to 47 days, with the average follow lasting 3.2 days.

Orangutans were primarily unhabituated at the beginning of the study. Unhabituated animals vocalized and engaged in agonistic displays directed towards human observers. It normally took 3 or more days before an unhabituated animal resumed normal behavior.

Comparisons were made between the behavior of habituated and unhabituated orangutans resulting in the decision to exclude unhabituated animals from the behavioral analyses.

A core sample of 27 individuals was followed extensively. These included 12 adult females, 8 developed adult males, 5 undeveloped adult males, 1 adolescent male, 1 adolescent female (who became an adult during the study) and 3 juveniles. Over 20 additional orangutans used the study area on occasion. Five females were thought to be cycling at some point during the first year and a half of the four year study period. Some animals remained resident during the entire study period, whereas others were absent for large periods of time, and still others were only infrequent visitors.

STUDY SITE

This study was conducted at the Cabang Panti Research Site in Gunung Palung National Park, West Kalimantan, Indonesia, on the island of Borneo (1°13'S, 110°7'E). The park includes approximately 100,000 ha of uninhabited tropical rain forest, providing a large area for orangutan movement. The study area is primarily pristine primary rain forest except that Ironwood, *Eusideroxylon zwageri*, and gaharu, *Aguilaria malaccensis*, trees have been extracted by hand logging in some areas. These are not orangutan fruit trees. However, the large ironwood trees would have provided potential establishment sites for strangler figs which are eaten by orangutans. Illegal hand logging is a recurrent problem in the marginal areas of the park, but has not encroached into the study site. The mean annual rainfall at Cabang Panti is 4300 mm (Leighton unpublished data) and is relatively evenly distributed throughout the year. Some years have a dry month with less than 100 mm of rainfall, which usually falls between June and September. Occasionally, longer droughts of several months duration are observed.

The Cabang Panti Research Site, established by Mark Leighton in 1984, occupies approximately 2100 hectares (ha) in the core of the National Park. This site is distinguished by a rich mosaic of seven distinct habitats (Figure 2.01). The western portion of the study area, at approximately 1-20 m elevation, is characterized by freshwater swamp forest, peat swamp forest, and forests on alluvial benches along river courses. The eastern portion rises in elevation and is bordered by two mountain ridges, that extend up to approximately 1000 m at their highest point. Forest on lowland sandstone is found at the

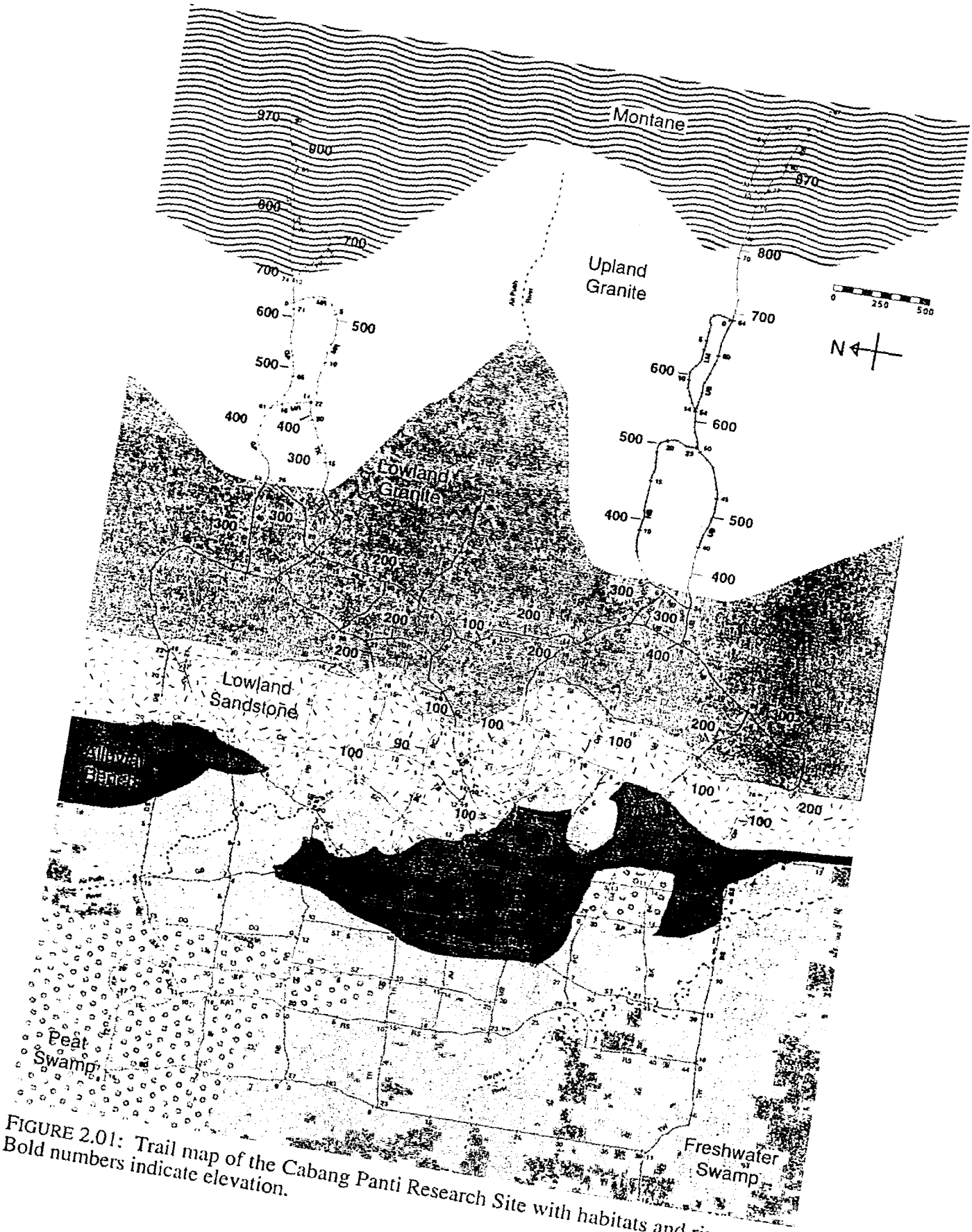


FIGURE 2.01: Trail map of the Cabang Panti Research Site with habitats and rivers shown. Bold numbers indicate elevation.

foothills of the mountain at approximately 20 - 100 m elevation. This grades into forest on lowland granite at approximately 100 - 400 m elevation, sub-montane forests on upland granite at approximately 400 - 700 m elevation, and mossy cloud forest above approximately 700 m elevation. The *Air putih* river flows down the valley between these mountain ridges and provides the primary means of access to the study area. The *Bayas* river flows through the southeastern corner of the site. Orangutans were followed in all habitats except for the sub-montane and montane forests. Although they were sighted sporadically in these areas, the steep terrain precluded regular monitoring.

During the course of my study new trails were made to expand the effective area for orangutan follows. Trails are essential for navigation and efficient travel in hard to access areas such as swamp forests. Although orangutans are, of course, followed off trail, trails are key to being able to return to the base camp after the orangutan makes a nest and to return to the nest in the pre-dawn hours. The trail system was composed of 43.2 km of cut trail when my study began in August 1994. An additional 9 km of trail were cut by Tim Laman and me in 1994-1995, 4.65 km of trail were made by Jamie Jones and Libra Hilde in 1996, 1.85 km were added by Andy Marshall and Cassie O'Connor in 1997, and an additional 0.8 km were cut by Ramsay Ravenal later that year. New trails were added in areas heavily frequented by orangutans, almost doubling the effective area for orangutan follows below 300 m from approximately 650 ha (Figure 2.02) to approximately 1200 ha (Figure 2.03). This has greatly improved the ability to follow individual animals through a wider portion of their home range.

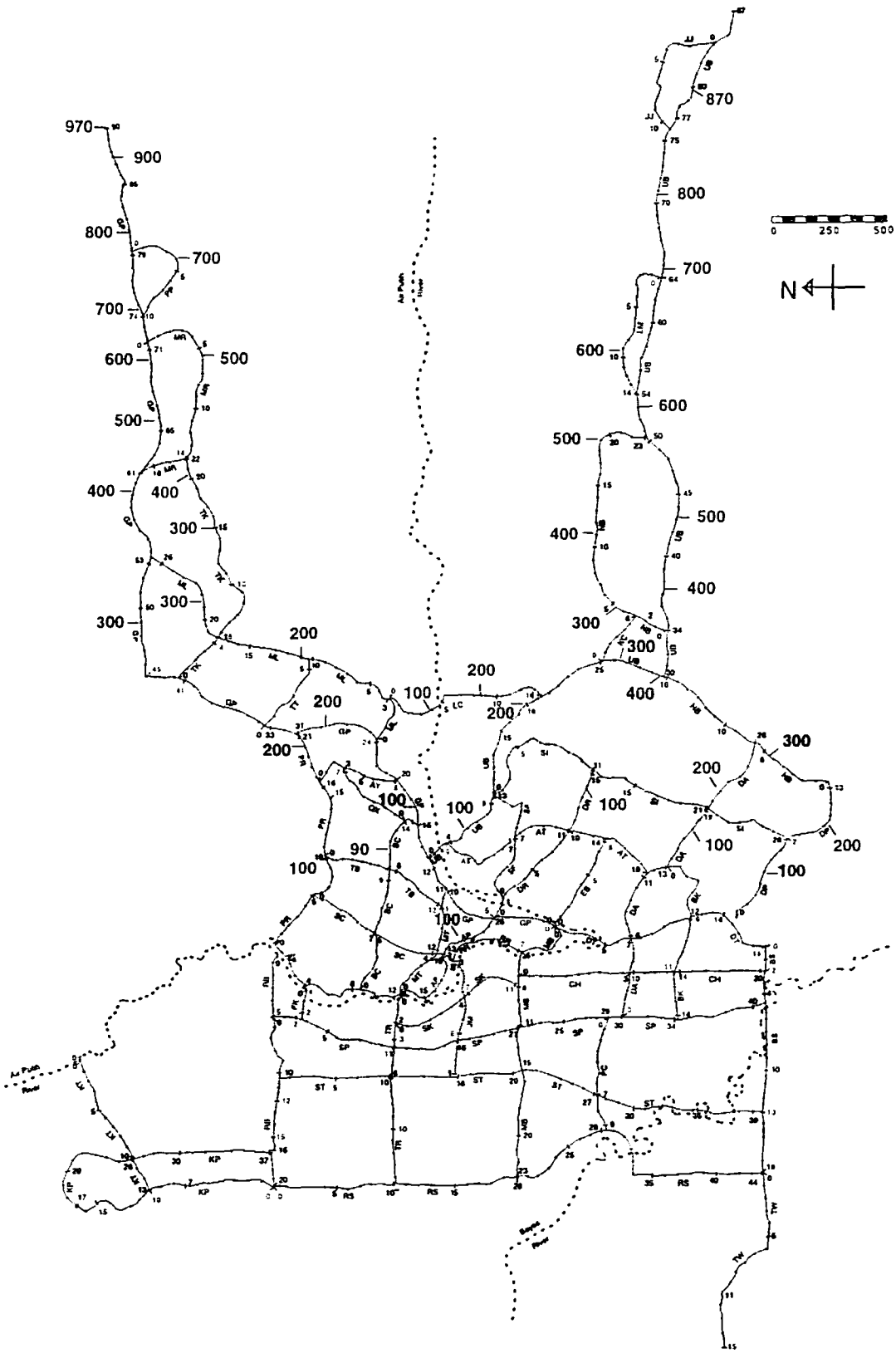


FIGURE 2.02: Map of the Cabang Panti Research Site as of August 1994. Trails are marked off in 50 m segments and trail names are indicated.

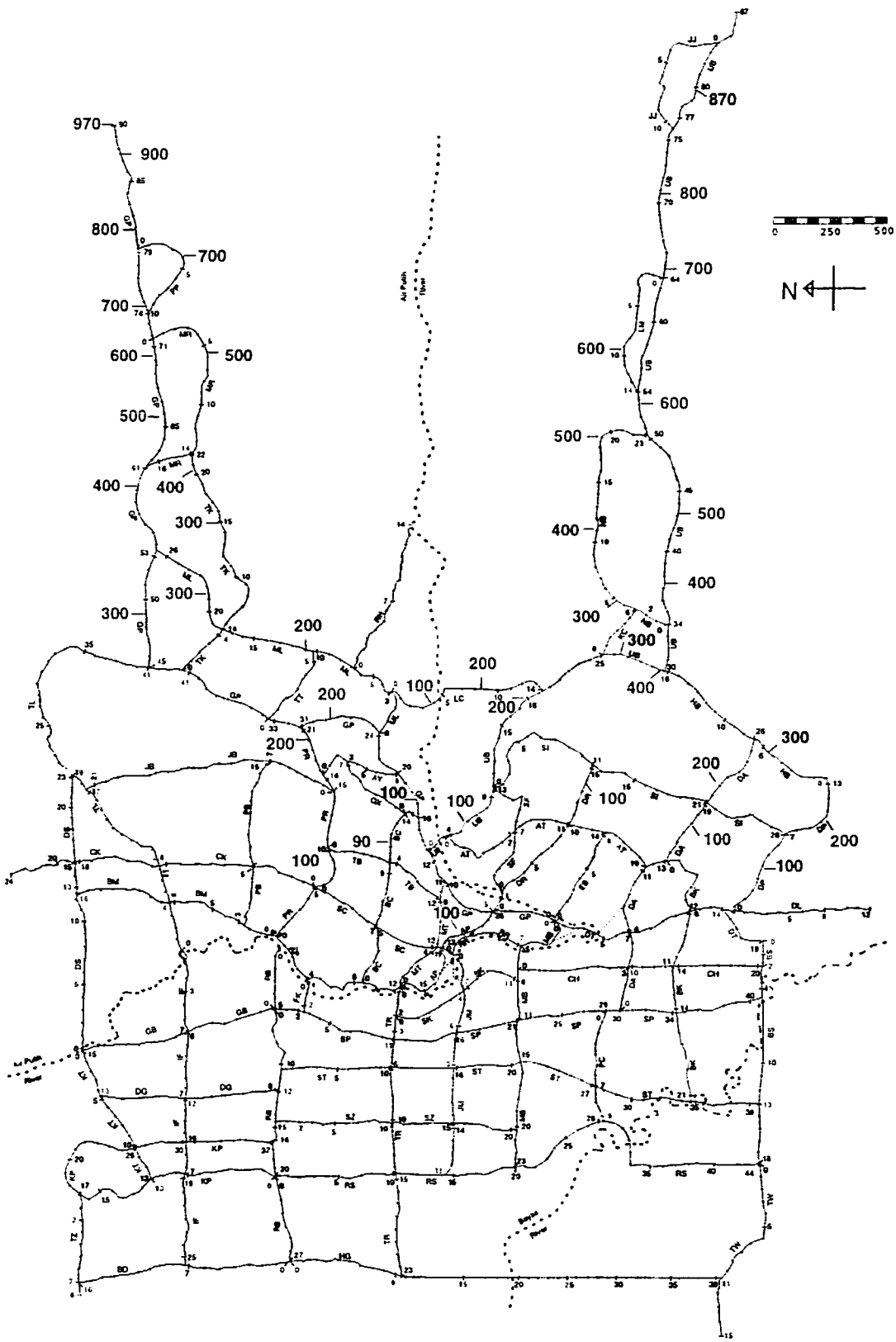


FIGURE 2.03: Map of the Cabang Panti Research Site as of January 1, 1998 showing the expansion into the lower half of the study site where orangutans are most frequently found.

PREVIOUS ORANGUTAN RESEARCH AT THE SITE

Orangutans have been followed at Cabang Panti off and on since 1984. Between 1984 and 1991 orangutan observations were recorded as part of Mark Leighton's vertebrate census monitoring study. When an orangutan was sighted, the animal's location, activity, food item if eating and a feeding rate were recorded. Orangutans were not individually identified. John Mitani conducted research on orangutan social behavior and male vocalizations at the site for 14 months from April to May 1988 and August 1988 to July 1989 (Mitani *et al.* 1991). His study subjects were 2 adult males, 4 adult females with their offspring, 2 sub-adult males and 3 adolescent females, as well as 5 non-resident individuals.

PILOT STUDY

During the Fall of 1992 I conducted a pilot study of orangutans at Cabang Panti. The project focused on two primary goals: (1) to test the feasibility of the field methods used for this research, particularly the ability to collect daily orangutan urine samples; and (2) to establish a descriptive and photographic database of the orangutans inhabiting the study site in order to initiate research on known individuals.

A total of 15 individual orangutans were followed providing 327 hours of focal follow data. I was able to clearly observe the animals 92% of time. During the remaining 8% of observation time the animals were difficult to observe because they were either feeding, resting inside a tree crown or traveling outside my direct field of vision. Orangutans are normally quite noisy travelers, thus I could reliably assess whether an animal was moving even if it was not directly observable. I was able to obtain an accurate estimate of feeding rate throughout 85% of each feeding bout. Orangutans are usually noisy eaters as well,

and often drop food items to the ground while feeding. Thus, lack of visible or audible movement while an animal was in a tree crown was usually a signal that feeding had stopped. A total of 23 urine samples were collected from 10 individuals. I was able to successfully obtain urine in 100% of my attempts.

Detailed descriptive data sheets were completed for all orangutans in order to identify key features. A sample orangutan identification sheet is shown in Figure 2.04. Multiple photographs of each individual and videotape footage were taken by either Tim Laman or myself in order to form a complete descriptive and photographic record of each orangutan encountered. Orangutans at this study site were individually recognized and named by John Mitani three years prior to the initiation of my pilot study. I thus attempted to ascertain whether the current resident individuals were the same as those followed by Mitani. This was done through consultation in the field with one of Mitani's field assistants who still worked at the study site, through reviewing Mitani's orangutan descriptions, and through showing Mitani photographs of individual animals. However, except for possibly one adult female (Kristen and her two offspring), no animals could be positively identified by either Mitani or his assistant as the same individuals whom they followed in 1988-1989.

Name: Tumor Belly Code: TB Relatives:

Sex: M Estimated birth date: Age Class: Mature adult

Size: Comparison: About the same size as Roman, but older.

Key features: Large tumor on belly near belly button; Very floppy cheek pads, but well formed; Wart on right cheek, below corner of right eye.

Color of face: Black

Face shape: Long

Facial Marks:

Eyes: Small, wide set

Ears:

Forehead: Fairly deep mark

Throat sac: Big throat pouch

Cheeks: Floppy, not fat; on right side sticks out

Hair on top-head: Flat on top and in front

Hair on side-head: Not much hair

Hair on back-head:

Hair on neck:

Hair on chin: Large beard

Overall body color:

Overall body shape: Very large, fluffy

Bald patches: Back has disinctive bare patch with sharp edges.

Back: Like Herman - Very distinct, clear edges, can see spine quite clearly.

Chest: Dark orange

Shoulders: Lots of hair, dark orange

Arms: Very fluffy

Legs:

Belly: Large tumor on belly near belly button.

Hands/fingers:

Feet/toes: Very hairy toes. Left index toe has a wound on knuckle as of 1995

Rear:

Genitals:

Vocalizations:

Companions:

Trails seen on: SC, MB, RB

First recorded by: CK, IS Date: 4 Dec 94 Unique Individual? Yes

Alias:

Could also be: Herman, Peter

Cannot be: Anyone else

Comments: This may be male found dead in February 1995. TB not seen since after February 1995.

Figure 2.04: Sample orangutan identification record.

ESTABLISHMENT OF CURRENT STUDY

Field Team

In August 1994 I initiated the current study. Because orangutans are primarily solitary, they are difficult to locate and once found it is desirable to follow them from dawn to dusk in order to maintain contact. At least one and preferably two orangutan followers are required for each animal. Thus, a large staff was needed to enable me to find orangutans and to follow multiple individuals simultaneously. Six Indonesian men from the surrounding villages were hired as full-time field assistants for the project. Additionally, I trained seven field assistants who were conducting phenological surveys for Mark Leighton to follow orangutans. I hired these additional individuals to rotate into the project as needed, depending on their availability. Since the initiation of the project, additional men have been hired as field assistants, resulting in a staff, as of January 1999, of 10 full-time orangutan followers.

All field assistants received extensive training. Training sessions were conducted both in groups and individually during an approximate three-month training period. During the initial training period, all field assistants followed orangutans and collected data simultaneously with myself, or in subsequent years, with another supervisor or an experienced assistant. Until data could be satisfactorily collected independently, all field assistants followed orangutans in teams of two, taking simultaneous data. An individual's data were judged satisfactory when his simultaneously collected data matched my own.

Several measures were taken to assess inter-observer reliability and to reduce any inter-observer bias. First, all orangutan followers were rotated between study animals every half or full-day so that there was no systematic bias between who collected data on which

animals. Individual followers were also equally assigned to follow all age-sex classes of orangutans. Second, throughout the study, I either collected the data myself or was present during part of the day in approximately 75% of the follows. When more than one orangutan was being followed on a given day, I often spent part of the day with each field assistant-orangutan pair. When following with field assistants I collected data simultaneously with them to check that data was being collected properly and to maintain quality control and continued training. When not conducting written data checks I verbally tested the assistants' evaluation of the orangutan's behavior, height, distance traveled, feeding rate, etc. throughout the follow. I also supplemented their field records with additional behavioral notes and independent feeding rates. In this way all field assistants data were standardized to my own data collection judgments and I was able to maximize accuracy and consistency in data collection among all field assistants. Third, periodic tests of data that could be quantified and recreated (e.g. travel distance, height in canopy, tree dbh, etc.) were conducted of all field assistants. In these tests I rigged markers of known height or distance and checked the reliability of the assistants' estimates. Fourth, all day training sessions with the entire staff were done periodically to reinforce all aspects of data collection. Fifth, I checked over all data that was collected each day to look for any discrepancies or missing pieces of information.

In addition to the Indonesian field assistants, other Western scientists and students were also part of the field team. These individuals, Jennifer Burnaford, Andrew Marshall, Christine Perez, Mary Ford, and Sera Blair, assisted me in training, supervision, and data collection during periods when I had to be absent from the field. They were trained in a similar manner as described for the field assistants.

Sampling Regime

Orangutans usually range individually over large areas, making them difficult to find and follow. Thus, a combination of strategies was used to locate the animals. Orangutans were found through walking trails, walking off-trail transects, combing an area where an animal had been previously seen or last contacted, and checking fruiting trees that were known to be favored by orangutans. Individuals were often found by either hearing their movement through the canopy or locating the sound of dropping fruit. Orangutans often vocalized when first seeing someone, which was sometimes the first sign to the searcher that the animal was present. The time it took to find an orangutan depended on the number of people searching, the intensity of the search effort, the availability of fruit and the presence of the primary investigator.

Between August 22, 1994 and November 21, 1998, 20,619 hours of observation were conducted on individual animals. This includes 2272 partial or full day follows. Observation time is defined as the time from the first contact with a focal animal or arrival at the nest, to the time the animal was lost or was left at the night nest. Follow durations during the first year ranged from less than a day to 47 days, with the average follow lasting 3.16 days. The ability to conduct such long-term follows has greatly improved over the course of the study as habituation of the animals and knowledge of their movements and ranges has increased. For example, the mean follow length from the beginning of the study until November 1998 is now 6.70 days.

Once contacted, focal animals were followed until they made a night-nest and were re-contacted by arriving at the nest before dawn the next morning. Typically, one member of the field team followed the orangutan from 5:00 to 11:30 at which time they switched with a second individual who followed the animal from 11:30 to 18:00 or until the animal had

bedded down for the night. During the initial field assistant training period, 2 to 3 people followed each animal during each shift. Currently, many follows are conducted by one individual who follows from 5:00 to 18:00. Some circumstances warranted two individuals following the same animal simultaneously. These were if (1) the animal was in a difficult or dangerous area to access, such as in the swamp forest at the edge of the study site or in very steep areas on the mountain and/or (2) the animal was an adult male who had a history of chasing people. If two people were needed to conduct one follow, and that follow was of a female with a dependent juvenile offspring, the second person took data on the juvenile.

Due to the large range and elusive nature of orangutans it was not possible to locate specific individuals or a specific age-sex class of individual on an "at will" basis. Thus, target animals were normally located and followed opportunistically. When possible, target animals were selected based on priority of the animal to be followed, density of orangutans, and manpower available to search for animals. Female orangutans who were thought to be cycling were given the highest priority, followed by females with dependent offspring, fully developed adult males, undeveloped adult males and juveniles.

Three methods were used to determine whether a female was likely to be cycling: (1) I looked for females who did not have an infant or whose youngest offspring was judged to be over 4 years of age. (2) Urine from individuals who met the first criterion was tested daily using the product Hemastix to detect the presence of blood in urine, indicative of menstruation, and the likelihood of ovulation was tested using the product Ovuquick. The use of Hemastix to detect menstruation is routinely used in zoos (Rogers 1989; Smith 1989; Masters and Markham 1991). Ovuquick is a product designed to indicate ovulation in humans. This test detects the presence of LH (luteinizing hormone) in humans. It is unknown whether the quantity of LH produced in wild orangutans is adequate to trigger a

positive result in this test. Thus, a positive test result could be used to indicate the presence of LH, but a negative result could not rule out the occurrence of ovulation. (3) The possibility that a female was pregnant was established by using a urinary HCG kit also used in zoos (Davis 1977; Hodgen *et al.* 1977) and through assessing whether the labia and vulva were swollen and whitish, indicative of pregnancy (Fox 1929). Again, the effectiveness of using human HCG kits is unknown for wild orangutans, and thus a negative result could not rule out pregnancy. Changes in the labia and vulva proved to be more reliable indicators of pregnancy.

Females who were thought to be cycling were followed for as many days as possible in order to obtain data for complete ovarian cycles. If such a female was encountered while following an orangutan from a lower priority age-sex class, the follower switched to following the cycling female. When cycling females could not be found, females with young offspring, developed adult males and undeveloped adult males were followed. Such animals were typically followed between 3-10 days. If the density of orangutans was high, animals in one of these "lower priority" age-sex categories would be followed for 3 days, and then abandoned in favor of looking for cycling females or other individuals. If the density of orangutans was low, and it was difficult to locate orangutans in any of the age-sex classes, then an animal from one of these categories was followed for up to 10 days and then abandoned to search for a new individual.

Habituation of Animals

During the first three months of the study, the animals were largely unhabituated. Although some of these animals had probably been followed prior to this study, I found through subsequent observation that habituation is lost if an animal has not been followed for more than one year. The degree of habituation was assessed by recording all occurrences of vocalizations and agonistic displays directed towards human observers. All unhabituated animals vocalized when initially contacted. Typically, they would either run away from the observer or hide in a tree crown, tree crotch or in a nest.

To assess the behavioral differences exhibited by habituated versus unhabituated animals in response to people, we (Setiawan, Knott and Budhi, 1996) sub-sampled data from 33 half or full-day follows. The sample consisted of 11 follows from 2 developed adult males, 6 follows from 2 adult females with offspring, 11 follows from 5 adult females without offspring, and 5 follows from 5 undeveloped males. The sample included 6 unhabituated animals and 8 habituated animals. Focal animals were selected based on the objectives of sampling multiple individuals in each age-sex class and obtaining as many follows from each class as possible during the sample period.

Data were collected on travel distance and travel height in the canopy, aggressive behavior and vocalizations, nest placement and vigilance. During each observation period an instantaneous sample (Altmann, 1974) was taken every five minutes of orangutan height in the canopy. All occurrences of aggressive or threatened behavior patterns and vocalizations, either directed toward human observers or other orangutans, were recorded on an *ad lib* basis. Aggressive and threatened behavior fell into the following categories: staring at the human observer, tree shaking, branch shaking, and branch throwing. Vocalizations included kiss-squeaking, grumphs and lork calls as defined by

MacKinnon (1974). The distance between the nest-site and the last visited food tree was estimated to the nearest meter by pacing. Nest height above the ground was also estimated to the nearest meter. Additionally, we measured the dbh (diameter at breast height) of the nest tree using a dbh meter tape.

Vigilance was defined as either actively scanning or staring at a particular spot in the immediate or distant vicinity of the animal. All data on vigilance were collected by a single observer, eliminating the problem of inter-observer reliability. Passively "staring into space" was not counted as vigilance. Obvious bouts of scanning for food or travel path were also not counted as vigilance. The presence or absence of vigilance was recorded during continuous 5-minute intervals, timed with a countdown timer, throughout each orangutan follow. Intervals when the animal was not in clear view were excluded from the sample. When vigilance was observed, the length of each vigilant bout was recorded. A bout of vigilance was measured from the initiation of vigilance until the animal either switched its focus to another behavior or resumed passive "staring into space." This sampling method for vigilance proved feasible with orangutans due to the small percentage of time they spent engaging in vigilant behavior.

We classified animals as habituated or unhabituated based on the number of aggressive/threatened behavioral patterns displayed in combination with alarm vocalizations. The median number of vocalizations for the 6 unhabituated animals was 116.5 times during each follow, whereas the 8 habituated animals had a median of 1.5 vocalizations per follow. These unhabituated animals had not been followed previously. Habituated animals had been followed periodically for a period of several months.

Mann-Whitney U-tests were used to assess behavioral differences between habituated and unhabituated orangutans. Distance traveled and time spent being vigilant were divided by

total observation time for each follow. Significant results ($p \leq 0.05$), presented in Table 2.01, indicate that in addition to aggressive displays and vocalizations, unhabituated orangutans reacted to a perceived threat from humans by traveling greater distances per unit time, traveling at greater heights in the canopy, building nests that were higher and farther away from the their last food source, and engaging in more vigilant behavior than did habituated animals. Unhabituated animals also tended to build their nests in larger trees and to have longer bouts of vigilance, but these differences were not significant.

Due to the above behavioral differences between habituated and unhabituated animals, data from unhabituated animals was not used for any behavioral analyses. To determine which animals were sufficiently habituated to warrant inclusion in the sample, I tabulated the number of vocalizations directed towards the observer emitted by each animal on each day. Then I divided the sample into follows with 0-5 vocalization (403 follows), 6-10 vocalization (67 follows), 11-15 vocalizations (35 follows), 16-20 vocalizations (22 follows), 21-25 vocalizations (15 follows), 26-30 vocalizations (10 follows), 26-30 vocalizations (9 follows), 31-35 vocalizations (7 follows), 36-45 vocalizations (9 follows), and 46 vocalizations or more (13 follows). Using ANOVA and Scheffe-F test comparisons, I found that animals that gave more than 20 vocalization per day spent significantly more time resting and less time eating than animals that emitted fewer than 20 vocalizations per day. Thus, animals that vocalized more than 20 times per day at the observer were categorized as unhabituated and eliminated from further analyses. Normally it required 3 or more days of continuous follows before an animal ceased vocalizing and appeared to resume normal behavior.

TABLE 2.01: Mean values of behavioral patterns exhibited by habituated and unhabituated animals. Significance was tested using the Mann-Whitney U test and values are presented under p. Standard errors are presented in parentheses. Average travel height for each follow was calculated from the travel height values recorded every five minutes during the follow. Sample size, *n*, is number of follows. Data is from Setiawan, Knott and Budhi (1996).

	Travel Distance/ Time (m/hr)	Travel Height (m)	Nest Height (m)	DBH of Nest Tree (cm)	Distance from last food tree to nest tree (m)	Time spent vigilant/obs. time (sec/hr)	Avg. length of vigilance (sec)
Habituated	40.7	21.0	20.2	32.2	14.1	154.7	87.5
(n=27)	(5.95)	(0.64)	(1.2)	(3.78)	(3.02)	(20.92)	(4.97)
Unhabituated	89.5	25.1	26.00	45.2	25.00	412.4	93.9
(n=6)	(18.43)	(1.50)	(1.98)	(9.99)	(2.57)	(128.89)	(26.58)
p value	*.01*	*.01*	*.04*	*.18*	*.02*	*.04*	*.79*

Orangutan Study Population

A core of 27 individuals were individually recognized, named and followed extensively (Table 2.02). These 27 individuals were adults or juveniles over an estimated 4 years of age. In addition, several of the females were accompanied by younger juveniles or infants but data was not generally collected separately on these individuals. Interactions between mother and infant or other juveniles less then 4 years old were recorded on the mother's data sheet. Orangutans were divided into 9 age-sex categories (Table 2.02): adult females, developed adult males, undeveloped adult males, adolescent females, adolescent males, juvenile females, juvenile males, male infants and female infants.

Developed adult males were those with fully developed cheek pads. Undeveloped males were those with either no cheek pads or developing cheek pads. I believe this to be a more appropriate distinction than "adult" versus "sub-adult" males since there is ample evidence that "sub-adult" males are capable of fathering offspring and are functionally adult animals (Kingsley, 1988; Schürmann and van Hooff, 1986). Adolescent females were those who were known or suspected to have separated from their mothers within the past 2 years and were traveling independently. Once a female had her first offspring she was classified as an adult. Adolescent males were those that had separated from their mothers and were now traveling independently or, if their mother was not known, they were individuals that appeared to be very young, still much smaller than adults in body size, and with no sign of cheek pad development. Younger individuals tended to have lighter colored hair and pale eyelids. Juvenile males and females were offspring with an apparent or known age of over 4 years. They were still traveling with their mothers, but usually locomoted independently. Infants were those individuals that were estimated or known to be less than 4 years of age. They often or always traveled on the mother's body. A more exact age estimation was also

given for all dependent offspring and adult animals were further distinguished as young, mature or old.

Over 20 other orangutans occasionally used the study area and were followed briefly (Table 2.03). Unless highly distinctive features were present, an unhabituated animal that was only followed briefly could not be distinguished from other individuals of that age-sex class. However, there were usually some individuals of the same age-sex class that these individuals *could* be distinguished from. Thus this list represents a maximum number of animals that were seen to use the study area during this time. No formerly captive orangutans have been released into the park.

Between August 1994 and July 1998, 5 individual females who were regularly encountered appeared to be cycling: Marissa, Beth, Kristen, Kate and Shea. Beth and Kristen became pregnant during the first year. Shea was followed from November 1994 to December 1995 and then was not encountered again. Kate was followed in 1994 when she was an adolescent female and then found and followed again in 1997 — this time with an infant. Marissa has been the most likely candidate over the past five years to be in "the waiting time to conception" and thus she has been followed extensively, with over 4646 hours of observation collected on her to date. She was believed to be pregnant as of July 1998, and gave birth in late October 1998.

The continual presence of new, unhabituated animals in the study area highlights the point that the orangutans who used the study area were not a fixed group. Some individuals appeared to be resident for months at a time, then they might not be found again for 1 year or more. Other animals appeared to only pass through the study area.

TABLE 2.02: Observation time and age sex-class of orangutan study subjects that could be positively identified between August 1994 and December 1995. Individuals that changed their age class* or infant/juvenile categorization are listed twice, with summaries provided for each category.

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
AB	AF	—	yes	3	34
AR	JM	—	—	4	24
BF	DM	—	—	30	334
BN	DM	—	—	10	88
BT	AF	no	no	39	387
BT	AF	yes	no	122	1370
CR	DM	—	—	8	88
EK	AF	yes	no	8	45
EM	JF	—	—	7	68
EM	AF	no	no	68	662
ER	IF	—	—	2	7

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

TABLE 2.02: Continued

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
EZ	AF	yes	yes	42	423
EZ	AF	yes	no	117	1259
EZ	AF	no	yes	2	17
EV	AF	no	no	3	27
FK	DM	—	—	29	306
GG	UM	—	—	10	80
JK	UM	—	—	14	150
JM	DM	—	—	121	1030
JR	UM	—	—	3	21
KL	FA	—	—	43	448
KR	AF	no	yes	13	101
KR	AF	yes	yes	99	1021

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

Table 2.02: Continued

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
KT	FA	—	—	11	82
KT	AF	yes	no	80	876
LE	UM	—	—	2	18
LL	AF	no	yes	7	63
LN	FM	—	—	5	57
MR	AF	no	yes	436	4657
MS	JF	—	—	244	2557
OK	UM	—	—	5	28
PH	UM	—	—	2	9
RB	UM	—	—	38	207
RC	UM	—	—	9	96
RM	DM	—	—	237	2035

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

Table 2.02: Continued

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
RS	AF	yes	no	10	90
RY	DM	—	—	11	85
SE	AF	yes	no	8	71
SH	AF	no	no	21	201
TB	DM	—	—	24	186
TK	AF	no	yes	5	43
TM	UM	—	—	3	29
TN	AF	no	no	2	13
TY	UM	—	—	3	24
ZL	FA	—	—	3	28
ZR	AF	no	yes	21	218

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

TABLE 2.03: Observation time and age sex-class of orangutan study subjects that were followed briefly and could not be positively distinguished from all other individuals between August 1994 and December 1995. Unnamed, unidentified individuals are grouped together.

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
AK	IF	—	—	1	9
AN	AF	yes	yes	3	30
AR	DM	—	—	2	4
BL	UM	—	—	3	30
BR	UM	—	—	4	37
CE	AF	yes	no	1	5
CN	AF	?	?	2	19
GE	DM	—	—	1	9
FM	FA	—	—	3	27
FP	AF	no	no	3	17
FT	AF	yes	no	3	9

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

TABLE 2.03: Continued

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
HM	DM	—	—	1	8
JR	UM	—	—	3	21
MH	AF	?	?	2	14
MU	AM	—	—	4	31
MV	AM	—	—	3	26
MW	AM	—	—	3	25
PG	AF	no	no	2	14
PT	AF	no	no	3	19
RO	UM	—	—	1	2
SA	UM	—	—	3	14
SB	UM	—	—	3	12
SM	DM	—	—	3	29

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

TABLE 2.03: Continued

Animal	Age-sex class*	Dependent offspring under 4 years of age	Dependent offspring over 4 years of age	Number of days followed	Observation hours
SP	UM	—	—	3	25
SR	AF	?	?	3	27
ST	UM	—	—	3	15
TM	DM	—	—	2	16
Unidentified Females		—	—	131	996
Unidentified Developed Males		—	—	37	232
Unidentified Undeveloped Males		—	—	20	92

* Age-sex class abbreviations: DM = developed adult male, AF = adult female, UM = undeveloped adult male, FM = adolescent male FA = adolescent female, JF = juvenile female, JM = juvenile male, IF= infant

• CHAPTER 3 •

CHANGES IN FRUIT AVAILABILITY

CHAPTER SUMMARY

The aseasonal rain forest of Borneo is characterized by substantial supra-annual fluctuations in fruit production due to mass flowering and mast fruiting in the dominant Dipterocarpaceae tree family and numerous other synchronously fruiting families. A consequence of these mass synchronized fruitings is that they are followed by long periods of low reproductive activity among forest trees. This is a phenomenon unique to the Southeast Asian tropics. Tree flowering and fruiting phenology were documented at Gunung Palung through monitoring 567 orangutan fruit trees, providing an indication of fruit available to orangutans that was independent of the behavior of the animals. A mast fruiting was observed between September 1994 and February 1995 during which the dipterocarps and over 30 other genera of orangutan fruit trees produced fruit. Fruit availability was low for an extended period between March 1995 and March 1996 following the mast fruiting event. Other peaks in orangutan fruits which did not include dipterocarp masting occurred between April and September 1996 and between March and June 1997. These natural changes in fruit availability provided an excellent opportunity to study the effects of variation in food abundance on orangutan behavior and physiology. This chapter provides a summary of changes in fruit availability at Gunung Palung. In subsequent chapters data will be presented on how these changes in fruit production influenced orangutan diet, activity, hormonal patterns and social behavior.

INTRODUCTION

In ecological studies, temporal patterns of food availability are an important variable in understanding the interaction between an animal and its environment. For primarily frugivorous animals like orangutans, monitoring fruiting phenology in the forest provides an assessment of food availability that is independent of the diet and activity of the study subjects. Changes in fruit availability have proven important for understanding behavior in many primate species, such as blue monkeys in Rwanda (Kaplin *et al.* 1998), howler monkey in Guatemala (Crockett and Rudran 1987a, 1987b), orangutans in Sumatra (te Boekhorst *et al.* 1990) and in Borneo (Leighton and Leighton 1983), gorillas in Gabon (Tutin *et al.* 1991) and in the Virungas (Watts 1998a, 1998b), chimpanzees in Uganda (Wrangham *et al.* 1998; Conklin-Brittain *et al.* 1998) and in Tanzania (Matsumoto-Oda *et al.* 1998), and bonobos in Zaire (White 1998; Furuichi *et al.* 1998; Hashimoto *et al.* 1998). In this chapter I present data on variation in the fruit resources available to orangutans which will form the basis for interpreting the behavioral and physiological changes I measured through direct study of the animals.

Mast Fruiting

The tropical rain forests of Southeast Asia, home of the orangutan, are unique in several ways. Borneo and Sumatra and the surrounding regions including much of peninsular Malaysia, Java and the Philippines represent a region that is highly aseasonal even by tropical standards. This area does not have regular annual dry seasons with mean monthly rainfall of less than 100 mm (Appanah 1993). This contrasts with most parts of the neotropics and tropical Africa which have much more predictable annual wet and dry seasons and thus plant phenological patterns of flowering and fruiting that are more seasonal on an annual basis (reviewed in Appanah 1993).

Another unique feature of Southeast Asian rain forests is the dominance of the forest by one tree family, the Dipterocarpaceae. This family of trees typically makes up 50 to 80% of all canopy trees in these forests (Appanah 1993; Rabenold and Bromer 1989). The combination of aseasonality and the dominance of the dipterocarps appears to have produced another unique phenomenon in these forests, that of mass flowering and mast fruiting (Ashton *et al.* 1988; Appanah 1985, 1993). This phenomenon occurs at varying intervals of two to ten years, when a large number of species including the dipterocarps and species from many other families flower and then fruit in synchrony. Instead of being triggered to flower by annual seasonal changes, the trigger for mass flowering appears to be a climatic event occurring at rarer intervals. A wide range of climatic triggers have been associated with mast fruiting, such as extended droughts (Ashton 1964; Medway 1972) and periods of low night-time temperature. It is now believed to be associated with El Niño events and other peculiar weather patterns (Ashton 1988; Ashton *et al.* 1988).

The evolution of mast fruiting has been hypothesized to be a mechanism to escape seed predation through satiation of potential predators (Janzen 1974). Janzen (1974) speculates that this system evolved in Southeast Asia because the climate is more uniform than other tropical regions, allowing a change in climate to serve as a cue for mast fruiting. In their long-term study of dipterocarp mast fruiting and seed predation at Gunung Palung, Curran *et al.* (in press) have found evidence to support Janzen's predator satiation hypothesis.

Mast fruitings are bursts of plant reproductive activity when up to 88% of all canopy species can produce fruit after years of inactivity (Medway 1972; Appanah 1981; van Schaik 1986). Thus, most of the forest's reproductive potential is concentrated during the mast periods. Consequently, non-mast years can be pronounced periods of low fruit availability (Appanah 1985). At Gunung Palung major mast fruiting events have occurred

in 1987 and 1991, and a lesser masting event, with fewer dipterocarp species participating, occurred in 1995 during this study (Curran *et al.* in press).

Fruit Abundance and Vertebrate Frugivores

Studies in all parts of the tropics have shown that fruit availability fluctuates in rain forests (McClure 1966; Terborgh and Diamond 1970; Fogden 1972; Medway 1972; Waser 1977; Struhsaker 1978; Gautier-Hion 1980; Opler *et al.* 1980; Raemakers *et al.* 1980; Hilty 1980; Waser and Case 1981; Foster 1982; Wong 1983; Leighton and Leighton 1983). In addition to community level fluctuations in fruit availability, individual tropical trees usually produce variable sized fruit crops each time they fruit (Janzen 1978; Howe 1983; Wheelwright 1986).

Of particular relevance to the animal communities in tropical forests is the degree of unpredictability of periods of abundance and scarcity. According to Terborgh (1986) one can make the generalization about tropical rain forests that "the more uniform the climate, the more unpredictable and irregular will be the production of resources by vegetation." The more pronounced wet and dry seasons in Africa and in the neotropics (Janzen 1974) correspond with heavier fruit production during predictable, annual wet seasons compared to the dry seasons (Smythe 1986). Borneo, with its more uniform climate (Fogden 1972) represents the more unpredictable end of the spectrum. Because of the mast fruiting phenomenon in Southeast Asian forests, frugivores in this region face the most extreme fluctuations in food availability. These dramatic mast-fruiting peaks are often followed by long periods of fruit scarcity (Appanah 1985).

Fleming and colleagues (1987), concluded that because of these differences in fruiting seasonality, compared to African or South American rain forests, Southeast Asian rain forests are characterized by a higher degree of spatial and temporal patchiness in food availability. They have suggested that a number of features of Southeast Asian vertebrate communities may reflect adaptations to deal with less predictable resources. Compared to similar species in South American and African forests, Asian frugivores tend to have larger average body size, range farther, have more dietary generalization, higher inter-specific dietary overlap, lower densities and exhibit specialized adaptations to long distance travel such as brachiation (Fleming *et al.* 1987).

Because the dominant dipterocarp trees fruit so infrequently they cannot be a reliable source of food for vertebrates (Medway 1972; Janzen 1974). Their dominance also means that there is less space for other fleshy-fruit producing trees in these forests (Janzen 1974). This in turn limits the number of animals that can be supported. Consequently, overall animal biomass is substantially lower in Southeast Asia than in other rain forests (Appanah 1985). MacKinnon *et al.* (1996), for instance, report that primate biomasses are considerably lower in Southeast Asia, particularly in Borneo, than forests in South America or Africa. Lower fruit production appears to have consequences throughout different food webs in the forest. It is believed to result in a lower insect biomass because of fewer resources for guilds of flower and fruit feeding insects (Janzen 1974). The fact that Southeast Asian forests have ten times fewer amphibians and reptiles than do Central American forests (Inger 1980) has been attributed to lower insect biomass due indirectly to mast fruiting.

Reproduction in a number of Southeast Asian frugivores seems to be tied to cycles of fruit availability. For example, a correlation between reproductive activity and periods of high fruit availability has been found in forest rats (Medway 1972) and many species of Asian

birds (Fogden 1972). Fogden (1972) found that some frugivorous birds species in Borneo lose weight and do not breed successfully during unpredictable periods of fruit scarcity. Long tailed macaques have been found to reproduce primarily during periods of high fruit availability (van Schaik and van Noordwijk 1985). Gibbons have also been found to conceive more readily during periods of high fruit availability, with mating and births peaking during years of greatest fruit production (Chivers and Raemaekers 1980). Thus it is reasonable to expect that orangutan reproductive biology may also have been shaped by these unique fruiting patterns of Southeast Asia.

The critical component of mast fruiting for frugivores is not so much the peak of fruit availability but the long period of low fruit availability that follows. Lean periods of food production are critical for understanding the selective forces that have shaped the evolution of most species. Food scarcity provides a strong selective force for the evolution of adaptations that enable animals to survive these periods. It is thus argued here that the particularly high variance in resource availability in Southeast Asia is critical for understanding the proximate and ultimate forces which have shaped orangutan behavior and physiological functioning. In particular, the extended periods of fruit shortage coupled with the unpredictable nature and the magnitude of the fruit peaks may explain why orangutans are so extreme, compared to other primates, in a variety of physiological and behavioral measures.

In this chapter, I present data on how the availability of important orangutan fruit resources varied over a 3-year period at Cabang Panti. Monitoring these changes allowed me to study how orangutan physiology and behavior responded to these fruit fluctuations. I will argue in subsequent chapters that orangutans have evolved a suite of adaptations to take advantage of periods of rich fruit production in order to survive the extended period of severe fruit scarcity experienced in the forests they inhabit.

METHODS

Climate

Daily minimum and maximum temperatures were recorded at 1.5 m height in the shade. Daily rainfall was measured with a plastic rain gauge located in the clearing at the main camp.

Phenology

Relative changes in fruit availability were assessed through monitoring of 753 orangutan fruit plants. The trees (including some lianas) were selected based on records of orangutan census observations collected between 1986 and 1993 by Mark Leighton and his assistants. I set up phenology transects based on these records that included all trees and lianas in which orangutans had been observed feeding, and that were within 25 m of the trail. Trees were distributed along 12 different phenology routes, 2 in each of the following habitat zones found at Cabang Panti: peat swamp, freshwater swamp, alluvial terrace, lowland sandstone, lowland granite, and upland granite. These routes correspond to the trails covered in the original census routes used to generate these lists. Each phenology route was approximately 3 km long.

The trees included in the sample were reassessed after the third year of my study and only those taxa that orangutans had been seen feeding on within this 3-year study period were included in the analysis. Additionally, the original sample included some trees from which only the leaves or bark were eaten, and these were also eliminated from the analysis. The resulting sample described here was composed of 567 trees, all of which are taxa which were fed on by orangutans during this study.

Ninety-three percent of the trees in the sample were identified to genus and represent 56 genera. Species have been determined for 15% of these trees. The trees were identified prior to my study by Mark Leighton as part of his earlier census observations. Further identifications of unknown trees were made by Campbell Webb, Tim Laman and Ismail Rachman. The tree list covers 93% of the known fruit tree genera that orangutans fed on within my study period. Sample sizes of species included in the list ranged between 1 and 42 individuals, and averaged 9.38 ± 9.64 trees per genus (mean ± standard deviation). All trees were reproductively mature.

Beginning in September 1994, these trees were monitored monthly by myself or my assistants for the presence of buds, flowers, and immature, mature and ripe fruit. Each tree was scored as either "X" = no reproductive activity, "B" = flower buds, "F" = flowers, "I" = immature fruit, "M" = mature fruit, and "R" = ripe fruit. Immature fruits were defined as those that were not yet full-sized. Mature fruits were full-sized, but at a stage before ripening. Ripe fruits were those evidencing species-specific changes in color and fruit pulp softness. If two reproductive categories were present in the same tree, the most mature category was used for analysis. Each transect was sampled at approximately the same time every month.

Three measures were taken to assure accuracy and reduce inter-observer bias. First, all observers were rotated each month between different transects. Second, transects were periodically checked by a second observer. Third, samples of all reproductive parts were brought back to the field camp so that I could confirm the reproductive stage that was recorded.

Fruit crop sizes were also recorded. This was accomplished by counting the actual number of fruits in a subsample of the tree crown, and then estimating the number of fruits in the total crown by extrapolation. An approximately exponential scale was used for estimating fruit crop size in which each greater category was double the size of the previous one: A = 1 - 10 fruits; B = 11 - 25; C = 26 - 50; D = 51 - 100; E = 101 - 250; F = 251 - 500; G = 500 - 1000; H = 1001 - 2500; I = 2501 - 5000; J = 5001 - 10,000; K = 10,001 - 25,000; L = 25,001 - 50,000; M = 50,001 - 100,000; N = 100,001 - 250,000. If the crop size was on the border between two categories, the larger category was recorded. Fruit crop sizes are not presented in the current chapter.

Samples of reproductive parts were picked up from beneath each tree and brought back to the research camp to confirm the identification and ripeness stage of the fruit by either myself or another expert. These samples were later dried in a kerosene drying oven and kept as field reference samples. The samples could then be compared to fruit picked up during orangutan observations in order to identify the species or genus consumed.

The trees and lianas in this sample are representative of the species fed on by orangutans. Those species that were fed on more often were more likely to be included in the sample. Thus, the proportional representation of species in the sample is roughly correlated with the relative importance of each species in the orangutan diet. An exception is that mast fruiting tree species such as the dominant dipterocarp trees are not well represented. This is due to the fact that this list of orangutan food trees was compiled primarily during non-mast periods. Thus I believe that the fruit abundance peak demonstrated during the mast by this sample underrepresents the increase in fruit abundance in the environment at that time. Ideally, I would like to use tree density information along with phenology data to better quantify fruit availability but determining the density of orangutan food trees in this forest of over 2000 tree species was beyond the scope of this study. Similar methods of

assessing fruit availability were undertaken by Tutin *et al.* (1991) who monitored 10 individuals of 60 species eaten by gorillas and chimpanzees in Gabon and were not able to account for density.

Analysis

The number of trees and lianas in each of the reproductive categories was summed for each of the phenology transects every month. From this, the total number of trees per month that were either fruiting or flowering was calculated. The actual number of trees checked each month sometimes varied as trees died or could not be relocated. Thus, results are reported as the monthly percentage of checked trees that were either fruiting or flowering.

Additionally, for each of the 56 tree and liana genera, I determined for each month whether any trees of that genus were fruiting and compiled a list of the number of genera fruiting per month. This provides a measure of changes in the diversity of genera that were fruiting.

RESULTS AND DISCUSSION

Climate

The mean daily low temperature was 23.0 °C (S.D. = 1.4), and the mean daily high temperature was 30.9 °C (S.D. = 2.4) . The mean annual rainfall between 1994 and 1996 was 4488 mm (Figure 3.01). Annual rainfall ranged from 3902 mm during 1994 to 5141 mm in 1996. A long period of drought was experienced at the beginning and right before the initiation of my study, with only 33 mm of rain falling in July 1994 and 7 mm in September 1994. During this period there was an associated period of low temperature which, coupled with the drought, may have been part of the weather pattern that triggered the mast fruiting. Except for this drought period, rainfall was variable, unpredictable, and consistently high with never less than 200 mm falling within a single month.

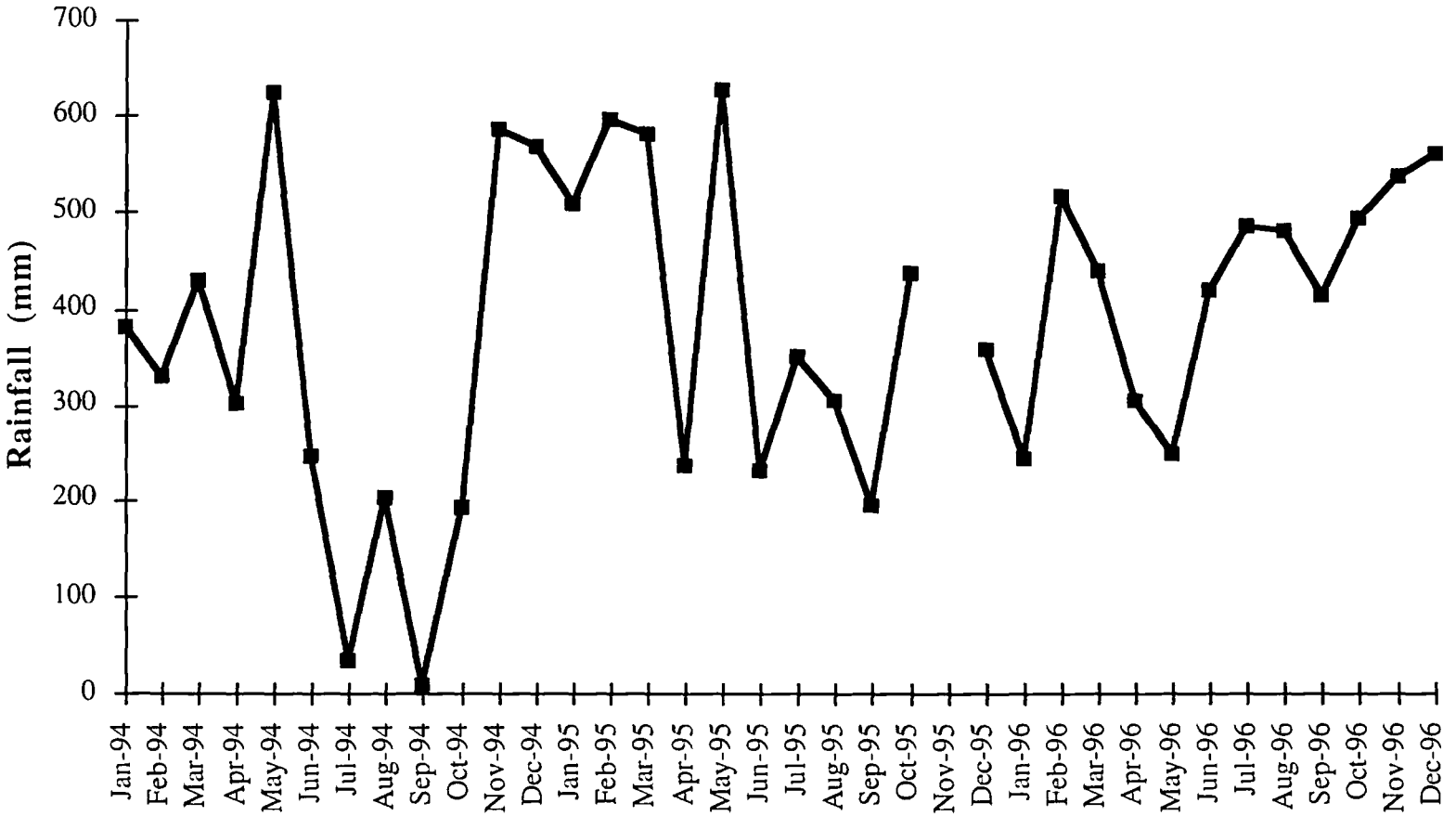


FIGURE 3.01: Monthly total rainfall (in mm) recorded at the Cabang Panti Research Site between January 1994 and December 1996. The gap in November 1995 indicates a period when rain data was not collected. Note that the pattern of rainfall was not predictable and that except for the drought that occurred between July and September 1994, there was never less than 200 mm of rain each month. The drought of 1994 preceded the mast flowering and fruiting that occurred at the beginning of my study period.

Phenology

The forest at Cabang Panti experienced dramatic changes in fruit availability during the period sampled (Figure 3.02). This was due to a mast fruiting event between September 1994 and February 1995 in which a large portion of trees flowered and then fruited in synchrony. The mast was also documented by Curran *et al.*'s (in press) seed traps. Five times as many of the orangutan fruit trees being monitored bore fruit during the month of highest orangutan fruit availability, December, compared to March, the month of lowest fruit availability. After the mast fruiting, between March 1995 and March 1996 there was an extended period of low fruit availability in which only 3 to 9% of trees in this sample fruited in contrast with up to 24% during the mast. As will be shown later, this was a particularly difficult period for the orangutans. In addition to the mast fruiting of 1994-1995, there were two other important peaks in fruit production between April and September 1996 and between March and June 1997. During these fruiting peaks a number of orangutan fruit species fruited in synchrony, but mast fruiting of the dipterocarps did not occur. A second mass flowering and mast fruiting episode began in August 1997.

Figure 3.03 shows the percentage of trees with ripe fruit. Ripe fruit is preferred to immature or mature fruit by orangutans (Leighton 1993). Thus, the percentage of ripe fruit was used as the most relevant measure of orangutan fruit availability to compare to variables of nutritional intake, energetic expenditure, energy balance and hormonal levels presented in later chapters.

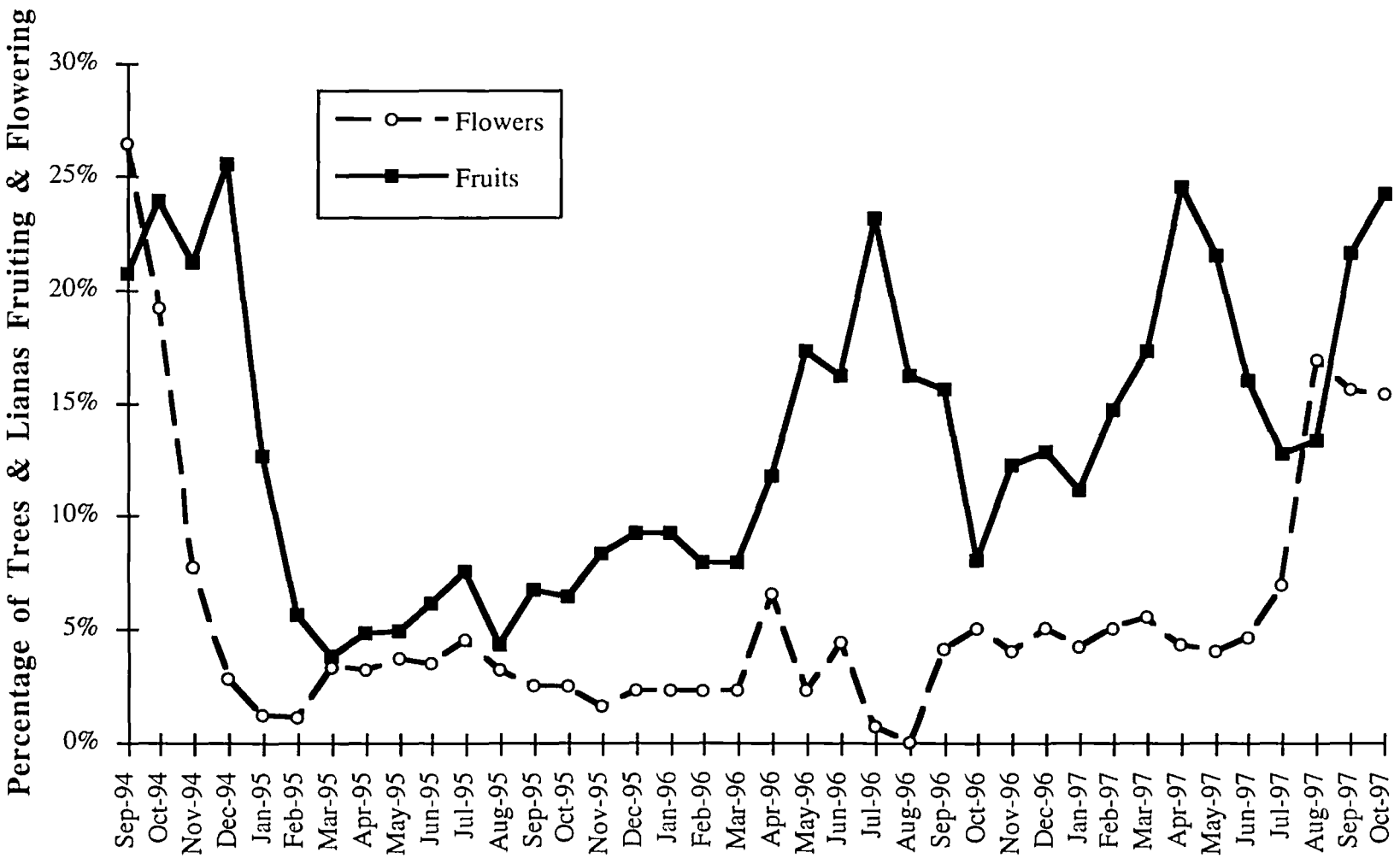


FIGURE 3.02: Percentage of trees and lianas (n=567) flowering or fruiting between September 1994 and October 1997. A mast flowering and fruiting occurred from October 1994 to February 1995 and again in July 1997. Other major fruit peaks occurred April-September 1996 and February-June 1997. Fruit availability was very low for an extended period from March 1995 to March 1996.

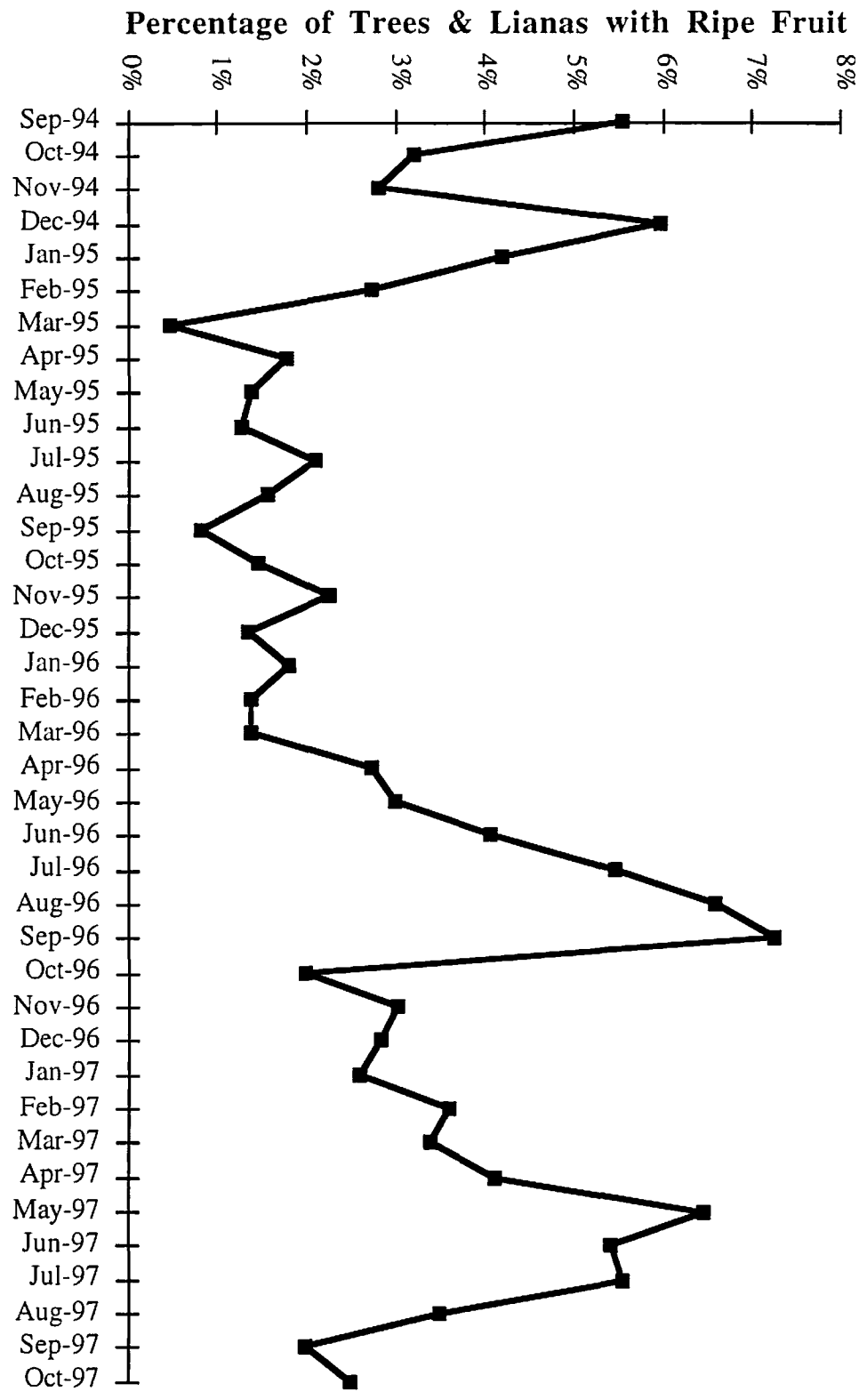


FIGURE 3.03: Percentage of trees and lianas (n=567) with ripe fruit over a 38 month period between September 1994 and October 1997.

The diversity of taxa fruiting each month is shown in Figure 3.04. A total of 36 genera were fruiting during the mast of 1994-1995. Fewer taxa fruited during the other two fruit peaks. Between April and September 1996 27 genera fruited and between March and June 1997 29 fruit tree genera fruited. During the prolonged period of fruit scarcity, only 8 to 14 genera fruited per month.

Figure 3.05 shows the flowering and fruiting pattern of a sample of trees in the genus *Dipterocarpus*, representing the dipterocarp trees that are the dominant canopy trees in this forest and are the primary masting family. Seventy-five percent of the dipterocarps in this sample were fruiting in December 1994. Dipterocarps did not flower again until June 1997. Because dipterocarp trees make up only a small percentage of the trees in the phenology sample, the actual magnitude of the peak in fruit availability may not be well reflected in my phenology graph. For example, the species *Dipterocarpus sublamellatus* is the most common tree species in the alluvial habitat where it occurs at a density of 26 individuals per hectare (Cannon and Leighton, unpublished manuscript). With three quarters of the *D. sublamellatus* trees fruiting across the approximately two hundred hectares of alluvial habitat, on the order of 4000 *D. sublamellatus* trees, each with crop sizes of over one thousand fruits were available to orangutans in this part of the study area alone. Needless to say, despite intensive feeding on *D. sublamellatus* fruits by orangutans in early 1995, only a very small fraction of the fruit crop was consumed before it was ripe and the seeds fell to the ground. Of course in addition to this species, numerous other dipterocarp and other tree species were fruiting at the same time. The dipterocarp mast fruiting period was thus unique during this study in that fruit resources in great excess of what could possibly be consumed by orangutans and other animals were available in the forest. This observation is supported by the findings of Curran *et al.* (in press), also from Gunung Palung, which showed that during the mast fruiting episodes of 1987 and 1991, vertebrates consumed less than three percent of the available dipterocarp fruits.

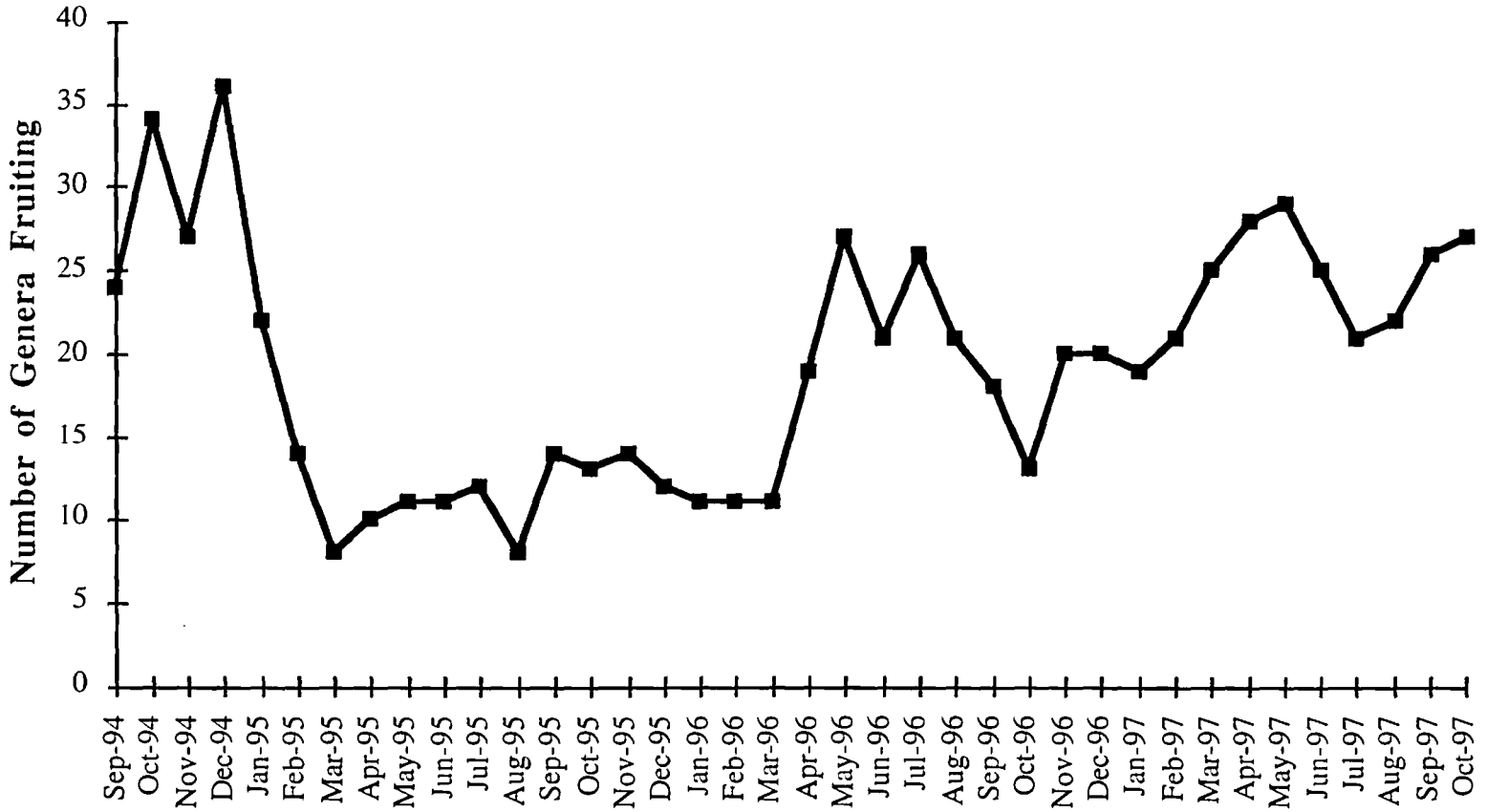


FIGURE 3.04: Number of genera (n=56) from a sample of 567 trees that were fruiting over a 38 month period between September 1994 and October 1997. A peak of 36 genera were fruiting during the mast of 1994-1994. During the extended period of low fruit availability between March 1994 and March 1996 only 8 to 14 genera fruited each month. During the other fruit peaks between April and September 1996 and between March and June 1997 a maximum of 27 and 29 genera fruited respectively.

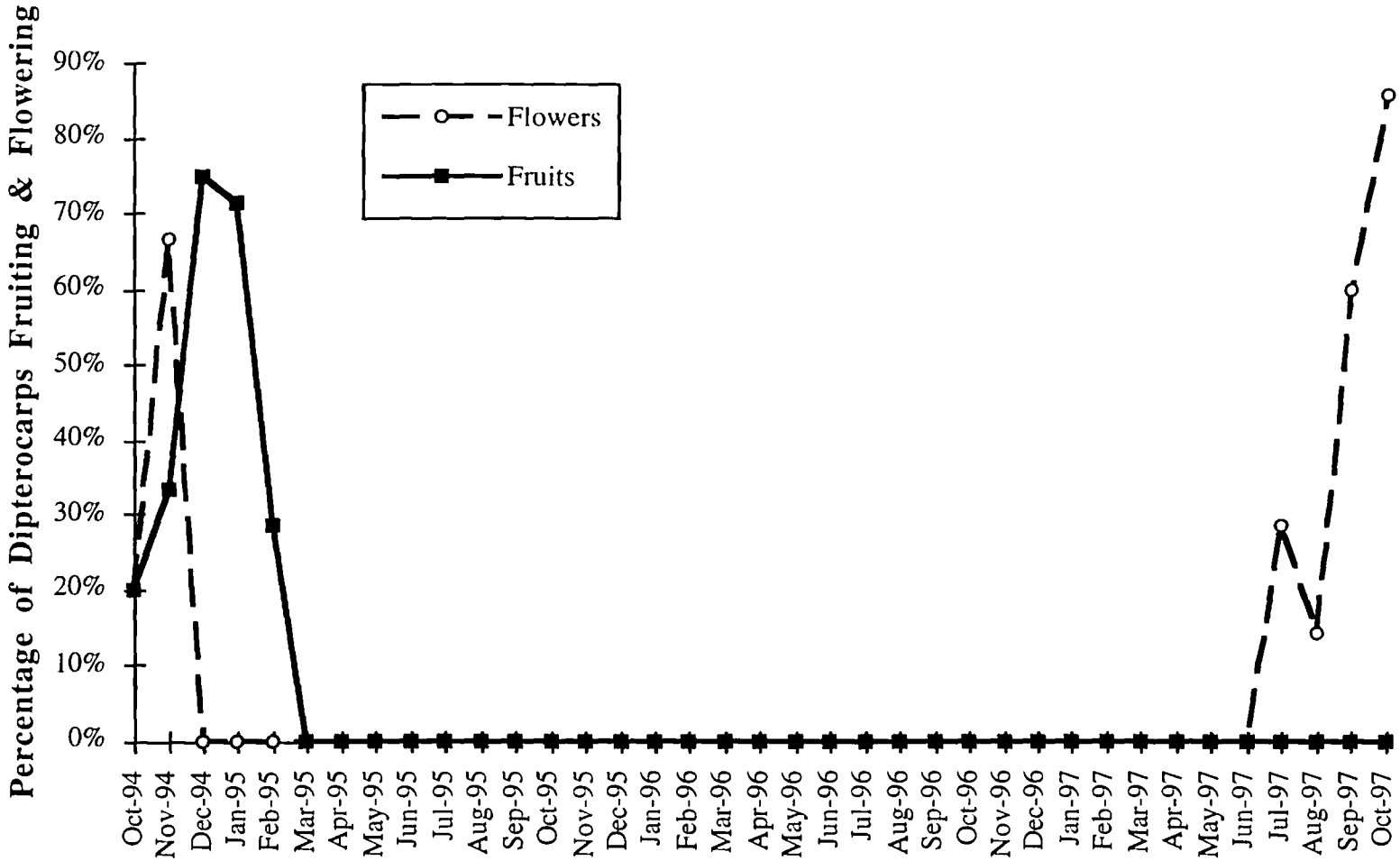


FIGURE 3.05: Percentage of trees (n=7) in the genus *Dipterocarpus* flowering or fruiting over a 37 month period between October 1994 and October 1997. A mast flowering and fruiting occurred between October 1994 and February 1995 and then again beginning in July 1997. No dipterocarp flowering occurred between March 1995 and June 1997. Dipterocarps represent 50-80% of the trees in this forest, thus a significant portion of the fruit trees potentially available to orangutans were non-reproductive during this period.

Figures 3.06 - 3.10 demonstrate some of the fruiting patterns of non-dipterocarp species that were important orangutan fruit sources during the study period. *Artocarpus* (Figure 3.06) and *Baccaurea* (Figure 3.07) followed the dipterocarps and fruited during the mast of 1994-1995. They also experienced secondary peaks between February and July 1997 and a few trees in these genera fruited at other times.

One of the major genera responsible for the fruit peak between April and September 1996 was *Palaquium* (Figure 3.08). This species also fruited in the 1994-1995 mast. It is found in the peat swamp forest in high densities (Cannon and Leighton, unpublished manuscript). Other important orangutan fruit species, such as *Diospryos* (Figure 3.09), were found to fruit on a more regular basis each year.

Some trees in the genus *Ficus* (Figure 3.10) were fruiting throughout the 3-year period presented here. This pattern of consistent fig availability has led to the categorization of figs as a "keystone species" on which animals can rely during period of low fruit availability (Leighton and Leighton 1983; Terborgh 1986). This was found to be the case is my study; orangutans avoided figs during the mast and consumed them most heavily during the period of lowest fruit availability.

SUMMARY

These data illustrate the general pattern of changing fruit availability revealed through this set of orangutan fruit trees. They demonstrate that orangutan fruit availability greatly fluctuated throughout the study, with a mast fruiting peak, two other fruit peaks, and an extended period of very low fruit availability. The existence of long periods of low fruit availability between fruit peaks is probably the most important feature of the orangutan's environment. These patterns will be compared in subsequent chapters to the diet, activity

levels, reproductive functioning and social behavior of the orangutans sampled. These data will illuminate the physiological and behavioral adaptations of orangutans to the pronounced boom and bust nature of the Bornean rain forest they occupy.

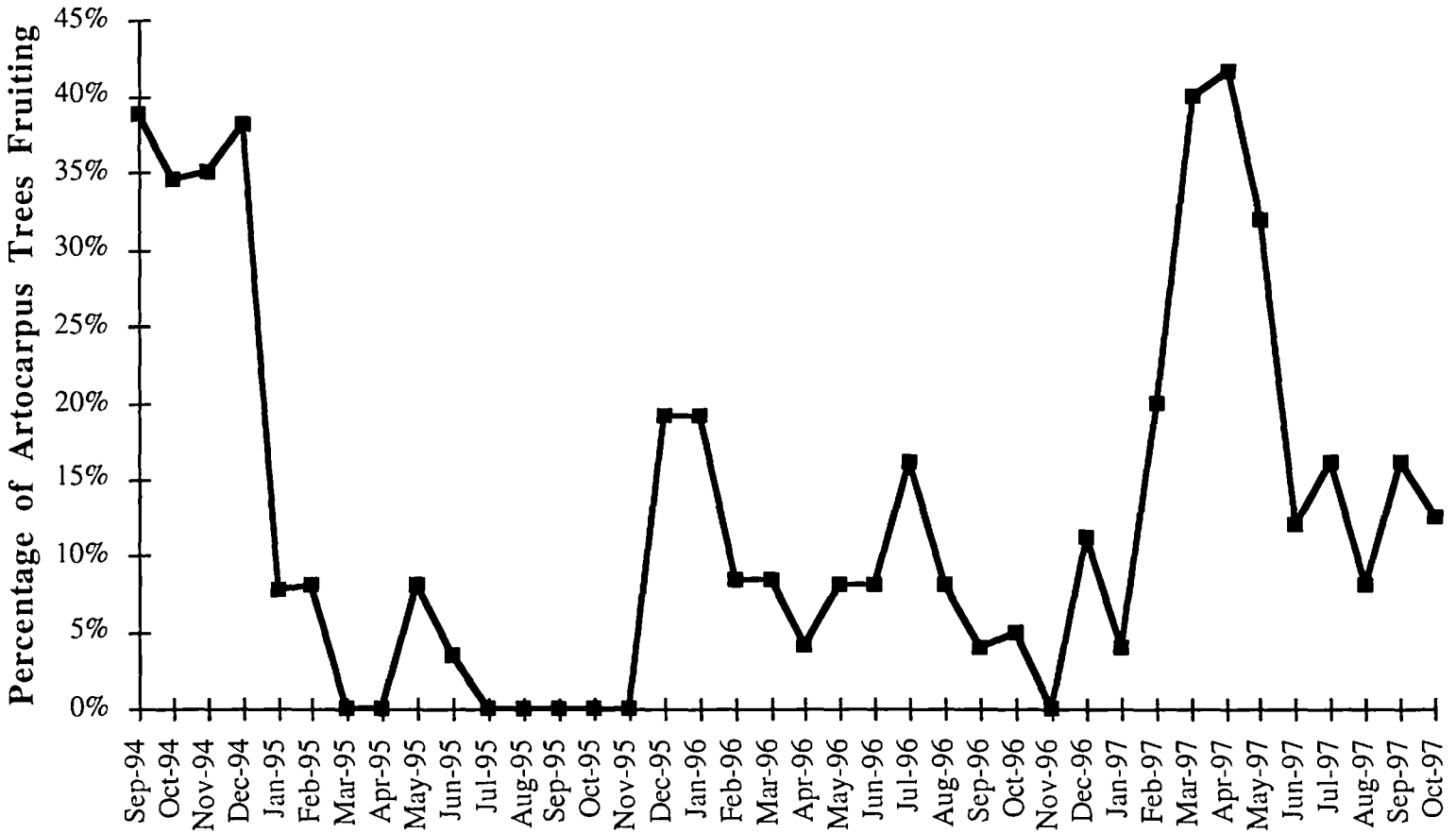


FIGURE 3.06: Percentage of trees (n=32) in the genus *Artocarpus* fruiting over a 38 month period between September 1994 and October 1997. Two major fruiting peaks were observed during this period, one during the Dipterocarp mast of September 1994 to February 1995 and another between February and July 1997.

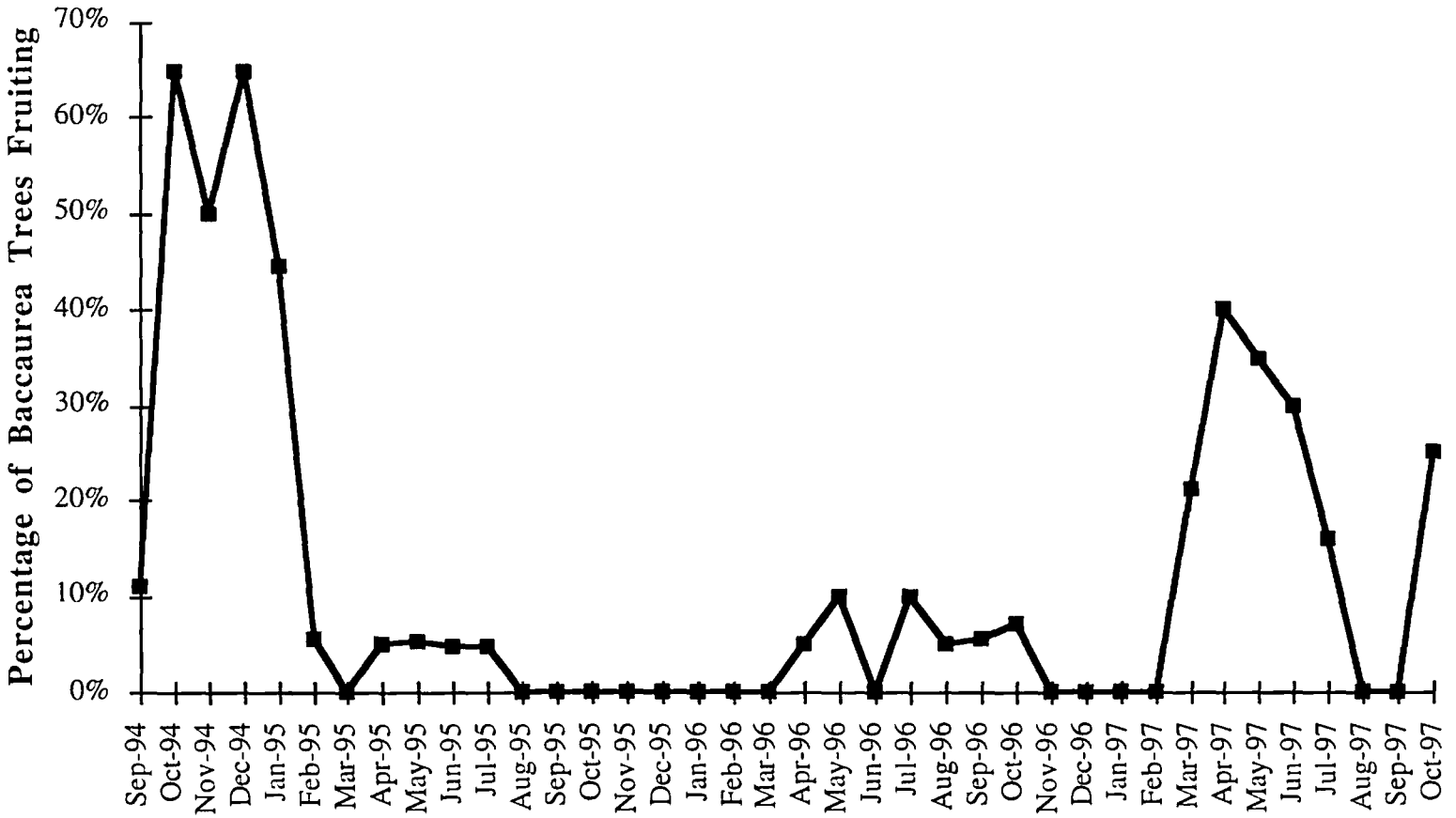


FIGURE 3.07: Percentage of trees (n=22) in the genus *Baccaurea* fruiting over a 38 month period between September 1994 and October 1997. A major peak was observed in the fruiting of this genera during the Dipterocarp mast of September 1994 to February 1995 as well as a minor peak between March and July 1997.

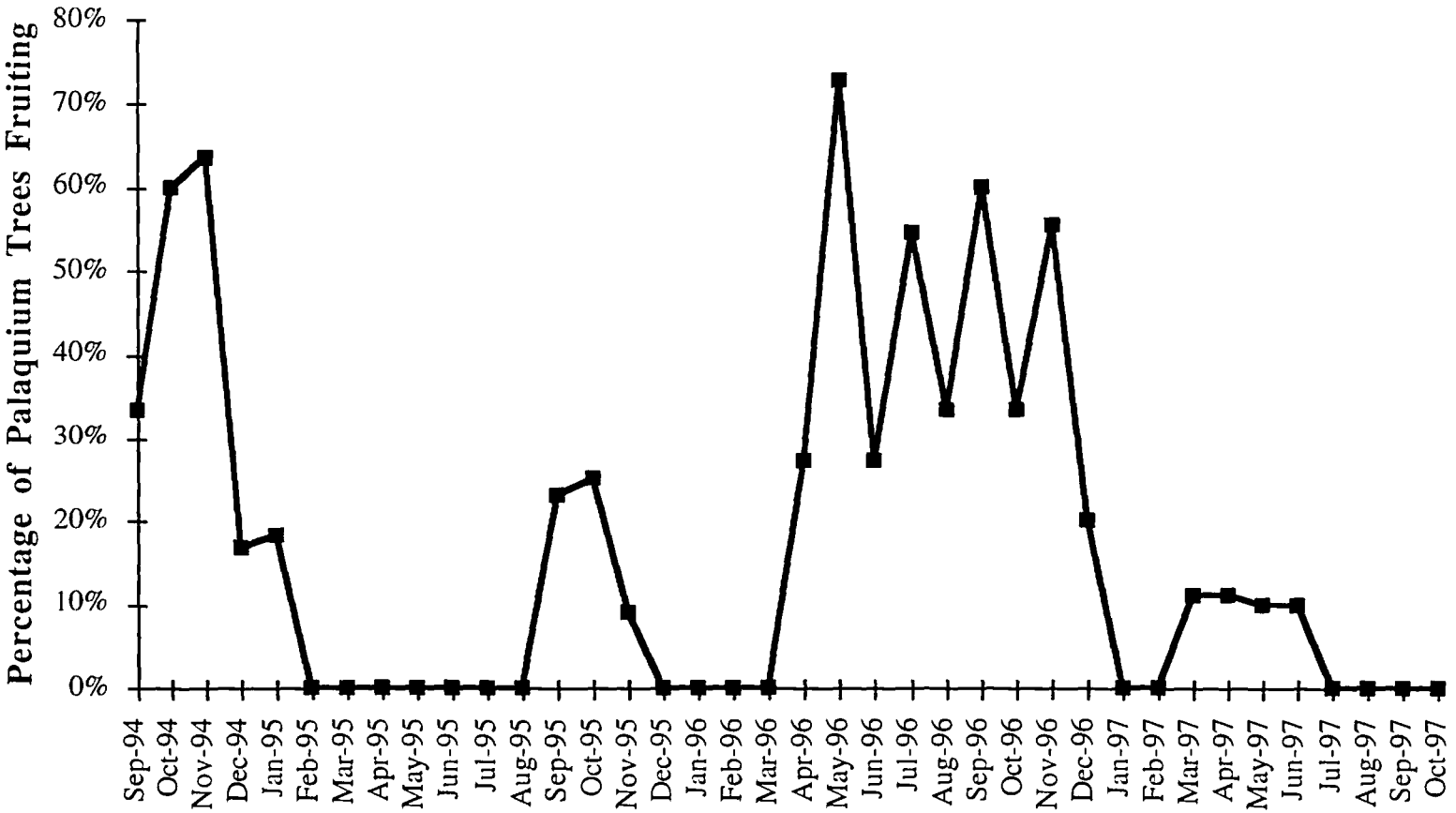


FIGURE 3.08: Percentage of trees (n=15) in the genus *Palaquium* fruiting over a 38 month period between September 1994 and October 1997. Major peaks in *Palaquium* were observed during the mast of 1994-1995 as well as between April and December 1996. Two smaller peaks were also observed during the sample period.

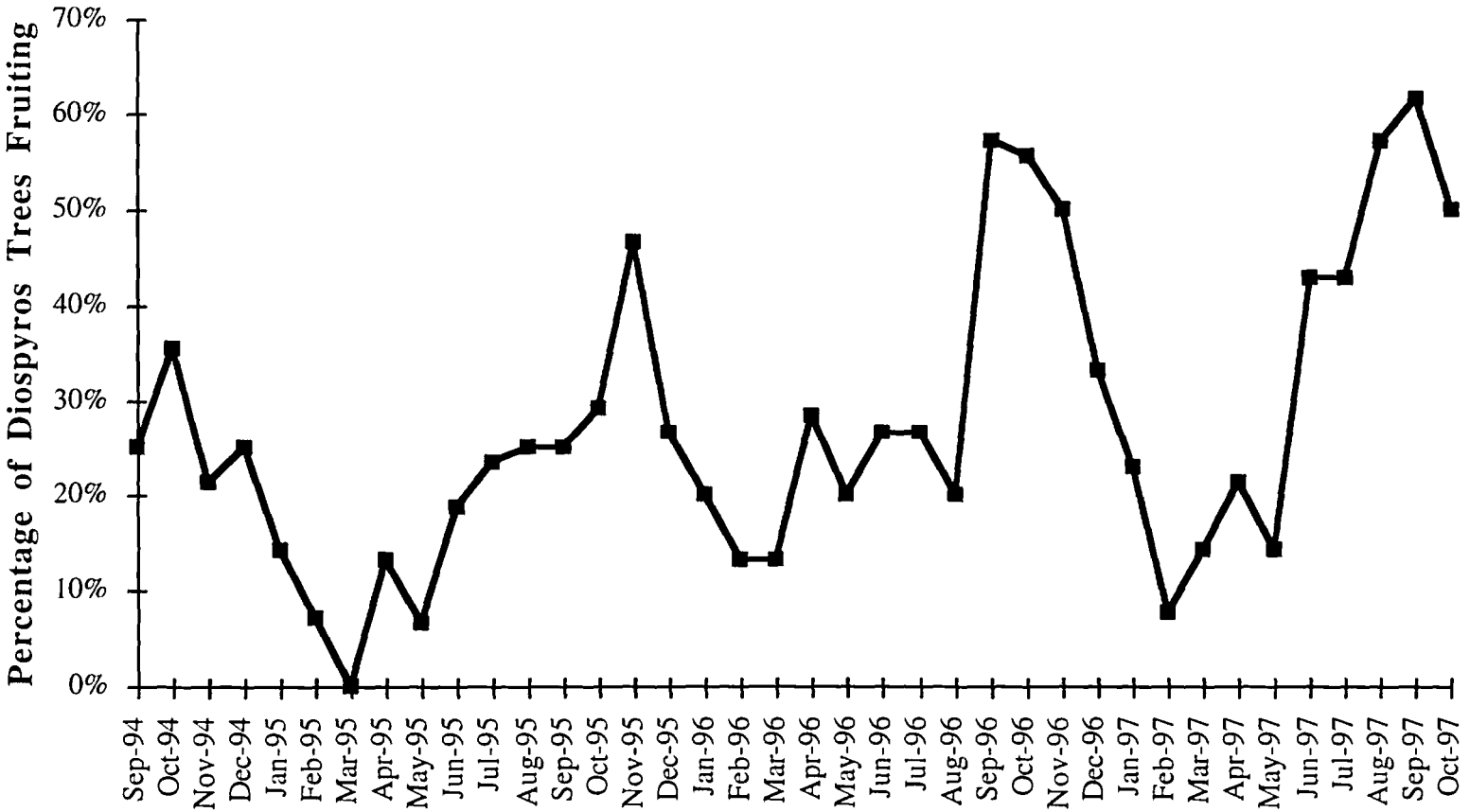


FIGURE 3.09: Percentage of trees (n=19) in the genus *Diospryos* fruiting over a 38 month period between September 1994 and October 1997. Over 30% of the *Diospryos* trees in this sample fruited during the mast of 1994-1995. Three larger peaks were observed during the remainder of the sample period.

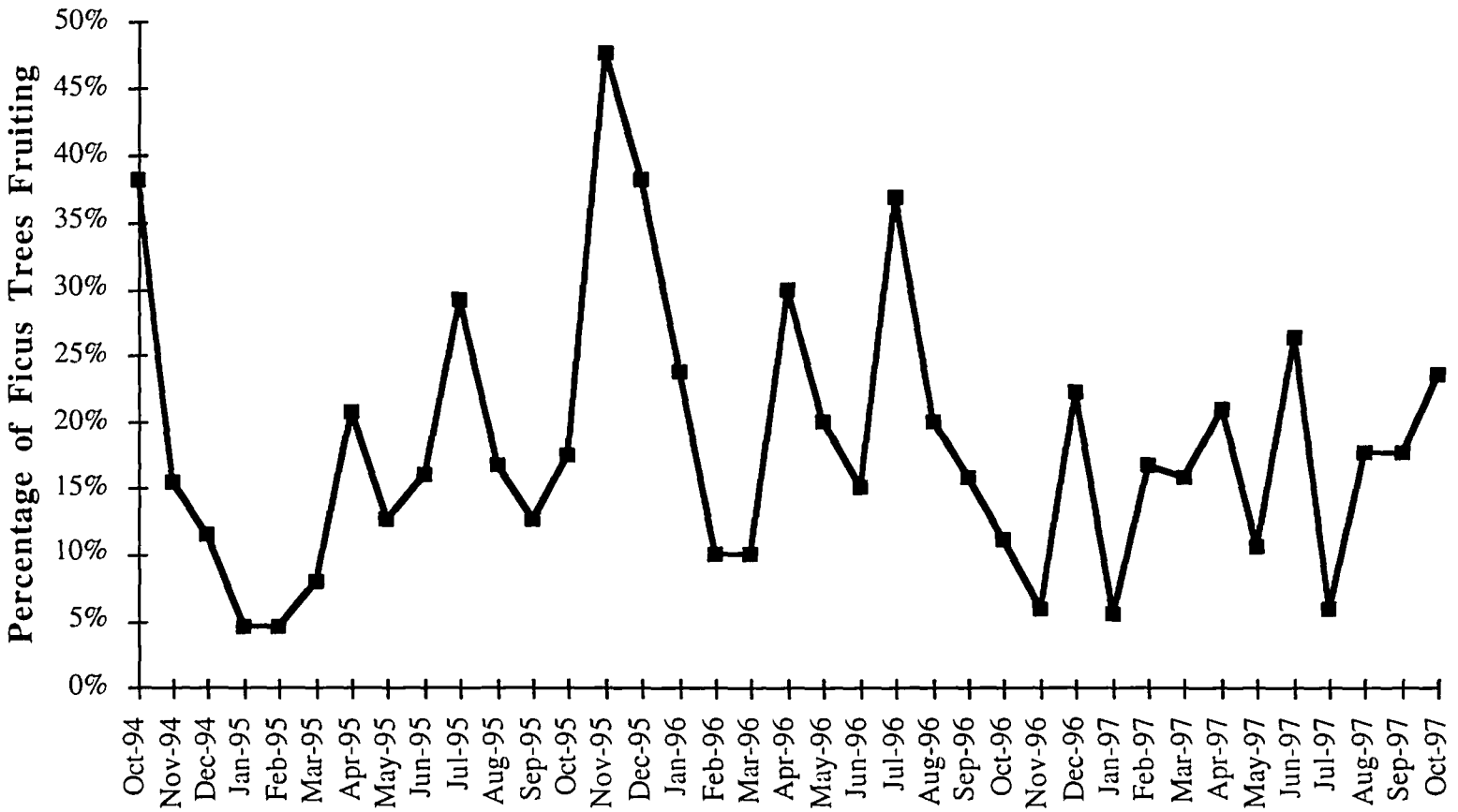


FIGURE 3.10: Percentage of trees (n=33) in the genus *Ficus* fruiting over a 37 month period between October 1994 and October 1997. Some individuals in the genus *Ficus* were fruiting during all months of the year, with numerous fruiting peaks observed over the sample period. Thus, some figs were always available to the orangutans.

• Chapter 4 •

Diet and Nutritional Intake

CHAPTER SUMMARY

Orangutans live in an environment characterized by sporadic peaks in fruit abundance interspersed with periods of low fruit availability. It has been suggested that orangutans cope with this variability in food resources by storing fat reserves during periods of plenty to cope with later food shortages. However, data on variation in orangutan nutritional intake across different fruiting seasons has been lacking. In this chapter I present the first quantitative data on changes in energy and nutrient intake of wild orangutans.

Across a fourteen month study period which spanned a mast fruiting peak and subsequent seven month period of low fruiting, I observed dramatic changes in the proportions and total amounts of fruit, leaves, flowers, pith, insects, and bark making up the orangutan diet. Data from 693 daily follows totaling 5989 observation hours were analyzed indicating that during periods of highest fruit availability, fruit made up almost 100% of the orangutan's diet in contrast with fruit-poor periods when orangutans resorted to alternative foods such as leaves, pith, insects, and bark in greater proportions and fruit declined to as little as 30% of their diet.

The nutritional makeup of the orangutan diet was determined by analyzing samples of the most important 93 food types eaten by orangutans and combining this information with detailed field data on feeding rates from 2441 feeding bouts. I found that when fruits were available, they were highly preferred over other food categories. Contrary to hypotheses about the importance of protein in ape diets, orangutans did not appear to be selecting foods to maximize protein intake but instead maintained a stable amount of protein in their diet all year. Instead, by maximizing intake of carbohydrate-rich fruits when they were available, they took in as much as twenty times as many calories a day during fruit-rich periods as during fruit-poor periods. These findings strongly support the hypothesis that orangutans

are building up fat reserves during fruit-rich periods to help sustain them through low-fruit periods.

Despite their differences in body size, male and female orangutans, in general, had similar diets and maintained similar diet quality. Both males and females showed the dramatic changes in diet with fruit availability. One interesting difference was that males were able to maintain a slightly higher quality diet during some months by increasing feeding on certain large, high calorie fruits like *Neesia* and *Durio* that may have been easier for larger males to open.

Detailed information on the nutritional intake across different seasons such as I have provided here is not yet available for other wild great ape populations. Based on the data that is available on other great ape diets, however, it appears that while all apes experience fluctuations in calorie intake related to fruit availability, the month-to-month differences for other species are unlikely to be as pronounced as reported here for orangutans. This unique aspect of the orangutan's environment may help us to understand certain aspects of orangutan behavior, physiology, reproduction and ultimately evolution.

INTRODUCTION

The goals of this chapter are three-fold. First, I document the magnitude of changes in orangutan diet, caloric intake, and nutrient consumption across the study period. Second, I test the hypothesis that changes in fruit availability are associated with significant differences in the types of foods orangutans eat, their caloric intake and the nutrient composition of their diet. Third, I examine whether there is a sex difference in any of these dietary and nutritional parameters, and if so identify the probable reasons for this variation. I also test the hypothesis that males have a less nutritious diet than do females.

Orangutans have been observed to modify time spent feeding (Rodman 1977; MacKinnon 1974; Mitani 1989), diet composition (Galdikas 1988), and food selectivity (Leighton 1993) in response to the availability of fruit. Earlier studies of orangutans (MacKinnon 1974; Rodman 1977; Rijksen 1978) documented how orangutan food type consumption fluctuates across sample periods. All studies have indicated that orangutans have high periods of fruit consumption, with bark and leaves, and to a lesser extent insects, filling in as fruit consumption declines. It was the impression of these earlier researchers that these changes were due to fluctuations in fruit availability, although this was not measured directly.

Sugardjito *et al.* (1987) and Galdikas (1988) added a phenology component to their studies to test these assumptions. Changes in the availability of figs versus non-figs were investigated by Sugardjito *et al.* (1987). They found that figs were eaten more readily when other non-fig fruits were in short supply. Galdikas (1988) measured changes in phenology through monitoring 690 trees in a plot (all species, not just orangutan fruits). She found strong seasonality in fruit availability but does not directly compare this to diet composition. She does show substantial monthly fluctuations in food type consumption.

Leighton (1993) modeled orangutan diet selectivity through examining multiple selection criteria. His food preference results are compared to extensive phenological data. He reports that orangutans preferred pulp and seeds of non-fig fruits over other food types as demonstrated by how the food type composition of the diet fluctuated with increasing fruit availability. He also found a strong relationship between fruit availability and fruit consumption and a negative relationship with fig and bark + leaf eating. Diet selection was heavily influenced by the energy content of the foods rather than protein.

The present study adds to this body of work on orangutan diets by presenting the first data quantifying seasonal changes in food choice, caloric intake, and nutrient composition of the diet in wild orangutans. It also contributes new observations of sex differences in diet and nutrient selectivity. Recent studies (Wrangham *et al.* 1998; Conklin-Brittain *et al.* 1998) have documented seasonal changes in the nutrient composition of the wild chimpanzee diet. This study adds to this great ape literature by presenting the first data on estimated changes in caloric intake and grams consumed of any wild great ape. In addition, because of the large sample size of observation hours compared to previous orangutan studies, the data presented here provide substantially more information on orangutan feeding patterns than has been previously documented. Although dietary modification has been studied previously in orangutans the magnitude of these changes in terms of caloric consumption, grams eaten and nutrient composition of the diet has not been previously quantified. Through combining data on calories consumed with records of time spent feeding and diet composition we can more rigorously assess diet adequacy, allowing us to measure the physiological and behavioral impact of fruit seasonality on individual animals.

I also investigate possible sex differences in the composition, caloric value and nutritive contribution of orangutan diets. Rodman (1979), found that the male in his sample had

fewer separate feeding bouts and fed longer in each bout than did the females. He suggests that females are more selective in their food choice, and thus have a higher quality diet. Rodman thus sees large body size in males as constraining food choice. An alternative hypothesis is that because of their large size males are able to stay longer at preferred food sources due to exclusion of other animals. If males did have a lower quality diet we would expect them to either consume fewer calories or eat a less nutritious diet than females. Lipid provides the densest source of calories to the diet (9 Kcal/gram), followed by carbohydrates and proteins (4 Kcal/gram). Fiber only contributes calories to the diet to the extent that an animal is capable of fermentation. Thus, I would expect that if males had a less nutritious diet it would be higher in fiber and lower in lipid, carbohydrates, and protein than that consumed by females. The hypothesis that males consume a less nutritious diet than do females can now be tested using the nutritional data presented here.

It has long been hypothesized that orangutans appear to have a pronounced ability to store food resources as fat (MacKinnon 1974; Wheatley 1982, 1987; Leighton 1993). However, no quantitative data exists to support this hypothesis. Such an adaptation would be important in allowing orangutans to take advantage of the supra-annual fluctuations in fruit availability, as a result of mast fruiting, by building up fat to sustain them through periods of low fruit availability. As shown in Chapter 3, the mast fruiting season of 1994-1995 was followed by a dramatic drop in the availability of orangutan fruits. This fruit-poor period was sustained for seven months. If orangutans were able to store excess food as fat during mast seasons it would help buffer them during these critical fruit shortage periods. Presented here is the first direct evidence that orangutans are responding in this way to fluctuating fruit availability.

Documenting the degree to which orangutan diets fluctuate is essential for understanding their physiological adaptations and interpreting their foraging decisions. Such fluctuations

in fruit production are important because of the ultimate effect they may have on fitness through a variety of proximate mechanisms, such as weight loss, disease, and hormonal functioning. A significant drop in energy balance could have serious consequences for both survivorship and reproduction. Thus, fruit seasonality, in particular the ability to survive fruit-poor periods through fat storage and utilization of fall-back foods, may have been an important selective force on orangutan evolution.

METHODS

Feeding Observations

Data were collected continuously on focal animals throughout full or partial day follows. The time of initiation and termination of all feeding bouts was recorded. Using a stopwatch feeding rates were obtained as follows: The observer counted the number of fruits the animal put in its mouth within a one-minute period, waited two minutes and then took another feeding rate, etc. until, if the bout was long enough, 10 such feeding rates were obtained. After that, an additional feeding rate was taken for one minute out of every five minutes in order to adjust the record for changes in feeding rate. In cases where several fruits were put in the mouth at a time, we recorded the number of mouthfuls eaten per minute as well as the number of fruits in each mouthful. Feeding rates were averaged over the bout, or subdivsions of the bout. I controlled for inter-observer bias as explained in Chapter 2. Additionally, for each species of fruit eaten I examined whether there was any systematic bias in feeding rate estimates by different observers.

Feeding rates for fruits that took more than one minute to eat were recorded by timing the period between picking one fruit and picking the next fruit. Thus, both methods

(fruits/minute and minutes/fruit) included harvesting as well as processing time. In some cases, such as when large durian or *Neesia* fruits were eaten, the total number of fruits eaten could be counted. Also noted was the part of fruit eaten (seed, pulp, seed coat, husk or a combination of these), the percentage eaten of each respective part, and the maturation stage of the fruit (immature, mature or ripe).

Processing of Food Samples

Fruit

Samples of fruit were collected either from the ground or by tree climbing by field assistants. Fruits representative of those eaten by the orangutans were chosen based on observing the size and maturation stage of fruits the animals selected. Ripe fruits were often knocked down by orangutan movement through the tree, making this collection possible. Trees were climbed to obtain fruit or leaves if an appropriate sample could not be found on the ground.

At least five samples of each fruit type or species were obtained. At the research camp, these fruits were divided into component parts (e.g. seed, pulp, husk) and weighed wet. They were then dried in a kerosene drying oven averaging 40-50°c for approximately two weeks. After drying, samples were weighed again, providing an estimate of the average grams of dry weight for each fruit. In some cases, particular fruit species were eaten throughout their maturation process. Thus, we continued to collect and weigh fruits at increasing stages of development. Dried samples were sealed in plastic bags and brought back to Harvard University for nutritional analysis.

Leaves

Feeding rates for leaves were obtained in the same way as for fruits, with the maturation stage (young or mature) and the leaf part (blade or bud) recorded. Young leaves were defined as those that were typically found at the end of twigs and that were different in color and softer in texture than mature leaves. Leaves were collected as described for fruit above. For each feeding bout, all the collected sample leaves from that tree were combined and weighed while wet. After drying, the total dry weight was divided by the number of leaves collected to determine the number of grams per leaf.

Bark

Bark consumption was measured by determining the surface area of bark that had been extracted by the orangutan and then calculating the grams of edible material that were consumed. First, if possible, all outer bark discarded by the orangutan after feeding was collected. At the research camp, the length and width of each piece of bark was measured in order to calculate the total area of bark that was fed upon. Each piece of bark was examined and an estimation of the percentage of bark actually eaten (usually the inner cambium) was recorded. Uneaten pieces of tree bark were used to make informed estimates. The remaining portion of the cambium not eaten by the orangutan was then removed. Each sample was weighed and the total grams of bark consumed from each piece could be calculated by dividing the weight of the sample by the proportion of edible material the sample represented. The total number of grams consumed during a feeding bout could then be determined by summing the grams consumed from each piece of bark. This also provided a measure of grams of edible cambium consumed per surface area of bark fed upon.

If all the bark could not be picked up, then the percentage of bark pieces collected by the observer was recorded. All the collected pieces of bark were measured as above to provide the surface area of bark collected. This was divided by the proportion of bark pieces collected to determine the total surface area of bark upon which the orangutan fed. As above, the grams of bark for a given surface area were determined from the pieces that were collected and this number was multiplied by the total surface area of bark consumed to provide the total grams consumed during the bout.

If no bark could be collected, then the tree was examined to estimate the surface area of bark that was fed upon. The grams consumed from that tree were determined by dividing the estimated surface area of bark fed on by an average value of grams of cambium eaten per surface area (determined from other feeding bouts as described above). The samples that were used to obtain this average were matched as closely as possible to feeding bouts on the same tree species, by the same orangutan, and within the same time period.

Additional data on rates of bark consumption were obtained through tree climbing. Soon after an orangutan fed on the bark of a given tree we would return to that tree and a tree climber would (1) measure the area of bark that had been eaten by the orangutan and (2) peel off additional bark from the area adjacent to the feeding site. The first piece of information provided actual, as opposed to estimated, data on the surface area of bark eaten by the orangutan during the feeding bout. Secondly, the additional bark peeled off was brought back to the field camp and the cambium layer of the bark was extracted. This was weighed and dried and provided a very accurate estimate of the grams of bark available/surface area of bark. These data could be used to estimate the grams of bark consumed for feeding bouts in which we could not obtain a bark sample.

Pith

Orangutans fed on *Pandanus*, ratan and other epiphytes and pithy plants by typically extracting the soft, pithy portions and then discarding the remaining part. These discards were collected and used to estimate the amount of material that was missing and assumed to have been consumed. First, the width and length of each stalk was measured. Then, uneaten plants of the same species were collected, the grams of edible material were extracted and weighed, and the outer covering of these stalks was measured. This provided a measure of the grams of edible material per stalk of a given length from which grams eaten could be calculated.

Insects

Insect feeding was primarily confined to arboreal termites, although ants, terrestrial termites, and occasionally wasps or bee larvae were also consumed. Typically the orangutans employed one of three techniques when feeding on insects. In order to pick up individual insects they would either bring the source of the insects (wood, carton nest, or epiphyte) to their mouth and pick up individuals with their lips, use their fingers to pick up individuals from the nest, or use their lips and tongue to pick up insects that had run onto their hair. This last technique was used predominantly for ants that tended to flee when an orangutan opened one of their nests, whereas the first two techniques were used for termites that tended to remain in their nests. No tools were used by the orangutans. We counted the number of times per minute the orangutan brought the nest to it's mouth or it's mouth/lips to the nest during each of these bouts. The number of insects consumed in each mouthful could not be determined through direct observation. Thus, I examined these nests and, based on the density of insects per cm^2, I estimated that the orangutans were probably able to consume a maximum of 10 insects per mouthful. Because individual

termites only weighed 0.001 g (dry weight), even a doubling of this rate would have a negligible effect on caloric or gram intake estimates.

The orangutans would normally discard the source of the insects (wood, carton nests, or epiphytes) after feeding. Many individual insects always remained in these discarded nests. The nests were sealed in plastic bags and brought back to the field camp. Nests were then placed in plastic trays and the insects were plucked individually from the nests using special light weight "insect" forceps. Individuals were placed in glass bottles containing 70% ethanol and 30% purified water. Termites always remained close by their nest and did not attempt to leave the plastic tray. Ants, however, tended to flee, thus a Vaseline barrier was applied around the lip of the tray to prevent their escape during the collection process. Bottles were labeled with the collection date, time of collection, collector, animal and nest location. Additionally a written data sheet was filled out for each insect collection with the above information as well as a description of the type of nest, a description of the insect (color, etc.) and a drawing of the insect. Collection bottles were weighed when empty, when filled with solution, and after they were filled with insects in order to obtain the wet weight of the insects. All samples were brought back to the Nutritional Chemistry Lab where dry weights were obtained.

Nutritional Analysis

All nutritional analyses were conducted in the Nutritional Chemistry Laboratory in the Anthropology Department at Harvard University. Crude protein (CP) was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce and Haenisch 1947). The digestion mix contained Na_2SO_4 and $CuSO_4$. The distillate was collected in 4% boric acid and titrated with 0.1 N HCl. The detergent system of fiber analysis (Goering and van Soest 1970) as modified by Robertson and van Soest (1980)

was used to determine the neutral-detergent fiber (NDF), or total cell wall fraction. Lipid content was measured using petroleum ether extraction for 4 days at room temperature, a modification of the method of the Association of Official Analytical Chemists (AOAC, 1984). Dry matter (DM) was determined by drying a subsample at 100°C for 8 h and hot weighing. Total ash was measured by ashing the above subsample at 520 °C for 8 h and then hot weighing at 100 °C. Organic matter (OM) was calculated as 1 minus ash multiplied by DM. The remaining total non-structural carbohydrates (TNC) were estimated by subtraction (100 - (NDF + CP + lipid + ash)). The potential energy available from the NDF fraction was calculated following the guidelines of Milton and Demment (1988) and Conklin and Wrangham (1994). However, I used a lower estimate of Kcal/gram than Conklin and Wrangham (1994) because their estimate did not take into consideration the high lignin content of wild diets (Conklin pers. comm.). The digestion coefficient calculated by Milton and Demment (1988) was determined from chimpanzee feeding trials with a diet containing less than 3% lignin. Such trials have not been done for orangutans. Female orangutans have a similar body size to adult chimpanzees and should be able to digest at least this much fiber at comparable levels. However, this may be an underestimate of metabolizable energy available to adult male orangutans because their larger body size may lead to an increased capability for hind-gut fermentation.

Nutritional analyses have not yet been conducted on the insects fed on by orangutans in order to first allow for taxonomic identification. Orangutans fed primarily on canopy termites and ants which are poorly known from Kalimantan. Specimens will be identified by the Termite Research Group of the Natural History Museum, London, with the possibility that some new species may be identified. Thus, I used published literature on termite nutrient composition (Oyarzun *et al.* 1996) for those calculations.

Calculation of Caloric Intake and Nutrient Composition

The caloric and nutrient content of each feeding bout was calculated by combining feeding bout data with laboratory analyses as follows. First, I calculated the length of each feeding bout. This bout length was then multiplied by the mean feeding rate or divided by the handling time to provide the total number of food items consumed. As discussed earlier, in some cases the actual number of food items consumed was recorded. This number was then multiplied by the proportion of the food item eaten to provide an adjusted estimate of number of food items eaten. These values were multiplied by the average dry weight of each food item (grams/food item) to calculate the total grams consumed during each bout.

In cases where a fruit was eaten at different stages of development, and thus at different weights, I determined the appropriate dry weight to use for the calculation based on the date the fruit was eaten. If a feeding rate was not obtained for a given bout, then I used an average feeding rate for that food item matched as closely as possible to known rates for that food item by the same animal on the same day.

Total calories were calculated based on the energetic value of the nutrient fraction of each food item assuming the values of 9 Kcal/g lipid, 4 Kcal/g CP and 4 Kcal/g TNC, taken from values used for humans (National Research Council 1980). Grams of fiber (NDF) were multiplied by 0.543 Kcal/g. The Kcal of metabolizable energy per gram of each food item were multiplied by the grams of that food item ingested per bout to obtain a measure of the Kcal consumed during each feeding bout. All bouts from each day were then summed to calculate the total Kcal consumed/day.

In some feeding bouts the food item was unknown. Thus, the caloric content of these bouts could not be calculated. In order to estimate total daily caloric intake, the remaining

unanalyzed proportion of the diet for that day was extrapolated based on the average caloric intake per minute for that animal on that day.

Statistical Analyses

Due to the composition of the orangutan population individual animals were repeatedly sampled. Thus, in order to eliminate pseudo-replication within each month, I calculated for each individual the mean monthly value for each of the variables described in this chapter (i.e. Kcal's consumed, percent lipid, etc.). When comparing within one sex or between sexes I used these mean monthly values, weighting each animal equally in the analysis so as to eliminate pseudo-replication within each month. For analyses in which males and females were combined, I calculated the overall mean for each sex for each month, taking an average of individual averages and reducing the data to one value for males and one value for females per month. In this way each sex was weighted equally.

Percentage of trees in the phenology sample with ripe fruit was used as the fruit availability index. Linear regression was used to examine the relationships between food type and nutrient intake and fruit availability. When greater means were accompanied by greater variance I log transformed the data so that the variance would be independent of the means as recommended by Sokal and Rohlf (1981). The data set also included some zero values, thus the transformation "log (y +1)" was applied. ANOVA was used to test for differences between months in the various food intake and nutritional variables. Due to the presence of zero values, the Spearman-Rank Correlation test was used to test for relationships between categories of food type consumed. For comparison, the same test was used to compare between nutrient categories consumed.

As described previously, the opportunistic nature of the sampling meant that individuals were not sampled equally. Thus, weighting by individual over represents the contribution of animals that were sampled infrequently in a given month. For example, the mean for one animal may reflect 20 follow days, whereas another animal may be represented by just two follow days. In previous studies of orangutans the investigators did not control for individual animals (Rodman 1977, 1984; Galdikas 1988; Mitani 1989; Leighton 1993) and often just one animal of a given sex was followed (Rodman 1977). Thus, I also present, for ease of comparison with these previous studies, selected analyses in which each follow day is weighted equally. Non-parametric statistics are used in these analyses. Although biased towards animals that were sampled the most, these analyses may more accurately reflect the actual activity of animals that were found within the study area. It also allows for comparison of between-day variation. Animals were sampled in relation to their presence in the study area as well as our ability to find them. The same primary results are exhibited using both methods of analysis, but the absolute values differ depending on the method utilized.

Due to the small number of individuals in the population, comparisons between the sexes, broken down by month, could not be carried out when the data had been reduced to a mean value for each individual. Thus, in these comparisons I used each follow day as an independent sample. The more conservative Mann-Whitney U-tests were used in these analyses. However, this does not avoid the problem of pseudo-replication. Thus, such analyses should be viewed as preliminary.

RESULTS

Sample

Between August 1994 and December 1995 a total of 693 daily follows were conducted, constituting 5989 observation hours. For the purpose of nutritional and dietary analysis I eliminated all unhabituated animals from the sample (as described in Chapter 2) and confined the analysis to adult females and fully-developed adult males. Thus, undeveloped (sub-adult) males and juveniles were not included in the sample. Due to the large number of unhabituated animals at the beginning of the study, I focus here on the period between November 1994 and December 1995. Both the mast period of high fruit availability and the post-mast period of very low fruit availability are included in this time span. The resulting data set used for the analyses in this chapter is drawn from 313 daily follows from 14 adult males and 14 adult females. When an animal was followed from the time s/he arose until s/he went to sleep this was called a "full day" follow, making up 207 of the follows reported here. The number of animals sampled and the number of follows conducted for the subsample of the data presented in this chapter, broken down by month, by sex, and by follow length is shown in Table 4.01. Please refer to this table for sample sizes used in figures in this chapter. The total data set presented is taken from 3159 observation hours and 2441 feeding bouts. The median percentage of diet analyzed in these bouts was 98.9%. I examined the feeding rates obtained for each fruit species and found that no observer systematically under or over estimated feeding rates compared to other observers.

Analyses that report total daily intake are restricted to full day follows. This enabled me to test for differences between the *total amount* of each food type or nutrient consumed. Analyses that report variables as percentages of feeding time include both full and partial

day follows. This provides information on the relative *proportion* of various food types and nutrients in the diet.

All variables were calculated in three ways: as total or percent time spent feeding, as total or percent grams consumed, and as total or percent Kilocalories (Kcal) consumed. These three versions of the data provide different information. Minutes of consumption provides the most accurate representation of foraging effort—how much time an animal devoted to finding and eating particular foods or nutrients. Grams of consumption is roughly correlated with minutes spent feeding to the extent that the longer an animal spends feeding on an item the greater the number of grams that are consumed. However, foods that have longer processing times, such as insects or some types of plant matter, may provide fewer actual grams to the diet than is indicated by minutes spent feeding. Thus grams is the most accurate measure of how much of an item they were eating. Finally, Kilocalorie data tells us the actual caloric contribution to the diet of particular foods and nutrients. This is the most physiologically relevant measure of diet quality.

TABLE 4.01: Break down of number of animals and number of follows included in the dietary and nutritional analyses presented in this chapter. Numbers in parentheses refer to the subset which came from full-day follows.

Month	# Females	# Follows	# Males	# Follows
Nov, 1994	6(3)	14(4)	5(2)	7(2)
Dec, 1994	3(2)	8(5)	9(3)	17(3)
Jan, 1995	3(1)	16(10)	1(1)	14(3)
Feb, 1995	2(1)	14(7)	2(2)	15(5)
Mar, 1995	1(1)	1(1)	1(1)	5(5)
Apr, 1995	2(1)	10(8)	2(2)	13(12)
May, 1995	2(2)	24(23)	1(1)	5(5)
Jun, 1995	2(2)	20(18)	2(2)	18(14)
Jul, 1995	1(1)	3(2)	2(2)	14(9)
Aug, 1995	1(1)	10(10)	2(2)	13(8)
Sep, 1995	4(3)	15(13)	2(1)	8(3)
Oct, 1995	1(1)	26(22)	1(1)	3(1)
Nov, 1995	1(1)	17(12)	0	0
Dec, 1995	0	0	1(1)	4(2)

Seasonal Changes in Dietary Composition

In accordance with changes in fruit availability, orangutan diets varied dramatically during the course of the study (Figure 4.01). Differences in time spent feeding on different food types were highly significant between months in the consumption of fruit (ANOVA: $F = 4.5$, $p < 0.0001$), leaves ($F = 5.53$, $p < 0.0001$), pith ($F = 5.32$, $p < 0.0001$), and bark ($F = 3.74$, $p < 0.0004$). Flower and insect consumption was not significantly different between months in time spent feeding. Grams of consumption and Kcal's of consumption showed the same pattern.

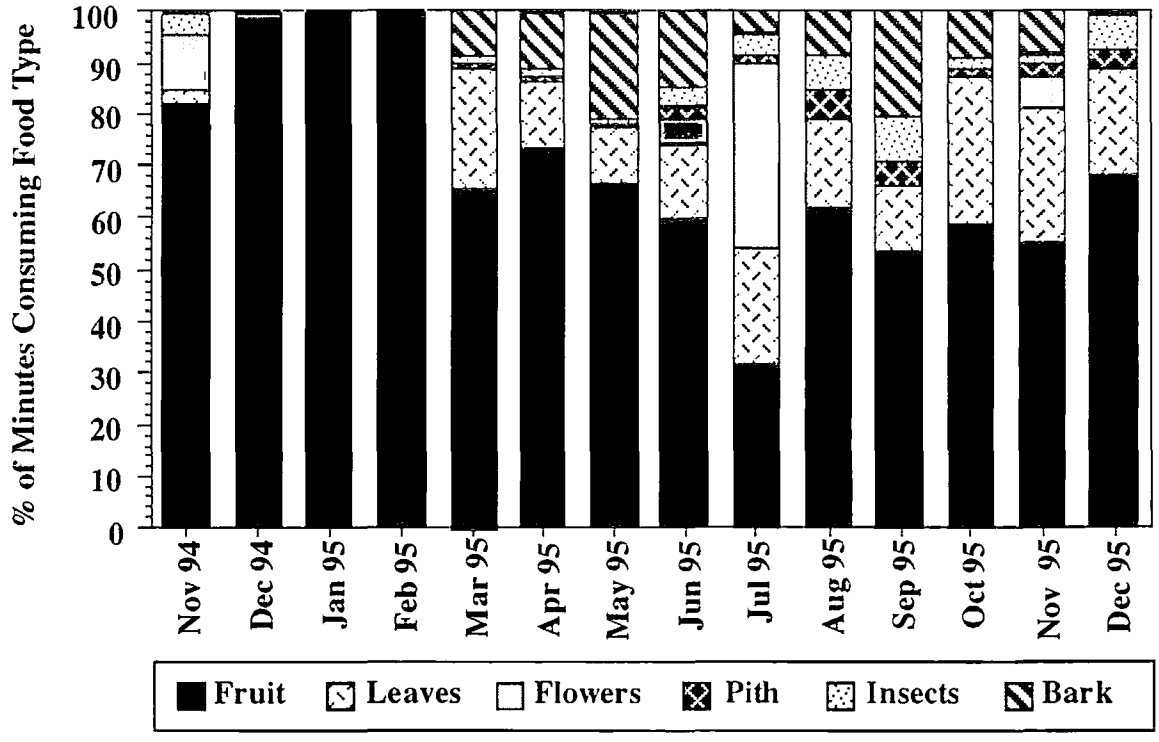


FIGURE 4.01 Percentage of time spent feeding consuming fruit, leaves, flowers, pith, insects, and bark from full and partial day follows of adult female and fully-developed adult male orangutans. Samples sizes are shown in Table 4.01

In November 1994, as the flowering period of the mast was coming to a close, the orangutans spent 10.7% of their feeding time eating flowers. During the peak period of fruit availability, December 1994 through February 1995, the orangutans fed almost entirely on seeds, whole fruit and pulp. Leaves, pith, bark, insects, and flowers combined, constituted less than 1% of the diet.

At the end of the mast fruiting in February, a period of severe fruit shortage began. Orangutans shifted to incorporating bark and leaves as fall-back foods. Insects and pith were fed on in lesser quantities. Fruit, however, remained the major dietary component except for the month of July. In July 1995, a significant portion of feeding time (35.5%) was spent consuming flowers in the genus *Gluta*. These were evidently preferred over the fruit that was available.

All food types do not make the same caloric contribution to the diet, thus Figure 4.02 presents the percentage caloric contribution of each food type to the overall diet. Although the pattern is similar, fruit contributed a significantly greater portion of the diet on a Kcal basis than on a time spent feeding basis (Paired T-Test, $P < 0.002$) due to the higher caloric value of fruits compared to leaves, bark, pith, insects and flowers. Thus, fruit yields the highest energy return per unit of feeding time and is likely one of the primary reasons that fruit is the preferred food type.

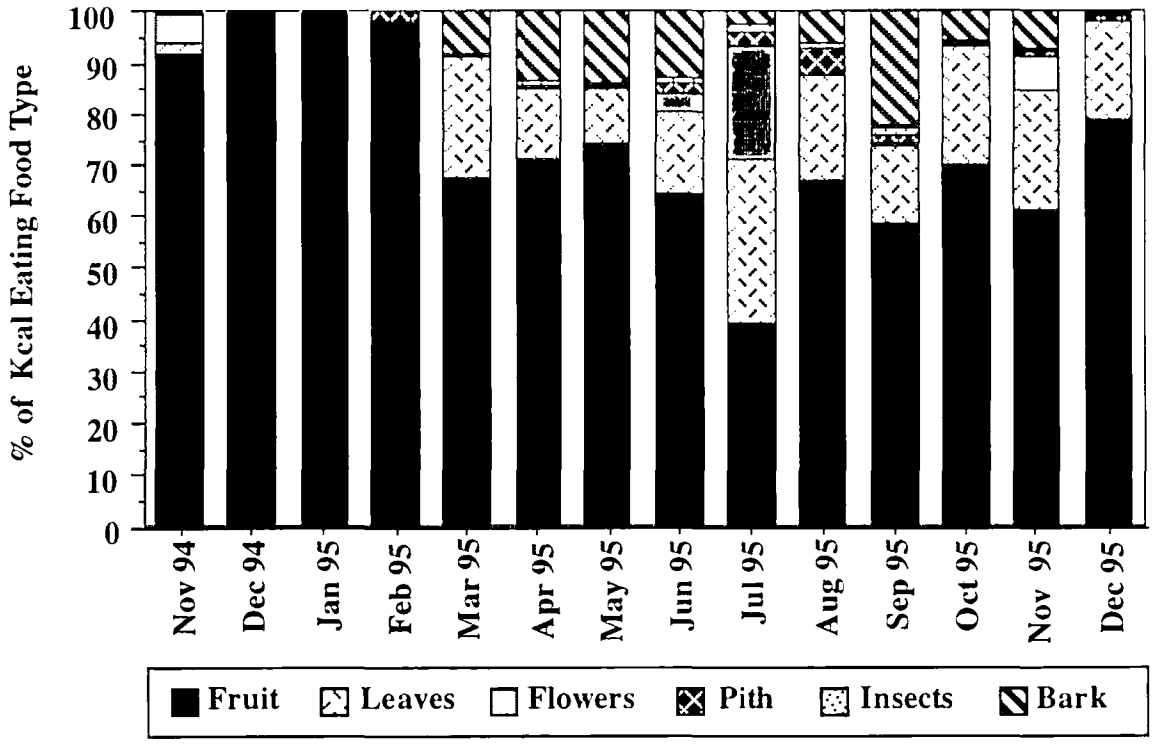


FIGURE 4.02: Percentage of Kcal's consumed from fruit, leaves, flowers, pith, insects, and bark from full and partial day follows of adult female and fully-developed adult male orangutans. Note that the relative contribution of fruit is greater in this analysis than when presented as minutes spent feeding, shown in Figure 4.01. Samples sizes are shown in Table 4.01

For comparison with other orangutan studies, Figure 4.03 presents time spent feeding data where each daily follow is weighted equally. The same general pattern is seen, with mean fruit consumption in December 1994 through February 1995 over 99%. However, in May and July the relative ranking of each food type's contribution to the diet is different than that presented in the analysis where individuals are weighted equally (Figure 4.01). In the individually weighted analysis orangutans ate 66.5% fruit, 20.9% bark and 10.9% leaves in May. Whereas in the follow-weighted analysis orangutans ate 41.23% bark, 36% fruit, and 18.5% leaves. In July, the reliance on flowers was 35.5% in the individually weighted sample and 16.8% in the follow-weighted sample. The relative food type ranking during the other months was the same in the two analyses.

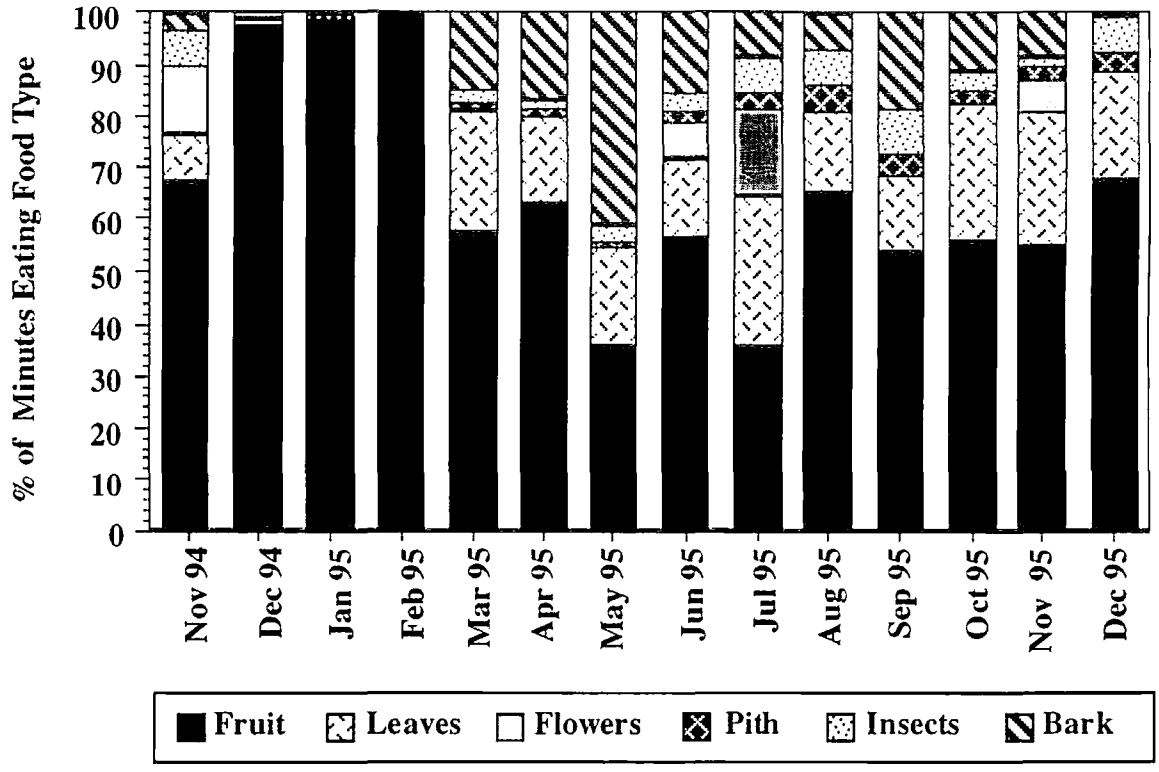


FIGURE 4.03: Percentage of the diet of adult male and female orangutans composed of fruit, leaves, flowers, pith, insects and bark on a percentage of time spent feeding basis where each follow is weighted equally. Samples sizes are shown in Table 4.01

Diet composition and Fruit Availability

Diet changed dramatically between the different months. To test how this related to changes in fruit availability in the forest I regressed the consumption of each food type, using the average monthly value for males and the average monthly value for females, against the percentage of trees with ripe fruit in the orangutan phenology sample (described in Chapter 3). Figure 4.04 A-E shows the mean Kcal's eaten per day of each food type compared to ripe fruit availability. As predicted, the Kcal consumption of fruit was positively correlated with the availability of ripe fruit (Liner Regression: all $p < 0.001$). Consumption of leaves, bark, pith, and insects were negatively correlated with ripe fruit availability. Flower consumption showed no relationship to the presence of ripe fruit. The same relationships were found when minutes of food type consumption and grams of food type consumption were regressed against ripe fruit availability.

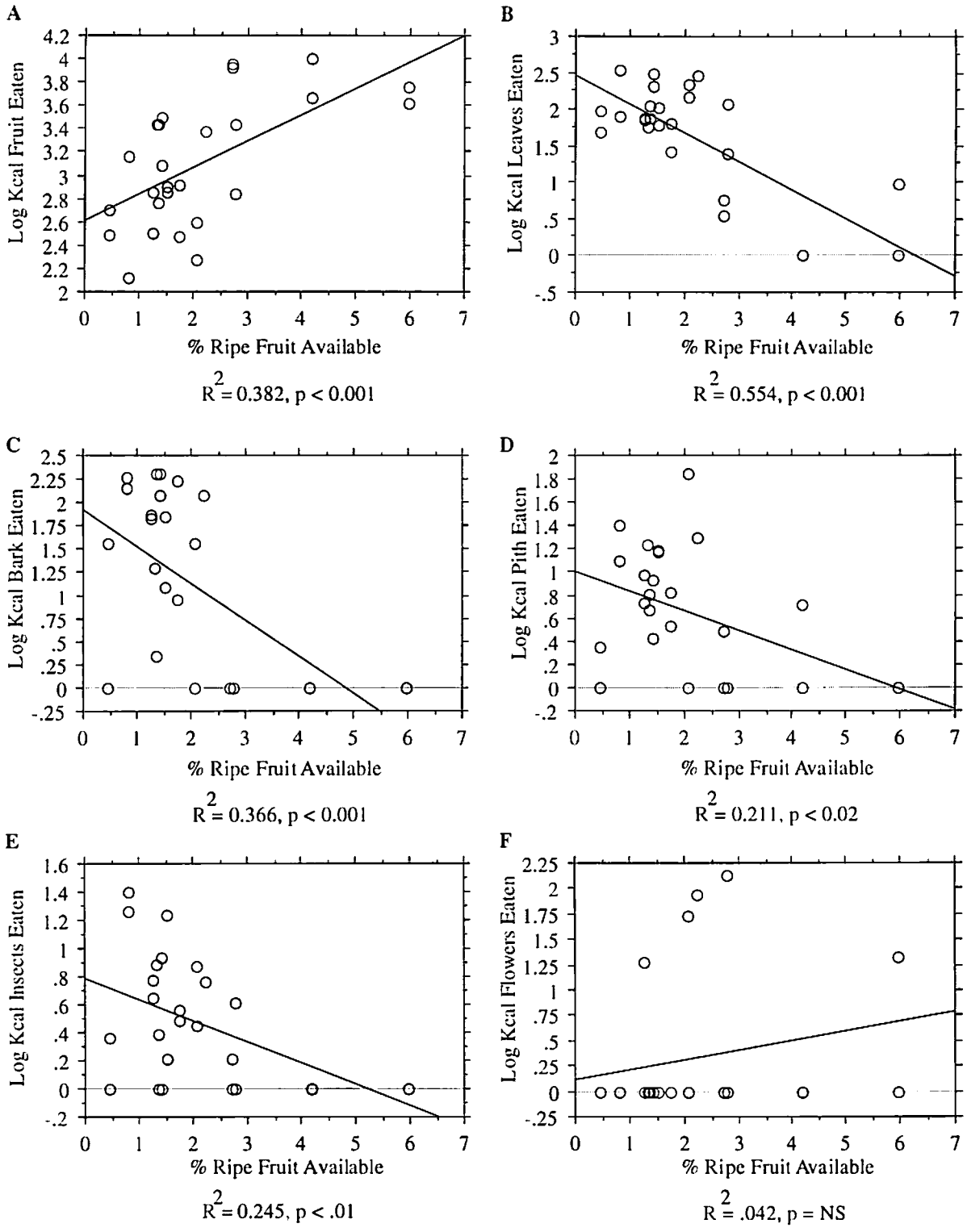


FIGURE 4.04: Regressions of percentage of trees with ripe fruit in the orangutan phenology sample compared to total dietary Kcal's obtained from fruit (A), leaves (B), bark (C), pith (D), insects (E) and flowers (F). Samples sizes are shown in Table 4.01

Relationships between Food Types Consumed

During the richest fruit period, orangutans ate high amounts of fruit and negligible amounts of the other food categories. However, this does not tell us how consumption of these different food types varied in relation to each other. Thus, correlations between different food types consumed is shown in the Spearman-Rank Correlation Matrix in Table 4.02. The consumption of fruit in the diet showed a significant negative correlation with the consumption of leaves, insects and bark. Consumption of leaves was positively correlated with pith, insect, and bark consumption. Pith consumption showed a very strong positive relationship with the consumption of insects and bark. Bark and insects themselves also showed a very strong positive correlation. Thus, as fruit availability and fruit consumption decrease, orangutans shift to eating these other co-varying food categories as fall-back foods.

TABLE 4.02: Matrix of Spearman Rank Correlation Coefficients (Rho) for relationships between Kcal consumption of different orangutan food types.

	Fruit	Leaves	Flowers	Pith	Insects
Leaves	-0.469*				
Flowers	0.235	0.284			
Pith	-0.276	0.422*	0.173		
Insects	-0.397*	0.477*	0.341	0.758****	
Bark	-0.392*	0.520**	0.161	0.700****	0.641***

* $p < 0.05$
** $p < 0.01$
*** $p < 0.005$
**** $p < 0.001$

Flower consumption varied independently of all other food types. As shown by the heavy reliance of orangutans on flowers in July 1995, flowers may be a highly preferred food item at times. Thus, flower consumption would be expected to vary as a function of the species of flowers available and the relative abundance of other preferred food items.

Sex Differences in Diet Composition

Examining the 12 months in which there is data from both males and females, no significant differences existed between males and females in the proportion of each food type consumed in the diet (ANOVA of individual means in each month, p = n.s.). Thus, male and female orangutans, in general, ate similar items, despite their difference in body size. Figure 4.05 (A-B) shows the percentage of feeding minutes consuming each food type in females compared to males.

I also investigated differences between males and females within each month. Due to the small number of individuals sampled each month, I could not compare between sexes using the pooled monthly means for each individual. Instead, I compared between the sexes by treating each daily follow as a separate sample as has been done by previous investigators. The days are not entirely independent, though, since some individuals are sampled more than once. I used the more conservative, non-parametric Mann-Whitney U statistical test to compare between the means.

In general, the percentage of time spent feeding on different food types was remarkably similar between males and females except during the months of April through July— part of the low-fruit period. As seen in the Mann Whitney U-test comparisons in Table 4.03, males spent a significantly greater percentage of time, Kcal's and grams consuming fruit in May and in June. Female diets were made up of a greater percentage of minutes eating bark in April and in May. In June and July, females consumed a greater percentage flowers than did males. All other food type comparisons within the different months showed no significant differences between the sexes ($P < 0.05$).

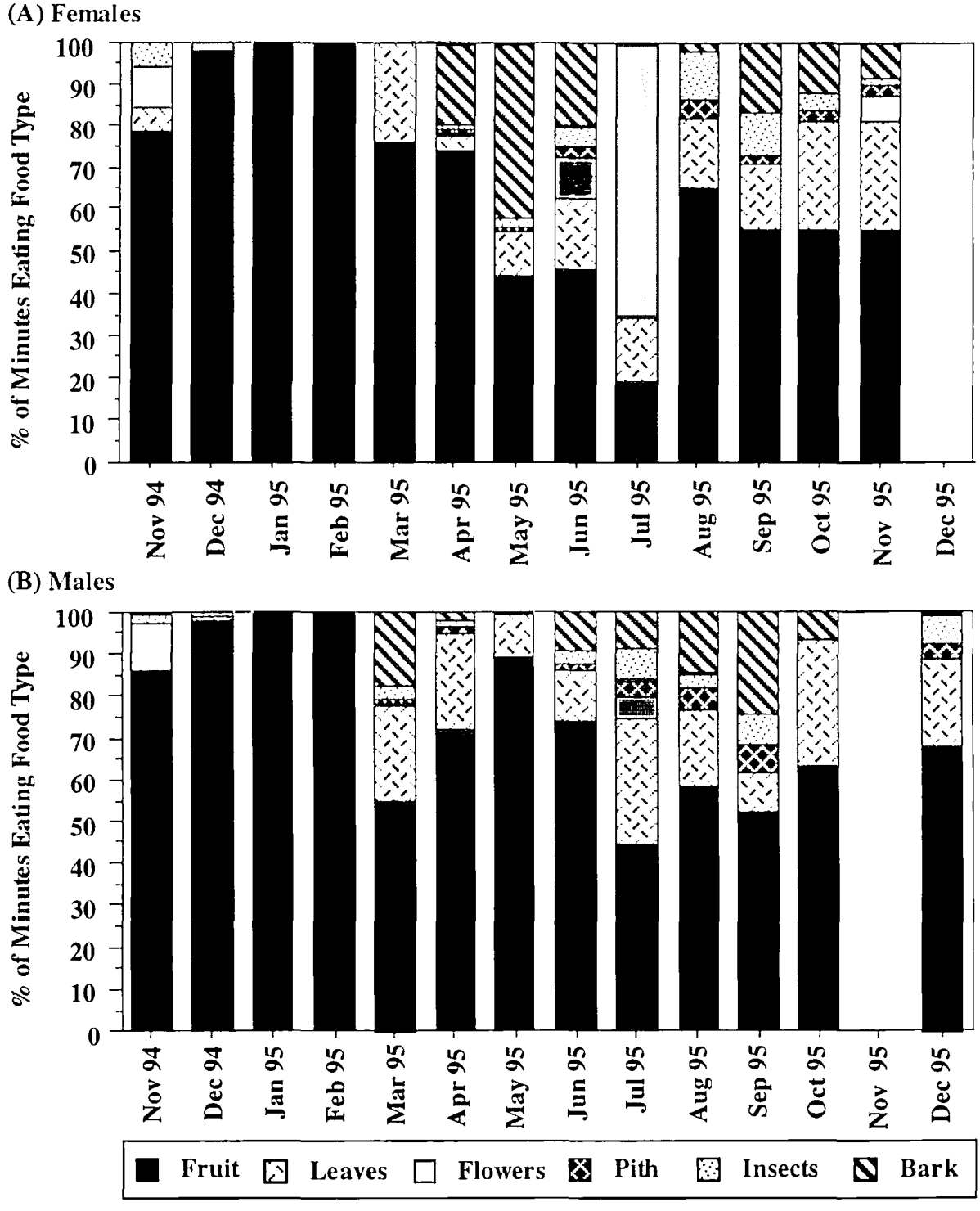


FIGURE 4.05: Percentage of the diet of adult female (A) and fully-developed male (B) orangutans composed of fruit, leaves, flowers, pith, insects and bark on a minutes spent feeding basis. Diet composition is similar in most respects, except for bark, fruit, and flower consumption in April through July. Samples sizes are shown in Table 4.01

TABLE 4.03: Mann-Whitney U tests comparing proportion of feeding time, grams, and kcal's consumed of each food type by adult male and female orangutans during both full and partial day follows. Reported are U values followed by level of significance.

Month		Fruit	Leaves	Flowers	Pith	Insects	Bark
Nov, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dec, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Jan, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Feb, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mar, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Apr, '94	Min	n.s.	n.s.	n.s.	n.s	n.s	U=30*†
May, '95	Min	U=4,****	n.s.	n.s.	n.s.	n.s.	U=0*****†
	Grams	U=14,**	n.s.	n.s.	n.s.	n.s.	U=0*****†
	Kcal	U=7***	n.s.	n.s.	n.s.	n.s.	U=0*****†
June, '95	Min	U=70,****	n.s.	U=99*†	n.s.	n.s.	n.s.
	Grams	U=92**	n.s.	U=99*†	n.s.	n.s.	n.s.
	Kcal	U=78***	U=112*†	U=99*†	n.s.	n.s.	n.s.
July, '95	Min	n.s.	n.s.	U=2*†	n.s.	n.s.	n.s.
Aug, '95		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sep, '95		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Oct, '95		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < .05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$, ***** $p < 0.0005$, † Females consumed a higher pecentage than did males

I also examined the *total amount* of each food type consumed on a minutes, Kcal and grams basis from full-day follows only. Results (Mann-Whitney U-tests, Table 4.04, samples sizes are shown in Table 4.01) were similar, in general, to the previous diet percentage analysis in that males and females were not significantly different in most comparisons. However, in some cases even though the proportion of different food items in the diet was the same, the *absolute amounts* consumed differed between the sexes. In January, although the percentage of food items consumed was similar between males and females (Figure 4.05), the minutes, Kcal and grams spent eating fruit was greater for males than for females. In April and May females consumed significantly more bark than did males. In May, as well, males ate significantly more fruit than did females. In July females ate significantly more flowers. Finally, in September, interestingly, females ate more grams and Kcal's of fruit than did males, although the relative proportion of time spent feeding on fruit was not different between males and females (Table 4.03). This seems to be due to less time spent feeding overall by males in September (see Chapter 5). All other food type comparisons within the different months showed no significant differences between the sexes ($P > 0.05$).

TABLE 4.04: Mann-Whitney U tests comparing total minutes, grams, and kcal's consumed of each food type by adult male and female orangutans from full-day follows.

Month		Fruit	Leaves	Flowers	Pith	Insects	Bark
Nov, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dec, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Jan, '94	Min	U=3*	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	U=3*	n.s.	n.s.	n.s.	n.s.	n.s.
	Kcal	U=3*	n.s.	n.s.	n.s.	n.s.	n.s.
Feb, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mar, '94		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Apr, '94	Min	n.s.	n.s.	n.s.	n.s	n.s	U=14**†
	Grams	n.s.	n.s.	n.s.	n.s.	n.s.	U=16*†
	Kcal	n.s.	n.s.	n.s.	n.s.	n.s.	U=16*†
May, '95	Min	U=5***	n.s.	n.s.	n.s.	n.s.	U=0****†
	Grams	U=18,*	n.s.	n.s.	n.s.	n.s.	U=0****†
	Kcal	U=8***	n.s.	n.s.	n.s.	n.s.	U=0****†
June, '95		n.s.	n.s.	n.s	n.s.	n.s.	n.s.
July, '95	Min	n.s.	n.s.	U=20*†	n.s.	n.s.	n.s.

* $p < .05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$, † Females consumed a higher pecentage than did males

TABLE 4.04 (continued): Mann-Whitney U tests comparing total minutes, grams, and Kcal's consumed of each food type by adult male and female orangutans from full-day follows.

Month		Fruit	Leaves	Flowers	Pith	Insects	Bark
Aug. '95		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sep. '95	Min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	U=3.5*	n.s.	n.s.	n.s.	n.s.	n.s.
	Kcal	U=3.5*	n.s.	n.s.	n.s.	n.s.	n.s.
Oct. '95		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

* $p < .05$

Sex Differences in the Relationship between Diet Composition and Fruit Availability

Figure 4.05 indicated that there may be some sex differences in fruit consumption by orangutans. This difference was significant in May. Thus, I examined the relationship between percentage of trees with ripe fruit and Kcal's of fruit eaten in separate linear regressions for males and females (Figure 4.06). The relationship was positively correlated for both males and females, but less of the variance in fruit eaten by males was accounted for by ripe fruit availability. Males may be less constrained by the low-fruit period because they are able to rely on fruits not as easily accessible to females, such as unripe *Neesia*.

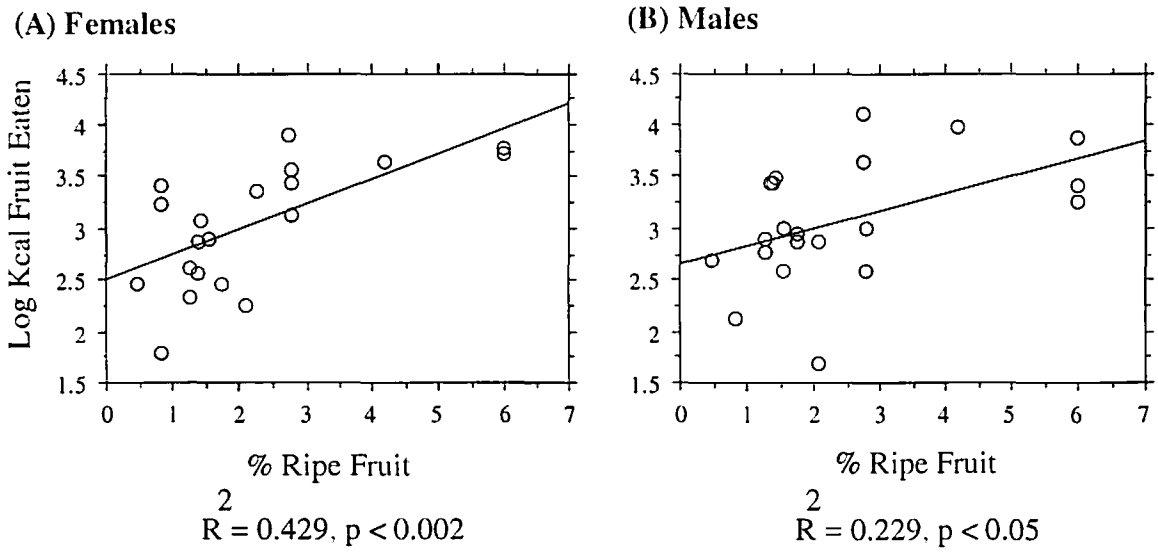


FIGURE 4.06: Regressions of percentage of trees with ripe fruit in the orangutan phenology sample compared to the total Kcal of fruit eaten per day (log transformed) for adult female and fully-developed male orangutans. Samples sizes are shown in Table 4.01

Nutrient Content of Orangutan Foods

Nutritional analyses have been conducted on 93 of the foods most commonly eaten by orangutans at Cabang Panti between August 1994 and December 1995. Appendix I provides the nutritional data on each orangutan food analyzed. Fruit was not only more abundant during the mast, but mast foods were significantly higher in caloric content than were non-mast foods (Mann-Whitney U-test, $n = 10$, $p < 0.05$). Table 4.05 compares the average caloric value of the five most commonly eaten foods during the mast period versus the five most commonly eaten foods during the non-mast period.

TABLE 4.05: Kcal/100 g of the five most commonly eaten mast foods vs. the five most commonly eaten non-mast foods[a]

	Part Eaten	%TNC	% Lipid	% Crude Protein	%NDF	Total Kcal/100 (g)
Mast Foods						
Baccaurea sp.	seed	39.8	14.9	11.8	33.5	359
Castanopsis sp.	seed	65.3	0	5.7	29.0	300
Dipterocarpus sublamellatus	seed	78.0	4.1	5.1	12.8	376
Durio sp.	pulp/seed	40.2	2.0	16.2	41.6	266
Sindora sp.	seed	59.1	6.7	7.4	26.8	341
Non-Mast Foods						
Average Bark	-	12.3	3.4	10.0	74.3	176
Average Leaves	-	18.5	2.1	11.9	67.5	177
Epiphyte Leaves	-	22.6	2.2	4.0	71.2	165
Polyalthia sumatrana	seed	2.0	3.0	6.8	88.2	110
Neesia sp.[b]	seed	31.7	46.0	12.4	9.9	596

[a]Values are percentage weight of organic matter. TNC is Total Nonstructural Carbohydrates. NDF is Neutral-Detergent Fiber. Total Kcal/gram were calculated assuming the values of 9 Kcal/g lipid, 4 Kcal/g CP and 4 Kcal/g TNC and an NDF coefficient of 54.3%.

[b] *Neesia* seeds were eaten predominantly by adult males during May.

Seasonal Differences in Caloric and Gram Intake

Total Kilocalories Consumed per Day

Data on caloric intake were analyzed using two subdivisions of the data: total daily caloric intake and mean intake/hour. For the purpose of calculating total *daily* caloric intake, I only considered data from *full* day follows of habituated, adult animals (Figure 4.07). Dramatic differences in caloric intake existed between the months (ANOVA, $P < 0.0001$). During the mast period of high fruit availability (December 1994 - February 1995) orangutan daily caloric consumption ranged between, approximately, 4000-11,000 Kcal on average. This was up to twenty times the amount of calories consumed between March and September 1995 when mean daily Kcal consumption ranged between, approximately, 600 Kcal and 1700 Kcal (except for the month of May for Males).

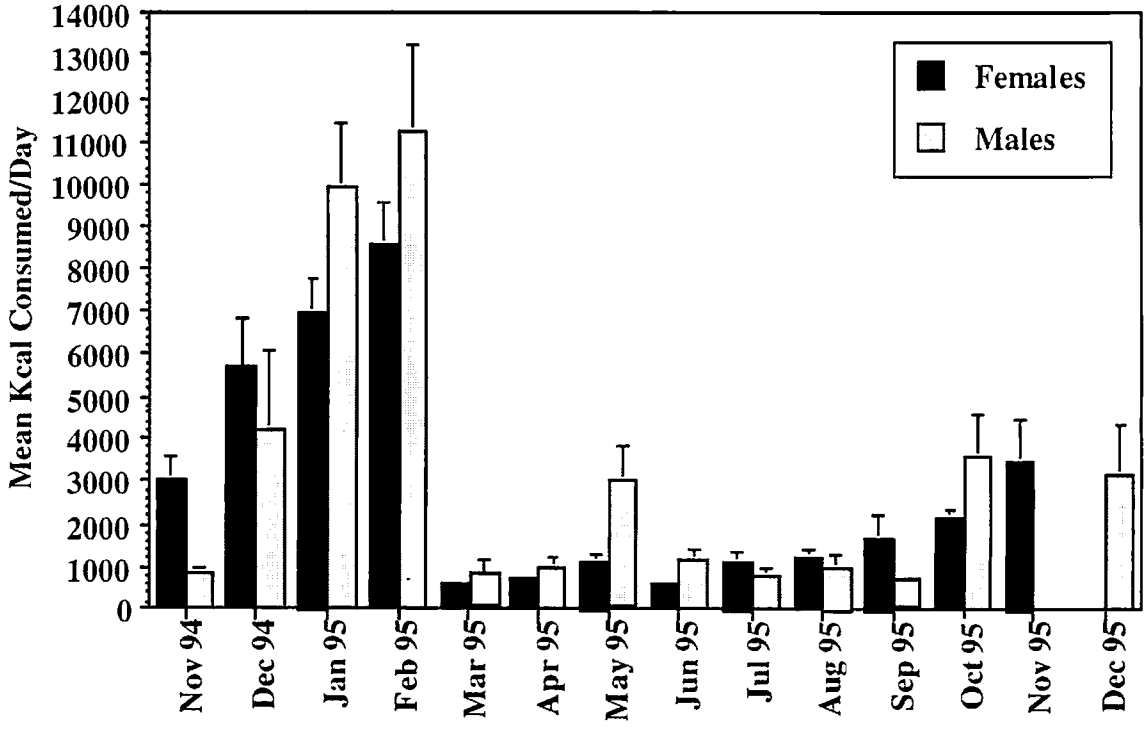


FIGURE 4.07: Total daily caloric intake (Kcal) from full-day follows of adult female and fully-developed adult male orangutans between November 1994 and December 1995. Samples sizes are shown in Table 4.01

In October through December 1995 orangutan caloric consumption was more intermediate, ranging between approximately 2000 Kcal/day and 3500 Kcal/day. Figure 4.08 shows the strong positive relationship between Kcal consumed/day and percentage of trees with ripe fruit between November 1994 and December 1995.

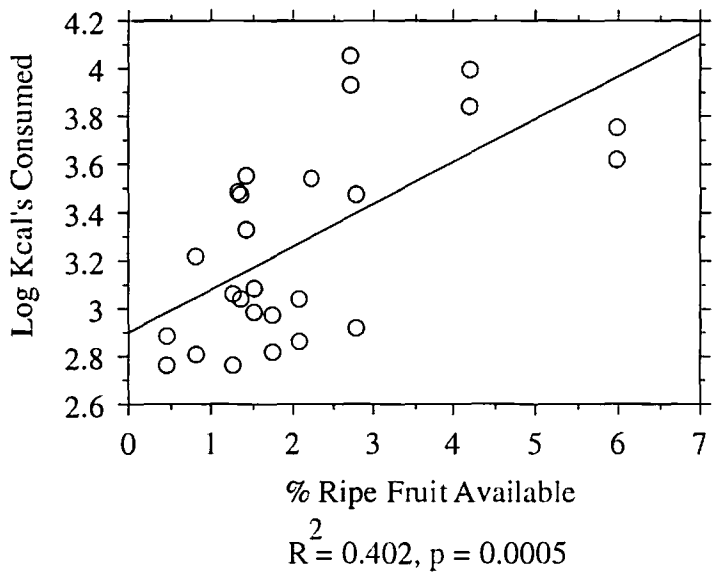


FIGURE 4.08 Regression of Kcal consumed/day against number of trees with ripe fruit from full day follows of adult female and fully-developed adult male orangutans.

Sex Differences in Total Daily Caloric Consumption

As shown in Figure 4.07, males and females followed the same trend across the sample period with increasing caloric consumption between November 1994 and February 1995, decreasing consumption during the post-mast months, and more intermediate levels reached during October through December 1995. Differences between males and females in total daily consumption across the whole year were first tested using an unpaired T-test on the individual mean Kcal's (log transformed). The means were not significantly different.

Next, I looked for differences between months. As explained previously the number of individuals within each given month is too small to allow for comparison of individual monthly means. I used a Mann-Whitney U-test to compare between males and females in each of the months.

In most months the mean daily caloric intake was greater for males than for females. However, this difference was only significant in May ($p < 0.01$) and June ($p < 0.05$). These were the two months with the highest sample sizes for full-day follows (May, follows = 28, individuals = 3; June, follows = 32, individuals = 4). Thus, non-significant results may be due to small sample sizes in some months. Interestingly, in some months the mean caloric intake was higher for females than for males. This difference was significant in September ($p < 0.05$). Even though male orangutans weigh roughly twice as much as females, as will be explained in Chapter 5 the caloric requirements of the two sexes are not as different as this size differential would imply due to the extra costs in females of lactation, pregnancy and infant/juvenile carrying. Nevertheless, the very highest daily values of caloric intake are seen in males in January and February 1995.

The significant difference in caloric consumption between males and females during May 1995 appears to be due to the consumption by males of lipid-rich *Neesia* seeds. *Neesia* seeds are contained within large (14.3 x 10.2 cm) fruits with a hard husk and the seeds are embedded in a layer of irritating hairs. I found that these seeds contained 46.0% lipid. In May, males spent 74.5% of their feeding time eating these seeds, whereas females spent only 1.9% of their feeding time eating *Neesia*. This difference in *Neesia* consumption is also reflected in the higher proportion of fruit in the diet of males in May and June as revealed in the previous sections.

Sex Differences in the Relationship between

Total Daily Caloric Consumption and Fruit Availability

I also examined the relationship, through linear regression, between the percentage of ripe fruit available and the mean Kcal's consumed/day (log transformed) for each individual animal, separated by males and females (Figure 4.09). As suspected, based on the trend for males to eat more than females during most of the fruit-poor months, the relationship between Kcal's consumed/day and ripe fruit availability was not as tight for males as for females.

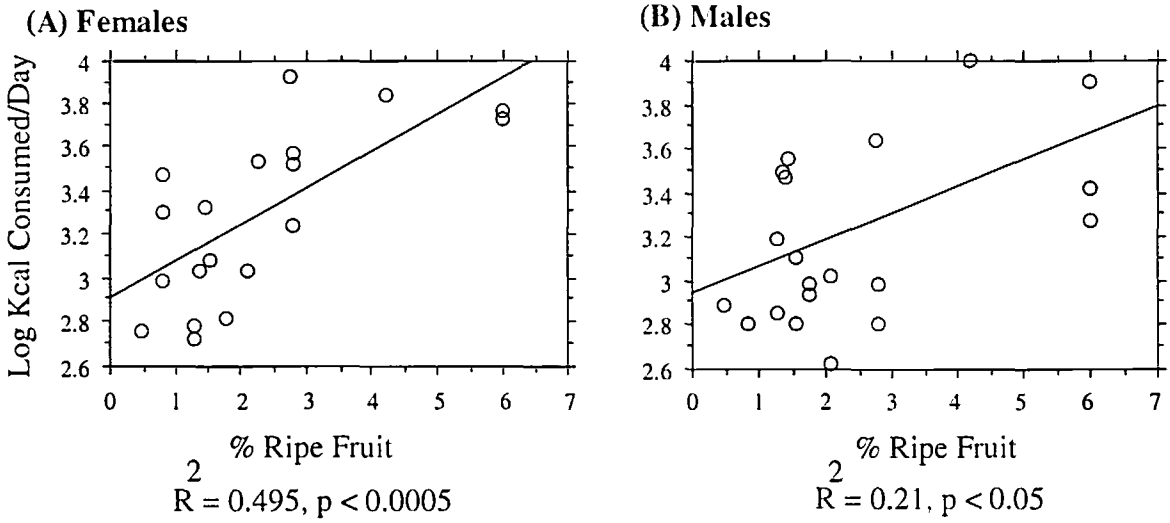


FIGURE 4.09: Regressions of percentage of trees with ripe fruit compared to the total daily Kcal consumption (log transformed) for (A) adult female and (B) fully-developed male orangutans.

Total Grams Consumed per Day

I also examined the total number of grams of dry weight consumed/day in order to assess differences in the amount of *total* plant material consumed. Animals, of course, are limited

by the total volume of food they can consume on a given day. This analysis revealed the same contrast between the periods of high and low ripe fruit availability as shown in Figure 4.07, with significant differences between the months (ANOVA, $P < 0.0001$). However, an important differences exists between food intake examined on a grams eaten versus a Kcal basis—the magnitude of the difference is not as great when grams eaten are considered. The average grams of dry weight consumed per day between March 1995 and September 1995 was 468.4. This is opposed to 2261.8 grams/day in December 1994 through February 1995, a 5-fold difference in grams intake as opposed to a twenty-fold

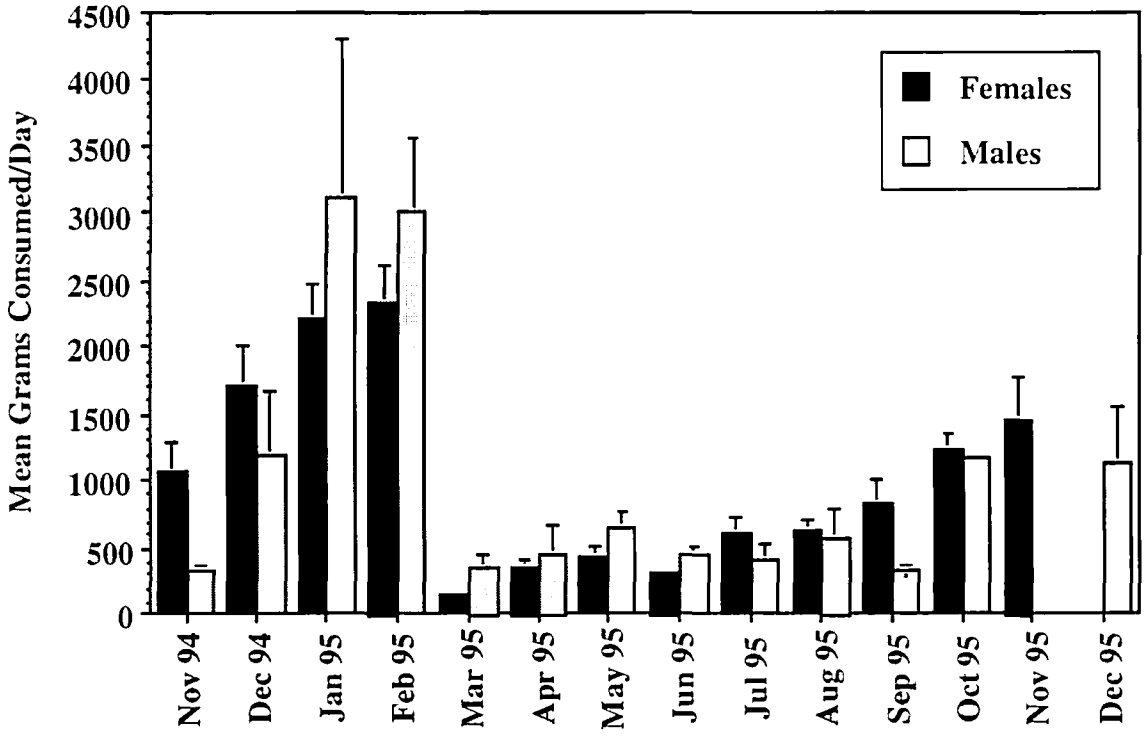


FIGURE 4.10: Total grams of food intake from full-day follows of adult female and fully-developed adult male orangutans between November 1994 and December 1995. Compare the magnitude of the difference between months to changes in mean daily caloric intake in Figure 4.07. Sample sizes are shown in Table 4.01.

difference in caloric intake. The orangutans were able to increase their caloric intake by a far greater margin than their grams of intake because of the different composition of the plant foods consumed during the two periods. As shown in Table 4.05, mast foods, in general, were significantly higher in caloric content, but lower in fiber.

A significant, positive relationship between the percentage of trees with ripe fruit and total grams eaten also existed as shown in the regression in Figure 4.11.

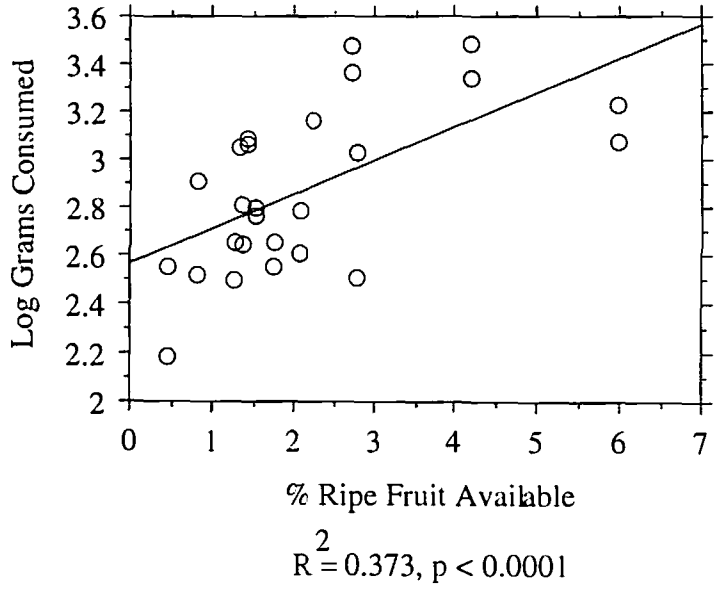


FIGURE 4.11: Regression of grams consumed/day against percentage of trees with ripe fruit for full-day follows of adult female and fully-developed male orangutans

Total Kilocalories Consumed per Hour

The second sub-division of the data examined total Kcal's consumed per waking hour. This allowed me to include partial day follows in the analysis and thus have a larger sample size for monthly and sex comparisons. Significant differences were again found between the months (ANOVA, $P < 0.0001$), and significantly more calories were consumed per hour in the mast compared to the post-mast period (Scheffe F-test comparisons between months). The magnitude of the differences (Figure 4.12) are not as great as when considered on a total daily caloric intake basis because, as will be shown in Chapter 5, the total time spent awake was greater in the mast months than in the post-mast months.

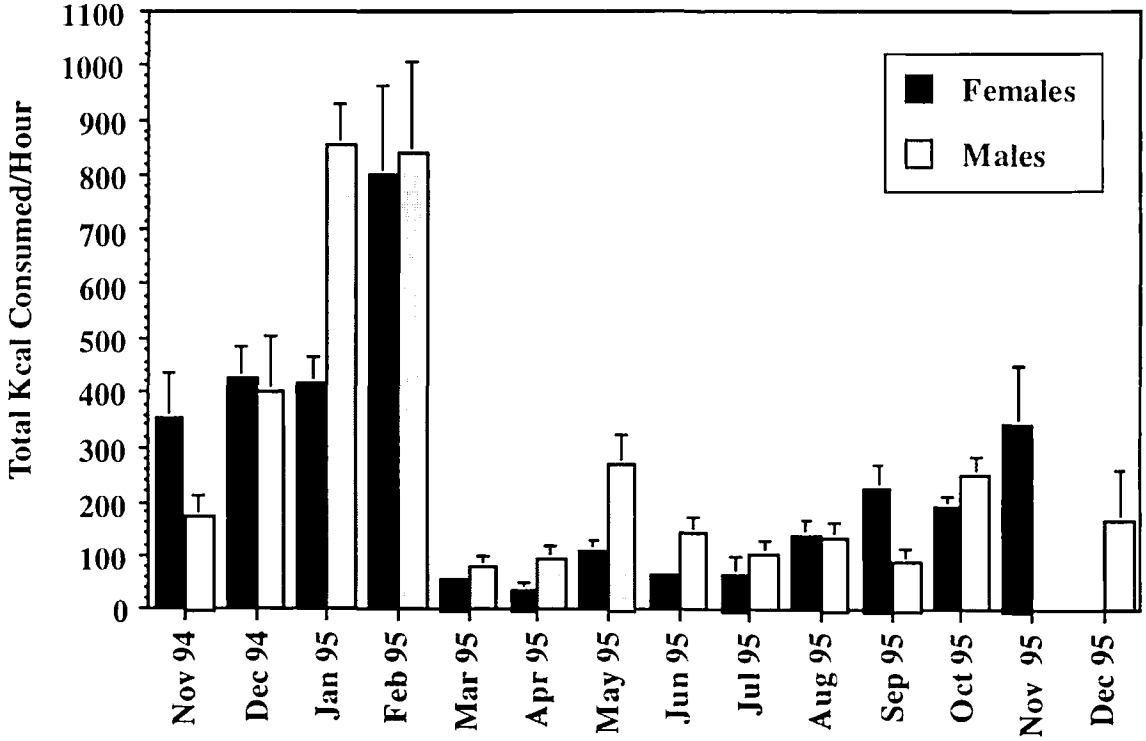


FIGURE 4.12: Total Kcal's consumed per hour of time awake in full and partial day follows of adult female and fully-developed adult male orangutans between November 1994 and December 1995. Sample sizes are shown in table 4.01.

The relationship between Kcal's consumed/hour and number of trees with ripe fruit was shown to have a significant positive relationship as demonstrated in the regression in Figure 4.13.

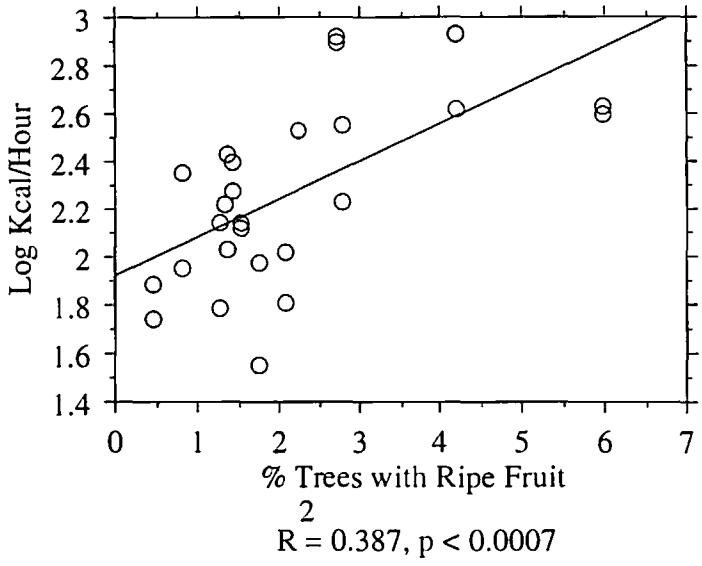


FIGURE 4.13: Regression of Kcal's consumed/hour against percentage of trees with ripe fruit. Data are from full and partial day follows of adult female and fully-developed male orangutans.

Several individuals in this study were followed during periods of both high and low fruit availability and thus provide a means of assessing whether the general pattern already described holds for particular individuals. Within individual comparisons are also advantageous because all the data for a particular individual can be used in statistical tests. For these analyses I compared daily caloric intake during the fruit-rich period (November 1994 to February 1995) to the fruit-poor period (March 1995 to September 1995). (Definitions of fruit-rich and fruit-poor periods are described in Chapter 3 and are based on the percentage of trees fruiting in the sample.) Using unpaired, two-tailed, T-tests I compared the mean caloric intake during the two periods and found that differences between the two groups were highly significant (RM: $p < 0.001$; FK: $p < 0.005$; EZ: $p < 0.003$) for each animal (Figure 4.14).

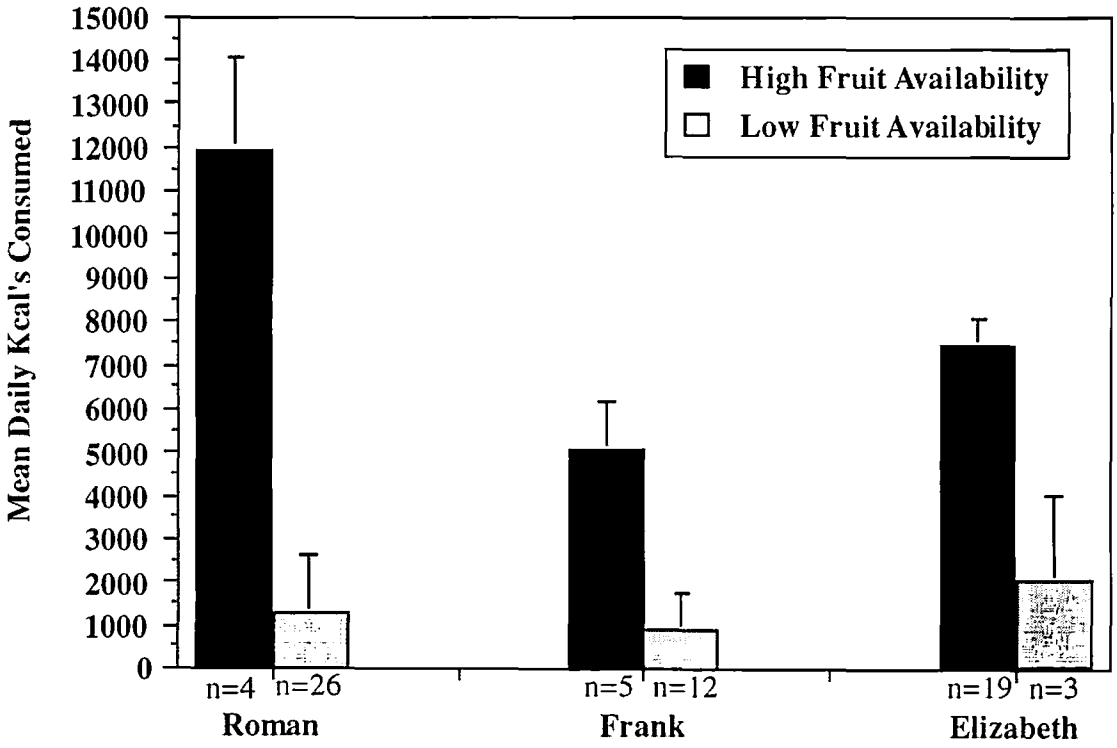


FIGURE 4.14: Comparison of mean daily Kcal's consumed during the high and low fruit availability periods (n = number of full-day follows) for two fully-developed adult male orangutans (Roman and Frank) and one adult female orangutan (Elizabeth).

Individual comparisons also show interesting contrasts between individuals. For example, Roman's high caloric intake during the high-fruit availability period may be related to his apparent ranking as the dominant male. This is based on his observed ability to deter other animals from entering preferred fruit resources that he was occupying, his ability to displace other orangutans at food sources and his rate of long calling. He long called at a rate of 1.7 ± 2.4 (SD) times per day compared to 0.2 ± 1.0 (SD) times per day for Frank. These were significantly different rates ($n = 112$; T-test, $p < 0.002$). Roman also spent significantly more time eating (240 minutes $\pm$ 110 SD, $n = 44$) than did Frank (155 minutes $\pm$ 84 SD, $n = 19$) over the whole study period (full-day follows and partial day follows over 500 minutes, unpaired two-tailed T-tests, t value = -3.002, $p < 0.005$).

Nutrient Composition

Nutrient Percentages in the Diet

Three measures were used to calculate the nutrient composition of the diet: minutes spent eating each nutrient, grams eaten of each nutrient and Kcal's eaten of each nutrient. All nutrient data is presented as percentage of organic matter. This means that I have subtracted the inorganic, or percent ash, of the sample from the mean 100°C dry matter weight. Combining all data from all adult animals (equally weighting animals, months and sex), the nutrient content of the orangutan diet between November 1994 and December 1995 can be characterized as 28.7%, carbohydrate, 5.2% lipid, 9.7% protein and 41.3% fiber on a minutes spent feeding basis. Significant differences were found between males and females, between seasons, between months and between males and females during particular months and seasons.

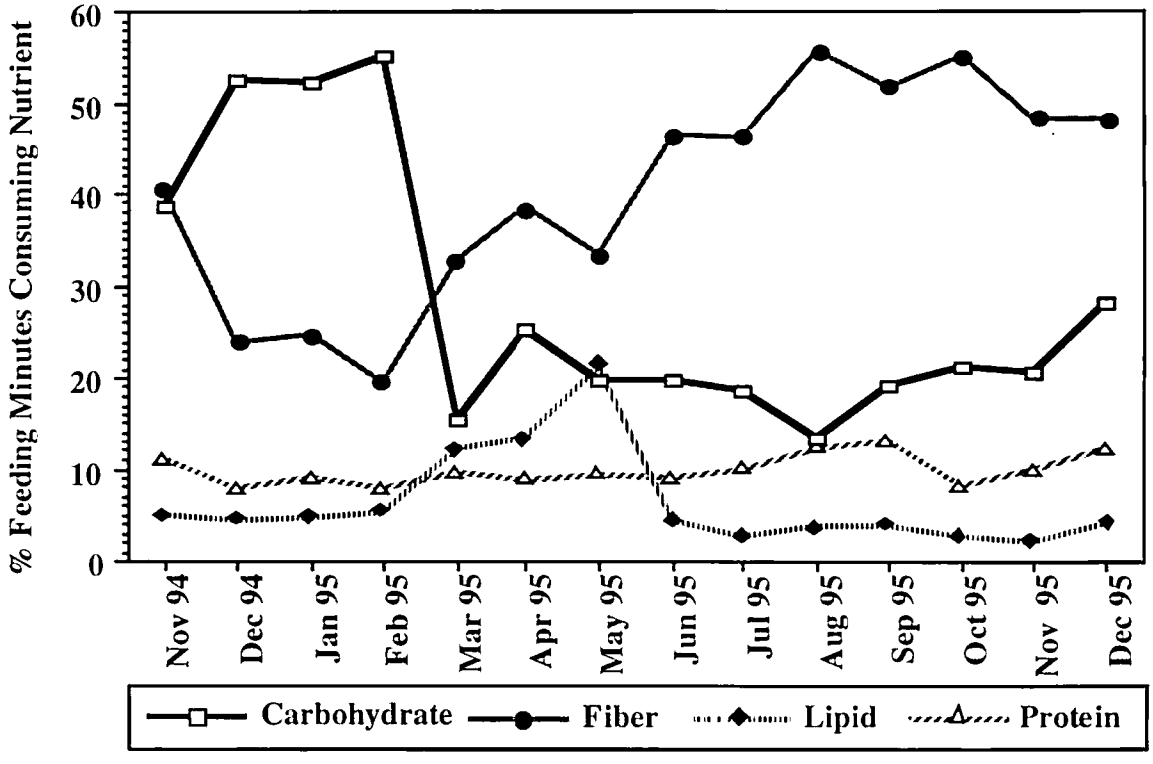


FIGURE 4.15: Changes in the nutrient content of the diet on a percentage of minutes spent eaten basis between November 1994 and December 1995 from full and partial day follows of adult female and fully-developed male orangutans combined.

Examining just full-day follows using ANOVA, there were significant differences across the 14-month period in the percentage of carbohydrate, fiber and protein in the diet on a time spent feeding, grams eaten, and Kcal basis (all $p < 0.05$). Percent Kcal's of lipid consumed was also significantly different ($p < 0.02$). Contrasts between months (Scheffe F-test; Table 4.06) revealed that the percentage of carbohydrate, in particular, was significantly different, particularly on a grams eaten basis (Figure 4.16) between many of the high fruit months (November 1994 through February 1995) and many of the low-fruit months (March through September 1995). The average percent of grams eaten that was carbohydrate was 57.7% in November 1994 through February 1995, whereas levels dropped to 20.7% between March through September 1995.

The percent fiber in the diet rose during the post-mast period, with the highest percent fiber consumption reached between June and December 1995 (mean 60.8%). The lowest fiber months were December 1994 through February 1995 (mean 24.1%). Pair-wise comparisons between months showed fewer significant differences than for carbohydrate, with grams of fiber consumption in February 1995 compared to June through September 1995 standing out as significantly different (Table 4.06).

Protein intake ranged between 5.3% and 16.0% throughout the year. Significant differences were found between February and July ($p < 0.01$) and February and September ($p < 0.05$). Percent lipid intake averaged 7.2% in the two periods November 1994 to February 1995 and again in June 1995 to December 1995. However, lipid consumption rose between March 1995 and May 1995, averaging 16.8%. This was the period when some orangutans were consuming *Neesia* as well as other lipid-rich seeds. Although differences in percent Kcal consumption of lipid was significantly different across the months ($p < 0.02$), no pair-wise comparisons were significant.

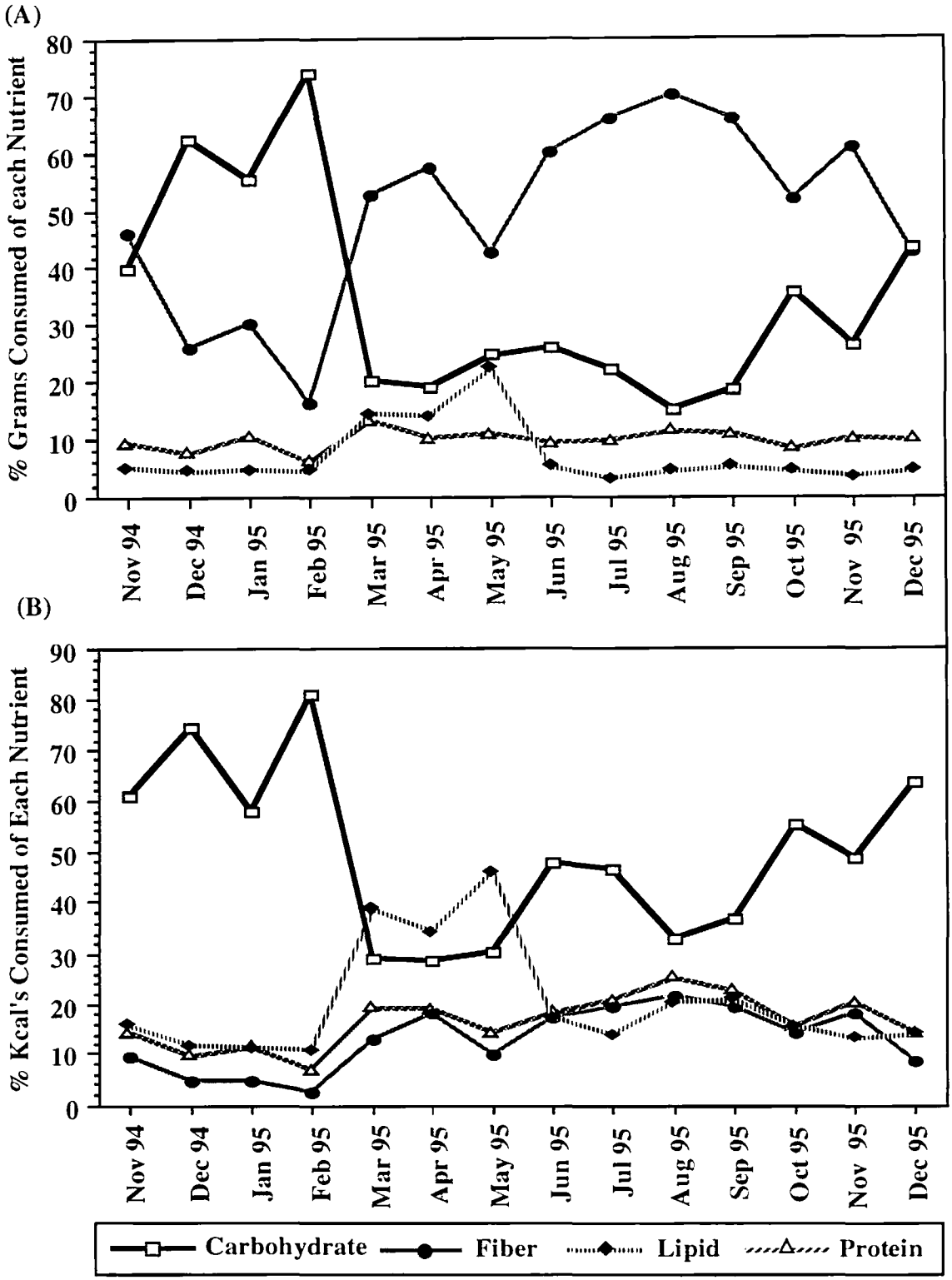


FIGURE 4.16: Changes in the percent nutrient content of the diet on a percent grams (A) and percent Kcal (B) consumption basis between November 1994 and December 1995 for adult female and fully-developed male orangutans combined.

TABLE 4.06: ANOVA, Scheffe F-test results comparing percentages of carbohydrate (C), protein (P), and NDF (N) in the diet of adult male and female orangutans during full-day follows. Lipid was not significnatly different between any months. No other pair-wise comparisons were significant.

Month	Measure	March	April	May	June	July	August	September
Nov, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	n.s.	n.s.	n.s.	n.s.	n.s.	**C***	n.s.
	Kcal	n.s.	**C***	n.s.	n.s.	n.s.	n.s.	n.s.
Dec, '94	Min	n.s.	n.s.	n.s.	**C***	**C***	**C******	**C****
	Grams	n.s.	**C****	n.s.	n.s.	**C***	**C******	**C*****
	Kcal	**C***	**C*****	**C****	n.s.	n.s.	**C*****	n.s.
		n.s.	n.s.	n.s.	n.s.	n.s.	**P***	n.s.
Jan, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	n.s.	n.s.	n.s.	n.s.	n.s.	**C***	n.s.
	Kcal	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Feb, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	**C*****	**C***
	Grams	**C***	**C****	n.s.	**C***	**C***	**C*****	**C*****
		n.s.	n.s.	n.s.	**N***	**N***	**N***	**N***
	Kcal	**C***	**C*****	**C***	n.s.	n.s.	**C****	n.s.
		n.s.	n.s.	n.s.	n.s.	n.s.	**N***	**N***
		n.s.	n.s.	n.s.	n.s.	n.s.	**P****	**P****

* p < .05, ** p < .01, *** p < .005, ****p < 0.001

Total Nutrient Intake

Total nutrient content from full-day follows shows interesting contrasts compared to the diet analyzed on a percentage basis. In particular, no significant differences (using ANOVA) were found in *total* fiber consumption on a grams or Kcal basis (p = n.s.), although minutes spent eating fiber was significantly different between the months ($p < 0.02$). Thus, although the overall percent fiber contribution to the diet changed across the year, the absolute amount of fiber did not vary significantly. This can be seen in Figure 4.17 which shows the total grams of each nutrient consumed across the sample period.

Carbohydrate consumption showed significant differences across the sample period in Kcal's ($p < 0.0001$), grams ($p < 0.0001$), and minutes ($p < 0.0001$) of consumption. Pair-wise comparisons (ANOVA, Scheffe F-test, Table 4.07) between months showed many significant differences between December 1994 - February 1995 compared to March 1995 - September 1995. Total gram consumption of carbohydrates peaked between December 1994 and February 1995. Carbohydrates contributed the highest Kcal percentage to the diet throughout the year, except for March and May 1995 when the mean intake of lipid was greater than for carbohydrate due to the reliance on *Neesia* and other lipid-rich seeds. All differences in mean lipid intake, however, were not significant across the year. Grams ($F = 3.982$, $p < 0.005$) and Kcal's ($F = 3.883$, $p < 0.005$) of protein intake showed significant differences across the year, but no pair-wise comparisons were significant.

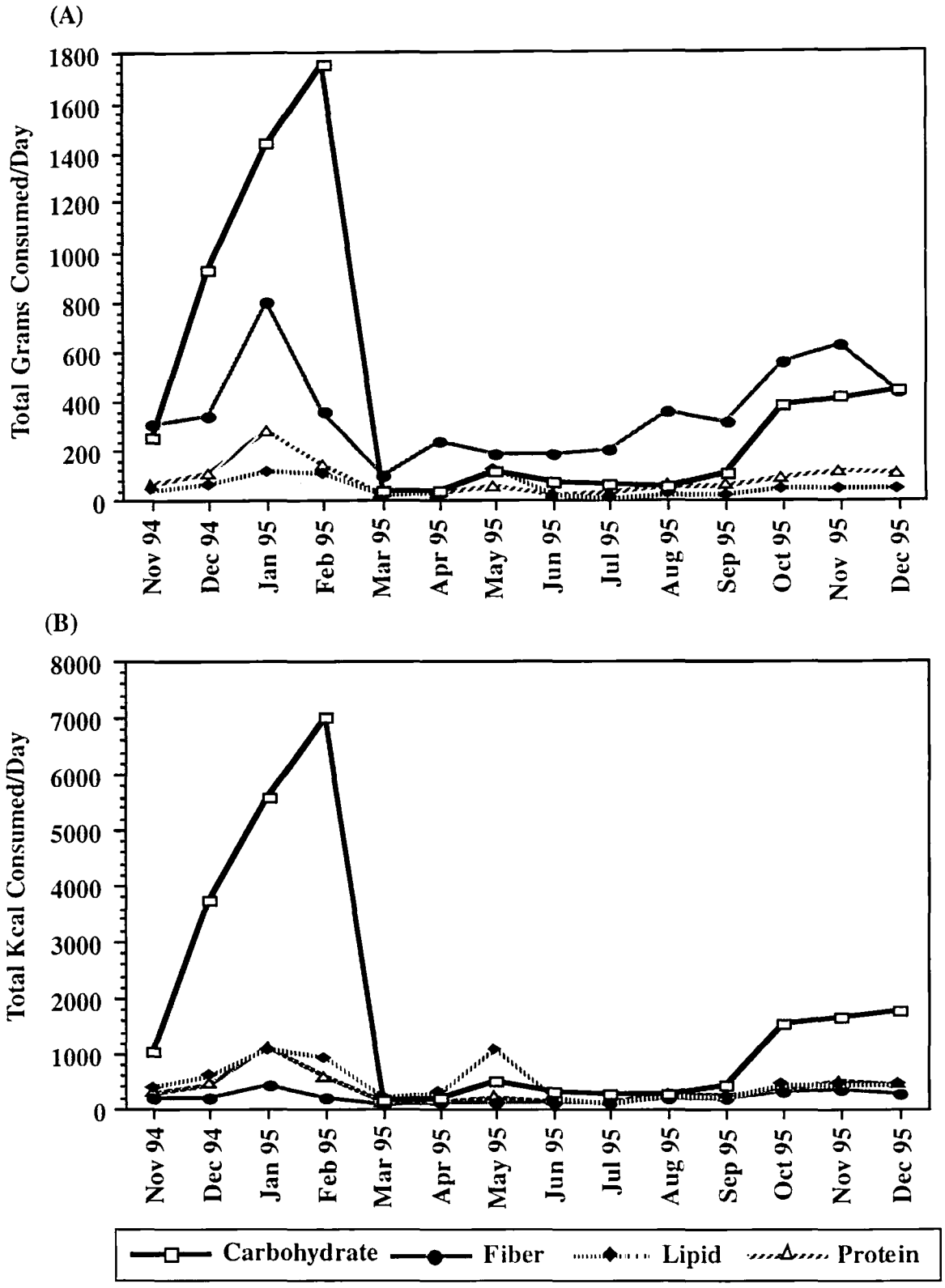


FIGURE 4.17: Changes in the total grams (A) and Kcal's (B) of nutrients in the diet of adult female and fully-developed male orangutans between November 1994 and December 1995.

TABLE 4.07: ANOVA Scheffe F-test results comparing monthly total nutrient consumption n the diet of adult male and female orangutans during both full-day follows. Only carbohydrate (C) was significantly different in these pair-wise comparisons. No other pair-wise comparisons were significant between months.

Month	Measure	March	April	May	June	July	August	September
Dec, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	C*	n.s.
	Grams	C*	C**	n.s.	C*	C*	C*	n.s.
	Kcal	C*	C**	n.s.	C*	C*	C*	n.s.
Jan, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	C*	C**	n.s.	C*	C*	C*	n.s.
	Kcal	C*	C*	n.s.	C*	C*	C*	n.s.
Feb, '94	Min	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grams	C***	C***	C*	C**	C**	C***	C*
	Kcal	C***	C***	C*	C**	C**	C***	C*

* $p < 0.05$
** $p < 0.01$
*** $p < 0.005$
**** $p < 0.001$

Nutrient Composition and Fruit Availability

I also examined the relationship between changes in the nutrient content of the diet and fruit availability (Figures 4.18 - 4.19). As ripe fruit availability increased, the percentage of grams of carbohydrates consumed also increased (Figure 4.18). The relationship is negative with percent grams intake of fiber, protein and lipid. All relationships are significant. Thus, it is the carbohydrate portion of the diet which is preferentially increased with high fruit consumption.

However, when we consider the *total* intake of nutrients, carbohydrate, fiber and protein all show a significant increase with increasing fruit availability (Figure 4.19). As was shown in Figure 4.10 there was a tremendous increase in the amount of food consumed during the fruit-rich period. Lipid intake did not show a significant relationship with fruit availability. This was likely due to the reliance on *Neesia* when it fruited during the middle of the relatively poor-fruit period. As seen in Table 4.05, Neesia seeds have an extremely high lipid content of 46%. An increase in dietary consumption of lipid provides a way for orangutans to increased their total daily caloric intake when carbohydrate-rich fruits are not as readily available.

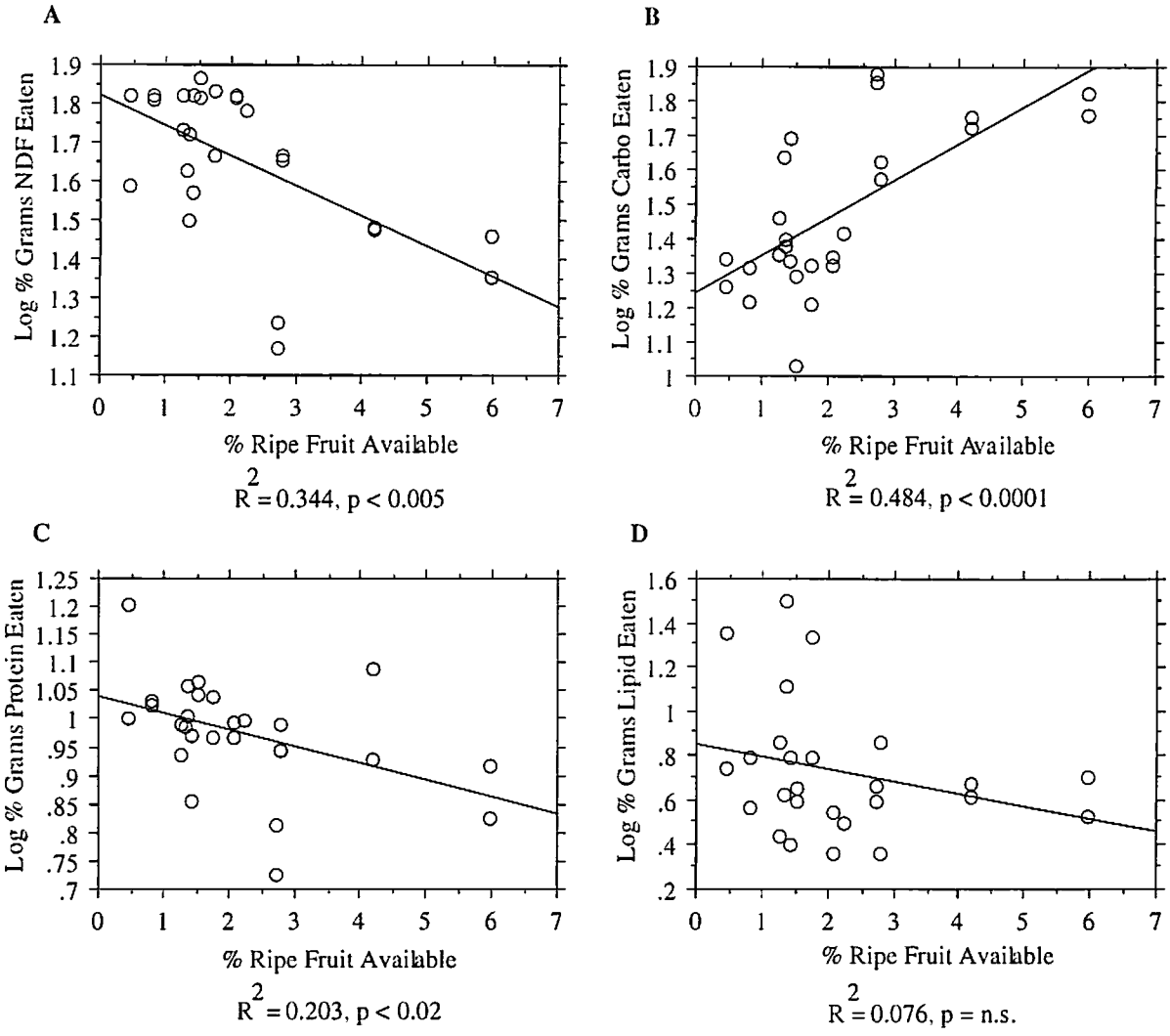


FIGURE 4.18: Percentage of grams consumed of (A) fiber, (B) carbohydrate, (C) protein, and (D) lipid compared to percentage of trees with ripe fruit.

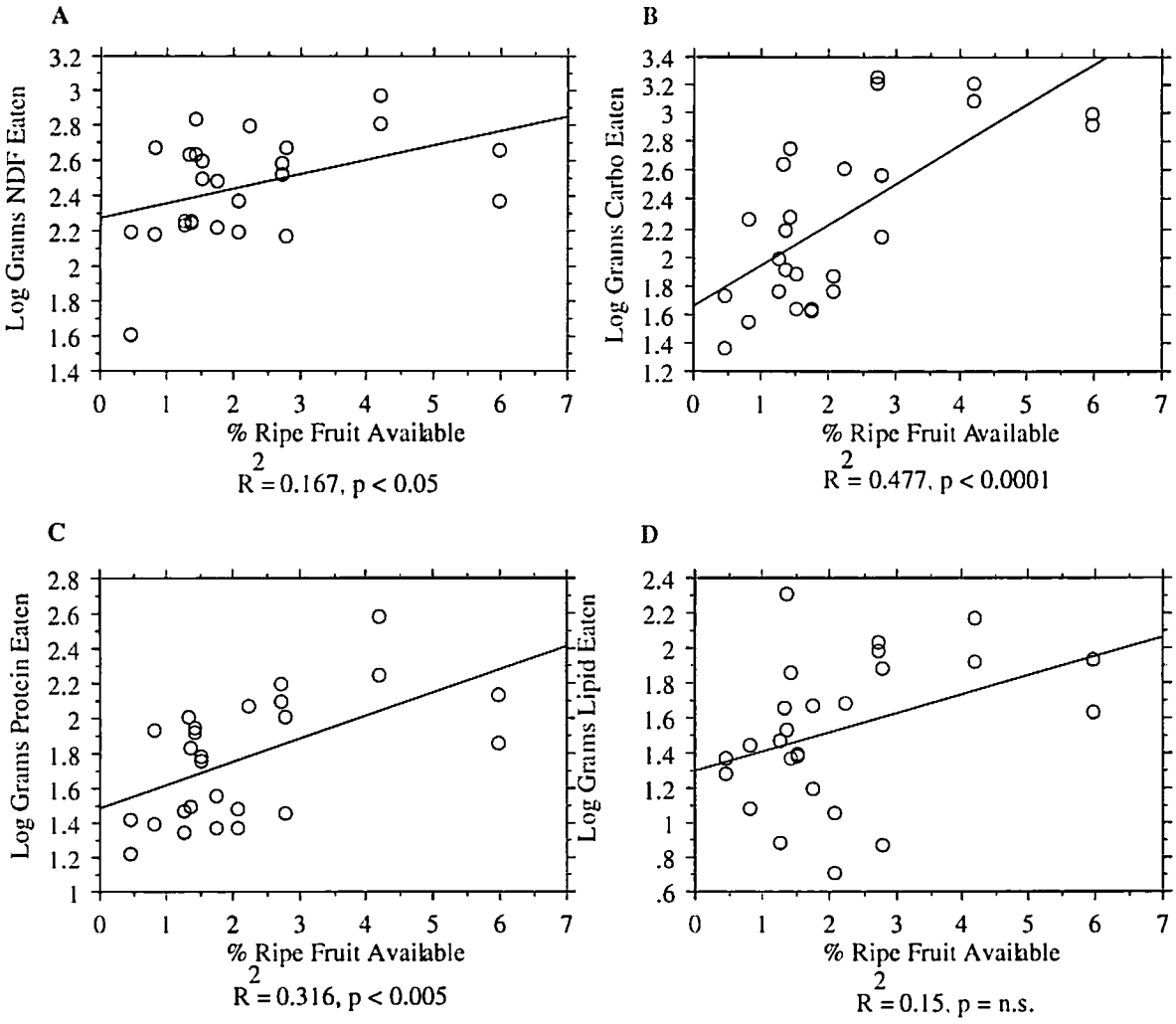


FIGURE 4.19: Total grams consumed of (A) carbohydrate, (B) fiber, (C) protein and (D) lipid compared to percentage of trees with ripe fruit.

Relationships among Nutrients Consumed

During the fruit-rich period orangutans increased their consumption of carbohydrates, but how did the consumption of the different nutrients vary with each other? Did other nutrient categories increase in parallel? A Spearman rank correlation matrix between the different nutrient fractions is shown in Table 4.08. There was a strong negative relationship between fiber and carbohydrate consumption. Carbohydrate was also negatively correlated with protein consumption. Thus, as carbohydrates increase the fiber and protein content of the diet decreased. Fiber and protein had a significant positive relationship. This is not surprising given the generally higher protein and fiber content of leaves and bark (Table 4.05). No significant relationships were seen between fiber and lipid, carbohydrate and lipid and protein and lipid.

TABLE 4.08: Matrix of Spearman Rank Correlation Coefficients (Rho) for relationships between percent gram consumption of the different nutrients.

	Fiber (NDF)	Carbohydrate	Protein
Carbohydrate	-0.914***		
Protein	0.327*	-0.509**	
Lipid	-0.247	0.011	0.185

* $p < 0.05$
** $p < 0.005$
*** $p < 0.0001$

I also examined the relationship between the *total* gram consumption of the different nutrients in order to assess whether orangutans maintained a certain "ideal" intake of particular nutrients, regardless of the make-up of the diet. I found that total intake of all

nutrients was positively correlated. Thus, as overall consumption increased, total consumption of all nutrient fractions increased in concert.

TABLE 4.09: Matrix of Spearman Rank Correlation Coefficients (Rho) for relationships between total gram consumption of the different nutrients.

	Fiber (NDF)	Carbohydrate	Protein
Carbohydrate	0.548**		
Protein	0.882***	0.791***	
Lipid	0.449*	0.669***	0.676***

* $p < 0.005$
** $p < 0.0005$
*** $p < 0.0001$

Sex Differences in Nutrient Composition

Significant differences were also seen between males and females in the nutrient content of the diet. As earlier, I use Mann-Whitney U-tests to compare between males and females. I analyzed two versions of the data set: (1) full day follows only and (2) full and partial day follows combined. Full day follows allow for the most controlled comparison between males and females and between months because the entire daily diet is represented. However, because only 66% of the follows were full days, analyzing just full-days may over-represent certain follows, particularly when males and females are viewed separately. Combining full with partial day follows has the advantage of allowing the entire data set to be used, thus increasing the sample size. However, because partial day follows only reflect a portion of the feeding bouts that day, this may over-represent feeding on particular items. Thus, I report here the significant differences that were consistent between the two

analyses. No females were followed in December 1995 and no males were followed in November 1995, thus those two months could not be compared. Statistics reported in the text are for full and partial day follows combined.

The nutrient composition of the diet was not significantly different between males and females in most months (Figures 4.20 - 4.21). The exceptions were in January, May and June. In January males had a higher percentage of Kcal's coming from protein (15.43%) than did females (7.66%) ($U = 58$, $p < 0.05$). Examination of the actual diet during this month showed two interesting differences between males and females. Females had a more diverse diet, they ate foods from 12 genera (11 fruit) whereas males ate 8 genera of fruits. Second, the percentage of time spent feeding on *Durio* was strikingly different between males and females. Males spent 44.0 % of feeding minutes eating *Durio* compared to 6.6% in females. *Durio,* or durian, is a large (mean wet weight is 347 grams and mean length and width are 10.9 cm x 10.7 cm), aromatic fruit protected by a hard husk and extremely sharp, long spines. The husk is 68% of the total wet weight of the fruit and for humans is impossible to open without a tool such as a machete. As shown in Table 4.05 durians are quite high in protein compared to other mast-fruits.

The second difference between males and females was in May and June. In May and June males ate significantly more lipid on both a percent Kcal's (May: $U = 2$, $p < 0.001$; June: $U = 98$, $p < 0.05$) and percent grams (May: $U = 2$, $p < 0.001$; June: $U = 94$, $p < 0.05$) basis. Females ate significantly more Kcal's ($U = 14$, $p < 0.01$) and grams ($U = 12$, $p < 0.01$) of fiber in May than did males. Males also had higher percent protein in their diet in May ($U = 23$, $p < 0.05$). As described in the section on sex differences in caloric intake this was when males were predominantly eating lipid-rich *Neesia* seeds. As can be seen in the graph in Figure 4.20, the percent lipid in the diet also increased for females relative to most other months, but the increase was much greater for males. The *Neesia* season

finished during June, but males ate 13% *Neesia* in June compared to 0% for females. It appears in Figure 4.20 that females had a greater percentage of lipid in the diet in March compared to males, but this difference is not significant due to the small sample size.

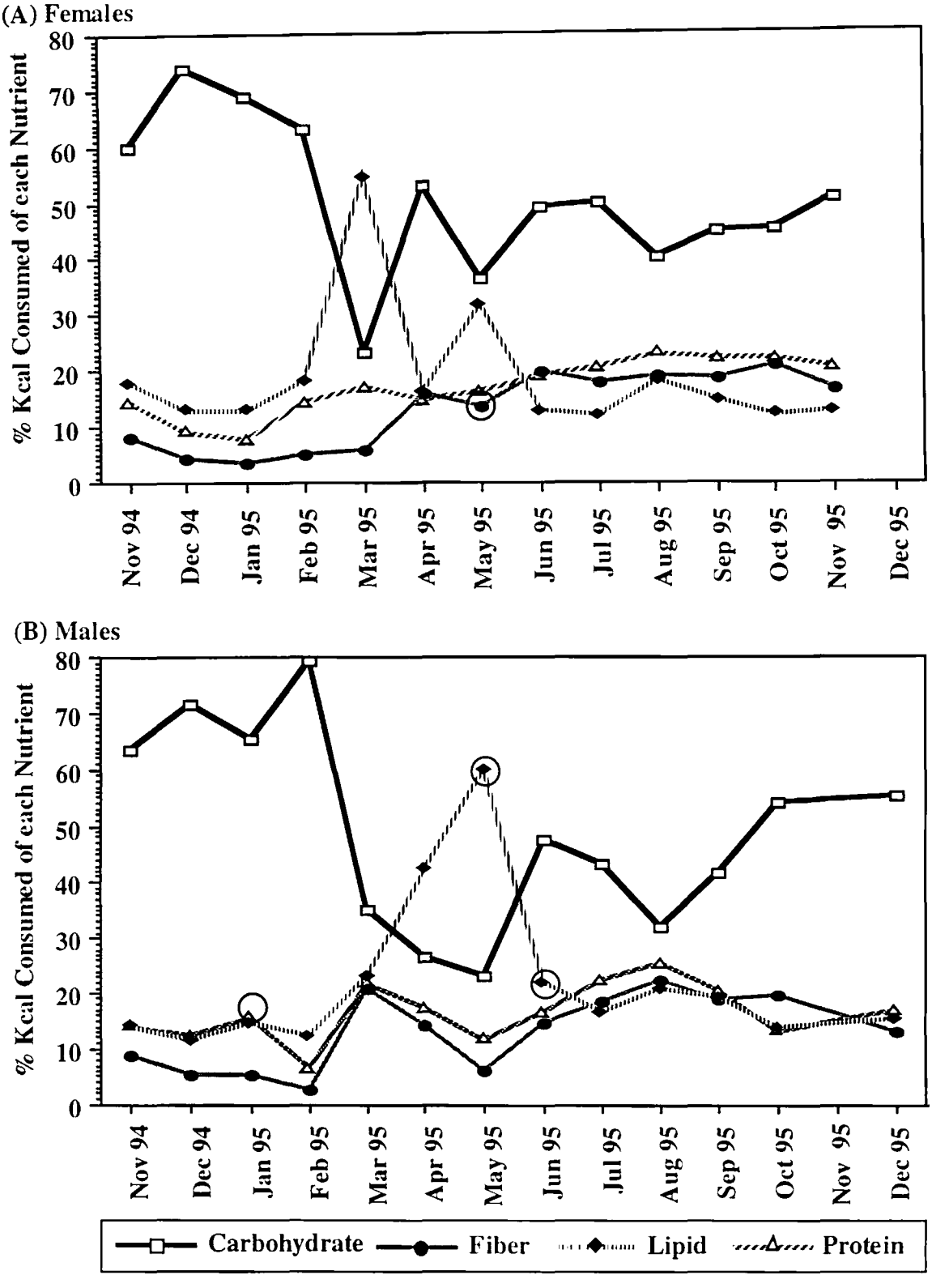


FIGURE 4.20: Changes in the percent nutrient content of the diet on a percent Kcal consumption basis for adult female (A) and fully-developed male (B) orangutans. Circled points are significantly higher than the same nutrient in the opposite sex for that month.

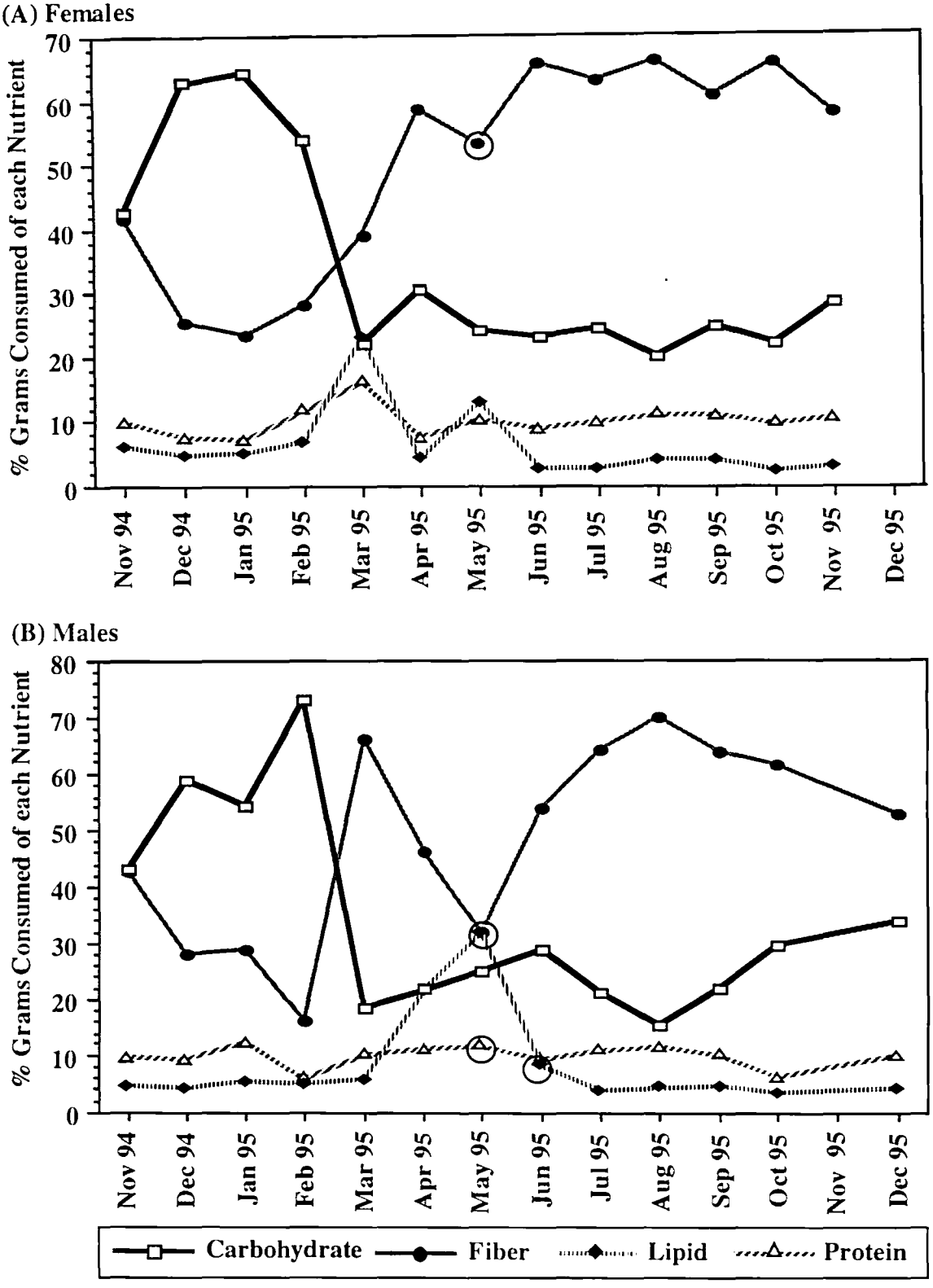


FIGURE 4.21: Changes in the percent nutrient content of the diet on a percent grams of consumption basis for adult female (A) and fully-developed male (B) orangutans. Circled points are significantly higher than the same nutrient in the opposite sex for that month.

DISCUSSION

Variability in Diet, Calories, and Nutrient Consumption

The evidence presented here supports two major new conclusions about the interaction between fruit availability, feeding behavior and dietary intake in orangutans. First, orangutans are maximizing their caloric intake when fruit abundance is high by consuming very large quantities of carbohydrate-rich fruit (including pulp and seeds). Leighton's (1993) examination of orangutan diet selectivity showed that carbohydrate-rich fruits were preferred by orangutans when they were available. This study, in which data on daily caloric and nutrient intake was collected for the first time, showed that orangutans consumed large quantities of these preferred foods during periods of high availability. Second, during periods of low fruit availability, such as following a mast fruiting, orangutan caloric intake can be drastically low. Available fruit is eaten during these low periods, but leaves and bark, and to a lesser degree pith and insects, are consumed as fall-back foods. These dramatic boom and bust periods of caloric intake have not been documented before in orangutans. Orangutans seem to cope with these periods of food stress, nutritionally, by relying on leaves and bark, in particular, as fall-back foods.

Differences in the types of food consumed provide the first line of evidence for substantial differences in dietary intake. Orangutans showed significant variation between months in the food types that were eaten. As was predicted, based on previous studies of orangutan food preferences (Leighton 1993), a significantly greater proportion of their diet was fruit during the mast period of high fruit availability compared to the post-mast period. Orangutans were still predominantly frugivorous throughout the year, except for occasional months when fruit consumption fell to less than 50%. In most low-fruit months leaves were the most important secondary food source, followed by bark. Pith and insects were

less important as fall-back foods, but were increasingly eaten as fruit availability decreased in terms of time spent feeding, but not as Kcal's of consumption. This may be because insects and pith have higher handling and extraction times relative to the caloric return. Differences in actual grams of consumption and total caloric intake are necessary to assess the impact of dietary changes on orangutan physiology. This type of data is considerably more difficult to obtain than minutes spent feeding on particular food items, but without such data we can only make qualitative impressions about differences in diet: bark and leaves would seem to indicate a lower quality diet than fruit but direct measurement is needed to quantify the difference in diet quality. Caloric intake variation is extreme and is far greater than just a time-spent-feeding or food-type analysis would intake.

Data on total daily caloric intake show that orangutans consumed as much as twenty times the calories during the mast fruiting peak compared to the fruit low periods. This difference is striking for both the magnitude of the peak and the severity and length of the low caloric intake period. Because of the different composition of the plant foods consumed during the two periods, the orangutans were able to increase their caloric intake by a far greater margin than their grams of intake. These data strongly support the hypothesis (MacKinnon 1974; Wheatley 1982, 1987; Leighton 1993) that orangutans are building up fat reserves during the fruit-rich periods and that these fat reserves are essential for sustaining them through the fruit-poor periods. However, data on energy requirements and changes in energetic expenditure are needed to assess whether calories in excess of requirements are being ingested during the fruit-rich periods and whether caloric needs can be met during the fruit-poor periods. These data are presented in Chapter 5.

It is possible that some of these excess calories eaten by orangutans may have been undigested and excreted in feces. Increased food intake increases gut passage time van Soest (1994), thus it's possible that there may have been greater nutrient loss during the

high-fruit period. This could be tested by collecting all fecal matter during a daily follow, analyzing it is caloric content and then subtracting that value from the estimated caloric intake.

Additionally, the existence of such extended fruit-poor periods emphasizes the importance of fall-back foods for orangutans. When fruit availability was low, a large proportion of their diet was composed of bark and leaves, and to a lesser extent pith and insects. These four food types showed a strong negative relationship with fruit availability and fruit consumption. Periods of low food availability can be strong selective forces in animal evolution, thus we can look to particular adaptations of orangutans to enable them to take advantage of these more reliable, but less nutritious resources. First, the large body and gut size of orangutans enable them to handle a highly fibrous diet. Second there may be features of their dentition that are necessary to remove bark from living trees. It was my observation that juvenile orangutans always ate bark by peeling away strips from a section that their mother had already opened. Thus, features of the adult dentition and cranial musculature may enable them to perform this task.

Overall, carbohydrates provided the most calories throughout the year. Leighton (1993) found that orangutans preferred fruits that were high in carbohydrates and that their foraging decisions maximized caloric intake. The results presented in this chapter support that conclusion. The methods differ in that Leighton's (1993) data are drawn from census observations of orangutans and the data in my study come from daily follows. During the low-fruit period orangutans males in particular were able to increase their caloric intake by concentrating on lipid-rich *Neesia* seeds. The total grams of fiber intake did not vary across the different months or between the high and low fruit periods. Although plenty of leaves and bark were available during the fruit-low period, orangutans did not increase their caloric consumption by increasing the *total* grams of fiber eaten. I believe this implies that

they are already eating near their limit of fiber consumption and cannot increase calories through increased fiber intake.

Finally, these data also suggest that dramatic seasonal fluctuations in fruit availability were an important selective force in the evolution of large body size in orangutans as suggested by Wheatley (1987). Orangutans prefer carbohydrate-rich fruits, but when these are not available they turn to lower quality, high-fiber food items. Large gut size enables them to effectively process a high fiber diet and large body size in itself helps to buffer against food-poor periods.

Comparison with Humans

It is interesting to consider how maximum caloric intake in orangutans compares to humans. Can and do humans consume as many calories as I have estimated for orangutans — on the order of 8,000 - 11,000 Kcal/day? Average caloric intake of Americans reported by Marston and Peterkin (1980) was 3500 Kcal. However, athletes routinely consume diets higher in calories. Mean energy intake was 7195 Kcal/day in elite cyclists (Gabel and Aldous 1990) and 7815.3 Kcal/day in "Tour de France" racers (Saris, *et al.* 1989). Perhaps the most appropriate comparison is in athletes who are trying to maximize their caloric intake. In a 4-year study of university athletes Short and Short (1983) found that football players had a mean intake of 5,270 Kcal/day. On average 1.7-5.3% of the players averaged over 10,000 Kcal/day throughout the fall playing season. One individual (6 ft, 3 in, 118 kg) averaged more than 11,000 Kcal/day with a one day total of 14,626 Kcal. Other maximum intakes were 9270 in basketball players, 7337 in crew members, and 14,962 Kcal in wrestlers. These humans are similar in body weight to the largest adult male orangutans (83.6 kg, Rodman 1984). Thus, it is reasonable to expect

that they also would be able to sustain such high caloric intakes. Given their larger gut capacities and their ability to ferment fiber orangutans should also be able to consume a much greater gram weight of food than do humans.

Sex differences

In many ways, male and female orangutans were very similar in the composition, nutrient make-up, and even caloric contribution of their diets. Thus, as a species, orangutan males and females seem to be consuming similar items and maintaining a similar diet quality despite their difference in body size. This is likely due to the high costs of reproduction in females. For example, in Figure 4.14, comparing two males and one female, the caloric intake of the female tended to be intermediate between the two males. This female was carrying one lactating offspring and was accompanied by an older juvenile and thus likely had high reproductive costs. Between the two males, Roman traveled further each day, dominated fruit sources and exhibited a high rate of long calling. Frank, on the other hand, was much more cryptic. He rarely long called, did not travel very far each day and thus may have had lower energetic costs, despite the fact that he was bigger than Elizabeth. In addition, although males are larger, if a large percentage of their greater soft tissue is due to fat, rather than metabolically more active muscle, this could reduce some of the expected differences. Males did eat significantly more calories in May and June than did females. During the months of greatest food consumption, January and February, the mean caloric intake tended to be greater for males, although this difference was not significant. It will be interesting to examine individual differences in depth in the future to understand more of these patterns.

I found no evidence that males had lower quality diets across the study period. In fact, the opposite tended to be true. Males were able to maintain a higher quality diet during the

fruit-poor period than were females. This was evidenced by higher caloric intake, higher percent and total lipid intake, and lower percent and total fiber intake during May and June. In addition, their protein intake was higher in January. Why were males able to eat a higher quality diet during these two periods than were females? Interestingly, the difference in both periods seems to have been due to the intake of large, heavily protected, but nutrient and calorie-rich fruits—*Durio* and *Neesia*. Both cannot be opened by humans without a tool due to the large, heavy husk. *Durio* is additionally protected by needle-sharp spines and *Neesia* seeds are protected by fiberglass-like irritating hairs. Three possible reasons may explain the sex difference in feeding on these two fruits: difficulty in opening the fruits, tolerance of the plant's defenses, and dominance of certain fruit trees.

Neesia fruits are ripped open by orangutans at Cabang Panti and *Durio* is gingerly forced apart using leverage at key points on the husk. It may be that adult males, being twice the size of females and having greater strength, are more successful at prying open these heavily protected fruit, especially when they are still unripe.

It also may be that adult male orangutans are more willing to suffer the costs of combating the plants' defenses. The spines of *Durio* could easily cause injury and, if not handled correctly, could pierce the skin. My observation was that forest durians had even sharper spines than did the domesticated variety which is highly prized but handled cautiously. The irritating hairs in *Neesia* may make the consumption of their seeds costly. The handling time of these two fruits is considerable and if females find it more difficult to open them, the cost/benefit ratio of consuming these fruits versus other foods available may be lower for males than for females.

That *Neesia* is difficult to extract is also evidenced by the observation of van Schaik and Fox (1996) that orangutans in Suaq Balimbing forest in Sumatra use tools to extract these

seeds from ripe fruits that have split open. They find that there is no sex difference in ripe *Neesia* eating, with adult males, females and juveniles all using tools to extract *Neesia* seeds. Unripe *Neesia*, however, which need to be forced open, were eaten more by males at Suaq, as at Gunung Palung (van Schaik and Knott 1998).

Finally, in the case of *Durio*, these trees are extremely rare in the forest. During the course of the study, less than 10 of these trees were known to be fruiting in the whole study area. The adult male, Roman, appeared to dominate the durian tree with the largest crop size. On several occasions females and undeveloped males were seen to wait until Roman had finished eating before entering the tree. Thus, females may have more limited access to these trees. No such observations were made of *Neesia*, however, which is a fairly abundant tree in the freshwater swamp forest.

Rodman (1979) observed that males had longer and fewer feeding bouts than did females. He supposed that this meant that males were forced, due to their large body size, to eat a diet that was lower in quality. I also found that diet diversity was higher in females but this did not equal higher diet quality. The data presented here support an alternative hypothesis that large body sized enabled male orangutans to utilize food resources that females either couldn't use or were prevented from using. Large, developed males may stay longer at a given food source because they can exclude other animals. Additionally, large males may be better able to tolerate secondary compounds present in plants due to their large gut capacity and thus may be able to feed longer on a given food species.

These data also show that male caloric intake and diet quality were slightly more buffered during the low-fruit period than was found in females. Caloric intake, fruit consumption and carbohydrate consumption were strongly correlated with fruit availability in both sexes, but the relationships were not as tight in males as in females.

Comparison with other Apes

Striking similarities and differences exist between chimpanzees and orangutans in percent of minutes spent eating each nutrient when the data presented here are compared to the chimpanzee data in Conklin-Brittain *et al.* (1997, 1998). These values were obtained in the same lab using identical procedures and are thus highly comparable. The only difference is that Conklin-Brittain *et al.* (1998) present their data on a percent room temperature dry matter basis and my data is presented on an organic matter basis. This means that the inorganic, ash portion (mean = 4.8%) has been subtracted from the weight of my samples. Differences between the two measures should be small.

Conklin-Brittain *et al.* (1997) report an average crude protein value of 9.5% over a one year period, compared to my finding of 9.7% crude protein for orangutans over 14 months. There is no evidence in either my study or in Wrangham *et al's* chimpanzee study that either ape ever tried to maximize protein intake. This is an important finding in light of hypotheses regarding the role of protein in determining interbirth intervals (Tutin 1994), in optimal foraging in primates, and in understanding human evolution. Instead of trying to maximize protein intake, it appears that orangutans and chimpanzees maintain low but adequate levels of protein regardless of season. Multivariate analysis of factors influencing fruit selection in orangutans by Leighton (1993) showed that protein content did not influence fruit choice.

Second, lipid intake was 5% in orangutans compared to 2.5% in chimpanzees. Chimpanzees had a diet significantly higher in lipid during their period of highest ripe fruit abundance. This was not the case with orangutans. Orangutan lipid consumption peaked during the low-fruit period when the high-lipid *Neesia* seeds were relied on, particularly by adult males. Peak lipid consumption in chimpanzees was 8.5% during the high fruit

season compared to peak lipid consumption of 16% in orangutans. Lipid was as high as 32% in adult male orangutans in May. These differences in lipid consumption may, in part, reflect differences in the fruits available in these two forests. Orangutan fruits, in general, appear to be higher in lipid than chimpanzee fruits (Conklin-Brittain, pers. comm.). Thus, percent lipid intake may not reflect differences in preference as much as differences in habitat between the two species. Regardless, the presence of high-lipid fruits provides an important avenue for orangutans to increase their caloric consumption.

Intake of fiber was greater, overall, in the orangutans, 41%, compared to the chimpanzees, 34%. In contrast, the orangutans had a carbohydrate (TNC) intake of 29% across the year compared to a mean of 39% for chimpanzees. Thus, on a carbohydrate versus fiber comparison, orangutans had lower quality diets overall than did chimpanzees. However, orangutans also experienced greater variability in carbohydrate and fiber consumption than did chimpanzees. Comparing maximum and minimum monthly averages, orangutan carbohydrate consumption ranged between 11% and 66%, compared to 32% and 48% for chimpanzees. Fiber consumption ranged between 11% and 56% in orangutans versus 20% to 37% in chimpanzees. These data suggest that orangutans do experience greater seasonality in the quality of the diet they consume than do chimpanzees.

Total grams and total Kcal's consumed have not yet been calculated for other great apes, although such calculations are planned (Wrangham pers. comm.). Such a comparison between orangutans and the other great apes would be necessary to fully test the hypothesis that the peculiar fruiting dynamics of Southeast Asian rain forests have led to a pronounced fat storage adaptation in orangutans compared to the other great apes. Chimpanzees and gorillas certainly experience fluctuations in fruit availability, but phenological studies indicate that fruit fluctuations in African rain forests are not as pronounced on a supra-annual level due to the absence of mast fruiting. The corresponding periods of extended

months of low-fruit availability may also not be as extreme in Africa compared to Southeast Asia. The comparison of this study with that of Conklin-Brittain *et al.* does suggest that the fluctuations in nutrient consumption are far greater in orangutans than in chimpanzees. Thus, I would hypothesize that gorillas, particularly the more highly frugivorous lowland gorilla, and chimpanzees even more so than gorillas, would show fluctuations in caloric consumption related to fluctuating fruit availability, but that these differences would not be as pronounced as reported here for orangutans.

Future Analyses

The data set presented here provides for a wealth of future analyses which are beyond the scope of this thesis, some of which I will mention here. Additional data exist on patch size, the presence of secondary compounds and the level of water soluble carbohydrates. These will be useful in analyzing orangutan dietary selectivity in comparison with Leighton's (1993) study. The path length between food sources, the tree species eaten, patch size, caloric return of each feeding bout, etc. will be useful in testing various aspects of optimal forging theory. Fruit consumption has been further broken down in terms of plant part (seed, pulp, skin), and nutrient composition has been broken down by food part (e.g. percent of each nutrient from fruit, leaves, flowers, insects, pith, and bark). This may help us understand why particular food items are selected — for example why are insects eaten even though they have such a low rate of caloric return.

Furthermore, the interaction between social and feeding behavior could be analyzed by looking at the foraging decision of particular individuals. Because orangutans are for the most part autonomous, we might expect a higher degree of variability between individuals than in other primates where travel and foraging decisions are strongly influenced by group

membership. Some males seemed to adopt a cryptic strategy, avoiding other males and not consuming as many calories as the more "dominant" males. The effect of individual strategies on understanding foraging in orangutans warrants further investigation. Finally, males and females in general have similar dietary quality, but do the strategies they use to obtain these nutrients differ? Bringing in more of the variables I have collected related to orangutan feeding behavior may help to answer these questions.

• CHAPTER 5 •

ORANGUTAN ENERGY EXPENDITURE

CHAPTER SUMMARY

Energy expenditure was quantified on a daily basis in order to estimate the total energetic requirements of wild orangutans, and to see if their expenditure of energy varied with the environmental changes in fruit production. The computational approach to calculating energy expenditure I used allowed an estimation of the partitioning of energy to different activities and was a non-invasive method feasible to use on wild orangutans.

Detailed data were collected on the total minutes orangutans allocated to different activities during the day, as well as horizontal and vertical distances traveled and body position during different activities. I adapted models developed for calculating energy expenditure in humans and other primates to orangutans to produce estimates of energy expended for each follow day.

Activity data showed that orangutans spent more time awake during the high fruit periods. Both males and females spent more time traveling during the high fruit period and also traveled further each day. Males also spent more time feeding during high fruit periods, but females did not. In contrast to adult males, there was a dramatic increase in the amount of time adult females spent in the company of other orangutans during the high fruit period, which seems to account for their additional time spent awake. These social interactions included gatherings of females with offspring in the same fruiting trees as well as undeveloped adult males consorting with females.

The calculated caloric expenditure of orangutans only varied slightly between high and low fruit periods, although these differences were significant between the time periods. Not considering the costs due to reproduction, both males and females expended more calories during the fruit-rich period. The higher expenditure during the high fruit period appears to

be explained by a significantly greater increase in caloric expenditure due to travel. Across both fruit periods, male daily caloric expenditure was 3100 - 3400 Kcal's per day, while female expenditure, including costs of maternal care was 2300 - 2400 Kcal's per day. These values calculated from time spent in various activities agree well with general expectations for active humans when adjusted for body size.

The energy expenditure data presented in the chapter provide the information necessary to compare with intake estimates in order to be able to examine the question of whether orangutans are experiencing caloric excess or deficit during different fruit availability periods.

INTRODUCTION

The question of how an organism allocates available energy is essential in the understanding of animal behavior and ecology. The most common approach to this question has been to look at time allocation profiles of an individual or group's behavior. This allows us to understand how activity patterns vary depending on different patterns of food availability, sex and sociality. A more detailed approach is to quantify the Kcal's expended for various behaviors in order to measure energy expenditure. This enables us to actually estimate the costs of particular behaviors to the animal and to assess whether an individual's energetic needs are being met. Both methods are used in this chapter to quantify changes in orangutan energy expenditure.

By studying how an animal partitions its time and energy resources, it is possible to begin to understand the relative importance of each behavior to the animal, the priorities set by the animal in determining how to allocate energy, and the extent to which behaviors may be constrained or determined by ecological factors. Adjustment of behavioral activity provides an animal with flexibility in dealing with excess or insufficient energy resources (Coelho 1986).

Determination of energetic expenditure requires detailed data on the duration of discrete behaviors that differ in the degree of energy expended. Very few primate field studies actually report total time spent in particular activities (Coelho 1986). When time allocation data has been reported, it generally has been limited to instantaneous sampling of broad behavioral categories: resting, eating, traveling, grooming, etc., rather than absolute bout lengths. Only a few studies have attempted to estimate energetic expenditure directly (Coelho 1986; Coelho *et al.*, 1976, 1979; Nagy and Milton 1979a, 1979b; Wheatley 1982; Rodman 1979; Muruthi 1989; Altmann and Samuels 1992; Leonard and Robertson 1997).

Although the most physiologically accurate method to determine energetic expenditure is the use of doubly labeled water (e.g. Nagy and Milton 1979a, 1979b), the computational method of estimating energy has several other advantages, as described by Coelho (1986): (1) in addition to modeling energy usage on a daily basis, the way an animal partitions energy expenditure throughout the day can also be determined (2) observation-based estimates of energy expenditure provide information on how energy is partitioned to particular behaviors (3) the relative importance of each behavior can be evaluated and (4) the method is non-invasive and thus can be used in situations where manipulation of the animals is not feasible.

The goal of this chapter is to quantify changes in energy expenditure in orangutans, comparing the periods of high and low fruit availability in my sample period. I examine changes in (1) activity patterns (2) travel distance, and (3) the amount of energy (Kcal) expended. This enables me to determine whether and how orangutans vary levels of energetic expenditure depending on the resources available and it provides estimates of caloric expenditure that can then be compared to intake estimates. These data also provide information on the levels of nutritional intake that are necessary to meet caloric requirements.

Background on Energetic Computations

In this section, I provide a review of the methods that have been used to calculate energetic expenditure in primates that I have applied to orangutans.

Resting Metabolic Rate

Resting metabolic rate (RMR) is the amount of energy used by an inactive individual under thermoneutral conditions (Passmore and Durnin 1955). RMR has been shown to scale to the three-quarters power of body weight in a diverse number of mammalian species (Kleiber 1932; Brody 1945). Thus, the number of Kcal's expended per day to meet resting or basal caloric needs can be defined as in Kleiber:

$$RMR = 70 \bullet Wt^{0.75}$$

where:

RMR = Resting Metabolic Rate (Kcal/day)

Wt = Body Weight (kg)

Primates do not differ significantly from this allometric relationship, despite their large brain size (Coelho 1986; Leonard and Robertson 1997). Bruhn (1934) measured actual RMR in multiple trials on 1 young orangutan and found that the predicted RMR differed from actual RMR by only -1%.

Non-Locomotory Costs

Coelho's Equations

The most commonly used method for estimating non-locomotory activity in primates is the model developed by Coelho (1974, 1976, 1986) and colleagues (Coelho *et al.* 1976, 1977, 1979). Because the costs of specific activities have not been determined directly for non-human primates, they scale empirical values obtained for humans (Consolazio 1971; Passmore and Durnin 1955; Webb 1973) to other primates based on metabolic body size

($W^{0.75}kg$). The cost of the activity (A_i) is defined as the energy expended by an actor of a given mass ($W^{0.75}$ kg) performing an act (D_i) for length of time (T_i).

$$A_i = D_i \bullet W^{0.75} \bullet T_i$$

where:

D_i = energy cost (Kcal/minute) for a particular act

W = body weight (kg) of an actor

T_i = amount of time spent performing an act (D_i) in minutes

Coelho (1986) provides estimates of the caloric costs (D_i) of 172 activities based on a baboon ethogram. These values include the cost of basal metabolism a well as the cost for the performance of the activity above basal levels.

In this model a pregnant animal's activity expenditure values are increased by a value of 1.25 and a lactating animal's energy by 1.5 (Coelho 1974, 1986). In evaluating this method, Coelho (1986) found close agreement between the results of his study on howler monkeys (1976, 1979) using the above values for energetic expenditure to those found by Nagy and Milton (1979a, 1979b) using doubly labeled water, when the costs of lactation and pregnancy were accounted for.

Coelho's methods have also been followed by Altmann *et al.* (1993) and by Leonard and Robertson (1997) in the calculation of non-locomotory costs. Altmann used Coelho's values directly to determine the costs of various baboon behaviors. Leonard and Robertson use Coelho's methods in a study of comparative bioenergetics and it's application to the study of hominid evolution. They divide all activities into five categories: (1) inactive (sleeping or dormant) (2) resting (3) feeding (4) locomotion and (5) other (e.g. socializing, grooming) and then use energetic values adapted from Coelho (1974; Coelho *et al.* 1976)

for the costs of these activities (except for locomotion). Leonard and Robertson take Coelho's energetic values and convert them to energy constants, K_i , that are multiples of RMR. Caloric costs for individual activities are then calculated as follows:

$$C_i = K_i(RMR)T_i/24$$

Where:

C_i = Energy cost in Kcal

K_i = Energetic cost for each activity

RMR = Resting Metabolic Rate (Kcal/day)

T_i = Time in hours spent in some activity

Moen's Equations

A second method of calculating non-locomotory costs used in primate studies is application of Moen's (1973) equations as done by Wheatley's (1982). These equations were developed from domesticated animals, such as sheep, and are multiples of basal metabolism. These are also used, in conjunction with information from Iwamoto (1978), by van Schaik and van Noordwijk (1985) to estimate energy expenditure in long-tailed macques (*Macaca fascicularis*).

Costs of Locomotion

Taylor's Equations

The most commonly used method for estimating locomotory costs are the equations developed by Taylor *et al.* (1970, 1973, 1982) and colleagues. They conducted a series of

experiments to estimate the cost of terrestrial locomotion in animals. Their 1970 formula (based on domesticated animals) for an animal traveling at any velocity for 1 km is:

$$M_{run} = 8.5W^{0.60} + (6.0/V) \cdot W^{0.75}$$

where:

W = Body weight in kg

V = Velocity

Leonard and Robertson (1997) follow the equations from Taylor *et al.* (1970) and Taylor and Rowntree (1973) for quadrupedal locomotion. They convert Taylor's equation for ml O2 g^{-1} kg^{-1} into Kcal's by using a respiratory quotient (RQ) of 0.9. Consumption at this RQ indicates that 1 liter of oxygen consumed equals 4.92 Kcal (McArdle *et al.*, 1986). In Leonard and Robertson's (1997) formulation, the cost of locomotion (C_{loc}) is estimated as:

$$C_{loc} = (0.041Wt^{0.60})DR + (0.029Wt^{0.75})T_{loc}$$

where:

DR = day range in meters

T = Time spent in the activity

Wt = Body weight in kg

Later, Taylor *et al.*. (1982) revised their equations using wild animals in specific mammalian orders. One of these groups was primates. Their primate sample was somewhat problematic in that in addition to stump-tailed macaques, hamadryas baboons and bush babies, it includes tree shrews, but it arguably provides more accurate estimates than using just the "average" animal.

Altmann and Samuels (1992) applied Taylor *et al.*'s (1982) allometric exponents of energetic expenditure in primates to their study of savanna baboons. Their energetic equation, which substitutes 20.1 KJ for 1 ml O_2, is:

$$E = (20.1)((0.523)M_b^{(1-0.298)}) + (0.345\ M_b^{(1-0.157)})$$

where:

E = KJ/Km

M_b = Body Mass (kg)

Using data on the time and distance traveled for several "categories" of baboons, they estimated how far each female traveled at each speed and then calculated the energetic expenditure per day for the distance traveled at that speed. In Altmann *et al.* (1993) they use the above equation plus Coelho's estimates of activity-specific expenditures to model energy balance in baboons.

Tucker's Equations

Coelho (1974) uses Tuckers' (1970) equations to estimate the caloric costs of locomotion.

$$Kcal/kg \cdot km = 0.100(10)^E$$

where:

$E = 1.67W^{-0.126}$

W = Body weight of the actor in kg

Previous Application of Energy Expenditure Equations to Orangutans

Energetic expenditure has been calculated for orangutans by Rodman (1979), Wheatley (1982) and Leonard and Robertson (1997). Each study used a somewhat different method. Orangutans lend themselves to this type of analysis because they are relatively slow moving and, because the party size is normally one individual, continuous activity data is often collected on orangutans.

Rodman

In Rodman's (1979) study of orangutan activity patterns he uses Taylor *et al.*'s (1970) equations to estimate the cost of traveling. Rodman found that orangutans in his study (42 full day follows on 1 adult male, 2 adult females and 1 juvenile female) traveled a median distance of 0.4 km/day in 75 minutes, giving a velocity of 0.32 km/hr. The cost of traveling horizontally across a given day range (M_{hor}) at 0.32 km/hr was estimated as:

$$M_{hor} = 17.1\ D \cdot W^{0.75}$$

where

D = day range in km

W = body weight in kg

Rodman addresses the fact that this locomotory cost is for a true quadruped and thus does not adequately model the costs of arboreal travel which is constantly interrupted, requiring frequent detours and vertical displacement. He states that travel costs due to arboreality would be increased due to constant acceleration and deceleration in the canopy. Rodman thus estimates the cost of arboreal travel as twice the cost of travel on the ground, using the following equation for vertical travel:

$$M_{vert} = 2.3DW$$

The derivation of this formula is not explained. He then estimates the total cost for basal metabolism (M_{tot}) and travel as:

$$M_{tot} = 70W^{0.75} + 34DW^{0.75} + 2.3\ DW$$

Given a day journey of 0.4 km and estimated weights of 90 kg for the adult male, and an average of 45 kg for the adult females, he estimated caloric expenditure to be 2530 Kcal for the male and 1495 Kcal for the two adult females in his study. These values do not account for lactation, pregnancy, or other non-locomotory activities.

Wheatley

In his study of orangutans and *Macaca fascicularis*, Wheatley (1982) estimates total daily energy expenditure by using additional equations developed by Moen (1973). He uses this method instead of that used by Coelho (1976) in order to account for horizontal and vertical travel separately. Moen's equations come from domesticated animals studied in laboratories or pastures and are hourly rates. Reproductive costs of lactation and pregnancy are not included. Daily energy expenditure is calculated as the sum of basal metabolism and the activity expenditures as follows:

$$\text{Resting} = (70W^{0.75})1.1/24$$

$$\text{Walking 1 km on level} = 0.59WD$$

$$\text{Vertical ascent of 0.1 km} = 6.45WH$$

$$\text{Foraging} = 0.54W$$

where:

W = Weight in kg

D = Distance in km

H = Vertical height ascended expressed as percentage of km on the level

In applying these formulas, Wheatley calculates arboreal locomotion as the sum of level walking and vertical ascent and descent multiplied by time engaged in travel. He assumes, arbitrarily, that half of the day range is spent in vertical ascent and half in horizontal descent. Because the cost of vertical descent is approximately equivalent to the cost of walking on the level (Moen 1973) he applies the equation for the cost of walking to the cost of vertical descent. Then he doubles the sum of these locomotory costs to account for non-linear travel. Based on the average activity budget for one adult male orangutan from 3 days of observation, he estimates a caloric energy requirement of 2333 Kcal/day for a 55 kg orangutan.

Leonard and Robertson

Leonard and Robertson (1997) calculated daily energetic expenditure in a variety of primates. They use a day range for orangutans of 300m/day that they say comes from Rodman (1977, 1984), but is smaller than the value Rodman used in his own calculations. Rodman's calculations for day range are significantly smaller than those determined in this and other studies (Galdikas 1988) and are based on a small sample limited to a single season. Thus they are likely not representative orangutan values. They also use Brauhn's data for RMR which provides a slightly higher RMR than is predicted from Kleiber's equation. They calculate energy expenditure to be 2500 Kcal/day for males and 1499 Kcal/day for females. Leonard and Robertson consider these to be *minimum estimates* of energy expenditure because the costs of thermoregulation, digestion and reproduction are

not considered. They also believe these to be underestimates because they state that there is a tendency in field studies to underestimate actual activities times and because the costs of locomotion are based on laboratory not field data.

Goals of this Study

For this study I follow Altmann (1993) and Leonard and Robertson (1997) and adapted the model developed by Coehlo (1986) for calculating non-locomotory energy expenditure in orangutans. For the cost of locomotion, I follow Altmann and Samuels (1992) in using Taylor's 1982 equations, rather than the Taylor's 1970 and 1972 equations used by Rodman (1979) and Leonard and Robertson (1997). Although not specific to orangutans, these primate-based models are likely to be more appropriate than earlier models for the "average" animal.

The studies described above used mean levels of expenditure across multiple animals to derive estimates of energy expenditure. In this study I attempt to quantify energy state more thoroughly by calculating energetic expenditure in each animal for each day of activity. Calculating each animal's expenditure individually allows me to compare between animals and between time periods. I also record the body position during each type of activity in order to assess more subtle energetic differences caused by different postural behaviors (e.g. eating while sitting vs. eating while hanging). This may be especially important for orangutans given their extremely variable body positions resulting from habitual arboreality. I also estimate vertical travel directly rather than arbitrarily calculating it from horizontal travel as did Rodman (1979) and Wheatley (1982).

METHODS

Data Collection

Data were collected on primary activities, secondary activities and body positions of focal animals on a continuous basis in order to quantify time spent at various levels of energetic expenditure. These data allow for a more fine-grained interpretation of changes in orangutan energetics than has been possible in previous studies. A gridded data sheet was used to record all categories of data, with codes used for each data type. I tested for inter-observer reliability and minimized inter-observer bias as described in Chapter 2. Through testing I determined that all observers were able to reliably estimate actual travel distance and height in the canopy. No systematic differences were found between observers in the coding of activity categories, body positions or substrates utilized.

Primary Activities

The time of initiation and termination of each primary activity of the focal animal was recorded to the nearest 30 seconds as they engaged in these non-overlapping activities: feeding, food searching, traveling, nest building, resting, sleeping, day sleeping, fighting, playing, mating and socializing (see Table 5.01 for definitions). Resting bouts, because they were essentially the absence of other activity, were at least one minute long. In addition to transition times, instantaneous scan samples (Altmann 1974) of behavior of the focal individual were done every five minutes in order to maintain vigilance during long periods of orangutan inactivity and to allow for comparison with other studies where only instantaneous records were made.

TABLE 5.01: Definitions used for orangutan primary activities.

Activity	Definition
Feeding	Any type of feeding behavior in which the animal was actively eating, reaching for food or preparing food.
Food Search	Searching for food while not actively engaged in feeding. Primarily used when the orangutans were searching for termites.
Traveling	Movement between trees or on the ground.
Nest Building	Actively making a new nest or adding to an existing nest.
Resting	If an animal was not engaged in another primary activity for more than 1 minute, the activity was scored as resting.
Sleeping	Lying down in a nest either before getting up in the morning or after retiring for the evening.
Day Sleeping	Lying down in a nest during the day after having moved out of the night nest
Fighting	Engaging in an antagonistic interaction with another orangutan, including threatening or being threatened by another conspecific as well as actual physical contact
Playing	Engaging in a behavior either alone or with another individual judged by the human observer to represent play.
Mating	Actively engaging in intromission or positioning prior to intromission.

Socializing	Actively interacting with another orangutan that does not involve fighting, playing or mating. This category includes grooming and touching another orangutan.

Travel Data

Travel data were further quantified by recording the direction of travel and the vertical and horizontal distance in meters traveled during each bout of locomotion. Meters traveled within a tree during other types of activity were also recorded. Travel distances were estimated through pacing and through visual estimates. Day ranges were drawn on a grid map of the study site. Height of the animal in the canopy was recorded on a continuous basis.

Secondary Activities

Secondary activities were those which could be engaged in at the same time as primary activities. Urinating and defecating were recorded on a continuous basis. Displaying aggression towards a human observer, looking at the human observer, looking at another orangutan and vocalizing were recorded as one-zero (occurrence/no occurrence) during each minute of observation. The type of aggressive act such as throwing branches, tree shaking, branch shaking and using leaves to kiss-grunt were described on the data sheet. When an animal vocalized, the number of vocalizations of each type emitted during each five minute period were recorded. Vocalizations were further broken down into long calls, kiss grunts, grumphs and lork calls as defined by MacKinnon (1974). In addition, the duration of all visible lactation bouts were recorded, using a stopwatch, to the nearest second. The start and stop of all raining "bouts" were also recorded on a continuous basis.

Social Behavior

When an orangutan was in the presence of another orangutan (including mothers and infants) we made an instantaneous record of the distance of separation between the two individuals every five minutes. Contact between the two individuals was recorded as "0" separation, then recorded in 5 cm increments from 1-30 cm, in 10 cm increments from 30-100 cm, and in 50 cm increments from 1m to 5 m and from 1 m increments above 5 m. Whether the non-focal individual was in the same or a different tree as the focal individual was also recorded. If there were more than two individuals present, then there was likely more than one observer, in which case each observer chose a different animal to record this data on. Otherwise, the observer recorded the distance of separation between the focal animal and up to two other individuals, with additional separation distances recorded opportunistically. The presence of an infant clinging to his/her mother was recorded on a continuous basis.

Positional Behavior

Positional behavior was recorded by dividing orangutan body positions into the following broad categories: sitting, lying down, standing, hanging, on all four's, clambering and brachiating. Lying down and hanging were further subdivided to provide more detailed positional information. Each body position is defined by how the majority of the animal's body weight is supported. Table 5.02 defines these body positions. Positional behavior was recorded on a continuous basis by writing down the time of initiation and termination of each separate positional "bout."

TABLE 5.02: Definitions used for orangutan body positions.

Body Position	Definition
Sitting	The majority of the orangutan's weight was supported on it's rear end, and the upper body was in an upright position.
Standing	The majority of the orangutan's weight was distributed on two legs and the animal was standing on a horizontal surface. The animal may have been holding on to a branch with one or both of his/her hands.
Lying Down	The majority of the orangutan's weight was supported on his/her torso and the animal was in a horizontal or reclining position. Subdivided into lying on the side, lying on the stomach or lying on the back.
Hanging	The majority of the orangutan's weight was supported by suspending from one or more hand or foot. Further sub-divided by recording whether the animal was hanging from hands or feet, the number of hands or feet used and whether the animal was hanging in a vertical or horizontal position.
Quadrupedal	The orangutan's weight was distributed equally on his/her hands and feet while on a horizontal substrate.
Brachiating	The orangutan was actively locomoting primarily through suspension from both hands.
Clambering	Orangutan movement in which both hands and feet were used roughly equally.

Substrate Utilized

The substrate the orangutan was positioned on was also recorded on a continuous basis as animal's changed substrate type. Substrates were defined as: a branch, a tree crotch, the trunk, a liana and the ground (Table 5.03). The size of the substrate was recorded as belonging to one of the following categories: < 5 cm, 5-15 cm, 15-20 cm, 20-25 cm, 25-35 cm, etc.

TABLE 5.03: Definitions used for substrate types.

Substrate	**Definition**
Branch	The majority of the orangutan's weight was distributed on a branch.
Tree Crotch	The majority of the orangutan's weight was distributed on a tree crotch.
Trunk	The majority of the orangutan's weight was distributed on the trunk of a tree.
Liana	The majority of the orangutan's weight was distributed on a liana.
Ground	At least one of the orangutan's feet was on the ground.

In addition to continuous sampling, an instantaneous scan sample was done every 5 minutes in which all of the above data (primary activity, secondary activity, height in canopy, trail location if known, body position and substrate type) were recorded. This was to ensure continued vigilance during data collection as well as allowing me to analyze the

data by either summing bout length or as instantaneous samples. The following figures were generated for each animal, each day (Figure 5.01): Percentage of time awake spent in each activity, total minutes spent in each activity, average bout length of each activity, average number of bouts of each activity, and average height in each activity.

Date	Name	F/P H/U	I/E	Sex	Who	Total Obs Time	Ttl Time Awake	Ttl Time Asleep	Time Woke up	Time to Sleep	Ttl Bout Min	Ttl %	X	Avg Ht	Ttl Obs Min
8/9/95	Roman	F	H	M	DW LD	780.0	706.0	734.0	6:22	18:08	706.0	100.00	X	22.54	1126.17

	Eat	Rest/ Sleep	Travel	Nest	Rest	Mate	Food Search	Social 1	Social 2	Play	Fight	Day Sleep	No Act	Carry Offspring	Urinate	Defecate	Rain
% of Time	55.6	40.1	2.8	1.4	38.8	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.4	0.1	2.2
Known Time	55.6	40.1	2.8	1.4	38.8	0.0	0.0	0.0	0.0	0.0	0.0	1.3		0.0	0.4	0.1	2.2
Ttl min	392.8	283.3	20.0	10.0	274.3	0.0	0.0	0.0	0.0	0.0	0.0	9.0		0.0	3.0	1.0	15.5
Avg Bout	0:49:05	0:09:59	0:00:57	0:05:00	0:10:58							0:09:00			0:03:00	0:01:00	0:15:30
# bouts	8.0	26.0	21.0	2.0	25.0							1.0			1.0	1.0	1.0
Height	21.1	13.3	11.1	21.0	13.3												

	Hang	Sit	Lie Down	Stand	Quad-rupedal	Calm-ber	Brach-iate	Don't Know
% of Time	1.3	90.7	1.3	3.7	0.5	2.5	0.1	0.0
Known Time	1.3	90.7	1.3	3.7	0.5	2.5	0.1	
Ttl min	9.0	640.0	9.0	26.0	3.5	18.0	0.5	
Avg Bout	0:02:15	0:32:00	0:09:00	0:03:15	0:01:10	0:01:00	0:00:30	
# bouts	4.0	20.0	1.0	8.0	3.0	18.0	1.0	
Height	5.8	12.6	30.0	11.5	5.0	12.5	6.0	

	Ground	Branch	Crotch	Trunk	Liana	Nest	Don't Know
% of Time	0.3	80.7	16.8	0.0	0.8	1.4	0.0
Known Time	0.3	80.7	16.8	0.0	0.8	1.4	
Ttl min	2.0	569.5	118.5	0.0	6.0	10.0	
Avg Bout	0:02:00	0:37:58	0:09:52		0:02:00	0:05:00	
# bouts	1.0	15.0	12.0		3.0	2.0	
Height		15.0	12.8		18.3	21.0	

	Eat Hang	Eat Sit	Eat Lie Down	Eat Stand	Eat Quad.	Eat Calmber	Eat Brach.	Eat No Body Pos
% of Time	1.8	93.1	0.0	5.1	0.0	0.0	0.0	0.0
Known Time	1.8	93.1	0.0	5.1	0.0	0.0	0.0	
Ttl min	7.3	365.5	0.0	20.0	0.0	0.0	0.0	
Avg Bout	0:03:37	0:36:33		0:06:40				
# bouts	2.0	10.0		3.0				
Height	10.5	19.1		11.0				

	Rest Hang	Rest Sit	Rest lie Down	Rest Stand	Rest Quad.	Rest Calmber	Rest Brach.	Rest No Bod Pos
	0.6	94.6	0.0	1.5	0.7	0.0	0.0	2.6
	0.7	97.1	0.0	1.5	0.7	0.0	0.0	
	1.8	266.3	0.0	4.1	2.1	0.0	0.0	
	0:00:35	0:15:15		0:01:00	0:02:00			0:07:00
	3.0	17.0		4.0	1.0			1.0
	4.0	15.1		7.3	13.0			30.0

	Travel Brachiate	Travel Clamber	Travel Quad.	Travel Stand	Travel no pos	Dist Trvl	Dist Desc	Dist Clim	Av Dis Trv	Av Dis Desc	Av Dis Climb	Av Trv Vel
% of Time	2.5	90.0	7.5	0.0	0.0	279.0	39.0	43.0	8.5	4.3	3.6	5.4
Known Time	2.5	90.0	7.5	0.0								
Ttl min	0.5	18.0	1.5	0.0								
Avg Bout	0:00:30	0:01:00	0:01:00									
# bouts	1.0	18.0	2.0									
Height	6.0	12.5	1.0									

Avg Total Vocalization	Vocalization	Look Alarm	Kiss	long call	JP	JJ	T	H	Grumph
4.0	0	12	0	1	3	0	0	0	0	0	0

# Nests Built	DBH of Nest Trees	Height of Nests	Height of 2 Nest Trees
2.0	30.0	25.0	

Ttl oth OH	Avg party	Lgst party	Ttl w/babes	Avg w/babes	Lgst party with babes	Avg separation	% time same tree	% time different tree
0	1.00	1	0	1.00	1			

Figure 5.01: Sample summary of energetic data for one full-day follow.

Calculating Energetic Expenditure

For the purpose of calculating energetic expenditure, data on the orangutan's three primary activities and body positions were combined to generate the following activity/body positions: eat sitting, eat standing, eat lying down, eat hanging, eat quadrupedally, eat brachiating, eat clambering, rest sitting, rest standing, rest lying down, rest hanging, rest quadrupedally, rest brachiating, rest clambering, travel quadrupedally, travel standing, travel brachiating and travel clambering. Eat brachiating and eat clambering indicate that the orangutan was moving while in the process of eating. Rest brachiating and rest Clambering reflect an orangutan's movement within a tree during a resting bout. This allowed me to designate energetic values for these various activities that took into account the position of the animal. Activities which accounted for less than 2% of total observation time: nesting, mating, fighting, playing and food searching were not subdivided by body position for the purpose of this analysis.

The energetic cost of each activity was determined following Coelho (1986). The cost of the activity (A_i) was defined as the energy expended by an actor of a given mass ($W^{0.75}$ kg) performing an act (D_i) for length of time (T_i).

$$A_i = D_i \cdot W^{0.75} \cdot T_i$$

where:

D_i = energy cost (Kcal/minute) for a particular act

W = body weight (kg) of an actor

T_i = amount of time spent performing an act (D_i)

Each activity/body position was given an energetic value following Coehlo (1986). For example, I combined Coelho's energetic expenditure value for eating (chewing) with the energy expenditure for the body position and the energetic expenditure for object manipulation. Nest building was not included as a possibility on Coelho's list, thus I followed Coelho in referring to Consolazio (1971), Passmore and Durnin (1955) and Webb (1973) to determine an equivalent value. Table 5.04 provides the energetic values used to calculate non-travel expenditure. Eat clambering and eat brachiating were only given values related to eating, as the travel component of these activities is figured under locomotory costs. Rest clambering and rest brachiating are subsumed under the travel category (see following section).

TABLE 5.04: Caloric expenditure values used.

Energetic State	Energy cost (Kcal/min)
Eating-sitting	0.14
Eating-hanging	0.15
Eating-lying down	0.13
Eating-quadrupedal	0.15
Eating-standing	0.15
Eating-brachiating	0.07
Eating-clambering	0.07
Resting-sitting	0.07
Resting-hanging	0.08
Resting-lying down	0.06
Resting-quadrupedal	0.08
Resting-standing	0.08

Nest Building-Sitting	0.30
Fighting	0.53
Mating	0.14
Playing	0.15
Sleeping	0.06

Body Weight

Body weight (W) could not be measured directly in these wild orangutans, thus estimates were used. I used the values determined by Markham and Groves (1990) from re-examination of wild caught specimens. In this reanalysis, the authors found that previous weight estimates often included animals labeled "adult" that were not yet fully mature. Bornean males were found to weigh, on average, 86.3 kg (range 80 - 91 kg) and Bornean females had a mean weight of 38.7 kg (range 33 - 45 kg). I used these mean values for each age-sex class.

Costs of Locomotion

As stated earlier, I follow Altmann and Samuels (1992) in using Taylor's (1982) equations for estimating the costs of locomotion. These equations were specifically derived from primates, and although they are not specific for orangutans, Taylor (1982) states that they are more accurate than previous equations. I follow Wheatley (1982) in adding distance descended to horizontal distance traveled. My equation differs from Altmann and Samuels in being calculated in Kilocalories. The equation is:

((Ttl Distance Traveled + Ttl Distance Descended)•((0.523)•Estimated Body wt.$^{(1-0.298)}$)+((0.345•Estimated Body wt.$^{(1-0.157)}$)•(Ttl Minutes Traveling•60)))•.0048

Costs of Climbing

I follow Wheatley (1982) in using Moen's equation for the cost of vertical climbing (C_{vert}), which I've converted here to the cost of climbing one meter. It is as follows:

$$C_{vert} = 6.92 \bullet \text{Estimated Body wt.} \bullet (\text{Ttl Distance climbed}/1000)$$

Cost of Infant/Juvenile Carrying

The costs of infant carrying (C_{car}) beyond maternal energetic expenditure was modeled following Altmann and Samuels (1992) as follows:

C_{car} = (Kcal expended/day • minutes carrying • (Weight of Offspring/Maternal Body wt.)

As explained earlier, minutes spent carrying was recorded on a continuous basis. The weight of infant and juvenile orangutans could not be measured directly. I thus obtained, from zoos, records of known age and body weights of 5 young orangutans and used these to obtain mean weights at each age from birth to 8 years. I also referred to Leigh and Shea's (1995) model of orangutan growth rates, examined Pusey's (1990) weights for wild chimpanzee infants and juveniles and drew from my own observations of individuals. The captive orangutan data showed that these young animals grew at an approximate rate of 4 kg/year. Because we know that orangutans in the wild grow and reach maturity much more slowly (see Chapter 1), I could not justify using the mean captive weight, thus I adjusted this rate slightly and estimated that wild orangutan body weights would increase at

a rate of 3.5 kg/year after 1 year. Weights were as follows: birth = 2 kg, 1 year = 4 kg, 2 years = 7.5 kg, 3 years = 11 kg, 4 years = 14.5 kg, 5 years = 18 kg, 6 years = 21.5 kg, 7 years = 25 kg, 8 years as 28 kg.

Costs of Reproduction

I follow (Coelho 1974, 1986) in estimating the cost of pregnancy as 1.25 • total daily energetic expenditure and the cost of lactation as 1.5 • total daily energetic expenditure. These values were determined for humans and non-human primates based on nutritional studies reported by Crampton and Lloyd (1959) and Portman (1970). I accounted for the decreasing frequency of lactation with increasing offspring age by assuming a lactation cost of 1.5 for the first 2 years, and then 1.4 for year 3, 1.3 for year 4, 1.2 for year 5 and 1.1 for year 6 and later of lactation.

Statistical Analyses

The total number of minutes spent in each energetic state was determined by developing a database and extensive "scripts" using the Filemaker computer program. For each animal, I first calculated a daily value for each of the variables described in this chapter (i.e. daily caloric expenditure, time spend in each activity, etc.). From these daily values I calculated the mean value for each month for each animal. Then I grouped monthly values into the high fruit period (October 1994 - February 1995) and the low-fruit period (March - September, 1995). Each animal's monthly value is an independent sample, but animals that were sampled more than one month may appear more than once during the two fruit availability periods. Pseudo-replication has thus been greatly reduced by collapsing all follows into monthly means, but because I have collapsed months into two time periods it

has not been eliminated. Unless otherwise noted, the Mann-Whitney U-test is used to compare the means between the sample periods.

RESULTS

Sample

As explained in Chapter 4, between August 1994 and December 1995 a total of 693 daily follows, resulting in 5989 observation hours, were conducted. In this analysis of energetic expenditure I also only consider habituated adult female and fully-developed adult male orangutans. Data from one mortally wounded male (Rocky) is also eliminated here as in other analyses. All follow days included in nutritional analysis are included here, as well as additional days for which energetic analysis, but not nutritional analysis has been completed. Thus, the data presented in this chapter comprises a larger number of follow days than in Chapter 4. Data are from the period between October 1994 and December 1995 and are drawn from 448 daily follows of 186 adult males and 262 adult females. The total data set presented here is taken from 3791 observation hours.

Time awake, total daily energy expenditure and distance traveled/day are all taken from full-day follows. Data referring to percent of time awake engaged in a given activity are drawn from both full and partial day follows. Table 5.01 presents the number of follows conducted for the subsample of the data presented in this chapter, broken down by month, by sex and by follow length. Please refer to this table for an indication of the sample size used in the analyses in this chapter, unless otherwise indicated.

TABLE 5.01: Break down of number of animals and number of follows included in the energetic analyses presented in this chapter. Numbers in parentheses refer to the subset which came from full-day follows.

Month	# Females	# Follows	# Males	# Follows
Sep, 1994	5(1)	10(2)	1(0)	1(0)
Oct, 1994	11(1)	21(4)	7(2)	21(6)
Nov, 1994	11(5)	28(8)	6(2)	13(3)
Dec, 1994	3(2)	8(5)	9(3)	21(4)
Jan, 1995	8(4)	29(13)	1(1)	14(3)
Feb, 1995	6(4)	23(11)	3(2)	17(6)
Mar, 1995	1(1)	3(1)	1(1)	9(7)
Apr, 1995	2(1)	11(8)	2(2)	18(14)
May, 1995	2(1)	25(23)	1(1)	6(5)
Jun, 1995	2(2)	22(19)	2(2)	22(16)
Jul, 1995	2(1)	4(2)	2(2)	15(9)
Aug, 1995	1(1)	15(13)	2(1)	12(4)
Sep, 1995	3(3)	18(14)	2(1)	9(3)
Oct, 1995	1(1)	27(23)	1(1)	3(1)
Nov, 1995	1(1)	17(12)	-	-
Dec, 1995	-	-	1(1)	4(2)

Time Awake

The total number of minutes adult female and fully-developed adult male orangutans spent awake was compared between the periods of high and low fruit availability (Figure 5.02). Time awake was defined as time between moving out of the nest in the morning until lying down in a nest at night. Both adult females (Mann-Whitney U-test, $U = 12.5$, $p < 0.005$) and adult male orangutans (Mann-Whitney U-test, $U = 16$, $p < 0.02$) spent significantly more time awake during the high fruit as compared to the low fruit period.

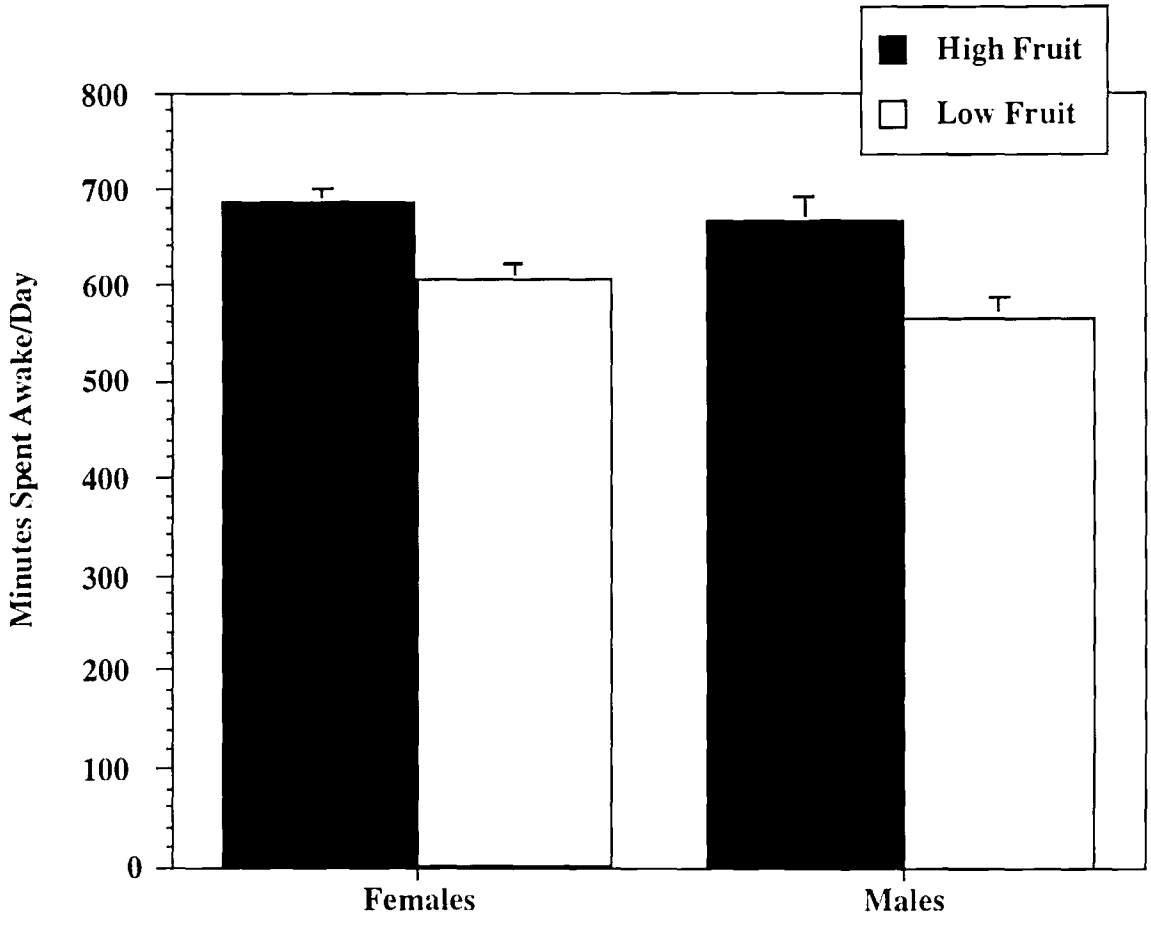


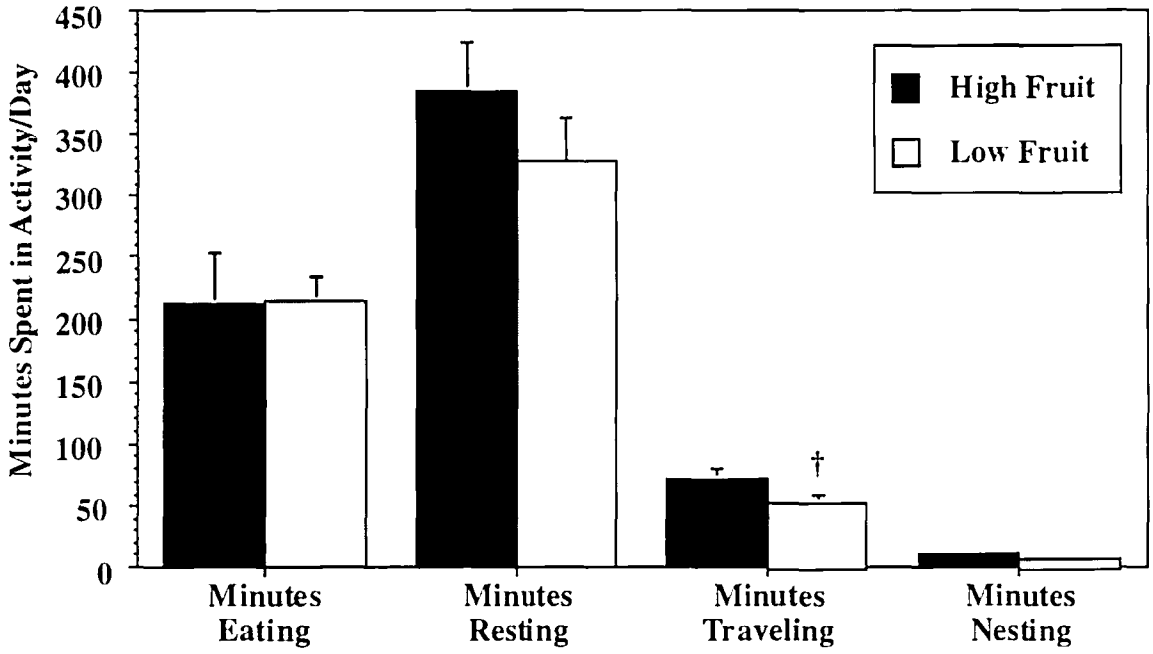
FIGURE 5.02: Mean total minutes spent awake (defined as time between night nests), per day, during periods of high and low fruit availability in 1994-1995 for habituated adult male and adult female orangutans. Standard errors of the data are shown. Sample size is mean monthly average for each animal. (High fruit: females n = 17 (43 follows), males n = 12 (22 follows); Low fruit: females n = 10 (61 follows); males n = 12 (115 follows)).

Activity Profile Comparisons

What were the orangutans doing during this additional time awake? To answer this I compared activity patterns between the high and low fruit periods (Figure 5.03). Females appeared to be spending more time resting and more time traveling during high as opposed to low fruit periods (Figure 5.03) although these differences were not significant. Males on the other hand, did not spend more time resting. Instead, they spent significantly more time feeding (Mann-Whitney U-test, $U = 20$, $p < 0.05$) during the high fruit period compared with the low fruit period. Like females, males also spent more time traveling during the high fruit period, and in their case, the difference was significant (Mann-Whitney U-test, $U = 11$, $p < 0.005$).

Comparing between the sexes, females spent significantly more time traveling during the fruit-poor period than did males ($U = 17$, $p < 0.005$). Other differences between the sexes were not significant.

(A) Females



(B) Males

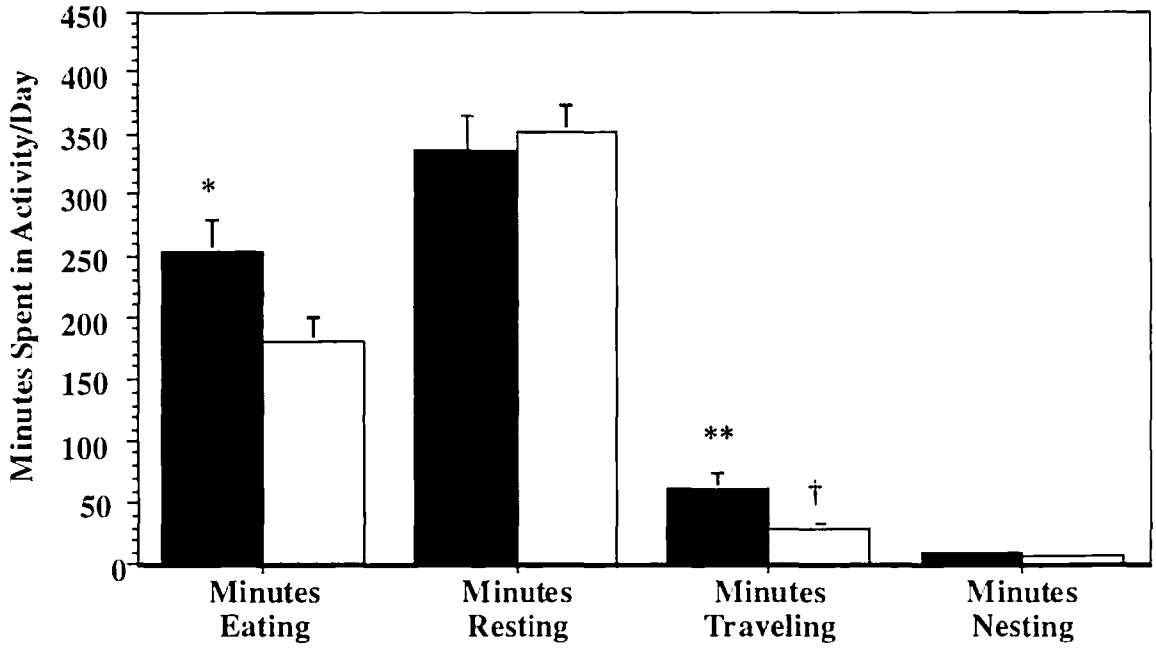


FIGURE 5.03: Mean number of minutes spent in each activity (full-day follows) during the periods of high and low fruit availability in 1994-1995 for habituated adult female (A) and fully-developed male (B) orangutans. Standard errors of the data are shown. In males, significant differences were found between the two periods in minutes spent feeding (*) and minutes spent traveling (**). Differences between periods were not significant for females. Between males and females, females spent more time traveling during the fruit-poor period (†) than did males. Sample size is mean monthly averages for each individual.

Changes in Social Behavior

An interesting contrast between males and females that may be affecting activity profiles is the percentage of time awake that was spent in the company of other adult orangutans (Figure 5.04). Males and females were very different in this regard. Females spent more time in the company of other orangutans, 12.9%, during the fruit-rich period compared to males, 0.05%. Females were spending this "social" time either with other female orangutans or with undeveloped adult male orangutans with whom they were consorting with or mating. No fully-developed males were seen to mate during this entire study period (although this has been seen in subsequent years of study). In the fruit-poor period females spent no time with other orangutans, and males virtually none (0.02%).

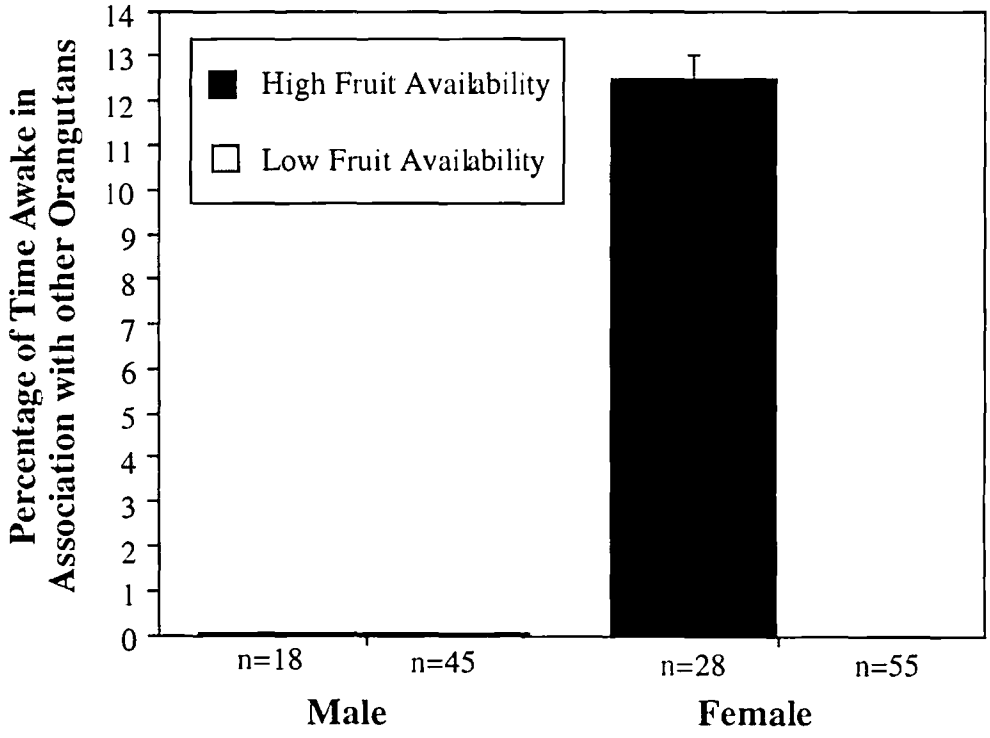


FIGURE 5.04: Mean percentage of time awake (defined as time between night nests) spent in association with other orangutans during periods of high and low fruit availability in

1994-1995 for habituated adult male and female orangutans. Standard errors of the data are shown. *N* is the number of full-day follows in the sample.

Distance Traveled

Highly significant differences were found in both males and females in the distance traveled per day between the high and low fruit periods (Figure 5.05). Females had a mean travel distance of 802 m during the fruit-rich period compared to 524 m during the fruit poor period ($U = 18$, $p < 0.02$). Males traveled 570 m during the fruit-rich period compared to 273 m during the fruit-poor period ($U = 17$, $p < 0.01$). Strikingly, females tended to travel further per day than males did in both periods. These differences were significant in the low-fruit period ($U = 11$, $p < 0.002$). Mapping of the orangutan ranges showed, through visual inspection, that males covered a much larger territory than did females. Thus, males tended to have much larger home ranges, but their day ranges were smaller than were females. Males were particularly sedentary during the fruit-poor period.

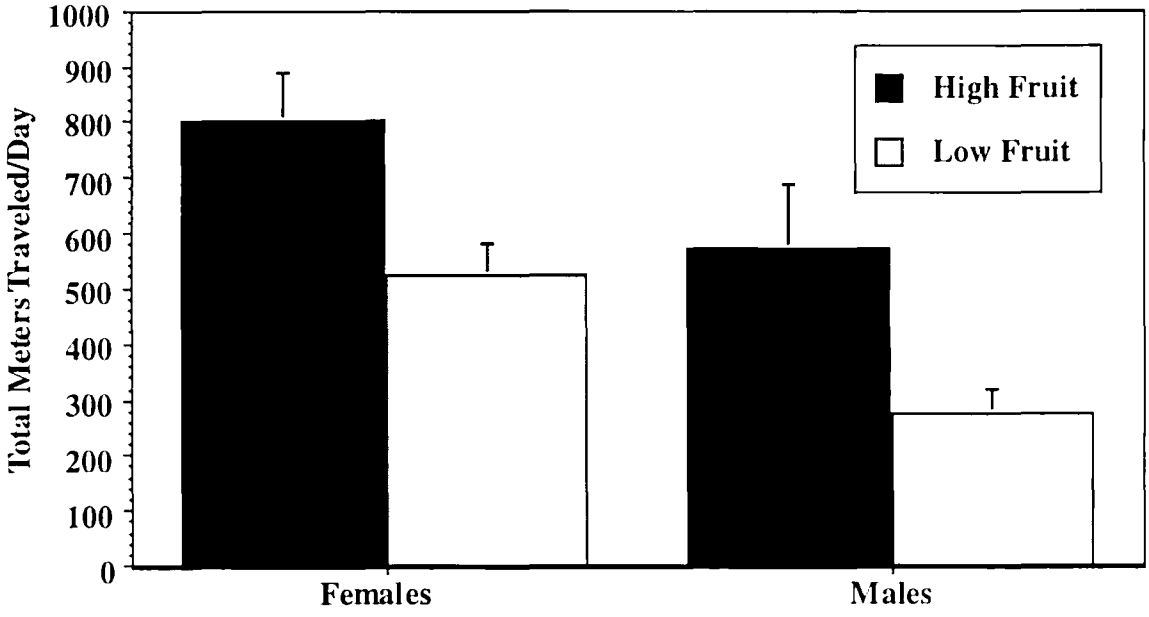


FIGURE 5.05: Mean number of meters traveled per day (full-day follows only) during the periods of high and low fruit availability in 1994-1995 for habituated adult female and fully-developed male orangutans. Standard errors of the data are shown. Differences between periods were significant for both males and females and females traveled significantly more than males during the fruit-poor period. Sample size is mean monthly average for each individual. (High fruit: females n = 17 (43 follows), males n = 12 (22 follows); Low fruit: females n = 10 (61 follows); males n = 12 (115 follows)).

Calories Expended

Next, I examined how these changes in activities and distance traveled were expressed in energetic expenditure (Kcal) terms. Looking at baseline costs (without factoring in reproduction or the costs of carrying offspring) both males and females expended significantly more energy during the fruit-rich period than the fruit-poor period. Females averaged 1900 Kcal expended per day during the mast period compared to 1800 Kcal during the fruit-poor period ($U = 34$, $p < 0.05$). Males had a mean caloric expenditure of 3400 Kcal per day during the high-fruit period, compared to 3100 Kcal during the low-fruit period ($U = 16$, $p < 0.05$). There was very small variance between individuals and between sample days. Males also expended significantly more energy during the high fruit ($U = 0$, $p < 0.0001$) and the low-fruit periods ($U = 0$, $p < 0.0001$) than did females. This is to be expected given the much greater body weight of males.

The costs of locomotion contributes the greatest differential to energy expenditure (Coelho 1986). Thus I looked at the costs of locomotion separately from overall energetic costs (Figure 5.06). Both males ($U = 15$, $p < 0.01$) and females $U = 35$, $p < 0.05$) expended significantly more energy in locomotion during the fruit-rich compared to fruit-poor periods.

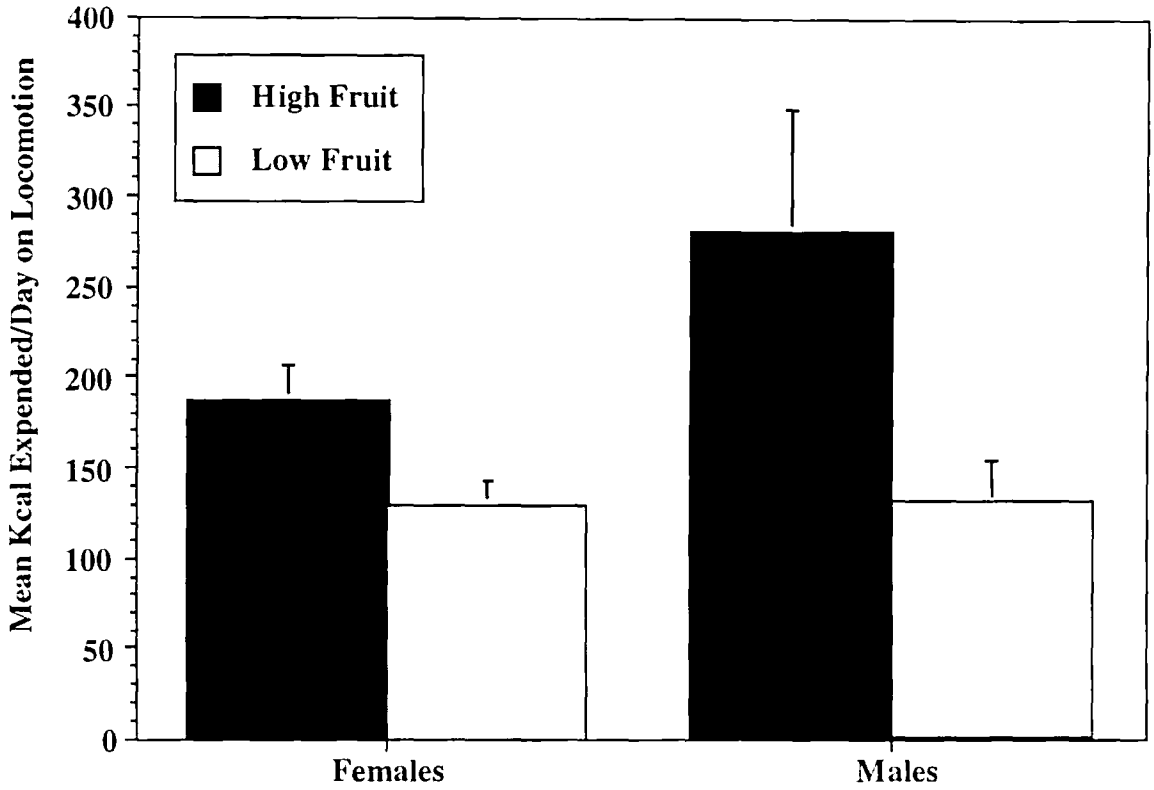


FIGURE 5.06: Energetic costs of locomotion, expressed as Kcal's expended per day, in adult female and fully-developed male orangutans during periods of high and low fruit availability. Standard error of the data are shown. Sample size is mean monthly averages for each individual. (High fruit: females n = 17 (43 follows), males n = 12 (22 follows); Low fruit: females n = 10 (61 follows); males n = 12 (115 follows)).

Energetic Expenditure including Maternal Costs

In females, it is necessary to figure in the additional costs of pregnancy, lactation and carrying offspring to daily energetic expenditure values. This raised energetic costs to a mean (over both periods) of 2300 Kcal for females. Differences between the high and low fruit availability period are no longer significant when these additional maternal costs are figured in to the energetic values (Figure 5.07). This is because the reproductive state of the females as well as the exact sample of females changed across these periods.

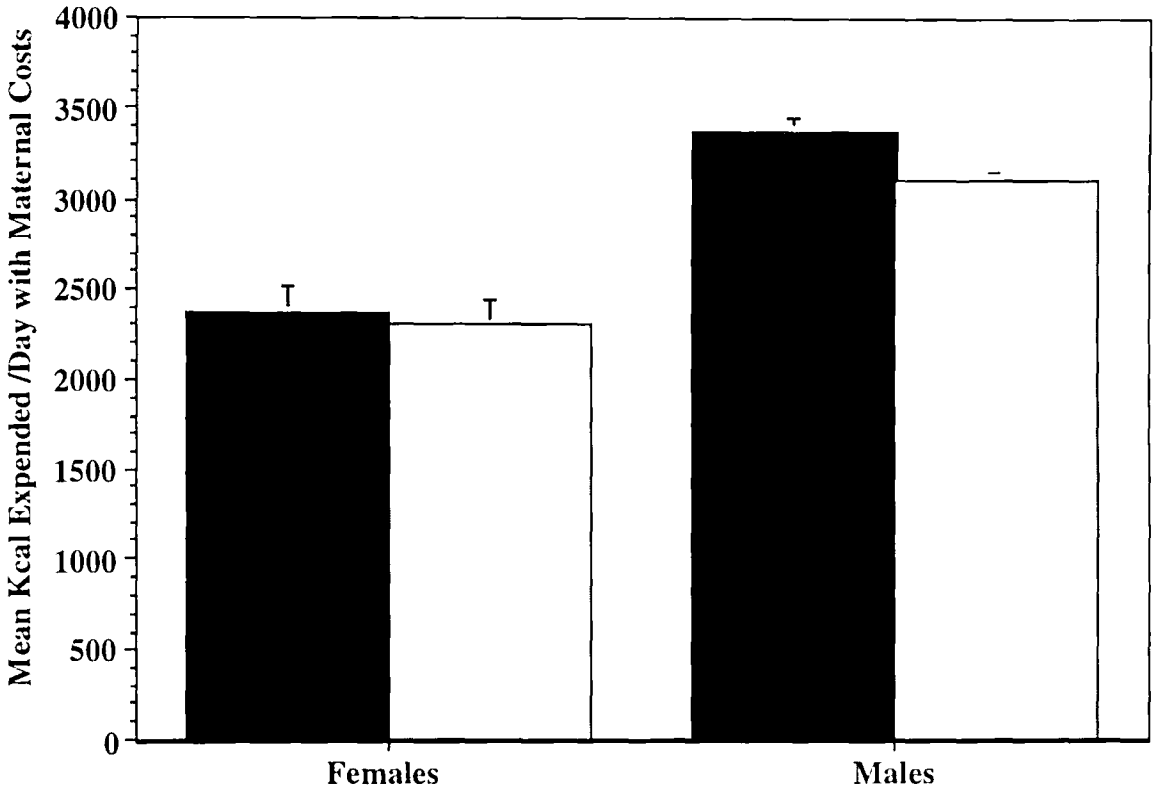


FIGURE 5.07: Mean total Kcal expended per day during periods of high and low fruit availability in 1994-1995 for habituated adult male and female orangutans (including maternal costs). Sample size is mean monthly average for each individual. (High fruit: females n = 17 (43 follows), males n = 12 (22 follows); Low fruit: females n = 10 (61 follows); males n = 12 (115 follows)).

DISCUSSION

Energy Expenditure and Activity Patterns

The data presented here estimate that during the fruit-rich period mean caloric expenditure in orangutans is 3400 Kcal/day for fully-developed males and 2400 Kcal/day for females (including maternal costs). In Chapter 4, I demonstrated that during the mast orangutans were consuming food at a rate of approximately 6300 Kcal/day between November 1994 and January 1995. Given that males spent approximately 250 minutes eating per day this results in a consumption of 1500 Kcal/hour. Thus, they would have been able to meet their daily energetic requirements in a little over two hours of feeding. However, during this high fruit season, much more feeding was observed. Why did the orangutans spend so much time feeding when they didn't "need" to? A possible explanation is that orangutans are maximizing their caloric intake when abundant, higher-calorie fruits are more available in order to build up fat reserves for lean periods (MacKinnon 1974; Wheatley 1982, 1987; Leighton 1993). If orangutans were only trying to maintain adequate levels of caloric intake I would have predicted that they would have spent less time eating during the fruit-rich compared to the fruit-poor period, due to the higher rates of caloric return. Instead, males spent significantly more time feeding during this period and females spent the same amount of time feeding.

Male and female patterns were opposite to each other in regard to resting and eating during the two fruit availability periods. Males increased feeding time, while females tended to increase their time spent resting during the fruit-rich period (this was significant for males). Why would females be resting more when fruit was abundant? A possible answer lies in the greater percent of time females spent in association with other orangutans compared to males. Two types of associations were seen. The first type of association was between

adult females and their offspring with other adult females and offspring. Females in such associations were observed to spend time "resting" while their offspring were engaged in play with each other. Often these types of multi-animal interactions occurred in large dipterocarp trees that could support several animals. After feeding in the same tree for some time, the mothers would rest while the juveniles played together.

The second type of interaction was mating and male-female consortships. Females were observed to mate with undeveloped males during the mast period. Although fully-developed males were seen in consortship with adult females, none of these males were observed to mate during this study period (although this has been observed in subsequent years). A typical mating interaction/consort initiation involved a female waiting, often in a frozen posture while an undeveloped male approached her. Such behavior was scored as resting on the part of the female. Additionally, on days when mating was observed females appeared to spend less time feeding than on days when mating did not occur. Sometimes they appeared to be actively trying to escape the male. This may be one reason that the time spent feeding did not increase for females during the fruit-rich period. These observations remain to be quantified through examination of the data collected.

An additional explanation for why females did not increase their feeding time during the fruit-rich period may be due to the size dimorphism between the two sexes. Females were already consuming a diet that was very high in calories and grams of intake. It may be that they did not increase their feeding time because they simply could not increase their grams of intake beyond the observed levels during the mast.

It is curious that both males and females did not increase their time spent feeding during the fruit-poor period given their very low caloric intake levels. Why didn't the orangutans spend more time eating the bark and leaves that were abundantly available during this

period? Several factors may help explain this pattern. First, orangutans may be conserving energy during the fruit-poor period by spending less time eating and traveling and more time asleep than during the fruit-rich period. The significant reduction in time awake, in distance traveled, and in males, time spent feeding and time spent traveling, is consistent with this hypothesis.

A second, related hypothesis is that although bark and leaves as a category are very abundant in the forest, all species of bark and leaves are not equally preferred or eaten. Individuals may travel a considerable distance between bark feeding bouts. Thus, it may be that the trade-off between expending energy to search out edible species of bark and leaves and conserving energy favors reduced foraging time.

Finally, a third and not mutually exclusive hypothesis, mentioned earlier in regard to females, is that the orangutans have reached a limit of fiber intake and cannot increase their caloric consumption through even greater ingestion of bark and leaves. Two reasons may help explain this strategy. As shown in Chapter 4, the total grams intake of fiber did not show a significant variation across the study period. Thus, it may be that orangutans consistently maintain a high fiber diet and that they cannot go significantly beyond this level of total grams of fiber ingested. It also may be that fiber intake is particularly extreme during both high and low-fruit periods due to high total amounts of food ingested during the mast and reliance on bark and leaves as fall-back foods during the low fruit period. Fiber intake could be lower during periods of intermediate fruit availability but such periods were not well represented in this study. Second, orangutans are hind-gut fermenters, which means that they are able to derive nutrients from fiber. According to van Soest (1994) increased intake depresses the digestibility (fermentation) of insoluble fiber. The longer food stays in the gut, the more nutrients are derived from the fiber. Increased food

intake increases gut passage time. Thus, it may also be that the orangutans are optimizing the amount of fiber intake compared to the gut passage time.

To further elucidate the relationships between fruit availability, nutrition, and energetic patterns it would be necessary to examine periods of more moderate levels of intake. For example, between October and December of 1995, intake levels averaged between 2000 Kcal/day and 3500 Kcal/day, approximately equivalent to expenditure levels. In future analyses of my data I will be focusing on this subsequent period.

Comparisons to Humans

Orangutan caloric requirements have not been measured directly in captivity, but considerable data exists on human caloric needs. How do my estimates of orangutan energetic needs compare to those obtained for humans? A rough estimate can be made by applying standard tables used to calculate human energy requirements based on body weight and activity level (ADA 1992). These provide an estimate of 40 Kcal/kg per day for a normal, active adult human. Applying this figure to orangutans and substituting body weights of 38.7 kg for wild adult females and 86.3 kg for wild adult males (Markham and Groves 1990), provides an estimated daily energy requirement of 1550 Kcal/day for females (without any maternal costs) and 3450 Kcal/day for males. These figures are quite similar to those calculated by my model.

Comparison with other Orangutan Studies

Wheatley's (1982) figure of 2,333 Kcal/day for a 55 kg animal is in the same range as what I've estimated. However, given the high degree of sexual dimorphism it may not be very useful to think of an "average" 55 kg orangutan in regard to energy requirements.

Rodman's (1979) figures for total energy requirements of 2530 Kcal/day for one adult male and 1495 Kcal/day, on average, for two adult females are lower than my estimates. However, he assumed a day range of only 400 m and his figures did not take account of additional energy requirements for pregnant or lactating females. Leonard and Robertson (1997) use 300 m as a day range figures and derive a Kcal expenditure value of 2500 Kcal/day for males and 1500 Kcal/day for females which they believe to be an underestimate.

The energetic expenditure results reported here differ from those generated by Rodman, Wheatley, and Leonard and Robertson (1997) in that I calculated an energetic expenditure value for each animal for each follow day, rather than calculating one value based on mean levels of expenditure. This has allowed me to compare between animals and between days in particular animals. Additionally, I have modeled the costs of pregnancy, lactation, and infant carrying and based my estimates of vertical ascent and descent on actual data. I thus believe that my data provide the most accurate estimates generated so far in regard to orangutan energy expenditure.

Finally, we can ask how these data on energy expenditure compare more directly with intake estimates. How much, if any, caloric excess or deficit were the orangutans experiencing during the two periods? This comparison is the subject of Chapter 7.

Possibe Refinements in Estimating Energy Expenditure

In studies of wild animals we cannot estimate energetic costs using respirometers and indirect calorimetry as is done in humans. Similarly, the use of doubly labeled water can not be done with most wild animals and cannot be used to determine the costs of specific activities. Thus, we are restricted in the estimation of energy expenditure to values derived

from humans and those domestic animals that can be studied in this way. However, studies that have been done by computing energy expenditure based on such values have comparable results to those which use more exact methods (Coelho 1986). Thus, I believe the computational method at least provides reasonable ball-park estimates that can be used in conjunction with energy intake estimates to assess relative changes in energy balance.

An additional area that warrants further investigation is the metabolic cost of lactation. I assumed that these costs fell off linearly after the second year based on my observations of changes in suckling frequency with increasing offspring age. However, the metabolic costs of lactation as juveniles grow and, at some point, decrease their suckling frequency remains to be quantified.

Finally, in estimating energetic expenditure several other influences could also be taken into consideration. It is possible that the orangutans are able to lower their basal metabolic rate during the fruit-poor period to help compensate for lower energy intake. Another source of energy expenditure not accounted for is the "thermic effect of food," which is the cost of elevated metabolism during digestion. This could have resulted in increased energy expenditure for males during the fruit-rich period when they spent more time feeding. This may be worth examining in future studies.

• CHAPTER 6 •

ORANGUTAN ENERGY BALANCE

CHAPTER SUMMARY

Energy balance is the difference between energy intake and energy expenditure and indicates whether energy intake is adequate to serve an organism's needs. In this chapter, I estimate changes in energy balance in orangutans in two ways, first through calculation from estimates of energy intake and expenditure, and second through measurement of ketones, a byproduct of fat metabolism excreted in urine.

Monthly mean energy balance values calculated for the study period for both males and females were positive during November 1994 through February 1995, the high fruit period. Subsequently, from March through September 1995, during the low fruit period, energy balance was negative. Thus there was a strong positive relationship between energy balance and ripe fruit availability.

The ketone analysis confirmed the same pattern. No ketones were found in urine samples collected during the high fruit availability months or the first month of low fruit availability. Starting in April 1995, after orangutans had been experiencing low nutritional intake, through March, ketones began to appear in a large proportion of urine samples. This indicates that the orangutans were metabolizing their fat reserves to make up for insufficient intake.

Particularly striking was the length of the period of negative energy balance—seven months. Thus, this was not simply a minor fluctuation in food availability and nutritional intake, but indicates an extended period of insufficient caloric intake. Orangutans appear to have survived this period due to two adaptations. First, the degree of caloric excess in the fruit-rich period indicates that they were storing excess energy as fat, from which they could draw on during the fruit-poor period. Second, as shown in Chapter 4, they were

able to dramatically change the composition of their diet so that they could consume leaves and bark as fall-back foods. These are important adaptations for living in an environment with highly variable food resources such as the rain forest of Borneo, and also has important implications for orangutan reproduction.

INTRODUCTION

Energy balance is defined as the difference between energy intake and energy expenditure. This is the most physiologically relevant value as it indicates whether energy intake is adequate to maintain body weight and the necessary functions of growth, maintenance and reproduction. Thus, intake and expenditure values are most meaningful when compared to each other.

Changes in body weight provide the most accurate estimate of changing energy balance. Measuring the physiological response of wild primates to changing food availability has only been accomplished, however, by weighing captured or provisioned animals (Mori 1979; Goodall 1986; Altmann *et al.* 1993). This is often not possible or desirable in studies of wild great apes. Thus, in this chapter I use two methods of estimating changes in energy balance. First, I calculate estimated energy balance by subtracting estimates of energetic expenditure from estimates of nutritional intake. Second, I present a new method (also described in Knott 1998c) of assessing weight loss through the measurement of ketones in urine. Ketones are produced when the body metabolizes its own fat reserves to produce energy. The production of ketones in response to excessive fat metabolism is a widespread phenomenon amongst mammals (Robinson *et al.* 1980), including humans (Fischbach 1988; Watson and Jaffe 1995). This method of measuring physiological indicators of weight loss provides a non-invasive way to quantify negative energy balance in wild great apes through simple field collection and analysis of urine.

The ketone method utilizes urinalysis strips which are used in human clinical laboratories to test samples for indicators of disease and physiological status. These are plastic strips with various reagents on pads that produce a color reaction when urine is applied. Tests used included blood (hemoglobin), specific gravity, leukocytes, bilirubin, ketones, glucose,

protein, urobilinogen, nitrite and pH. The specific gravity test provides a measure of concentration of urine which can be used in addition to or as a substitute for creatinine measures (Campbell 1994). The leukocyte test provides an indication of infection and ketones reflect the presence of fat metabolism. The presence of blood in urine is useful in assessing injury, disease and menstruation. This method has commonly been used in zoos to detect menstruation in orangutans (Rogers 1989; Smith *et al.* 1989; Masters and Markham 1991).

The goal of this chapter is to determine how energy balance varies with changing levels of energetic expenditure and nutritional intake in order to understand how much of an excess or deficit in energy is experienced during different time periods. I also evaluate the relative concordance of the two methods of estimating energy balance, through (1) calculation from intake and expenditure and (2) analysis of ketone production.

METHODS

Calculation of Energy Balance

Energy balance, as Kilocalories of excess or deficit, was calculated by subtracting the estimated energy expenditure value (Kcal) from the estimated energy intake value (Kcal) for each individual orangutan on each follow day. Nutrient intake and caloric expenditure values from the same individuals are available for the period between November 1994 and November 1995.

Ketone Analysis

Urine samples were collected from each focal animal on a daily basis when possible. Disposable plastic pipettes were used to collect urine from clean plastic sheets placed beneath urinating animals or pipetted directly from vegetation (Knott 1996b). Urinalysis strips (Boehringer Mannheim Chemstrip 10 with SG) made for human clinical analysis were used to test samples for the presence of ketones (Knott 1996b, 1997a, 1998c). These tests were conducted as soon after collection as possible, often while still in the field (see details in Chapter 7). The ketone test provides a semi-quantitative measure of the degree of ketosis. A daily ketone value was determined for each animal by giving the ketone test result a numeric value as follows: 1 = negative, 2 = trace, 3 = positive, 4= double positive. By assigning a number to the ketone test results I could compare relative levels of ketosis.

Statistical Analyses

Each individual's daily energy balance value was collapsed into a mean value for each month. In comparisons where males and females are combined I calculated the mean value for males and the mean value for females for each month. Differences between mean monthly values are then compared using ANOVA. Linear regression is used to compare energy balance to ripe fruit availability.

In order to reduce the problem of pseudo-replication and non-independence of data, the presence or absence of ketones was determined on a weekly basis for each animal that was sampled. This was computed as the mean from each animal's daily ketone values. As discussed in previous chapters, individual orangutans were not sampled equally, thus using daily means would over represent those animals more heavily sampled. Alternatively, monthly means gives too much weight to data collected from animals only sampled

occasionally. Thus, for these physiological values I compromise by computing weekly means. This allows me to take into account changes in physiological status over the course of the month. Each individual is thus represented no more than 4 times per month. A Mann-Whitney U-test is used to compare mean ketone levels between males and females.

RESULTS

Computed Energy Balance

The change in energy balance in Kcal's as determined using the computational method is shown in Figure 6.01. Only full day follows from habituated adult females and fully-developed males were used. Mean daily energy balance was positive during November 1994 through February 1995 — the mast period of high fruit availability. Energy balance gradually rose during this time as nutritional intake increased. In March 1995 through September 1995 — the low fruit availability period, energy balance was negative. This closely matches the period of low nutritional intake.

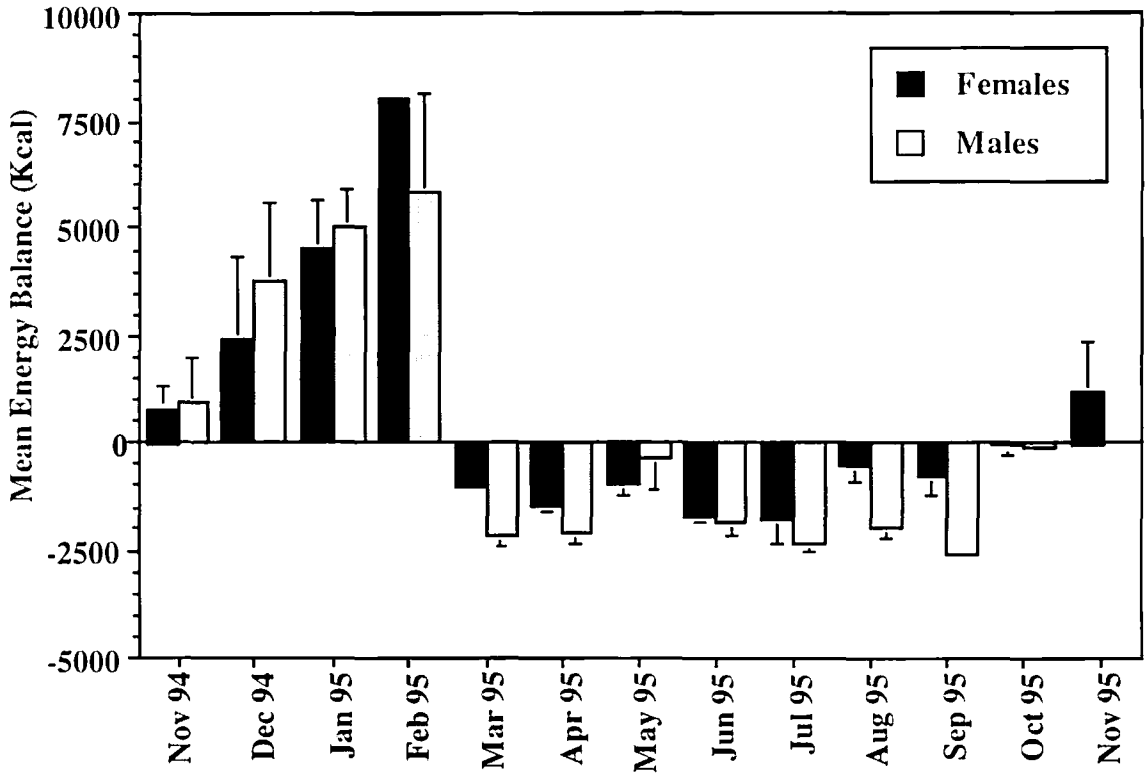


FIGURE 6.01: Monthly changes in energy balance (Kcal) between November 1994 and November 1995 from full-day follows of habituated adult female and fully developed male orangutans. Standard errors of the data are shown. Sample sizes are shown in Table 4.01.

In May, when males were eating *Neesia*, energy balance was still negative although the standard error indicates that it was fluctuating around zero. In October 1995, energy balance was very close to zero as fruit availability and nutritional intake increased. In November, values turn positive again as fruit availability, and particularly nutritional intake (as shown in Chapter 4), increased.

Comparing between months using the mean value for males and the mean value for females revealed highly significant differences between months (ANOVA, DF = 13, F = 25, $p < 0.0001$). Pair-wise comparisons (Scheffe F Test, all at least $p < 0.05$) indicated that these differences were significant between December 1994 and February, April, June, July and September 1995; between January 1995 and March through October 1995 and between February 1995 and November 1994 and March through November 1995. April 1995 and December 1994 were also significantly different. Thus, in this analysis of energy balance, April was the month of negative energy balance most significantly different from the others and February was the month of highest fruit availability most significantly different from the other months.

Energy Balance and Fruit Availability

As shown in the regression in Figure 6.02 there was a significant, positive relationship between energy balance and ripe fruit availability.

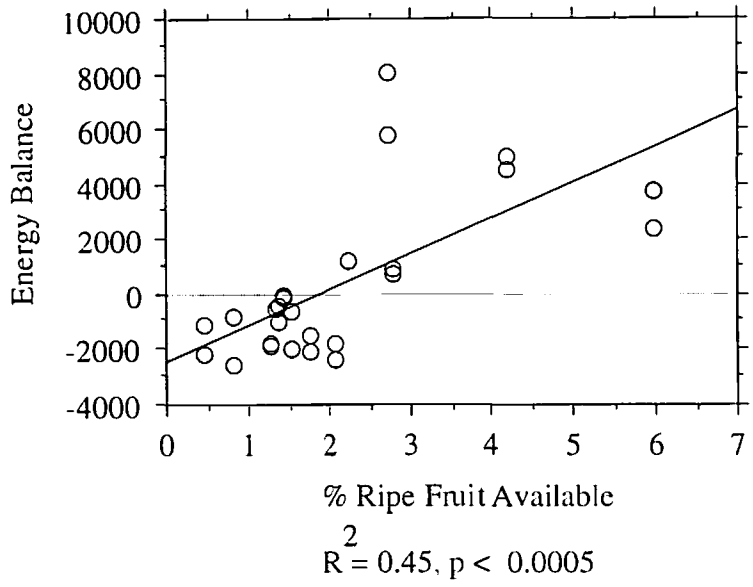


FIGURE 6.02: Regression of percentage of trees with ripe fruit in the orangutan phenology sample compared to energy balance.

Ketone Analysis

Between September 1994, and September 1997, a total of 996 urine samples were collected. Of this total, ketones were tested in 936 samples. Ketones were not tested if there was insufficient urine for the ketone test after samples were aliquoted for hormonal measurement. Ketone results between September 1994 and September 1995 are shown in Figure 6.03. This reflects 122 samples from 9 adult males and 135 samples from 13 adult females. The median time the ketone test was performed was 9 hours and 29 minutes after urine collection.

Urinalysis revealed that ketones were present in urine between April 1995 and September 1995, during the period of severe fruit shortage. No ketones were detected in urine during the mast months (November 1994 through February 1995) or during the high flower production period prior to that (September 1994 and October 1994). Ketone production exhibited a lag time effect, not commencing until April 1995, after orangutans had been experiencing low nutritional intake throughout the month of March. No ketones were observed in urine during August 1995.

Comparing weekly mean ketone levels from males and females during the period of low fruit availability (March through September, 1995), revealed that females had significantly higher levels of ketones in their urine than did males (Mann-Whitney U-test, $n = 46$, $U = 189$, $p < 0.05$).

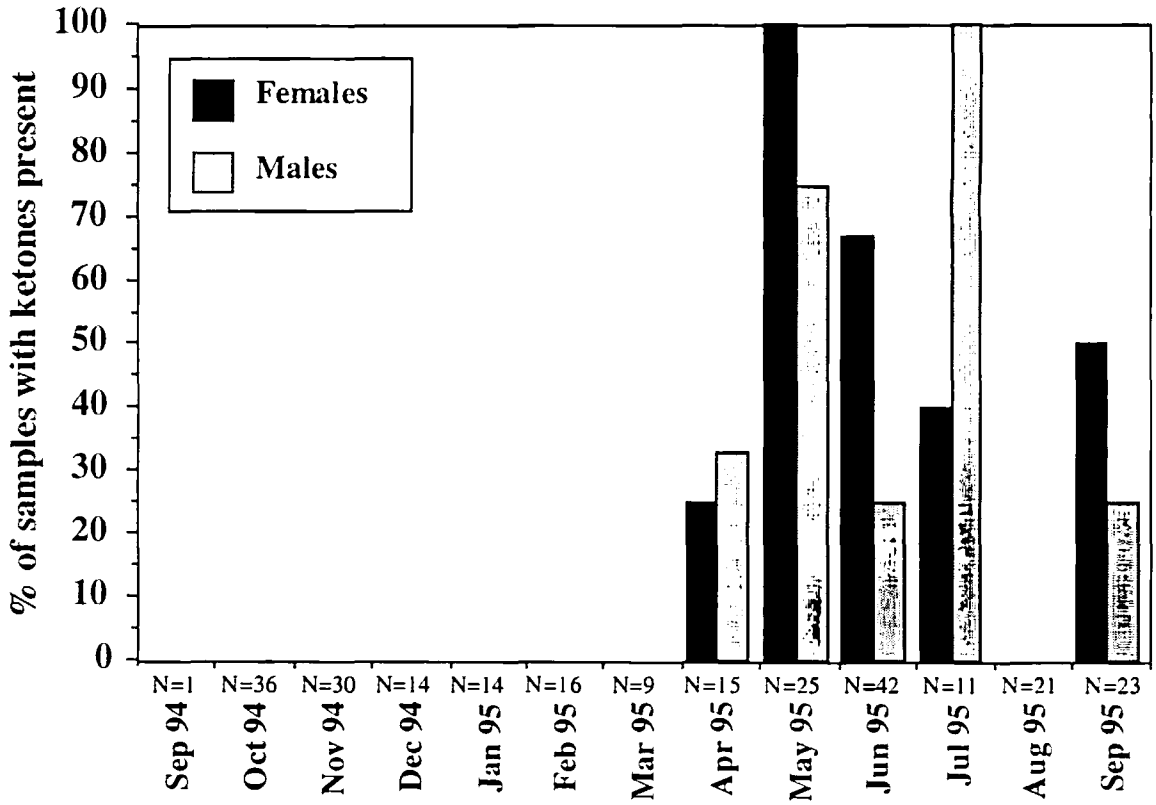


FIGURE 6.03: Percentage of urine samples containing ketones based on weekly ketone values calculated from 257 urine samples collected from 13 adult females and 9 fully-developed adult male orangutans from September 1994 through September 1995. *N* represents the total number of urine samples that were tested for ketones that month.

DISCUSSION

Fluctuations in fruit availability have significant effects on orangutan nutritional intake and energetic expenditure, but what does this tell us about diet adequacy? Although weight gain could not be measured directly, estimates of energy balance derived from intake and expenditure figures indicate that orangutans clearly had an excess of calories during the fruit-rich period. Two independent lines of evidence, energy balance computation and ketones, indicate that during the fruit-poor period orangutans were in negative energy balance and metabolizing their fat reserves.

A caloric consumption of 7700 Kcal/day over baseline energy requirements results in one kilogram of weight gain. Orangutans had a clear excess of caloric consumption during the mast fruiting period and thus, by definition, they must have been gaining weight during this period. Thus, when fruit is abundant orangutans are able to take advantage of this period of plenty to put on additional fat stores.

Among the great apes orangutans may be particularly adapted for fat storage because of the great supra-annual fluctuations in fruit availability in the Southeast Asian rain forests. This is supported by the particular propensity towards obesity in captive orangutans compared to other great apes (MacKinnon 1971). In captivity, orangutans tend to have higher rates of disease associated with obesity, such as diabetes, than do other great apes (Kemnitz 1994). As suggested by Wheatley (1982), the ability of orangutans to store large amounts of energy as fat allows them to subsist on lower quality foods in an environment where fruiting is unpredictable.

During the period of low fruit availability, when orangutans were feeding predominantly on bark, the production of ketones indicates that orangutans were losing weight and

energetically stressed (Robinson *et al.* 1980). Thus, the daily caloric intake of 600-1700 Kcal/day between March and September 1994 was not sufficient. This is in keeping with studies of humans which indicate that ketones are produced only in cases of starvation, or extreme weight loss (Robinson 1980). Of particular importance is the length of this period of negative energy balance. For a full seven months they appear to have been unable to meet their caloric requirements. Ketones were not detected in urine until April even though energy balance was already negative in March. Although orangutans may have started to lose weight in March, the weight loss may not have been severe enough at that point to produce ketones. Alternatively, this result may have been an artifact of the smaller number of samples tested during March or of the timing of the monthly phenology sampling.

What implications do these effects on physiological functioning have for understanding orangutan evolution? First, orangutans clearly have evolved the ability to exploit periods of high fruit abundance by storing excess energy as fat. This fat storage ability seems to enable orangutans to mobilize stored energy to survive periods of severe fruit shortage. It also provides the opportunity for orangutans to subsist in an environment in which fruit is patchily distributed in both space and time.

Second, if sustained, negative energy balance can lead to starvation and eventually death. Thus, periods of fruit shortage can serve as strong selective forces. Disease resistance may be compromised during periods of low fruit availability as more energy is needed to fight infection. For example, when calculating energy requirements, clinicians multiply the required Kcal/day by an injury factor to reflect the greater energy needs of sick individuals. Injury factors due to infection range from 1.0-1.8 (ADA 1992). Orangutans, particularly adult males, may at times experience high rates of infection due to injury (Knott 1996a, 1998b). Thus, if injuries are sustained during periods when caloric intake is marginal, it could severely compromise their survival ability.

Third, changes in energy balance may have a significant effect on orangutan reproductive functioning. Orangutans give birth in the wild on average only once every eight years (Galdikas and Wood 1990). We know that in humans changes in energy balance have a significant impact on hormonal functioning (Ellison *et al.* 1993). If similar mechanisms control reproduction in orangutans, such large fluctuations in fruit availability may have an effect on the wide birth spacing we see in orangutans. Prolonged periods of negative energy balance may compromise the ability of orangutans to conceive. The effect of changes in energy balance on orangutan hormonal functioning is examined in Chapter 8.

• CHAPTER 7 •

URINE COLLECTION, PRESERVATION, AND HORMONAL ANALYSIS

CHAPTER SUMMARY

Urine is an excellent medium for the measurement of physiological correlates of reproduction, behavior and health. However, hormonal analysis of urine from free-ranging animals has been limited due to the difficulty of preserving samples under field conditions. I report here on techniques which I have found effective for collection of urine from wild orangutans and the application of field methods for urine preservation on filter paper in the absence of refrigeration. A new laboratory method of steroid elution of urine from filter paper using methanol is described along with a series of experiments used to develop and validate this method.

In assays comparing estrone conjugate levels of captive orangutans, values measured from frozen urine were significantly correlated with values from matched samples dried on filter paper ($r = 0.96$). Creatinine measurements from frozen urine compared to urine dried on filter paper were also significantly correlated ($r = 0.96$). After storage for two years, both estrone conjugate levels and creatinine levels were still significantly correlated with frozen urine.

These data demonstrate the effectiveness of filter paper as a medium for preserving urinary steroid samples and the efficiency of methanol as a solvent for eluting estrone conjugates and creatinine. This method thus provides a viable alternative to the traditional procedure of freezing urine.

INTRODUCTION

Over the past 15 years analysis of urine has become accepted as one of the standard methods of studying primate reproductive physiology (Czekala *et al.* 1988). Such studies have allowed for the characterization of hormonal changes during pregnancy (e.g. Bonney and Kingsley 1982), lactation (e.g. Hearn 1984), development (e.g. Kingsley 1988) and the menstrual cycle (e.g. Dahl 1991) of many primate species. However, the great majority of these studies, and thus what is currently known about the hormonal control of primate reproduction, comes from research on captive animals (e.g. Graham 1981; Faiman *et al.* 1981; Shideler and Lasley 1982; Czekala *et al.* 1988; Masters and Markham 1991). Studies of captive animals have the advantage of being in a controlled environment. However, they may not adequately represent the physiology of free-ranging animals. Nutrition, activity levels and social behavior vary significantly between captive and wild populations. Thus we should expect to find differences between these populations in the physiological correlates of energetics and behavior.

Reproductive functioning of wild primates has largely been studied through behavioral observation alone. However, in animals such as orangutans that do not exhibit visual signs of ovulation, very little can be learned about their reproductive cycles in this manner. Knowledge of changes in hormonal levels can greatly aid our understanding of reproductive behavior and paternity in the wild. Thus, the collection and preservation of urine samples from the field can apply the more precise reproductive measures obtained from laboratory analysis to the study of free-ranging animals.

Data collected from the wild, in conjunction with what has already been learned from captive studies, can greatly augment our understanding of primate reproductive functioning. Collection of urine and analysis of hormones from the wild provides the

opportunity to study the ecological context of reproduction through addressing questions about the interaction between nutrition, energetics and ultimately food availability on reproductive hormones. Further, as demonstrated by Sapolsky (1982, 1986) and van Schaik *et al.* (1991), evaluation of the hormonal correlates of social behavior in the wild can be effectively used to study how rank, aggression and stress affect physiology and reproductive success. Hormonal analysis of urine also provides a way to investigate the effect of both male and female hormones on sexual behavior, mate choice and the timing of mating in the wild.

Until very recently logistical considerations have limited the analysis of primate urine samples to the captive setting. This is largely due to the lack of adequate storage facilities in the field. The few primate field studies that have analyzed urine from free-ranging animals have preserved and transported samples using a freezer, liquid nitrogen and/or dry ice (Andelman *et al.* 1985; van Schaik *et al.* 1991; Czekala *et al.* 1994). At many remote field sites, however, the ability to keep samples under these conditions is either difficult or impossible.

I thus report here a method I have developed for collecting, preserving and analyzing urine from free-ranging animals by using filter paper. I have successfully used this method with both orangutans and chimpanzees (Knott 1996b). Filter paper has previously been used by other investigators for urinary steroid preservation in humans and captive primates. However, this is the first time filter paper preservation has been used for wild primates. Shideler *et al.* (1995) describe the analysis of steroids stored on filter paper using enzyme immunoassays. Their procedure uses hole-punched samples from urine soaked filter paper that are directly introduced into enzyme assays. This cannot be done with radioimmunoassay which requires the additional step of elution of the sample from filter paper. Thus, I present here a new technique of steroid elution from filter paper and it's

application with radioimmunoassay. The experiments conducted to validate these methods are described.

METHODS AND RESULTS

FIELD METHODS

Urine Collection and Handling

Most primates, including orangutans, urinate upon awakening. Given that first morning urine is usually more concentrated, this is the ideal time to collect a sample. Orangutans characteristically urinate directly to the side of their nest or a few meters away. Thus to collect urine, a large (1.5 x 1.5 m), clean plastic sheet was placed on the ground beneath the sleeping nest before the animal awakened. The side of the nest from which the orangutan would exit could often be anticipated and the sheet placed accordingly, adjusting if necessary. The urine was collected from the sheet using disposable plastic pipettes and then transferred into plastic collection tubes. Volumes of urine over 15 ml could often be collected in this way. Plastic disposable gloves were worn for protection and to avoid contamination of the sample. Care was taken not to collect urine that had intermixed with feces on the plastic sheet.

Urine was also opportunistically collected during focal follows. The most effective way to do this was to keep a plastic sheet handy which could be quickly tossed beneath the urinating animal. Urine was also collected directly from vegetation, although this method usually yielded smaller volumes. A short-stemmed pipette worked best for small volume collection. Suspended drops on leaves could be captured directly into plastic bottles. All

collection vials were labeled in the field with an indelible marker to avoid later sample confusion and transported in a plastic bag.

I found 15 ml screw top centrifuge tubes convenient for collecting large samples and 1.5 ml snap tubes worked well for small samples (available from Fisher Scientific). Collection tubes of polyethylene should not be used as they have been shown to adsorb substantial amount of steroid (Banjeree and Levitz 1985). Ellison (1988) found that salivary steroid values obtained from samples collected in polystrene tubes were highly correlated (over $r = 0.85$, $p < 0.001$) with matched samples collected in borosilicate glass tubes. Thus, polystrene tubes were used for urine collection.

Between September 1994 and September 1998, 1211 urine samples were collected in this manner. Urine was sought primarily from adult animals, and was successfully collected during 75% of follows of non-juvenile animals. Sample volumes collected averaged 5.4 ml $\pm$ 5.2 (SD) and ranged from under 0.05 ml to 28 ml. The largest volumes of urine were obtained from plastic sheets, averaging 7.6 ml $\pm$ 5.31 (SD, n = 675, range 0.15 ml to 28.0 ml), versus an average of 1.9 ml $\pm$ 1.7 (SD, n = 411, range 0.05 ml to 13.0 ml) of urine obtained from pipeting off vegetation. (The remaining samples were collected using both methods, or the method utilized was not recorded.) Since only small volumes of urine are needed for hormonal analyses, the total volume of urine available was not always collected. Urine samples consisted primarily of early morning collections with 86.4% of samples collected before noon. The median time of collection was 6:35 a.m.

Urine Preservation

Urine samples were dried on pieces of filter paper using a method modified from a similar procedure employed for human and captive primate urine samples (Campbell 1994; Shideler *et al.* 1995). Highly absorbent filter paper (Schlicker and Schloom #16110) was cut into 2.5 x 2.5 cm pieces. Due to the high humidity of the rain forest, cut pieces of filter paper were stored in an air-tight container with silica gel desiccant to prevent moisture absorption. When urine was ready to be aliquoted, these pieces of filter paper were placed on a non-absorbent surface, usually aluminum foil or parafilm, for sample application. On each piece of filter paper the animal's name, collection date, sample letter and aliquot amount were written in pencil. Samples were aliquoted onto pieces of filter paper using a micropipette. During the pilot study urine was aliquoted using calibrated capillary tubes, but micropipettes were found to be easier to use and are more precise.

When possible, five replicates, each containing 200 µl of undiluted urine, were made. Fewer replicates were made when the sample volume did not allow for it. If adequate urine remained after the five initial samples were aliquoted, then five additional 200 µl replicates that were diluted with 0.1% sodium azide were made. Sodium azide is an antifungal agent and this precaution was taken in case the initial samples showed bacterial growth. This method has proved reliable for the stabilization of salivary samples (Ellison *et al.* 1986) and was used by van Schaik *et al.* (1991) for urine samples.

Urine samples were applied to filter paper as soon as possible after collection, usually in the evening after returning from the day's follow, to avoid contamination from bacterial growth. The median time between sample collection and filter paper application was 12 hours and 40 minutes (range 0 to 87 hours). Samples were aliquoted within 24 hours in 78.8% of cases, and within 48 hours for 99.8% of the samples.

After the urine was transferred to filter paper, the aluminum foil with the samples on it was placed in an air-tight container of approximately five liters in volume, containing approximately one half liter of silica gel. Filter paper with urine applied normally dried within twelve hours. The drying time depended on the number of samples in the container; the fewer number of samples the quicker the drying process. Urine samples dried in this manner exhibited no mold growth, thus only samples of urine not containing sodium azide were used for analysis.

After drying, samples were stored in transparent plastic slide sheets as recommended by Shideler *et al.* (1995). Slide sheets containing samples were also kept in a plastic container with silica gel to avoid the moisture absorption and mold growth which could occur in tropical rain forest conditions. The silica gel used for these procedures had a color indicator and was "cooked" once a week to maintain its effectiveness. Samples were also kept away from light and heat as suggested by Campbell (1994).

LABORATORY METHODS

Determination of Solvent

In developing the method for preserving hormones using filter paper, I first had to find an effective solvent for eluting urinary steroids dried onto paper. Thus I conducted several experiments to determine the best choice of solvent. In the first two tests, the recovery ability of methanol, ether, ethanol and acetylnitrile were investigated. In these tests 100 µl of titrated estrone sulfate (6500 cpm) were aliquoted onto matched 2.5 x 2.5 cm pieces of filter paper. After drying, each filter paper sample was folded in half and placed, using

forceps, into a 6 x 130 mm glass test tube. Each tube received 5 ml of solvent which was enough to fully immerse the filter paper. The filter paper was allowed to elute in the solution for approximately one hour.

After elution, the filter paper squares were removed from the test tubes by grasping the top edge of each square with forceps. As much of the solvent as possible was squeezed out of the filter paper by pressing the forceps against the side of the test tube. The forceps were cleaned with ethanol in between samples. Samples were placed in a heated dry bath, set at 37° C, and the solvent was evaporated using nitrogen. After the solvent was completely dried off, 2 ml of Tris buffer with a pH of 8.4 (0.1 M Tris, 0.9% NaCl, 0.1% NaN_3, 0.1% gelatin) were added to each sample tube. Each tube was then vortexed for two minutes, sealed with a rubber stopper and refrigerated overnight before counting. Sample aliquots equivalent to 40 µl of the original sample were counted and compared to 40 µl aliquots of tritiated estrone sulfate solution (6500 cpm).

In the next test I investigated the recovery ability of methanol compared to buffer. Methanol samples were eluted as described above. Buffer eluted samples did not require the evaporation and reconstitution step, thus sample aliquots could be counted directly. Samples were eluted in either 2 ml or 3 ml of Tris Buffer instead of the 5 ml used for methanol in order to prevent excessive dilution of the sample. This smaller elution volume necessitated additional folds of the filter paper samples. Sample aliquots equivalent to 40 µl of the original sample were counted and compared to 40 µl aliquots of tritiated estrone sulfate.

Results, shown in Table 7.01, revealed that methanol was quite effective at recovering the steroid from filter paper in both tests. Buffer recovered less than half of the steroid and

TABLE 7.01: Recovery of tritiated estrone sulfate eluted from filter paper, expressed as a percent of control samples not dried on filter paper.

Test Date	N	Buffer	Methanol	Ethanol	Ether	Acetylnitrile
10/12/93	12	—	88.1% ± 2.6	—	0.8% ± 0.1	—
10/18/93	6	—	79.7% ± 2.6	47.5% ± 1.8	0.6% ± 0.1	14.5% ± 1.3
1/29/94		41.9% ± 3.2 (n=4)	80.1% ± 5.4 (n=2)	—	—	—

ether was very poor at eluting the sample. Sample elution using buffer may have been inhibited by excessive folding of the filter paper, thus, this was modified in subsequent tests.

In addition to this first set of experiments using tritiated hormones in solution, I went on to further test solvents using actual urine samples. I compared estrone conjugate values determined from urine samples stored by freezing and matched samples stored on filter paper and then eluted. Six potential solvents were tested: methanol, ethanol, acetylnitrile, distilled water, Tris buffer (pH 8.4) and ether.

Urine samples were from three non-contracepting human females. In each test 2.5 cm x 2.5 cm pieces of filter paper were aliquoted with 200 µl of urine. Campbell (1994) showed that 3 cm x 3 cm pieces of filter paper are completely saturated at 250 µl. Thus, an aliquot amount of 200 µl was chosen because it would ensure that all of the hand-cut pieces of filter paper would be large enough to absorb the full 200 µl. The filter paper samples were dried in a container with silica gel in order to mimic field conditions. After drying, each filter paper sample was folded in half and placed, using forceps, into 6 x 130 mm glass test tube. Each tube received 5 ml of solvent. Tubes were sealed using rubber stoppers and placed in a refrigerator where they were allowed to elute for 24 hours. Samples eluted in methanol, ethanol, ether and acetylnitrile were dried and reconstituted as described previously. Samples eluted in water and buffer were directly assayed.

Urinary estrone conjugates were analyzed using radioimmunoassay by modifying procedures from Shideler *et al.* (1983), Czekala *et al.* (1987) and Ellison (1988). For samples eluted in methanol, ethanol, ether and acetylnitrile, aliquots of 0.1 ml of eluted sample (equivalent to 0.01 ml of undiluted urine) were combined with 0.3 ml of Tris assay buffer. For samples eluted in water and buffer, aliquots of 0.25 ml of eluted sample

(equivalent to 0.01 ml of undiluted urine) were combined with 0.15 ml of Tris assay buffer. Urine stored by freezing was thawed, and sample aliquots of 0.01 ml of urine were combined with 0.39 ml of Tris assay buffer. Antiserum which cross-reacts equally with estrone sulphate and estrone glucuronide (antiestrone glucuronide, 0.1 ml, 1:4500; D. Collins, Emory University) and tritiated estrone sulphate (0.1 ml, 6500 cpm, sp. act. 55 Ci/mmol: New England Nuclear, Boston, MA) were added to the urine and standard samples (50-8000 pg estrone sulphate). The assay was incubated at 15° C overnight. Charcoal-dextran (0.3 ml, 0.625% charcoal Norite A, 0.0625% in 0.1 M phosphate buffer pH 7.0) was used to separate bound and free steroid during a 10 minute incubation at 15° C. After centrifugation for 10 minutes the supernatant was decanted and mixed with scintillation fluid (Packard, Meriden, CT). Each vial was counted on a beta counter for five minutes each.

The Pearson correlation coefficients between counts of tritiated estrone sulfate determined from frozen urine and matched filter paper samples were calculated for each of the solvents used (Table 7.02). Several solvent tests were done as the assay procedure was being developed. Methanol elution resulted in the highest consistent correlations between hormonal values obtained through radioimmunoassay of frozen urine compared to urine dried on filter paper. Ethanol, ether, and acetylnitrile had consistently lower correlations with matched frozen samples. In addition to methanol, buffer and distilled water were also quite effective at eluting estrone conjugate from filter paper, and were in fact more effective than methanol in one test. However, in all other tests methanol was the most effective at eluting the steroid.

TABLE 7.02: Pearson correlation coefficients between counts of tritiated estrone sulfate values obtained from frozen urine samples and matched samples stored on filter paper and eluted with one of the solvents listed below. Signicant correlations are indicated by asterisks.

Test Date	N	Water	Buffer	Methanol	Ethanol	Ether	Acetylnitrile
8/14/93	12	—	—	.956****	.703**	—	.217
6/3/96	9	.882***	.819**	.706*	.524	.419	—
6/7/96	13	.656*	.862****	.864****	—	—	—

*P < 0.05, **P < 0.01, *** P < 0.001, **** P < 0.0001

The correlation between estrone conjugate values (pg/ml) for frozen urine and urine eluted from water, buffer and methanol was calculated for the third test. Results shown in table 7.03 show the high correspondence between frozen urine samples and eluted samples. Methanol elution resulted in the highest correlations with matched frozen samples.

TABLE 7.03: Pearson correlation coefficients between estrone conjugate values obtained from frozen urine samples and matched samples stored on filter paper and eluted with water, buffer or methanol. All procedures were significantly correlated with frozen urine, with methanol exhibiting the highest correspondence (n=13).

	Frozen Urine: Water Elution	Frozen Urine: Buffer Elution	Frozen Urine: Methanol Elution
r	0.853*	0.877*	0.929*

* $P < 0.0001$

Based on these experiments, methanol was thus chosen as the solvent to use for further method development. Water and buffer also demonstrated high correlations with matched frozen samples. Thus, they could be considered as potential alternative solvents if needed. However, methanol elution was also preferred because it allowed me to dry off the solvent and reconstitute the steroid at the desired concentration for the assay. Because water and buffer elutions were not reconstituted, but were taken directly into the assay, the final concentration of the sample was constrained by the 5 ml of solvent needed to completely immerse the filter paper during elution. A final concentration of 5 ml of solution results in a sample that is too dilute for the creatinine measurements to be described subsequently.

Filter Paper Removal

In the process of testing the solvents, I also investigated alternative procedures for removing the filter paper from the eluting solvent. These alternative procedures were to remove the filter paper after the solvent was dried off, to remove the filter paper when the top of the paper was partially exposed (avoiding putting the forceps into the solvent), to decant the solvent into a separate test tube before drying and to remove the paper using forceps before drying (cleaning the forceps using methanol in between samples). For each treatment, 3 x 3 cm pieces of filter paper were aliquoted with 100µl tritiated estrone sulfate (6500 cpm). The filter paper samples were dried and eluted with methanol as explained previously. After the solvent had been dried off, 1 ml of Tris assay buffer was added to each tube and vortexed for 2 minutes. Sample aliquots of 400 µl were decanted into scintillation vials and counted for 5 minutes in a beta counter. Results were compared to control aliquots of tritiated estrone sulfate (6500 cpm).

Removing the filter paper before drying and removing the filter paper after the top was exposed resulted in the highest recovery of tritiated steroid from the filter paper (Table 7.04). Allowing the paper to remain in the test tube during the drying process and then removing it resulted in a recovery of less than half of the other procedures, with a very high degree of variance. In this case the steroid adhered to the filter paper during drying, as determined by placing the eluted paper itself in a scintillation vial and counting it. Decanting the methanol into a separate tube and then drying resulted in a very low percentage recovery. The steroid may have remained adhered to the original test tube in this case. Based on these results I decided to remove the paper before the drying process. This allowed for more consistent treatment of samples than waiting until the top of the paper was exposed as all samples could not be removed with precisely the same degree of paper exposure.

TABLE 7.04: Comparison of procedures for removal of filter paper after elution. Results are expressed as the percentage of tritiated estrone sulfate recovered relative to control samples not dried on filter paper.

Test Date	N	Paper Removed after Drying	Paper Removed after Top Exposed	Methanol Decanted before Drying	Paper Removed before Drying
10/12/93	12	43.9% ± 22.3	88.1% ± 2.6	0.4% ± 0.1	—
6/14/96	10	29.4% ± 3.0	—	—	91.9% ± 3.2

Validation of the Filter Paper Elution Method with Creatinine

Daily urine samples were obtained from a non-contracepting human female to validate the effectiveness of the methanol elution method with the additional step of indexing hormonal values with creatinine. Creatinine is a product of muscle metabolism which is used to correct for concentration and is described subsequently. Samples of urine stored by freezing were compared to matched samples of urine stored on filter paper (in 200 µl aliquots). Urine was eluted with methanol as described above. The filter paper was removed from the test tubes after elution. Radioimmunoassay was performed on the eluted and frozen urine samples as described previously and values were compared. All hormonal values were indexed by mg of creatinine obtained from frozen urine samples.

Hormonal levels measured in urine preserved on filter paper exhibited a high correspondence to hormonal levels in urine preserved by the conventional method of freezing. In this validation study, estrone conjugates recovered from human urine exhibited a correlation of $r = 0.962$ between samples preserved on filter paper and matched frozen urine samples (Figure 7.01).

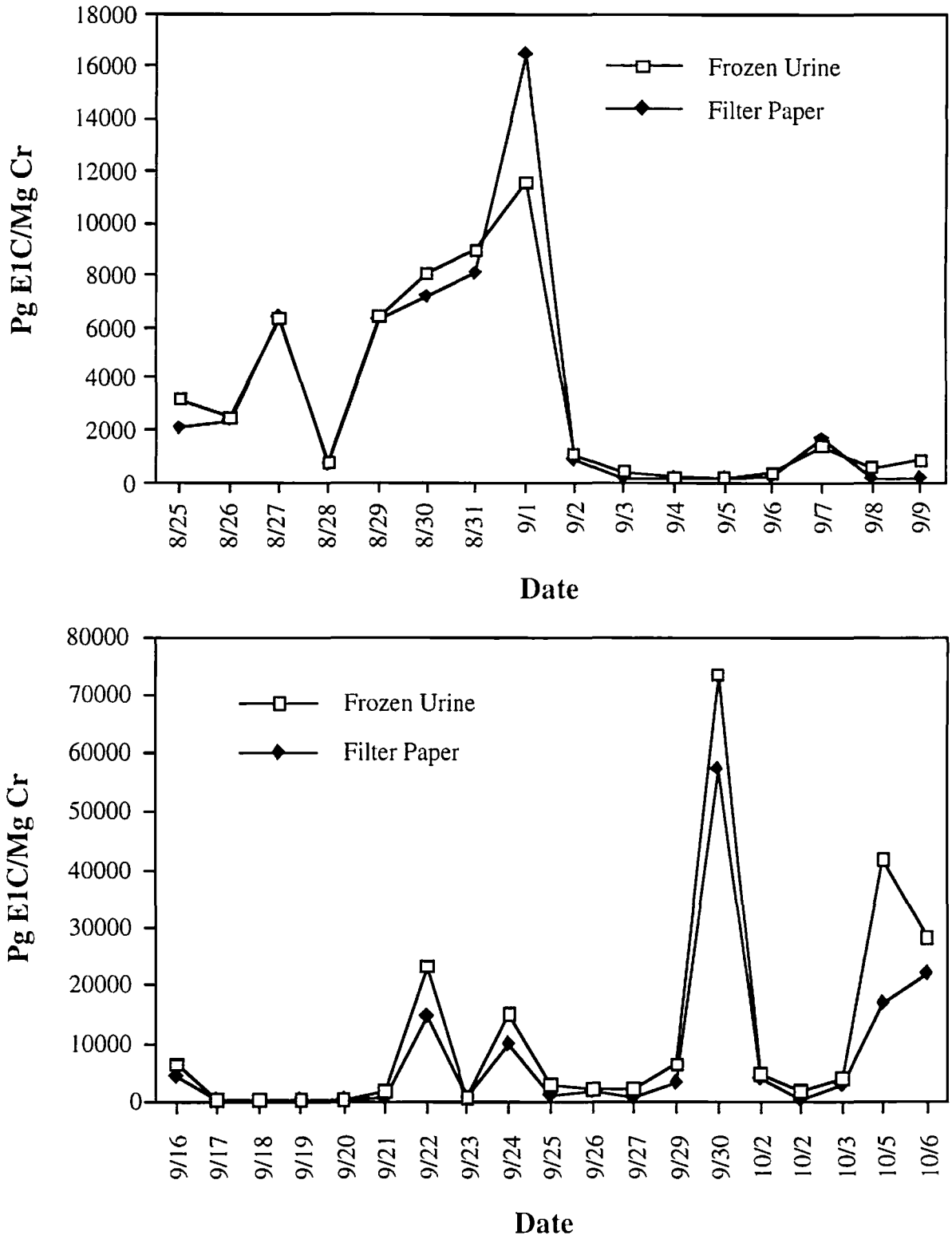


FIGURE 7.01: Comparison of estrone conjugate values using frozen urine and matched samples of urine dried on filter paper and eluted with methanol. Values obtained using the two methods were highly correlated ($r = .962$, $p < .0001$). Cycles are from a single human subject.

Validation of Method Using Captive Orangutan Urine Samples

After the filter paper elution method was validated for humans, the next step was to validate the method using urine from captive orangutans. This step was needed to assure that the levels of estrone conjugates found in orangutans could be measured using this assay. Permission was obtained for this study from the Orangutan Species Survival Program executive committee. Each participating zoo was sent an instruction sheet to standardize the collection and storage of urine samples; a log book to record samples collected, signs of menstruation and other behavioral notes; and several months' supply of disposable plastic pipettes for urine collection and vials for storing urine. All samples were stored in freezers at the respective zoos and frozen samples were mailed on dry ice to the Reproductive Ecology Laboratory. Sufficient samples for analysis were ultimately obtained from 2 cycling females from the San Diego Zoo and 4 cycling females from the Seattle-Woodland Park Zoo. The latter institution already had the urine collections on hand.

The urine was frozen upon receipt at Harvard. Using data that the zoos provided on menstrual bleeding, the samples were divided up into menstrual cycles. Five assays from 2 females, a total of 100 samples, were assayed. Frozen urine samples were thawed, pipetted onto filter paper and stored in a container with silica gel to mimic field conditions. Matched samples of urine stored by freezing and urine dried on filter paper were analyzed as described previously. In addition, in each assay I ran three pool samples from frozen urine and three matched pool samples from urine eluted off of filter paper. Pool samples came from human females. The mean interassay coefficient of variation was 9% for the frozen urine pools and 15% for the filter paper pools. The mean intra-assay coefficient of variation was 9.7%. The mean assay sensitivity was 2002 pg E1C/ml.

As seen in Table 7.05 a high correlation was found between estrone conjugate values from frozen urine and matched filter paper samples for all 5 assays from captive orangutans. All assays showed correlations of .918 or higher.

TABLE 7.05: Comparison of estrone conjugate values from frozen urine compared to matched samples eluted off of filter paper with methanol. A high correlation between the two procedures was observed in all assays.

Assay	n	r
Chinta 3/19-4/1	14	0.966*
Chinta 4/2-4/16	15	0.985*
Kelly 4/14-5/11	29	0.935*
Kelly 6/9-7/8	30	0.999*
Kelly 2/25-3/8	12	0.918*

* $p < 0.0001$

Creatinine Validation

Variation in fluid intake can have a significant effect on the concentration of steroids in urine. Thus, urinary steroid values must be indexed by an appropriate indicator of concentration. Creatinine, a product of muscle metabolism that is released in urine at a constant rate, is the standard measure used to index urinary steroid values. Creatinine is measured using the Jaffe reaction (Taussky 1954) in which a color indicator, picric acid, is added to the urine in alkaline solution (NaOH). A yellow-orange colored complex forms which deepens in hue with increasing creatinine concentration. Optical density values are

measured using a spectrophotometer and compared to values obtained from standard samples of creatinine.

I tested the ability of filter paper to retain creatinine after drying and the ability of methanol to serve as an elutive solvent. Procedures were modified from those described by Czekala *et al.* (1987) and Shideler *et al.* (1983). Shideler *et al.* (1995) used hole punches to sample pieces of urine-soaked filter paper disks. They found, however, that urine retention varied across the filter paper disks, confounding their ability to measure creatinine. They suggest that urine collected in a standardized way and kept dry after collection could be successfully analyzed for creatinine. Thus, I aliquoted a standard amount of urine (200 µl) on pieces of filter paper and eluted the creatinine from the entire piece of filter paper to avoid this problem.

All samples were aliquoted into microtiter plates. Working dilutions of 0.01 and 0.03 mg/ml of creatinine were used as standards, in 100 µl aliquots. Distilled water, also in 100 µl aliquots, was used as the zero dose to reflect the optical density in the absence of creatinine. Sample aliquots of 0.1 ml of urine eluted from filter paper were used (eluted samples are diluted 1:10). Pool samples were also run in each assay. Samples of three frozen urine pools were diluted 1:10 with distilled water and run in 0.1 ml aliquots. Matched pool samples dried on filter paper and eluted with methanol were run in 0.1 ml aliquots.

Sample and standard wells were aliquoted with 50 µl of 0.75 N NaOH and 50 µl of 0.02 N picric acid. All wells were read on a microtiter plate reader (Dynatec MR5000) after a development time of approximately 60 minutes. Standard and blanks were run in quadruplicate and urine samples were run in triplicate. If one replicate value was less than half of the average optical density of the other values it was rejected. During the elution

procedure a ten-fold dilution occurred, thus final values were multiplied by 10 to reflect mg creatinine/ml.

Results (Table 7.06) showed that creatinine was in fact retained on filter paper after drying and that methanol was an effective solvent. All assays showed a highly significant correlation between creatinine values from frozen urine and creatinine values from filter paper.

TABLE 7.06: Creatinine values measured from frozen urine compared to values obtained from creatinine eluted off of filter paper.

Assay	n	r
Chinta 3/19-4/1	14	0.987*
Chinta 4/2-4/16	17	0.958*
Kelly 4/14-5/11	29	0.952*
Kelly 6/9-7/8	30	0.919*
Kelly 2/25-3/8	12	0.964*

* $p < 0.0001$

Validation of Complete Method of Eluting Estrone Conjugates and Creatinine from Orangutan Urine Samples Dried on Filter Paper

For each of the assays of captive orangutan urine described above I calculated the pg Estrone Conjugate/mg Creatinine for each sample. Values obtained using the two methods were highly correlated as shown in Table 7.07.

TABLE 7.07: Comparison of pg Estrone Conjugate/mg Creatinine from frozen samples versus samples eluted off of filter paper.

Assay	n	r
Chinta 3/19-4/1	14	0.882*
Chinta 4/2-4/16	17	0.955*
Kelly 4/14-5/11	29	0.729*
Kelly 6/9-7/8	30	0.933*
Kelly 2/25-3/8	12	0.960*

* $p < 0.0001$

Storage Time

In this study, field urine samples needed to be stored on filter paper for up to one year before bringing back to the laboratory. Thus, the stability of urine stored in this manner was tested in several experiments. In the first experiment, urinary estrone conjugates from frozen urine were compared to values obtained from matched filter paper samples that were

stored for either three months or for less than one week. All samples came from non-contracepting human females. All filter paper samples were stored in a plastic container with silica gel, out of the light, at room temperature. Elution, radioimmunoassay and creatinine measurement procedures were followed as described previously. In this first experiment, samples stored on filter paper showed a close correspondence with urine whether they had been stored on filter paper for less than a week or for three months. All correlations were highly significant.

TABLE 7.08: Pearson correlation coefficients between estrone conjugate values determined from frozen urine samples (n=8) compared to matched samples dried on filter paper and stored for 3 months and matched samples dried and stored on filter paper for less than one week. All correlations were significant.

	Frozen Urine: 3 Month Filter Paper	Frozen Urine: 1 Week Filter Paper	3 Month Filter Paper: 1 Week Filter Paper
r	0.981*	0.879*	0.909*

*$p < 0.005$

In the second experiment, samples from captive orangutan females (described previously) were stored on filter paper for two years. These were compared to matched samples of frozen urine and urine dried on filter paper for less than 1 month. Three assays with 41 samples from two orangutan females were run in this series of experiments. Results showed that values from frozen urine were significantly correlated with both one-month-old filter paper samples and two-year-old filter paper samples. Tables 7.09-7.11 show these correlations for estrone conjugates, creatinines and pg estrone conjugates/mg cr.

TABLE 7.09: Pearson correlation coefficients between estrone conjugate values determined from frozen urine samples compared to matched samples dried on filter paper for either one month or 2 years.

		Urine: One-Month-Old Filter Paper	Urine: Two-Year-Old Filter Paper	One-Month: Two-Year-Old Filter Paper
Assay	n	r	r	r
Chinta 3/19-4/1	14	0.966***	0.927***	0.857***
Chinta 4/2-4/16	15	0.985***	0.958***	0.943***
Kelly 2/25-3/8	12	0.918***	0.764**	0.883***

* = $p < 0.05$; ** = $p < 0.005$; *** $p < 0.0001$

TABLE 7.10: Pearson correlation coefficients between creatinine values determined from frozen urine samples compared to matched samples dried on filter paper for either one month or 2 years.

		Urine: One-Month-Old Filter Paper	Urine: Two-Year-Old Filter Paper	One-Month: Two-Year-Old Filter Paper
Assay	n	r	r	r
Chinta 3/19-4/1	14	0.987***	0.632*	0.660*
Chinta 4/2-4/16	17	0.958***	0.735***	0.654**
Kelly 2/25-3/8	12	0.964***	0.659*	0.698*

* = $p < 0.05$; ** = $p < 0.005$; *** $p < 0.0001$

TABLE 7.11: Pearson correlation coefficients between values of Pg Estrone Conjugates/Mg Creatinine determined from frozen urine samples compared to matched samples dried on filter paper for either one month or 2 years.

		Urine: One-Month-Old Filter Paper	Urine: Two-Year-Old Filter Paper	One-Month: Two-Year-Old Filter Paper
Assay	n	r	r	r
Chinta 3/19-4/1	14	0.882***	0.852***	0.738***
Chinta 4/2-4/16	17	0.955***	0.949***	0.965***
Kelly 2/25-3/8	12	0.960***	0.947***	0.940***

* = $p < 0.05$; ** = $p < 0.005$; *** = $p < 0.0001$

Shideler *et al.* (1995) found that samples that had been soaked, dried and stored on filter paper for one year produced hormone concentrations that were quantitatively and qualitatively similar to results obtained from samples newly placed on filter paper. However, after 5 years of storage, hormonal results were qualitatively similar, but quantitatively they were 10-50% lower than those originally obtained. In my study I found that hormonal results obtained from filter paper compared to frozen urine were highly correlated at one month, 3 months, and two years, with a somewhat weaker correlation observed at two years.

Contamination

Urine collected under field conditions may sometimes come in contact with feces from the animal, and dirt, leaves, and bark from the canopy or the ground. An experiment to test the effect of contact between the urine and these substances was set up in the field during the pilot project of 1992. A large volume urine sample was collected from 3 wild orangutans and separated into 5 separate bottles. One bottle was left as uncontaminated urine. One bottle was intermixed with a small amount of feces from the animal as might happen if urine was collected from a spot next to where feces has dropped. The remaining bottles were intermixed with small amounts of dirt, leaves, and bark respectively, as might happen during routine sample collection. Sample aliquots of 200 µl were put onto filter paper. Samples were assayed by radioimmunoassay following the procedure described above.

Correlation coefficients between estrone conjugate values obtained from uncontaminated urine and matched urine samples that were intermixed with feces, dirt, leaves or bark are shown in Table 7.12. A high correlation was found between uncontaminated urine and urine intermixed with any of these contaminants.

TABLE 7.12: Pearson correlation coefficients between estrone conjugate values from uncontaminated urine samples (n=3) compared to samples that were purposely contaminated with feces (from the same animal), dirt, leaves or bark. All samples were stored on filter paper.

	Urine:Feces	Urine:Dirt	Urine:Leaves	Urine:Bark
r	0.983	0.987	0.999	1.000

SUMMARY

These sets of experiments demonstrate that the desiccation of urine onto filter paper and elution using methanol is an effective method for preserving primate urine samples for later hormonal analysis in the absence of freezer facilities. Both estrone conjugates and creatinine remained significantly correlated after two years of storage. However, because Shideler *et al.* (1995) found that samples had started to decay after five years it is recommended that samples be frozen after returning from the field and that assays be run as soon as is convenient.

These methods can be applied to any species in which urine can be readily obtained from individual animals. Collection and assay protocols may need to be modified depending on local conditions and the species involved. These methods for the non-invasive collection of urine from free-ranging orangutans and the preservation of urine without freezing provide an effective way to monitor primate reproductive physiology in the wild where urine collection is possible. They are particularly valuable in field conditions where freezing urine is not possible.

• CHAPTER 8 •

CHANGES IN ESTRONE CONJUGATE LEVELS

CHAPTER SUMMARY

Orangutans in this study experienced a dramatic fluctuation in fruit availability resulting from a mast fruiting peak followed by a prolonged period of low fruit availability. These environmental changes led to pronounced changes in their diet, nutritional intake, energy expenditure and energy balance. In this chapter I investigate the hypothesis that during the period of high fruit availability female orangutans would have higher estrone conjugate levels than during the period of low fruit availability.

To test this hypothesis, 179 urine samples were collected from wild adult female orangutans between September 1994 and December 1995 and were analyzed for estrone conjugates (E_1C). A new method of eluting urine stored on filter paper was used, as described in Chapter 7. Two non-pregnant females were followed extensively during both periods of high and low fruit availability and both showed a significant decrease in estrone conjugate levels during the low fruit availability period. Comparisons of weekly mean estrone conjugate values in 12 non-pregnant females also showed a significant decrease in estrone conjugates when fruit availability decreased.

Samples from captive orangutans were also obtained and measured for E_1C values. Comparison of these samples with those from wild females showed that captive females had significantly higher estrone conjugate values than did wild females. This result supports the hypothesis that the peculiar conditions of captivity, availability of a constant food source and low energetic expenditure, would lead to higher hormonal levels in captive orangutans.

Finally, data are presented on matings and conceptions observed during the course of the study period. All matings were observed during the months of highest fruit availability and

all matings were between undeveloped males and females whose youngest offspring was judged to be four years of age or older. The implications of these findings for studying orangutan reproduction and interbirth interval are discussed.

INTRODUCTION

The preceding chapters have shown that orangutans live in an environment with greatly fluctuating fruit resources, and that their nutritional intake, activity patterns and energy balance vary in accordance with these fluctuations. In this chapter, I will extend this line of inquiry to examine reproductive status in female orangutans with the ultimate aim of understanding how the environment influences orangutan reproduction.

Previous research on reproduction in orangutans, as well as other great apes, has focused almost exclusively on sexual behavior and characterization of reproductive parameters (Nadler 1982a, 1982b, 1986, 1988; chimpanzees: e.g. Tutin 1979, 1980; Tutin and McGinnis 1981; gorillas: e.g. Harcourt and Stewart 1978; Harcourt *et al.* 1980, Harcourt 1981). More recently, as long-term reproductive patterns and differences between study sites have become available, there has been an emerging recognition that nutrition, in particular, may be an important factor in understanding great ape reproduction (Tutin 1994). Goodall (1986) reports that there are seasonal influences on chimpanzee reproduction in Gombe National Park, Tanzania, and Wallis (1995, 1997) proposes, after examination of 17 years of Gombe reproductive data, that seasonal changes in diet may play a role, either through the content of the food or through direct social contact, to alter reproductive physiology. However, no direct data exists to confirm this speculation.

No studies have been conducted in the wild on female ovarian hormones in any of the great apes. Laboratory analyses of great ape hormonal functioning have focused on characterization of the menstrual cycles, pregnancy and lactation. Thus, this is the first study of hominoid ovarian function in the wild as well as the first study to explicitly investigate the ecological context of ovarian function in any ape. As explained earlier in Chapters 2 and 7, I developed methods for collecting urine samples in the field (Knott,

1996b), preserving them on filter paper, and extracting hormones from filter paper in the laboratory in order to be able to measure hormonal levels in wild orangutans in a non-invasive way.

Estrone conjugates (E_1C) were measured from these urine samples to provide an assessment of orangutan ovarian function. Levels of ovarian hormones as determined by radioimmunoassay are commonly used as measures of fecundity in both humans (Ellison *et al.* 1993) and non-human primates (Shideler and Lasley 1982; Monfort *et al.* 1986). Using this technique, urinary hormone excretion has been studied in orangutans during the menstrual cycle (Collins *et al.* 1975; Masters and Markham 1991) and during pregnancy (Czekala *et al.* 1981, 1983). This research indicates that urinary estrone conjugates peak both at mid-cycle and during the luteal phase (Collins *et al.* 1975; Masters and Markham 1991). Changes in measures of estrone conjugates provide a comparative index of adequate development of the ovarian follicle across cycles. Higher peak as well as mean levels of estrone conjugates have been associated with increased fecundity of orangutan ovarian cycles in captivity (Masters and Markham 1991).

I hypothesize here that periods of high fruit availability experienced by orangutans, through the intermediate variables of high nutritional status and positive energy balance, result in higher mean estrone conjugate levels compared to periods of low fruit availability. This is based on the hypothesis that orangutans have evolved similar responses to changing ecological conditions as has been found in humans (Ellison 1990, 1993). I test this hypothesis by comparing E_1C levels between the high and low fruit availability periods from this sample of wild female orangutans. The alternative, null hypothesis is that fruit availability and associated energetic changes show no relationship with estrone conjugate levels.

Ideally it would have been best to compare E_1C levels between whole menstrual cycles from the different fruit availability periods. However, due to the difficulty of locating and continuously following individual orangutans for entire months, this was not possible. What was feasible was to get repeated opportunistic urine samples from several different females throughout different parts of every month. Even though estrone conjugate levels normally vary within each month across the different stages of the menstrual cycle, we can still expect to detect differences between months (or groups of months) if between month changes in average E_1C levels are large enough.

If the hypothesis that energetics has a significant effect on hormone levels in orangutans is supported, a resulting prediction is that we would expect that captive animals receiving a highly nutritious diet year-round would have consistently higher hormone levels than would wild orangutans experiencing a variable food supply. Captive orangutans are observed to reach reproductive maturity earlier (Asano 1967; Lippert 1977; Masters and Markham 1991), have a shorter waiting time to conception (Lippert 1974) and shorter interbirth intervals (Lippert 1977) than do wild orangutans. These differences have been attributed to nutrition, although decreased activity levels in captivity is likely an additional factor. Because hormonal data from wild orangutans has not been available prior to this study we have not been able to evaluate possible hormonal differences between these populations. I thus test the hypothesis that captive adult female orangutans will have higher hormonal levels than do wild adult female orangutans.

In parallel with these hormonal data, I also report here on the temporal distribution of matings and pregnancies observed during the study to document any behavioral responses correlated with fruit availability, energetics and hormonal levels.

METHODS

Samples

A total of 179 urine specimens were analyzed for estrone conjugates from 17 wild adult female orangutans sampled between September 1994 and January 1996. Urine was collected as described in Chapter 7 by using a plastic sheet or pipetting directly from vegetation. Primarily first morning urine samples were utilized. Mean collection time was 7:52 a.m. Samples collected per individual female ranged between 1 and 76. Animals could not be sampled evenly as some subjects remained largely within the range of the study area and were frequently encountered, whereas other animals were only encountered sporadically as they moved through the research site.

Estrone conjugate values were also measured, for comparative purposes, in four captive orangutans from the Seattle Woodland Park Zoo. Animals were housed separately and urine collected under sterile conditions. A total of 185 captive urine samples were analyzed across several complete cycles. Mean values for these females thus represent an average across the entire menstrual cycle.

Sample Preservation

Urine samples collected from the wild were preserved by aliquoting 200 µl of urine onto 2.5 x 2.5 cm squares of highly absorbent filter paper. Samples were dried and stored in a plastic container of approximately 5 liters volume, containing approximately 1/2 liter of silica gel. Samples from captive orangutans were frozen immediately after collection and later shipped on dry ice to Harvard University's Reproductive Ecology Laboratory where a

portion of each sample was aliquoted onto filter paper and dried following the above procedure.

Estrone Conjugate Analysis

Estrone conjugates were eluted from the filter paper samples by placing them in 6 x 130 mm test tubes and then adding 5 ml of methanol. Tubes were sealed using rubber stoppers and placed in a refrigerator where they were allowed to elute for 24 hours. The filter paper was removed after elution was complete and the methanol was evaporated by placing tubes in a heated dry bath under nitrogen. Samples were reconstituted in 2 ml of Tris buffer.

Aliquots of 0.1 ml of eluted sample (equivalent to 0.01 ml of undiluted urine) were combined with 0.3 ml of Tris assay buffer. Antiserum (which cross-reacts equally with estrone sulphate and estrone glucuronide) and tritiated estrone sulphate were added to the urine and standard samples. The assay was incubated at 15° C overnight. Charcoal-dextran was used to separate bound and free steroid during a 10 minute incubation at 15° C. After centrifugation for 10 minutes the supernatant was decanted, mixed with scintillation fluid, and vials counted on a beta counter for 5 minutes each. Samples run in duplicate were compared to triplicate doses of the standard curve. Urinary estrone conjugate methods are explained in detail in Chapter 7 and described in Appendices II-IV.

Pool samples made from human female urine were used to assess the inter-assay coefficient of variation. Pools were made from samples collected during the luteal phase, the follicular phase and from the third trimester of pregnancy. Both frozen and filter paper pool samples were tested in each assay. The average inter-assay coefficient of variation was 23.0% for frozen urine pools (luteal pool = 17.2 %, follicular pool = 16.1%, pregnancy pool = 35.7%) and 19.1% for filter paper pools (16.1% = luteal pool, 13.3% = follicular pool,

pregnancy pool = 27.8%). The average intra-assay variability was 8.35%. These levels of inter-and intra-assay variation are typical for radioimmunoassay (e.g. Ellison *et al.* 1989; Lipson and Ellison 1996). Assay sensitivity was 1648 pg E$_1$C/ml on average.

Creatinine

Variation in urine concentration was corrected by dividing hormonal concentrations by the creatinine values for each sample. Creatinine measurements were obtained using the Jaffe reaction (Taussky, 1954) as described in Chapter 7. Working dilutions of 0.01 and 0.03 mg/ml of creatinine were used as standards, in 100 µl aliquots run in quadruplicate. Sample aliquots of 0.1 ml of urine eluted from filter paper were run in triplicate. Sample and standard wells were aliquoted with 50 µl of 0.75 N NaOH and 50 µl of 0.02 N picric acid. All wells were read on a microtiter plate reader after a development time of approximately 60 minutes.

Pool samples were also run in each assay. Samples of three frozen urine pools were diluted 1:10 with distilled water and run in 0.1 ml aliquots. Matched pool samples dried on filter paper and eluted with methanol were run in 0.1 ml aliquots. Inter-assay variability averaged 12.7% for the frozen samples (range 10.6-15.25) and 7.4% for the filter paper samples (6.3-8.9%).

Fruit Availability Categories

Samples were divided into two categories based on the relative availability of fruit at the time they were collected. As explained in Chapter 3, a total of 567 orangutan fruit trees were monitored monthly for the presence of fruit and flowers. The percentage of trees ripening fruit or flowering was calculated each month. As shown in Chapters 3 and 4, the

period from September 1994 to December 1996 could be divided into two distinct categories based on ripe fruit and flower availability, and also fruit consumption, by orangutans. Months spanning September 1994 to February 1995 represented a period of high fruit and flower availability and high caloric consumption by orangutans. Then, from March through September 1995 there was a period of very low fruit availability and caloric consumption. Thus, these two time periods were used for the comparison of hormonal data in this chapter.

Mating Behavior

Mating behavior, including consortships, attempted matings and actual matings were recorded on a continuous basis when they occurred. A separate, specialized data sheet was used for such events. The timing of mating behavior as well as the tree position, distance of separation between the male and female, and reactions of other animals were recorded. Six possible mating positions were recorded as well as eight types of vocalizations. Additionally, I attempted to further elucidate the differences between forced vs. unforced copulations by recording the occurrence and frequency of twenty-four behaviors related to copulation.

Statistical Analyses

Due to the high variance in number of samples collected per individual female, I examined the data in two ways. First, I compared mean hormonal values for each female across all collection days, or within a defined period of fruit availability. This resulted in samples that are independent of each other and could be rigorously compared. Second, in analyses where I wanted to characterize hormonal values found in wild orangutans compared to captive orangutans or between pregnant and non-pregnant orangutans, I calculated the

mean hormonal value (pg E_1C/mg Cr) for each individual. The cycle phase of each orangutan could not be determined visually because these animals do not have estrus swellings and I was not able to follow individuals continuously enough to determine the cycle phase through plotting their E_1C values. Thus, averaging across sample days provides an estimate of mean hormonal level across the cycle. Data in these first two types of analyses were log transformed when not normally distributed and means were compared using two-tailed T-tests since there was no pseudo-replication of individuals.

In the third type of analysis I wanted to include all data from wild non-pregnant females to compare mean pg E_1C/mg Cr values between the high and low fruit availability periods. Because some animals were very heavily sampled and others sampled rarely, I calculated the mean weekly value for each individual. This allowed the data from all females to be included in the analysis without over representing infrequently sampled individuals and reducing the data for well sampled individuals. However, it does not eliminate pseudo-replication completely. The non-parametric Mann-Whitney U-test was used to compare between samples in this analysis.

A lag time effect was also incorporated into fruit-season comparisons. Lager and Ellison (1990) found in humans that the effect of weight loss on ovarian hormones was greater in the month after the weight change occurred. Thus, I examined the data by first assuming there was no lag time, and then assuming a one and a two-month lag time.

RESULTS

Variation in Orangutan Estrone Conjugate Values

Data analyses fell into three general categories to meet the goals of this study. First, I characterized the levels of estrone conjugates found in wild adult female orangutans. Next, I tested the hypothesis that estrone conjugate values would be significantly higher in captive versus wild adult female orangutans. Finally, I tested the hypothesis that estrone conjugate values in wild female orangutans would be higher during periods of high fruit availability than during periods of low fruit availability.

Pregnant vs. Non-Pregnant Wild Adult Females

Of the seventeen wild female orangutans in this study, five could confidently be assigned to pregnant or non-pregnant categories because they were followed extensively for at least one year after samples were collected. Thus, I knew if a pregnancy had occurred. Two of these five females were pregnant, two of them were not pregnant, and one female became pregnant during the study and was thus in both categories at different times. Using data from these five individuals, average weekly estrone conjugate values between pregnant and non-pregnant females were compared, and as expected, mean values were significantly higher in pregnant females (two-tailed unpaired T-test, $n=6$, $t = 5.7$, $p < 0.005$). Pregnant females averaged 282,000 pg Estrone Conjugate (E_1C)/mg Creatinine (Cr) (SE = 66,000) and non-pregnant females averaged 19,000 pg E_1C/mg Cr (SE = 6000). The average weekly estrone conjugate values for the pregnant females ranged between 108,600 and 1,110,600 pg E_1C/mg Cr and for the non-pregnant females ranged between 8100 and 61,800 pg E_1C/mg Cr. Note that these ranges are non-overlapping.

The remaining twelve of the seventeen females were not followed long enough or continuously enough to positively determine whether or not they were pregnant when the samples were collected. Examination of their hormonal values showed that, except for one sample from one female, all values fell clearly within the range of either pregnant or non-pregnant values. Three females, with one sample each, fell in the pregnant range, with a mean pg E_1C/mg Cr value of 420,000 (SE = 125,000, range = 217,400 - 648,500 pg E_1C/mg Cr). These females had no accompanying offspring at the time, thus their apparent reproductive state is consistent with pregnancy. They were thus classified as "suspected pregnant." The remaining nine females fell in the non-pregnant range with a mean pg E_1C/mg Cr value of 20,300 (SE = 2600, range = 7300 - 32,900 pg E_1C/mg Cr). They were thus classified as "suspected non-pregnant." Figure 8.01 compares the mean pg E_1C/mg Cr values of females in the different groups.

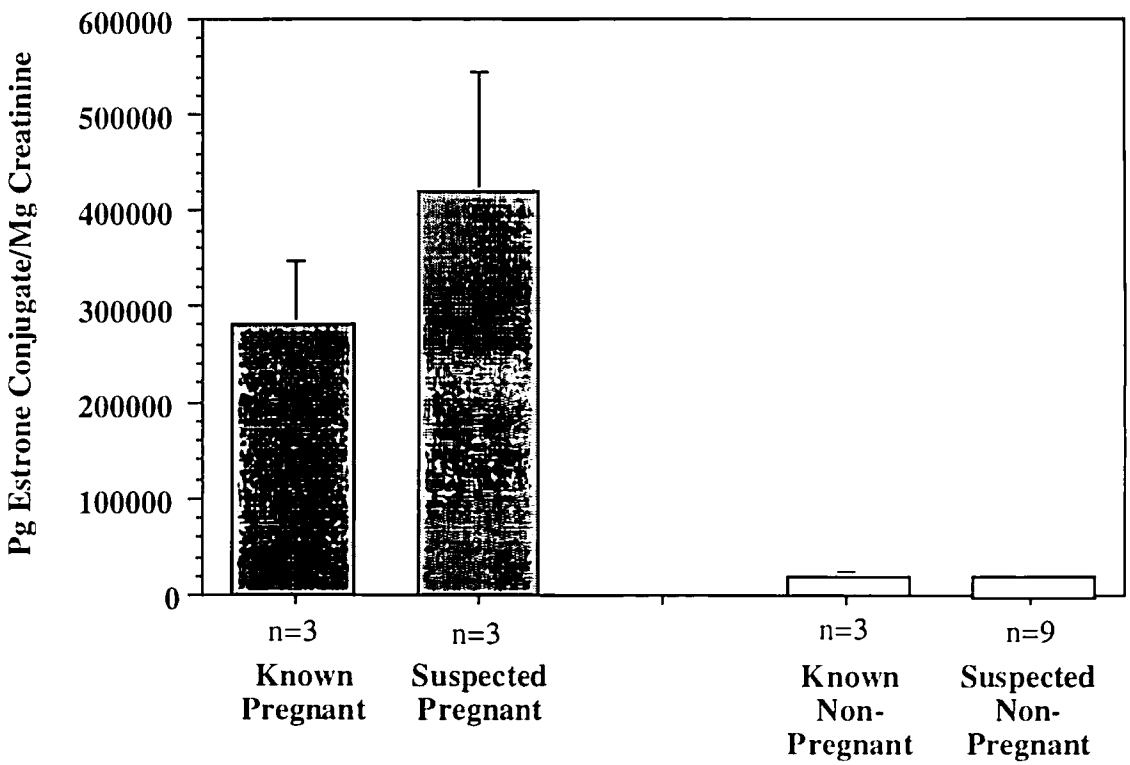


FIGURE 8.01: Comparison of mean estrone conjugate values for pregnant and non-pregnant wild orangutans. Sample size, *n*, is the number of individuals. The hormone value used for each individual was the mean of all E_1C values for that individual. Standard errors of the data are shown.

As indicated above, one female had a single sample value of 82,400 pg E_1C/mg Cr, falling between the ranges of pregnant and non-pregnant values. During the subsequent week she had sample values that were clearly within the pregnancy range. She was observed to mate several times during this two-week period. This value may represent a peak estrone conjugate level during a conception cycle, or may indicate the beginning of pregnancy. Thus, I did not include this sample in subsequent analyses because of its indeterminate status.

The overall mean value for pregnant females combining "known" and "suspected" categories was 351,000 pg E_1C/mg Cr (SE = 70,400; n = 6) and for combined "known" and "suspected" non-pregnant females was 20,000 pg E1C/mg Cr (SE = 2300; n = 12).

Estrone Conjugate Values in Wild vs. Captive Orangutans

The hypothesis that the energetic conditions of captivity would result in estrone conjugate values that were significantly higher than those found in the wild was tested by comparing mean estrone conjugate values from the 12 non-pregnant (suspected and known) wild orangutans to mean estrone conjugate values obtained from 4 non-pregnant captive orangutans. Values from captive females were determined from samples stored on filter paper in order to eliminate differences due to the storage method.

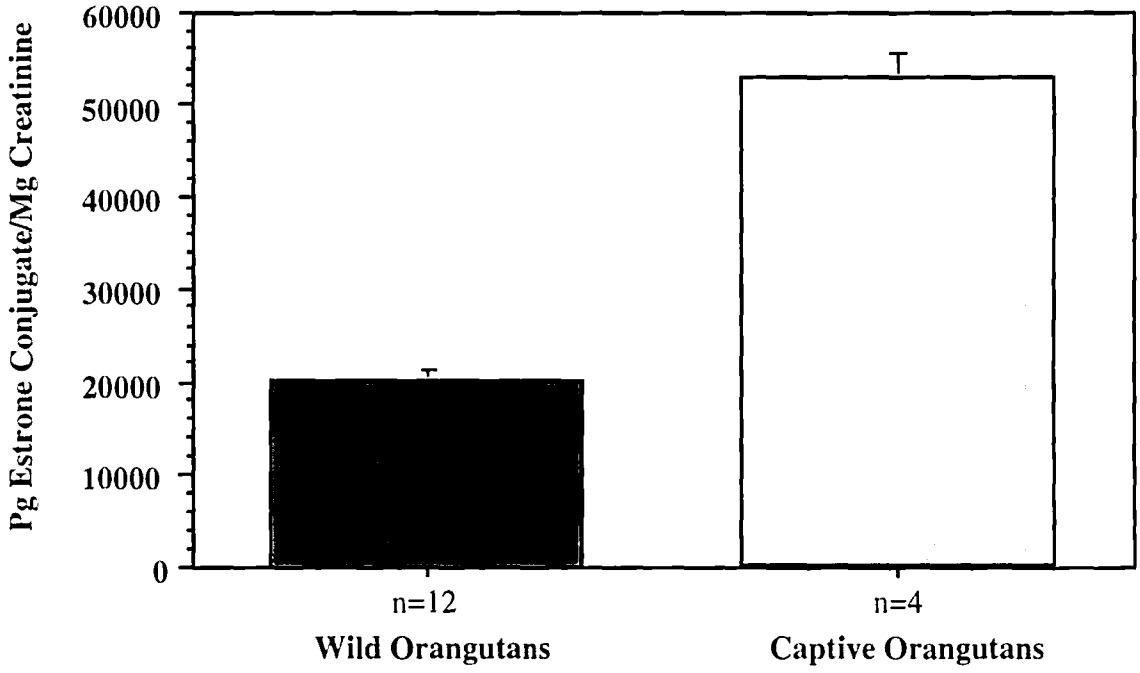


FIGURE 8.02: Comparison of mean estrone conjugate values for 12 wild non-pregnant orangutans compared to 4 captive non-pregnant orangutans. The hormone value used for each individual was the mean of all E_1C values for that individual. Standard errors of the data are shown.

Results (Figure 8.02) show that estrone conjugate values were significantly lower in the wild females than in captive females (two-tailed, unpaired T-test, n=16, $p < 0.0001$). Mean estrone conjugate values were 20,000 pg E_1C/mg Cr (SE=2300) for the wild orangutans and 53,000 pg E_1C/mg Cr (SE=1940) for the captive orangutans. Thus, the hypothesis that captive orangutans have significantly higher estrone conjugate levels is supported by this sample.

Estrone Conjugate Values and Fruit Availability

Comparison of Individual Changes in E1C Values during the High and Low Fruit Periods

The hypothesis that estrone conjugate values would be significantly greater during periods of high as opposed to periods of low fruit availability was first tested by examining the data from the two females (Marissa and Elizabeth) who were repeatedly sampled during both high and low fruit availability periods. These two females were the most heavily sampled individuals in the study. Ninety-three samples were collected from these females, representing 65% of samples from non-pregnant females. I concentrated specifically on sampling these individuals because I thought they were the most likely females, of those regularly encountered, to be cycling. An additional female, Kristen, was also sampled during both periods. She became pregnant and gave birth during the middle of the study period, thus her post-birth hormonal values would be expected to be depressed due to heavy lactation and she was not included in this comparison.

The data for each female was examined independently (using unpaired, two tailed T-tests) to assess whether there were significant changes in estrone conjugate levels between the two sample periods of high and low fruit availability. Estrone conjugate values were significantly lower during the low fruit availability period in both females (see results in Table 8.01). Because there might be a delay in ovarian responsiveness I also examined the data assuming a one and a two-month lag time. Significant differences were also found in both lag-time comparisons.

TABLE 8.01: Results of unpaired, two-tailed T-tests between the periods of high and low fruit availability for Marissa and Elizabeth. Estrone conjugate values were assigned to the high and low fruit availability periods with no lag time, a one month lag time and a two month lag time. T values are reported and *n* is the number of daily samples in each comparison.

	No Lag Time		1 Month Lag Time		2 Month Lag Time	
	n	t-value	*n*	t-value	*n*	t-value
Marissa:						
High Fruit	6	2.242*	6	2.637**	7	4.308***
Low Fruit	27		51		62	
Elizabeth:						
High Fruit	15	2.356*	15	2.100*	15	2.356*
Low Fruit	7		7		7	

* $p < 0.05$; ** $p < 0.005$; *** $p < 0.0001$

Figure 4.03 shows the comparison between the two periods for both females. Both females showed a similar percentage change in E_1C levels between periods (MR = 30%; EZ = 38%). These data strongly support the hypothesis that lower fruit availability was associated with lower overall E_1C levels in these sampled individuals.

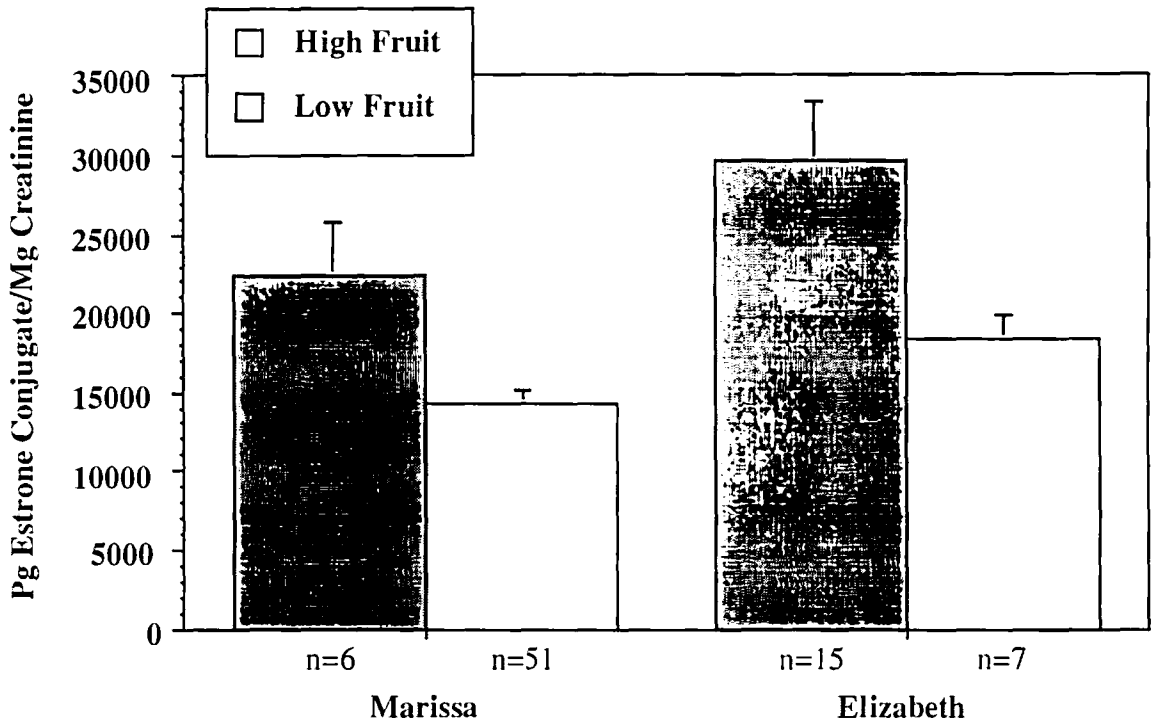


FIGURE 8.03: Comparison of mean estrone conjugate values (± SE) in the two non-pregnant orangutans that were sampled during periods of both high and low fruit availability. The number of daily urine samples (*n*) is indicated below each column. Data assuming a one-month lag time is used in this figure.

Comparison of Mean E1C Values for all Non-Pregnant Wild Orangutans during both the High and Low Fruit Periods

In the second comparison, the weekly mean estrone conjugate values for all non-pregnant females sampled during the study period were compared using a Mann-Whitney U-test (Figure 8.04). Although some individuals are represented more than once in this analysis, this design allows me to include all samples that were collected from non-pregnant females. It thus provides supplementary information to the previous analysis. One month and two month lag time effects were also incorporated. I found that in all of these comparisons as well (summarized in Table 8.02), estrone conjugate values were significantly greater in the high fruit availability period compared to the low-fruit period.

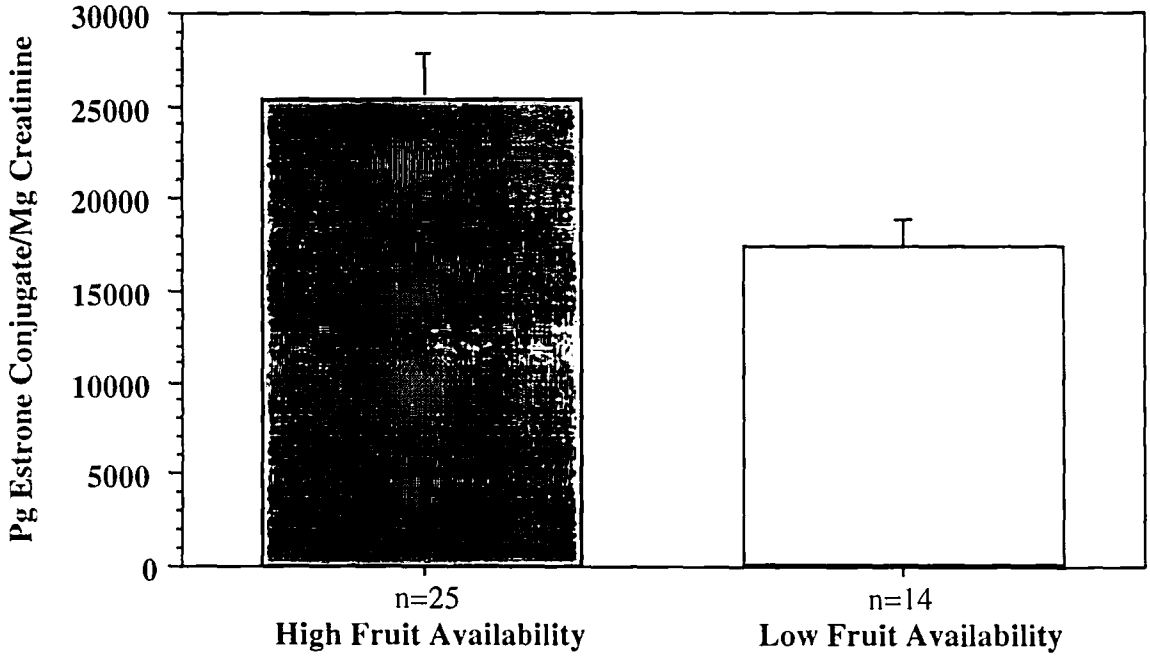


FIGURE 8.04: Comparison of mean weekly estrone conjugate levels in 12 non-pregnant wild orangutans. The number of weekly samples, *n*, is indicated. Values incorporate a one-month lag time. Standard errors of the data are shown.

TABLE 8.02: Results of Mann-Whitney U-test comparing weekly estrone conjugate values between the periods of high and low fruit availability for all non-pregnant wild orangutans. Estrone conjugate values were assigned to the high and low fruit availability periods with no lag time, a one month lag time and a two month lag time. U values are reported and *n* is the number of weekly samples.

	No Lag Time		1 Month Lag Time		2 Month Lag Time	
	n	U-value	*n*	U-value	*n*	U-value
High Fruit	25	92*	26	118*	27	117**
Low Fruit	14		17		20	

* $p < 0.05$; ** $p < 0.005$

Estrone Conjugate Values and Percentage of Ripe Fruit Available

The mean monthly estrone conjugate value for each individual female was calculated to compare against ripe fruit availability. Using linear regression, these estrone conjugate levels were regressed against the percentage of trees with ripe fruit as determined from the orangutan phenology sample. Results showed a significant positive relationship (R^2 = 0.403, $p < 0.0005$) between ripe fruit availability and estrone conjugate levels (Figure 8.05).

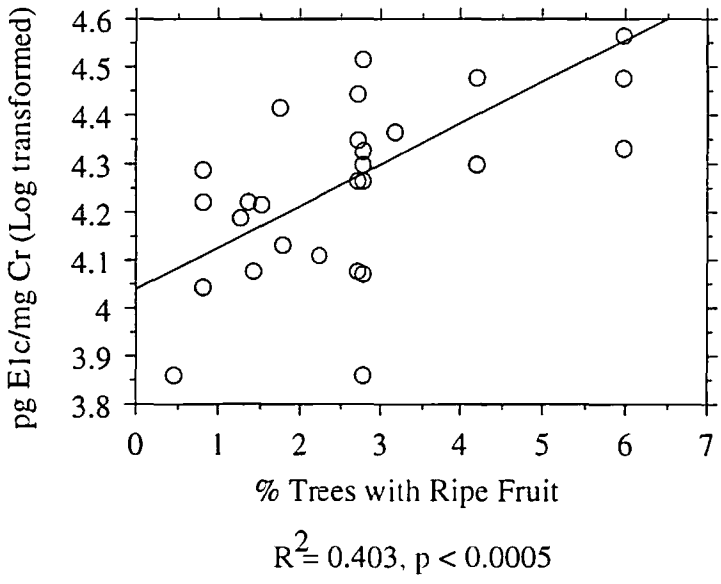


FIGURE 8.05: Regression of mean monthly estrone conjugate values (pg E_1C/mg Cr) for 12 non-pregnant wild female orangutans (n = 28) compared to the percentage of trees with ripe fruit in the orangutan phenology sample.

Timing of Matings and Conceptions

Evidence of matings and births provides additional corroboration of the relationship between fruit availability and reproductive functioning in wild female orangutans. Table 8.03 shows the matings that were observed between August 1994 and December 1996. All matings were between "undeveloped" males and adult females that either did not have an offspring or whose oldest offspring was judged over four years of age. Females whose oldest offspring was estimated to be less than four years old did not mate. No developed males were seen to mate although they were seen in consortships with females. All matings occurred during the mast period of high fruit and flower availability. Additionally, the three females who were known to have become pregnant all conceived during the high fruit availability period. No male-female associations or consortships were observed between February 1995 and December 1995. Subsequent observation has also shown that no females are known to have conceived during this post-mast period.

TABLE 8.03: Orangutan matings observed between August 1994 and December 1996.

		"Type" of Male		*"Season" of Copulation*	
	Hours Females Observed	Undeveloped Males	Developed Males	Mast	Non-Mast
Adult female with no offspring	729	7	0	7	0
Adult female with youngest offspring of estimated age over 4 years	1781	7	0	7	0
Adult female with youngest offspring of estimated age under 4 years	1277	0	0	0	0

DISCUSSION

The two primary hypotheses relating to orangutan ovarian functioning were strongly supported in this study. As predicted, captive female orangutans were found to have higher estrone conjugate levels than did wild orangutans. Energetics were not measured in these captive females, thus I cannot make a direct comparison with the wild. The possibility that there are some inherent differences between individuals in captivity and individuals in the wild can thus not be entirely ruled out, but I believe the general observation of accelerated or enhanced reproductive parameters in captivity supports the proposition that it is the unusual conditions of captivity—steady, adequate nutrition and low energetic expenditure levels—that account for this difference.

The hypothesis that females would have higher estrone conjugate levels during the high fruit period compared to the low fruit period was also strongly supported with this data. This is particularly striking because the sample size is small and cycle phase differences could not be controlled for. As stated earlier, mean differences between seasons would have to be particularly strong to overcome the natural cycle phase changes in estrone conjugate levels. This finding is in keeping with the dramatic differences that have been shown in previous chapters. Caloric intake and energy balance, in particular, showed extreme fluctuations in response to changes in fruit availability.

These results are further strengthened because the direction of change in hormonal levels observed runs counter to that expected as non-pregnant females progress through the stages of their interbirth intervals. Following pregnancy and lactation, if environmental influences were neutral, we would expect E_1C levels to gradually rise as full fecundity is resumed. In contrast to this expectation, the E_1C levels in these females show a dramatic *decrease* over

time, implicating fruit availability, and associated nutritional status and energy balance, as the critical variables.

In addition, differences were significant between the periods assuming a one or a two-month lag time. Although caloric intake and energy balance were increasing in October through December, females may still have been experiencing the effect of the extended period of negative energy balance due to the cumulative effects of low energy balance. The level of significance was greatest after two months for Marissa. However, this is confounded by the fact that sample size increased as well.

Perhaps equally dramatic was the finding that despite almost 6000 hours of observation of wild orangutans, mating was only observed during the fruit-rich mast period. Mitani (1985b) hypothesized that males were drawn into his study area because of the presence of ovulating females, whereas Leighton and Leighton (1983) found that orangutans switched habitats based on relative fruit production. These data support a third hypothesis that both of these factors may be attracting animals into areas of high fruit production because high fruit availability and female hormonal levels co-vary. Moving into an area of high fruit production would have both reproductive and survivorship advantageous for both males and females. It would enable females to increase their nutritional status and energy reserves, with a concomitant effect of increasing hormonal levels and presumably the probability of conception. Males would be rewarded with an opportunity to increase fat stores necessary for survival during fruit-poor periods as well as the opportunity to mate with females who had an increased probability of being fecund. Ultimately, however, males may have lower survivorship during these periods because of the intense male-male competition observed during these periods (Knott 1998b).

It is still unclear what actual proximate mechanism is responsible for mating occurring only during this time. One explanation could be that there is an increase in female sex drive that results in females seeking copulations with males. However, this has not been observed in this or any other study (Mitani 1985b; Galdikas 1979). It was my observation as well as Mitani's (1985) that it was males that were seeking these copulations. Why did the males put so much more effort into seeking mating opportunities during these periods and none during other periods? It could be argued that because several females already conceived during the fruit-rich period, that there were just no other fecund females in the area. This may partially account for the pattern, but, males mated with Marissa during the mast and the same males did not do so during the post-mast period, even though they were traveling in the same vicinity. Other non-pregnant females with older juveniles were not seen to mate during this post-mast period either. Additionally, in my three years of research subsequent to the results reported here I also found that mating was confined to high fruit periods.

One possibility is that males are responding to an olfactory or pheromonal signal produced by ovulating females. However, no evidence exists of such a signal. It could also be that high fruit availability raises testosterone levels in males, resulting in an increase in sexual activity. I have analyzed testosterone samples in both developed and undeveloped adult males (Knott 1997b), however, and found that levels were *not* higher during the fruit-rich period. In distinguishing between females, males may use the size of a female's offspring as a proximate cue as to her likely reproductive status. But, this does not explain why they limited their mating to the high-fruit availability period. Whether males and females "know" when conception is most likely, or if there is a mechanism by which high fruit availability could be correlated with mating remains to be explained.

The finding that only undeveloped males mated is also surprising given that females are reported to prefer larger males (e.g. Galdikas 1979). However, Mitani (1985b) observed the highest number of matings yet reported in one study of orangutans and he reports that only 16% of matings involved developed males. MacKinnon (1974) also found that fully developed males had a low mating frequency and he suggested that these males were protecting an area so that their sons could mate (a behavior that would actually be selected against based on evolutionary theory, since the advantage of mating yourself, if you are able to, outweighs the advantage of helping your offspring to mate (e.g. Hill and Hurtado, 1997)). Although both fully-developed and undeveloped males engage in forced copulations, Mitani found that 95% of sub-adult copulations were forced. It may be that undeveloped males mate with females regardless of her willingness to mate or her cycle phase and that fully developed males may be more selective. However, as mentioned earlier we have no evidence that males are able to detect ovulation. In Nadler's (1982b) test of sexual behavior in orangutans he found that fully-developed males that were not restricted from accessing a female mated with her on every day of the cycle. Additionally, undeveloped males may just be more adept at catching females given their smaller body size and greater agility compared to developed males.

Future Work

This has been the first study to measure ovarian hormone levels in any wild great ape. I have shown that estrone conjugate levels were correlated with changes in energetic status in wild adult female orangutans. This is what we would expect if orangutans were also influenced by the same energetic variables that affect reproduction in living humans. The very significant difference between estrone conjugate levels in captive and wild orangutans supports other evidence from zoos that the effects of captivity on energy balance, such as improved nutrition and decreased energy expenditure, are associated with accelerated

reproductive parameters. This study, however, is just a first step in the investigation of great ape reproductive ecology in the wild. I would hope that this would become a common feature of other great ape field studies.

The characterization of hormonal responses to changing energetic status could be further explored through the measurement of urinary progesterone, specifically pregnanediol-glucoronide (PDG). Progesterone is an important indicator of luteal adequacy and endometrial preparation. However, PDG levels appear to be low and difficult to measure in orangutans (Czekala personal communication). This will be the next step in analysis of the samples currently in hand. I would also like to measure luetenzing hormone (LH) and prolactin to study the effect of suckling on the menstrual cycle and to assess the role of lactation in the suppression of ovulation. This, however, would likely require freezing urine samples, and thus far it has not been feasible to bring a freezer into the rain forest given our remote location. This may become possible in the future. Additionally, since 1996 I have been preserving unfrozen urine in ethanol and in sodium azide and am currently evaluating these as additional alternative methods.

One of the limitations to studying orangutans, perhaps even more so than other great apes, is the difficulty in monitoring a large sample of individuals. Thus, despite over 20,000 hours of observation to date and a large team of field assistants, only a small number of individuals can be found within the study area in a given time period. A more complete picture of hormonal responses of orangutans to changes in food availability will only emerge after many more years of field work. Wild studies are also limited to broad scale effects. I found very significant differences in energy balance during my study and smaller scale fluctuations may not have been great enough to uncover a difference between fruit availability periods given the sampling limitations. Thus, in conjunction with wild studies, captive studies are needed to investigate whether other apes exhibit the same close

modulation of ovarian function in response to relatively small scale changes in energetic status as is seen in humans.

We do not yet know what levels of orangutan ovarian hormones are necessary for ovulation and conception to occur. In humans, women living under energetically stressed circumstances seem to be able to conceive despite having low levels of ovarian hormones. One possible explanation of this is that different populations have different "set-points" of ovarian function. This may be the same for other primates, particularly given the differences I found in estrone conjugate levels between captive and wild cycling females. Thus, a similar study to that done by Lipson and Ellison (1996) could be carried out in captivity to reveal the relationship between ovarian hormone levels and cycle fecundability. This would tell us about the general responsive of orangutan ovarian function but would not reveal the levels that were adequate for conception in the wild. To answer this, the ideal would be to collect daily samples from females during the waiting time to conception to compare with actual conceptive cycles. Such a data set may be possible to acquire over the long term.

Interbirth intervals in wild great apes are extremely difficult to obtain due to the length of these intervals and the relatively small number of individuals who have been monitored closely enough to determine these statistics. For example, Wallis (1997) was able to confidently determine the interbirth interval in only 11 cases for 6 females studied in Gombe National Park for a 20 year period between January 1964 and December 1994. Thus, although interbirth intervals and ultimately lifetime reproductive success are the most crucial parameters of interest, these data are extremely hard to acquire. Measurement of ovarian hormones provides a more immediate way to compare inter-individual, inter-site and inter-species differences in the modulation of female reproduction.

• CHAPTER 9 •

CONCLUSION AND IMPLICATIONS FOR ORANGUTAN AND HUMAN EVOLUTION

CHAPTER SUMMARY

This chapter reviews the major findings from this thesis and then discusses what implications these results may have for our understanding of orangutan and human evolution. I argue that orangutans appear to be able to survive periods of severe food stress due to at least five adaptations. First, they are buffered by their large body size since large animals have proportionately lower daily energy requirements and greater fasting endurance than do smaller animals. Second, the degree of excess caloric consumption observed in the fruit-rich period indicates that these orangutans were storing excess energy as fat, from which they could then draw during the fruit-poor period. Third, they were able to dramatically change the composition of their diet, consuming leaves and bark as fall-back foods instead of their preferred foods. Fourth, they lowered their energetic expenditure during fruit-poor times by traveling less. Fifth, both behaviorally and physiologically (in females) they lowered or ceased their reproductive effort.

Comparative data on fat stores and rates of obesity-linked diseases, such as diabetes, are lacking between the great apes. However, the finding of a susceptibility towards diabetes in captive orangutans suggests that, as in certain human populations like the Pima Indians and South Pacific Islanders, orangutans may possess enhanced fat storage mechanisms. Thus, the extended, unpredictable periods of severe food shortages that orangutans are subjected to may have selected for a "thrifty genotype" as has been argued for these humans groups.

This study helps understand the long orangutan interbirth interval by showing that (1) estrone conjugate levels are correlated with changes in energy balance and (2) orangutans are subjected to unpredictable, long-lasting and severe periods of food shortage and negative energy balance. I thus argue that the pattern of mast fruiting and overall low fruit

productivity in the rain forests of Southeast Asia is one of the major factors contributing to longer orangutan interbirth intervals compared to other apes.

Finally, I argue that understanding how physiological and reproductive systems of living hominoids respond to environmental perturbations is essential to building more informed models of human and great ape evolution. Humans also appear to have a particular propensity for building up fat stores and I discuss how this may have been an adaptation for surviving feast and famine, for reproduction and/or for supporting the high energetic costs of growing the human brain. My finding that orangutan ovarian function is also responsive to some of the same energetic variables as have been recognized in humans enables us to predict that early hominids also shared similar adaptations. I argue that this is especially important in understanding how humans could have shortened their interbirth interval, relative to other great apes, and yet maintained longer periods of nutritional dependency. I posit that some human adaptations, such as the sexual division of labor, tool use, hunting, etc. would have exerted influences that would have enabled us to shorten this interbirth interval.

INTRODUCTION

This chapter provides an overview and a discussion of the main results from this thesis. I first review the main findings pertaining to orangutan energetics and explore the implications of these findings for understanding orangutan evolution, making comparisons with other great apes where possible. The second section summarizes the results related to orangutan reproduction and discusses how these findings help us understand orangutan reproductive patterns and adaptations. Finally, I discuss what insights the data presented here may give us for understanding human evolution. Throughout, I incorporate some suggestions for future research both in the field and in captive or laboratory settings.

ENERGETICS

Summary of Results

Fruit Availability

Despite only small changes in temperature, the aseasonal tropical rain forests of Borneo are characterized by dramatic annual and supra-annual fluctuations in fruit availability. These forests are dominated by trees in the Dipterocarpaceae family which is distinguished by its unusual reproductive pattern. Triggered by climatic events, these trees fruit and flower on an irregular basis, once every 2-10 years (Ashton *et al.* 1988). They are joined by other tree families that normally produce fruit on a more regular basis, resulting in a phenomenon in which more than 90% of trees produce fruit during these "mast" fruiting events (Medway 1972; Appanah 1981; van Schaik 1986). This provides an overabundance of fruit for animals, such as orangutans, during these periods. Due to the concentration of

plant reproductive effort during masts, these synchronized fruiting events are often followed by long periods of low fruit availability. As a result, these forests have lower overall productivity and support substantially less animal biomass than do other tropical rain forests (Appanah 1985). These natural fluctuations in fruit productivity provide an excellent opportunity to study the effects of variation in food abundance on orangutan behavior and physiology.

The flowering and fruiting phenology of 567 orangutan fruit trees were documented over a three-year period at Gunung Palung, providing a measure of fruit availability that was independent of orangutan behavior. A mast fruiting was observed between September 1994 and February 1995 during which time the dipterocarps and over 30 other genera of orangutan fruit trees showed reproductive activity. Fruit availability was then low for an extended period between March 1995 and March 1996, following the mast fruiting event. Other peaks in orangutan fruits which did not include dipterocarp masting occurred between April and September 1996 and between March and June 1997.

Nutritional Intake

Because orangutans live in an environment characterized by sporadic peaks in fruit abundance interspersed with periods of low fruit availability, it has been suggested that they cope with this variability in food resources by storing fat reserves during periods of plenty to cope with later food shortages. However, quantitative data on changes in total energy and nutrient intake of wild orangutans during different fruiting seasons has not been collected before.

Extending over a fourteen month study period which spanned a mast fruiting peak and a subsequent seven month period of low availability, I observed dramatic changes in the proportions and total amounts of fruit, leaves, flowers, pith, insects and bark making up the orangutan diet. Data from 693 daily follows totaling 5989 observation hours were analyzed indicating that during periods of highest fruit availability, fruit made up almost 100% of the orangutans' diet. In contrast, during fruit-poor periods orangutans resorted to fall-back foods such as leaves, pith, insects and bark. These non-fruit items comprised from 40% to 70% of their diet during these low fruit periods.

The nutritional makeup of the orangutan diet was determined by performing biochemical analyses on samples of the most important 93 food types eaten by orangutans and combining this information with detailed data from 2441 feeding bouts in order to calculate total caloric, grams and nutrient consumption. I found that when fruits were available, they were highly preferred over other food categories. By maximizing intake of carbohydrate-rich fruits when they were available, orangutans took in up to twenty times as many calories a day during fruit-rich periods as during fruit-poor periods. These findings strongly support the hypothesis that orangutans are building up fat reserves during fruit-rich periods to help sustain them through low-fruit periods.

Despite their differences in body size, male and female orangutans, in general, had similar diets and maintained similar diet quality. Both males and females showed dramatic changes in diet with fruit availability. One interesting difference was that males were able to maintain a slightly higher quality diet (higher in calories and lower in fiber) during some months due to their exploitation of certain large, difficult to process, but high-calorie fruits like *Neesia* and *Durio* that may have been easier for larger males to open.

Energy Expenditure

Energy expenditure was quantified on a daily basis in order to estimate the total energetic requirements of wild orangutans, and to see if their expenditure of energy varied with changes in fruit availability and feeding behavior. Detailed data were collected on the total minutes orangutans allocated to different activities during the day, as well as horizontal and vertical distances traveled and body positions adopted during different activities. I adapted models developed for calculating energy expenditure in humans and other primates to orangutans in order to produce estimates of energy expended for each follow day. This allowed me to estimate the partitioning of energy to different activities.

Activity data showed that orangutans spent more time awake during the high fruit periods. Both males and females spent more time traveling (significant for males) during the high fruit period and also traveled further each day. Males also spent more time feeding during high fruit periods, but females did not. In contrast to fully-developed adult males, there was a dramatic increase in the amount of time adult females spent in the company of other orangutans during the high fruit period, which seems to account for their additional time spent awake. These social interactions included gatherings of females with offspring in the same fruiting trees as well as consortships between adult females and undeveloped adult males.

The calculated caloric expenditure of orangutans varied only slightly between high and low fruit periods, however these differences were statistically significant. Not considering the costs due to reproduction, both males and females expended more calories during the fruit-rich period. The greater expenditure from the high fruit period appears to be explained by a significant increase in caloric expenditure due to travel. Across both fruit periods, male daily caloric expenditure was 3100 - 3400 Kcal per day, while female expenditure,

including costs of maternal care, was 2300 - 2400 Kcal per day. Differences between periods for females were not significant when maternal costs were added in.

Energy Balance

Energy balance is the difference between energy intake and energy expenditure and indicates whether energy intake is adequate to serve an organism's needs. Thus, energy balance was calculated in order to examine the question of whether the orangutans were experiencing caloric excesses and/or deficits during the different fruit availability and consumption periods. This was accomplished in two ways: first, through calculation from estimates of energy intake and expenditure. and second through measurement of ketones, a byproduct of fat metabolism excreted in urine.

Monthly mean energy balance values calculated for the study period for both males and females were positive during November 1994 through February 1995, the high fruit period. Subsequently, from March through September 1995, during the low fruit period, energy balance was negative. Thus, there was a strong positive relationship between energy balance and ripe fruit availability.

The ketone analysis confirmed this same pattern. No ketones were found in urine samples collected during the high fruit availability months or the first month of low fruit availability. Starting in April 1995, after orangutans had already been experiencing low nutritional intake during the month of March, ketones began to appear in a large proportion of urine samples. This indicates that the orangutans were metabolizing their fat reserves to make up for insufficient intake. Particularly striking was the length of the period of negative energy

balance—seven months. Thus, this was not simply a minor fluctuation in food availability and nutritional intake, but indicates an extended period of insufficient caloric intake.

DISCUSSION:
ENERGETIC IMPLICATIONS OF FLUCTUATING FRUIT AVAILABILITY FOR ORANGUTAN EVOLUTION

I believe that these responses to fluctuations in fruit availability have important implications for understanding orangutan evolution. We can now ask, how have orangutans adapted to this pattern of fruit availability? What mechanisms have they evolved to cope with these fluctuations? Do orangutans differ from other great apes in their responses to seasonality and, if so, how?

Adaptations to Fruit Phenology Patterns

What are the major characteristics of the Southeast Asian rain forests that are pertinent for understanding orangutan evolution? Three major features distinguish the pattern of fruiting in these forests. First, there are dramatic supra-annual peaks in fruit availability (Ashton 1988), as well as smaller-scale, more frequent peaks. Second, supra-annual masting peaks are normally followed by extended periods of low fruit availability (Appanah 1985). Third, these supra-annual peaks, and the subsequent extended low fruit periods, are unpredictable (Ashton 1988). Overall, this fruiting pattern leads to forests in which fruit availability is more temporally and spatially patchy than in other tropical rain forests (Fleming *et al.* 1987).

The low fruit periods characteristic of Southeast Asian rain forests are of particular evolutionary importance as periods of inadequate food supply can exert strong selective pressures during animal evolution, with the severity and duration of food shortage periods being the most critical features. This is true throughout different ecological systems. For example, the ultimate effect of low food availability on evolution has been documented directly by Peter and Rosemary Grant, working with Darwin's finches in the Galapagos. They were able to demonstrate, through beak measurements over consecutive generations, that directional selection had occurred during a particularly brutal period of drought and subsequent food shortage (Grant and Grant 1993). In primates, Terborgh (1983, 1992) showed that of five sympatric new world monkeys, each species had a particular morphological adaptation that allowed them to consume a different back-up food, enabling them to survive the annual period of fruit scarcity, even though their diets were almost identical during fruit-rich periods.

The finding that during the low-fruit period orangutans experienced negative energy balance for an extended length of time, as measured through ketone production as well as through estimation of intake and expenditure, attests to both the severity and duration of the fruit shortage period. The orangutans I studied appear to have survived this period due to at least five adaptations. First, their large body size would have acted as a buffer. Second, the degree of excess caloric consumption in the fruit-rich period indicates that they were storing excess energy as fat, from which they could then draw during the fruit-poor period. Third, they were able to dramatically change the composition of their diet, consuming leaves and bark as fall-back foods. Fourth, they lowered their energetic expenditure during fruit-poor times by traveling less. Fifth, both behaviorally and physiologically (in females) they lowered or ceased their reproductive functioning and effort.

1. Body Size

Orangutans are the largest fully arboreal mammal and large body size can be an important adaptation in itself for survival during periods of low food availability. Because BMR scales to the 0.75 power of body weight (Kleiber 1975), larger species have lower daily energy requirements for their body size than do small mammals. Large mammals also have a proportionately greater mass of body fat (Lindstedt and Boyce 1985). Lindstedt and Boyce (1985) show mathematically that the ability to survive periods of low food availability, or "fasting endurance," is greatest in individuals of large body size. Increased fasting endurance in large-bodied animals may be an important factor contributing to "Bergman's Rule," that body size tends to be largest in the coolest regions of a species' range. This has traditionally been explained as due to decreasing costs of thermoregulation with increased body size. However, because cooler, temperate regions also tend to be more seasonal, increased fasting endurance may be an alternative or complementary explanation for Bergman's rule (Lindsey 1966; Calder 1984; Lindstedt and Boyce 1985). Thus, pronounced fluctuations in fruit availability may be one of the forces selecting for large body size in orangutans.

2. Fat Storage

The major function of adipose tissue in mammals is as a long-term energy store (Pond 1997). Because of the ability of large mammals to store a proportionately larger amount of lipid, fat storage in animals such as orangutans is a viable option for coping with low fruit availability. Pond (1997, p. 152) reviews the data on obesity in captive primates and compares this to other mammals, concluding that primates "may be more susceptible to obesity than any other group of mammals when living on an artificial regime of diet and exercise." McFarland (1997) suggests that cattarrhines, in particular, have evolved an

enhanced propensity to store fat as a way to maintain an energy balance that ensures one's own survival and, at the same time, in females enhances the survival and development of offspring. Because most cattarrhines are large-bodied, they can carry some body fat and still remain mobile and active, walking and foraging for long hours.

Fat storage patterns in primates are also influenced by survival and life-history features such as the need for mobility to escape predators and to forage for food and, in females, by the energetic requirements of reproduction (MacFarland 1997). Adult Bornean orangutans do not have any predators except for humans, and thus the necessity to escape predation through flight and agility is not a constraint on body size and thus on fat storage. Additionally, although the costs of locomotion are greater with larger body mass, orangutans use this body mass to their advantage. They regularly take advantage of their body weight to bend trees and grasp the next tree over, enabling them to cross relatively wide gaps without venturing out on small branches that wouldn't support their weight. Thus, the costs of being "too fat" are probably small for orangutans, making fat storage a particularly viable method of coping with an unpredictable food supply.

Orangutans show behavioral and perhaps enhanced physiological mechanisms that allow them to store excess energy as fat reserves. This study has demonstrated that orangutan caloric intake greatly exceeded their energy requirements during the period of high fruit availability. Such caloric excess indicates that they must have been building up fat deposits. Thus, orangutans clearly have the ability to exploit periods of high fruit abundance by storing excess energy as fat. The finding that they were utilizing these adipose stores through metabolism of fat tissue indicates that they can mobilize these stored energy reserves to survive periods of severe fruit shortage, confirming the opinion of other researchers (MacKinnon 1974; Wheatley 1982, 1987; Leighton 1993).

Diabetes and Fat Storage

What evidence is there that orangutans may possess specific physiological adaptations that promote fat storage? In the wild, orangutans appear to be able to accumulate large fat reserves (MacKinnon 1974; Wheatley 1982, 1987; Leighton 1993; this study) and rates of obesity in captive orangutans is widespread (MacKinnon 1971; Kemnitz *et al.* 1994). Of particular relevance to the question of physiological adaptations for fat storage is the documentation of diabetes mellitus in captive orangutans and a recent study by Kemnitz *et al.* (1994) on the insulin response of orangutans. Kemnitz and colleagues performed glucose tolerance tests on 9 captive orangutans, from 3 to 40 years of age, 2 of whom were thought to be developing diabetes. These researchers found low glucose clearance values in *all* the orangutans, based on both human and animal expectations of normal insulin response. They conclude that this indicates impaired glucose tolerance and increased susceptibility to diabetes mellitus.

Kemnitz *et al.* (1994) suggest that given these findings in *all* of their subjects, low clearance values may be a characteristic of the species under captive conditions. The subjects came from different genetic populations of orangutans and spanned much of the orangutan lifespan. The finding that the insulin response of orangutans predisposes them towards diabetes under the well-fed conditions of captivity can be likened to the human condition where certain populations, after the adoption of an "over-fed" Western lifestyle, develop high rates of obesity and diabetes due to a genetic predisposition. This has been most well studied in populations of Pima Native Americans and Pacific Islanders, particularly Somoans.

The Pima Indians have one of the highest rates of obesity and diabetes of any human population. In Pima adults between 20-34 years of age, over 90% exceed the age-specific

median body mass index and over 50% exceed the 90th percentile for body mass index (Knowler *et al.* 1982). Additionally, over 50% of adults over the age of 35 have diabetes (Knowler *et al.* 1982). This prevalence of diabetes has only been reported since the 1950's, despite medical studies of this population since the early part of the century (Knowler *et al.* 1982). In non-diabetic Pima Indians, similar to the non-diabetic orangutans, glucose clearance values are still low compared to other populations (Knowler *et al.* 1982), pre-disposing these individuals to later development of non insulin dependent (NID) diabetes.

NID diabetics are characterized by having excessively high concentrations of insulin in their blood, either due to the over-production of insulin, low insulin receptor density or a combination of the two (Knowler *et al.* 1982). NID diabetes and obesity are closely linked because of the role insulin plays in fat storage. High levels of circulating insulin facilitate the uptake of glucose, favor triglyceride synthesis, and have a direct influence on adipose tissue triglyceride storage (Anderson *et al.* 1982).

An especially efficient insulin response can therefore build up fat stores, but it may also predispose individuals to later development of diabetes as overabundant insulin or excessive fat reserves may lead to decreased receptor sensitivity or density. This may account for the low glucose clearance in the non-diabetic Pima Indians and in the Kemnitz *et al.* (1994) orangutan study. Both of these populations are described as having a high rate of obesity. The Kemnitz *et al.* study was limited to nine subjects, but this finding in 100% of the orangutans, derived from different genetic populations and from across the orangutan life-span, is striking. Increasing the sample size of individuals would be desirable, although the necessity of anesthetizing the orangutans limits the widespread administration of this test.

A Thrifty Genotype?

Neel (1962, 1982) proposes in his "thrifty gene hypothesis" that enhanced mechanisms to promote fat storage have been selected for in certain populations that were subjected to pronounced periods of feast and famine. Under such conditions, enhanced fat storage mechanisms would promote survival through boom and bust periods, but if such populations lived in a constant high-availability food environment, these people would be pre-disposed to the development of NID diabetes. The costs of developing diabetes would have acted as a strong selective pressure against such enhanced fat-promoting mechanisms in populations not as highly subjected to these pronounced feast and famine periods.

The proposition that the type of insulin response characteristic of those with a propensity towards diabetes is an adaptation to feast or famine is also supported by studies in mice (cited in Neel 1982). There are at least five strains of mice which display a genetic basis for diabetes mellitus, each resulting from different recessive genes. Homozygotes of each of these strains are all characterized by obesity. When given identical diets, the diabetes-prone strains gain weight at a faster rate than do normal controls. A fasting study of one of these strains showed that homozygotes were better able to survive caloric deprivation than were non-diabetic controls.

We know that human populations differ in their ability to store fat (Baker 1984). Populations with the highest rates of obesity also show a high prevalence of NID diabetes. Amongst pacific islanders, McGarvey (1991) showed that the degree of adiposity was related to the degree of modernization in four Samoan populations. This physiological tendency towards obesity in Samoans has been postulated as due to selection for survival during long ocean voyages with limited food supplies as well as survival after the cyclic occurrence of severe tropical storms, when starvation would have been a strong selective

pressure. The fattest individuals, along with any genetic tendencies towards fat storage which they possessed, would have been favored (Baker 1984; McGarvey 1991).

The dramatic changes in caloric intake that orangutans experience suggest that they are naturally exposed to feast and famine periods. Efficiently exploiting the abundant caloric resources found during fruit peaks would be highly advantageous for orangutans given the unpredictability of future food resources and the common likelihood of low fruit availability following such mast peaks.

All primates are, of course, capable of storing excess energy as fat (McFarland 1997). However, the necessity of relying on this mechanism should be governed by the severity of the low food availability periods one experiences. Animals subjected to periods of more severe fruit shortages, as is characteristic of the low productivity forests of southeast Asia, should have experienced increased positive selection on mechanisms to cope with these pressures. Enhancing the fat storage "potential" found in all primates, and in many or most other mammals, is one possible option. It may be an especially viable option in a large-bodied primate such as the orangutan, with little predation pressure on adults and a slow mode of locomotion.

Similarly, all primates, in theory, have the ability to increase caloric intake during food-rich periods. However, we need not assume that all species or all individuals would take equal advantage of surfeits in food production. Although all animals should benefit from periods of high food availability, the "optimum" amount of calories ingested would differ between species and between individuals. Animals may not always take in the maximum amount of calories possible, but should consume an optimal number of calories given the metabolic constraints on such caloric consumption and the costs of getting too fat. For instance, all animals are physiologically constrained at some point by the sheer volume of food they can

ingest. Those that rely on fast, efficient modes of locomotion may not be able to fatten up by doubling or even tripling their caloric intake due to the additional travel burden such body mass would pose. For example, in Malaysia which displays a similar environment to Borneo, Siamangs were found to decrease their time spent feeding during a super-abundant feeding period (Chivers and Raemaekers 1980). This implies that they responded to the high fruit availability period by fulfilling their caloric needs more quickly than at other times. Given the higher caloric content of mast fruits, they may have consumed more calories during this period, but may not have consumed the *maximum possible* calories. I would argue that orangutans are not as constrained by these considerations as are some other species. They are able to take full advantage of the opportunity to increase food intake and put on fat reserves.

Great Ape Comparisons

Do orangutans show greater physiological mechanisms promoting fat storage than do other great apes? If, as I have proposed here, orangutans are subjected to greater variance in cycles of feast and famine, then I hypothesize that they do. However, no detailed data exist comparing the anatomy and distribution of adipose tissue between the different ape species (Pond 1997). There are no published comparisons of the relative rates of diabetes between captive great apes and to my knowledge the insulin responsiveness of other great apes who have not been diagnosed with diabetes, has not been evaluated. Such comparative studies are apparently being undertaken by the "Great Ape Aging Project" (Joseph Erwin, pers. comm.) and should yield results to test this hypothesis. Another possible means of collecting such information is through the use of bioelectrical impedance. Although this requires the animal to be immobile, captive apes are routinely trained to present various body parts for inspection and to remain still during such examinations. Thus, I believe a

comparative study like this could be carried out in zoos and would shed considerable light on the genetic propensity for such response in hominoids.

In contrast to the great apes, diabetes and obesity have been well studied in humans. As mentioned, this research tells us that while all human populations can build fat reserves, some humans populations have genetic differences leading them to enhanced fat storage capabilities (Baker 1984). The existence of population level differences in fat storage ability within the human species suggests that between-species differences in the efficiency of fat storage may also exist.

In sum, I believe the data presented in this thesis strongly support the suggestion that orangutans are able to store large amounts of excess calories as fat. The pattern of fruit availability in Southeast Asia and comparative data on obesity and insulin reactivity in zoo animals suggests that orangutans may have an enhanced ability to store fat. I am therefore hypothesizing that orangutans are particularly adapted to fat storage compared to the other great apes. However, this hypothesis remains to be tested and I cannot conclude, based on the data available to date that the fat storage ability of orangutans is enhanced compared to other great apes. This will be a fruitful area for future research.

Sex-Differences in Fat Storage

Sex differences in body fat have been examined in relatively few primate species. Pond (1997) states that in most primates there are not detectable sex differences in fat distribution. However, where sex differences exist, females tend to be fatter than males. In one study of captive baboons, 5-year-old males had 6% body fat, whereas their female counterparts had 16% (Rutenberg *et al.* 1987). In a study of captive adult pig-tail macaques (*Macaca nemestrina*), Walike *et al.* (1977) found that males had 8.7% body fat

whereas non-obese females averaged 12.7%. Furthermore, Coelho (1985) found that captive female macaques were significantly fatter than male macaques.

Morbeck and Zihlman (1988) report that captive female orangutans have more body fat than do captive males. This was determined from examination of one 15-20 year old captive male and one 9-year-old captive female. Fat was subsumed with "other tissue," which comprised 44.3% of body weight in the female and 41.4% of body weight in the male. Percent fat—independent of other tissue—was not reported nor was the absolute amount of fat present. Thus, I believe there is still insufficient data to conclude whether or not there is a sex difference in relative percent body fat in orangutans, given both the imprecision of the measures, the small sample size and the disparate ages of the two individuals. Due to the high costs of reproduction, I would predict, however, that female orangutans would have a greater percent body fat than do males.

More evident, however, are sex differences in the *distribution* of fat deposits in *Pongo*. Males have extensive fat depots in their laryngeal sacs, upper backs and cheek pads. The cheek pads, characteristic of the fully developed adult male, are composed of 28% fat (Morbeck and Zihlman 1988). Winkler (1989), after dissecting the cheek pad region of 11 orangutans, concurs, reporting "massive fatty deposits" in the cheek pads of two fully developed adult males.

Thus, in orangutans, conspicuous fat deposits are also a secondary sexual characteristic. These fat stores may be used as an additional way that orangutan males can increase their apparent body size. As stated in Chapter 1, I believe that the primary function of the cheek pads in the adult male is to increase apparent body size. Fat deposits are an important component of this. Fat in the neck may also contribute to an overall perception of bulk. (Alternatively, fatty necks may also help deter lethal neck bites from conspecifics.) Fat is a

less expensive tissue than bone or muscle to build and maintain and can be more easily mobilized when needed. Increasing body mass through fat storage may be a more malleable and less costly way to enlarge body size above skeletal constraints. In support of this, when adult males are sick or injured, their cheek pads as well as laryngeal sacs become noticeably shriveled (personal observation).

The three posited modes of sexual selection—male-male competition, female choice (Darwin 1871) and sexual coercion (Smuts and Smuts 1993)—may have made large body size advantageous in developed male orangutans. Physical male-male contests are a rare, but important, component of developed adult male behavior. Two males died during my study, one definitely and the other probably due to the wounds inflicted during fighting with other males. At least six of the adult males followed had visible wounds due to male-male aggression. Adult males also had significantly higher mean leukocytes levels than did females (Mann-Whitney U-test, $p < 0.05$) (Knott 1996a). The presence of leukocytes in urine is consistent with the interpretation that these adult males were fighting infection. Severe infection can lead to an overall decrease in energetic status and ultimately can cause death. Thus, these male-male contests can be strong selective events. I have observed that relative male size appears to play a role in the willingness of males to engage in conflict. These fat deposits in developed adult males may therefore also serve as a sign of a male's health and the ability to survive periods of low fruit availability. Thus, they also may have been selected for through the mode of female choice. Finally, larger males may be more successful in forcing females to mate — through both the use of force and the threat of force as suggested by Smuts and Smuts (1993). Other studies (Mitani 1985b) found that the larger developed males engage in forced copulations less often than do the smaller undeveloped males, but it remains possible that females are more compliant due to a greater risk of injury from resisting males that are twice their size. Regardless of the mechanism,

large body size appears to hold a selective advantage for developed adult males, and fat storage may help to enhance it.

3. Fall-Back Foods

The fall-back foods that animals turn to during periods of scarcity are crucial for understanding evolutionary divergence. Closely related animals may have similar preferred diets, but the back-up foods they select may help explain their morphological and behavioral differences. Studies of sympatric primate frugivores suggest that when preferred fruits are scarce, dietary divergence is greatest. Such primate communities often exhibit substantial dietary overlap, with niche separation and the function of some morphological characteristics only becoming clear during periods of fruit scarcity (Gautier-Hion 1980; Terborgh 1983; Tutin *et al.* 1991). For example, Kinzey (1992a) addresses the seeming paradox that members of the Pitheciinae all have highly frugivorous diets, but substantial differences in their dentition. He argues (Kinzey 1992b) that these morphological differences in the dentition are due to selection for dietary specialization on different fall-back foods during periods of fruit scarcity. Similarly, Wrangham *et al.* (1992) show that chimpanzees rely on THV (terrestrial herbaceous vegetation) or pith as an important fall-back food. This focus on fall-back foods has lead (Wrangham 1986) to propose that the greater availability and patch size of THV in the bonobo habitat explains why bonobos are able to travel in larger parties and form more stable associations than do chimpanzees.

At Gunung Palung, orangutans dramatically shifted their diet to cope with changes in fruit availability. Leaves and bark were the primary fall-back foods. Their large gut capacity enabled them to eat and digest large quantities of these fibrous bark and leaves. In

addition, they also tended to consume more insects and pith during periods of low fruit availability, but in lesser quantities than bark or leaves. Pith in the orangutan diet mainly consisted of pithy arboreal plants (PAP), although males in particular sometimes came down to the ground to eat THV. Furthermore, while orangutans may occasionally eat THV, it is probably not a prime back-up food because it grows on the ground where orangutans rarely travel and its patchy distribution would make foraging on it inefficient.

During the three months of highest fruit availability, orangutans consumed over 95% fruit in their diet. In contrast, during the three months of lowest fruit availability, 40-70% of their diet was non-fruit vegetation. Thus, they were able to switch from their preferred diet of being largely frugivorous to becoming generally herbivorous. However, in spite of this shift in diet, they did not maintain caloric adequacy as shown through the calculation of energy balance and measurement of ketones. In other words, the orangutans were able to survive during this fruit-poor period, but they would not have been able to sustain themselves indefinitely on this classically insufficient dietary regime.

In evaluating the importance of fall-back foods in great apes, several key questions must be considered: (1) what is the nutritional value of the fall-back foods, (2) how efficiently can nutrients be extracted from these foods, (3) what proportion of the diet is made up of these fall-back foods and, (4) how long is the period during which fall-back foods are relied upon? I have shown that orangutans were producing ketones across a seven-month period, indicating that the fall-back foods they relied on were not sufficient to provide for all of their caloric needs. In contrast, Wrangham and colleagues (personal communication) have not detected ketones in the urine of chimpanzees in Kibale forest, despite testing since 1992. Similarly, ketones have not been detected in the urine of chimpanzees from Mahale (Huffman personal communication). Is this difference due to the nature of the fall-back foods? Alternatively, is the severity of the fruit-shortage periods greater for orangutans, or

is it a combination of both factors? The first year and a half of this study, which is reported in detail here, encompassed a period of very high and very low fruit availability. Subsequently, fruit availability has fluctuated, but not as dramatically, and although sporadic ketones have been detected in urine, another sustained period of ketosis has not been observed in the five years since the initiation of the study. Thus, it appears that during these ensuing periods of low fruit availability, fall-back foods and the other adaptations described in this chapter were sufficient. As I've argued, orangutans in these mast fruiting forests, are regularly, but unpredictably, subjected to lean periods of particular severity due to the nature of this phenological pattern. It may be that the greater availability of pith in African rain forests, as suggested by Wrangham (personal communication) is an important difference between the two ape habitats, but I would see this as just one of the factors contributing to the *experience* of greater fluctuations in fruit availability for orangutans. In the future, it will be interesting to perform more explicit comparisons of differences between species in fall-back food composition and consumption. This also highlights the importance of continuing long-term studies of individual populations so that the periodicity of severe events can be more precisely determined.

4. Energy Expenditure

Studies of the relationship between primate diet and foraging effort suggest that primates that eat high-energy foods with high spatiotemporal patchiness, such as fruit, have longer day ranges than do primates that eat more evenly distributed low quality foods, such as leaves (Milton and May 1976; Clutton-Brock and Harvey 1977). Orangutans conformed to this pattern. Male orangutans significantly decreased their time spent traveling and both sexes decreased their day range during the period of *lowest* fruit availability. This was

possible because they shifted to a more folivorous and evenly distributed diet during the fruit-poor period. Estimates of daily energy expenditure were also significantly lower during the fruit-poor compared to the fruit-rich period. Thus, relying on more abundant leaves and bark and shortening their day range was an effective strategy for conserving energy.

A similar finding was reported for gorillas by Goldsmith (1999). She found that Western lowland gorillas responded to decreasing fruit availability by increasing consumption of leaves, stems and bark and decreasing daily path length. In other primates that can switch between frugivorous and folivorous diets, equivalent results have also been found (Richard 1979; Bennett 1986). Siamangs have also been observed to incorporate more leaves in their diet and travel less during fruit-poor periods (Chivers and Raemaekers 1980), although this was based on data from a single group.

REPRODUCTIVE RESPONSES TO ENERGY AVAILABILITY

Summary of Results

Hormonal Changes

In order to explore reproductive responses, I developed new methods to enable collection of hormonal data from wild orangutans. Using these methods, I was able to collect data to test the hypothesis that during the period of high fruit availability female orangutans would have higher estrone conjugate levels than during the period of low fruit availability. Between September 1994 and December 1995, 179 urine samples were collected from wild adult female orangutans and were analyzed for estrone conjugates (E_1C). Two non-

pregnant females were followed during both periods of high and low fruit availability and both showed a significant decrease in estrone conjugate levels during the low fruit availability period. Comparisons of weekly mean estrone conjugate values in 12 non-pregnant females also showed a significant decrease in estrone conjugates when fruit availability decreased.

Samples from captive orangutans were obtained and measured for estrone conjugates. Comparison of these samples with those from wild females showed that captive females had significantly higher estrone conjugate values than did wild females. This result supports the hypothesis that the unique conditions of captivity, including the availability of a constant food source and low energetic expenditure, would lead to higher hormonal levels in captive orangutans.

Additionally, all matings and conceptions observed during the course of the study period occurred during the months of highest fruit availability. All matings were between undeveloped males and females whose youngest offspring was judged to be four years of age or older.

DISCUSSION:
IMPLICATIONS OF FLUCTUATING FRUIT AVAILABILITY ON ORANGUTAN REPRODUCTION

Ovarian Function

The finding that estrone conjugate levels were significantly lower during the fruit-poor period and that no matings occurred during this time suggests that orangutans responded to

this low-fruit period physiologically as well as behaviorally by not investing in reproduction. It was hypothesized in this study that females would have lower levels of ovarian function during periods of negative energy balance in order to modulate the probability of conception so that it would be more likely to occur when there were sufficient reserves for gestation and lactation. This was confirmed.

Primates evolved in the tropics where fluctuations in temperature are slight, but where fluctuations in food may be pronounced. Because day length close to the equator shows little variation, standard explanations of environmental influences on mammalian reproduction, such as photoperiod (Bronson 1989) seem insufficient. Like humans, apes have long interbirth intervals and exhibit high investment in single offspring. Furthermore, because of the unpredictability of fruit resources, apes like the orangutan cannot time their births to coincide with peaks of fruit availability. Thus, I would argue that apes have evolved, as in humans, to time reproduction so that conception is more likely during periods of positive energy balance. Van Schaik and van Noordwijk (1985) make the argument that non-seasonally breeding primates, such as great apes, should time reproduction to coincide with periods of high food availability in order to store reserves during pregnancy which can be drawn on later during pregnancy. As suggested by Ellison (1990), if the initiation of reproduction during a state of positive energy balance is associated with improved reproductive outcome it should be favored by natural selection.

We know through the work of Ellison and colleagues (1993) that human ovarian function is best understood within an ecological context in which hormonal functioning is very responsive to changes in nutritional intake, energy expenditure and energy balance. Studies of apes and other primates have suggested that nutrition and body weight can be important in understanding non-human primate reproductive functioning as well. However, the primate literature has not been guided by a unified theory of ovarian

responsiveness as is the case in studies of human reproductive ecology. I have suggested with this study that those same mechanisms that have become well known in humans may apply to great apes and perhaps other primates as well. This is a framework which can be used to guide informed investigations of primate reproductive ecology. It appears that, at least in orangutans, large changes in energy balance do affect ovarian hormone production. Whether this responsiveness is as tightly modulated as is seen in humans and whether the interaction between the different variables is the same in humans and the great apes will require many more future investigations.

Mating

The finding that no mating occurred during the fruit-poor period, despite the proximity and apparent reproductive availability of females, was somewhat surprising. I would have predicted that males should still attempt to mate with females even if the probability of conception was low during these times. The observation that this did not occur suggests that, for males, the probability of conception was indeed so low that mating was not attempted and/or the costs associated with mating were too high.

If fecundity is suppressed during this time in females, it may be that the possibility of conception is so low that males just do not attempt to mate. Perhaps there is a mechanism by which negative energy balance affects mating behavior. One possible factor to investigate would be testosterone levels. However, as stated in Chapter 8, my initial investigations have not shown a difference in levels of this hormone in males between fruit availability periods. This clearly warrants further investigation.

The costs of mating may also have deterred males from such copulating activity. Male mating costs include both energetic expenditure and risk of injury. Energetically, I found

that females traveled further each day than did males, in both high and low-fruit periods. Male energetic costs were also greater due to their larger body size. Thus, when calories were insufficient, males would suffer a much greater cost for consortship. Due to the lack of an estrous swelling, males would also have no way of pinpointing the time of ovulation and thus could not direct their mating effort to particular periods and/or individuals. In addition, as discussed earlier, the risk of injury and death due to male-male competition is serious in orangutans. The mortality risk from wounds would be predicted to be higher when the orangutans were more energetically stressed and thus had less reserves to fight infection.

Interbirth Intervals

One of the most intriguing questions about orangutans that this study has sought to illuminate is why they have the longest interbirth interval of any primate. I believe that the extended periods of low fruit availability and the overall low, non-mast, productivity of these forests set the stage for this life history pattern. The responsiveness of orangutan ovarian function to the consequent changes in energy balance are the key factors explaining the long orangutan interbirth interval. This study contributes the following to our understanding of orangutan interbirth intervals: (1) It quantifies physiologically relevant differences in energy balance associated with fruit productivity (2) It demonstrates that these periods of low fruit availability can be quite long and severe (3) It shows that estrone conjugate levels are correlated with these changes in energy balance and (4) It suggests that the rain forests of Southeast Asia may be particularly harsh, resulting in longer orangutan interbirth intervals compared to African apes.

We know from studies of other primates, and of humans, that changes in nutrition and energy balance can have an effect on the interbirth interval. For example, Lee (1987) found, in vervet monkeys of Amboseli, that groups with access to the lowest quality diet had longer interbirth intervals compared to those with higher quality diets. Bercovitch (1987) found that female olive baboons (*Papio anubis*) that weighed more had shorter interbirth intervals than lighter females. In another study of baboons, Strum and Western (1982) showed that decreases in access to food led to an increase in interbirth interval.

Among humans, studies in the Gambia as well as in Guatemala suggest that traditional, non-contracepting women who have supplemented diets have shorter interbirth intervals than those who do not receive supplementation (Prentice *et al.* 1986; Delgado *et al.* 1978). In Bangladesh, women who were heavier at the time of parturition had a shorter period of postpartum amenorrhea (Ford *et al.* 1989). A similar result was found among Mopan Mayan women of Belize, where the time to next conception was shorter in women who had a higher "fat body weight" (Fink *et al.* 1992).

These kinds of comparative studies, necessitating information about complete interbirth intervals and data on diet throughout the birth interval, would be difficult to carry out in orangutans due to the length of their interbirth intervals, their low population density and their tendency to shift ranges for extended periods of time. However, the findings reported here—lower estrone conjugate levels during periods of low nutritional intake and extended periods of negative energy balance—suggest that these times of low fruit availability are an important factor contributing to the length of interbirth intervals.

Negative energy balance could be affecting female orangutans regardless of their reproductive status at the time of the low fruit availability period. For example, in humans we know that supplementation during pregnancy, lactation and the waiting time to

conception leads to shorter interbirth intervals (Prentice and Prentice 1988). Negative energy balance drains maternal energy reserves, requiring time to recoup and thus lengthens the interbirth interval. Thus, an extended period of low energy balance should have an effect on interbirth interval regardless of the reproductive stage of the female, although it may be particularly detrimental during early lactation, the most energetically demanding period.

Food availability and periods of negative energy balance also had an effect on orangutan mating patterns. Without mating, of course, the probability of conception is zero. Thus, if orangutans are not even attempting to conceive during fruit-poor periods the length of such periods could have a dramatic effect on interbirth interval. I would predict that orangutans living in degraded habitats would have the longest birth intervals and that those living in richer habitats would have shorter interbirth intervals.

Great Ape Comparisons

Reproductive ecology, *per se*, has not been studied in other wild great apes, but several lines of evidence suggest that nutrition is an important factor in regulating chimpanzee interbirth intervals. First, just as in orangutans, chimpanzees and gorillas have shorter interbirth intervals and earlier age at menarche in captivity compared to the wild (Tutin 1994). Second, Wallis (1997) points out in her review of reproductive parameters from chimpanzees at Gombe National Park, Tanzania, that the individuals with the shortest interbirth intervals were all descendants of Flo. These family members were the most frequent visitors to the banana feeding station and thus Wallis speculates that they may have received better nourishment. No data were available on the relative food availability in the forest when the chimpanzees came to the feeding station, but such visitation may have been important for making up any caloric deficits. Third, seasonality in conceptions has also

been reported at Gombe, with the majority of conceptions occurring during the dry season. Without systematic data on phenology, caloric intake and energetic patterns we cannot positively ascribe this finding to changes in energetic status. However, Wallis (1997) speculates that changes in diet may have been important.

Juvenile Development

Finally, in understanding interbirth interval lengths we must also consider the needs of the dependent offspring. Galdikas and Wood (1990) suggest that differences in the length of suckling between the great apes may account for longer orangutan interbirth intervals. Indeed, suckling is probably the most important factor contributing to primate interbirth intervals. However, initial examination of my data on suckling patterns and dietary intake of infants and juveniles (not reported here) suggests that suckling is infrequent after 4-5 years of age and primarily occurs in the context of reassurance when juveniles have had trouble crossing canopy gaps. It does not appear to be a significant factor contributing to nutritional intake in these older juveniles. Thus, I would predict that this low level of suckling in older juveniles is not having a significant effect on maternal hormonal functioning.

Additionally, if orangutans do suckle longer than other apes it may be a result of low food availability. The length of lactation may be related to the ability of juveniles to turn to alternative food sources. Due to smaller body size and insufficient strength, juvenile orangutans may find it more difficult to access bark than do adults, and may nurse longer due to lower availability of more easily digestible fruit. I have observed that orangutan juveniles often wait until their mother has started peeling off a layer of bark and then they

strip pieces off the same area. Thus, orangutan juveniles may also be dependent on their mothers to help access some of these difficult to process fall-back foods.

Juvenile orangutans exhibit the slowest growth rates of any non-human primate (Horwich 1989). This slow rate of juvenile development may be influenced by the pronounced fluctuations in fruit availability in the Southeast Asian Rain forest. Orangutans feed predominantly on foods such as bark and leaves during fruit-poor periods, thus their survival ability may be highly dependent on their ability to extract adequate nutrients from these high fiber foods. Hind gut digestion of fiber is partly a function of body size, and thus it may be particularly difficult for juvenile orangutans to digest fiber given their small bodies. They may not be able to subsist as well on these fall-back foods and may require a more digestible, higher energy diet. Juveniles may thus be particularly vulnerable to nutritional stress during fruit-poor periods and the regular occurrence of such fruit shortages could be a contributing factor to the slow growth rates seen in wild orangutans.

SUMMARY

Orangutans were seen during this study to show adaptations to periods of low fruit availability that involved increasing caloric intake and fat reserves during fruit-rich periods and, during fruit-poor periods, breaking down fat reserves, relying on leaves and bark as fall-back foods, decreasing day range and energy expenditure, and down-regulating ovarian function and mating. Orangutans share many of these adaptations with other primates. However, the particular suite of features they show in response to changes in fruit availability, including the degree to which they are able to maximize caloric intake and fat stores and their reliance on such low quality foods such as bark, may be distinctive within the order. An additional way that orangutans (and many other Bornean vertebrates)

adapt to changes in fruit availability is through habitat movements as documented by Leighton and Leighton (1983). Examination of the data collected for this thesis supports their conclusion, although I do not present that data here.

A final point is that orangutans may have less latitude to respond to changes in fruit availability behavior by modifying their social grouping because they are already the most solitary diurnal primate. Wrangham (1977) describes how chimpanzees respond to low-fruit availability periods through decreasing party size. Orangutans do not have this option since they are already solitary. Indeed, this solitary lifestyle has been attributed to the sparse distribution and normally low availability of fruits in the orangutan habitat (Galdikas 1988; MacKinnon 1974; Rodman and Mitani 1987; Rijksen 1978; Rodman 1977, 1984; Schurmann and van Hoof 1986; Sugardjito *et al.* 1987). Thus, orangutans cannot use modification of social structure as a way to respond to low fruit availability and must rely on other strategies.

More detailed ecological comparisons between the different great ape species and between study sites are needed to assess whether the differences between rain forests are as great as what is suggested from the existing comparative literature. How severe are the periods of low fruit availability that other apes experience? Is it the availability and the distribution of fall-back foods or is it different fruiting patterns between rain forests that are of paramount importance? Most likely these are both salient features of the environment that provide clues as to how these animals have evolved. Complementary studies that are able to compare changes in total fruit availability, distribution and availability of preferred and fall-back foods, daily caloric intake, energy expenditure, ketone production, hormone production and social behavior would help to resolve these questions and help us to understand the evolution of differences between these closely related species.

IMPLICATIONS FOR HOMINID EVOLUTION

The last 30 years or so of great ape research has amassed a wealth of behavioral data that can be used to make predictions about the behavior of early hominids. We have only begun, however, to undertake great ape field studies that incorporate a physiological component. Understanding how physiological and reproductive systems of living hominoids respond to environmental perturbations is essential to understanding their evolution and adaptive significance. Adding these components to great ape behavioral studies allows us to build more informed models with which to reconstruct the behavior, morphology and the response to ecological pressures found in great ape and human ancestors. Below are some of the implications drawn from this study suggesting how environmental fluctuations may have impacted hominid evolution.

Seasonality in Human Evolution

Changes in environmental conditions have been proposed as catalyzing agents during critical junctures of human evolution (Vrba 1985a, 1985b, 1989; Rogers *et al.* 1994). Environmental fluctuations have become more and more extreme since the Miocene (Potts 1998). Starting at six million years ago, deep-sea cores reveal an isotopic record of oxygen enrichment, indicating a marked global cooling trend with accompanied drying (deMenocal 1995). This general trend, however, is characterized by a two- to three-fold increase in the degree of environmental fluctuations during the period of most recent hominid evolution (Potts 1998). The most extreme climatic oscillations seem to have occurred around 2.5 Ma, 1.7 Ma and 1.0 Ma (deMenocal 1995; deMenocal and Bloemendal 1995).

These large-scale changes may help explain major adaptive shifts during human evolutionary history, but such paleo-climatic analysis is limited to measuring change in tens

or hundreds of thousands of years. What we would like to know is the extent to which environmental variability affected the *individual lives* of early hominids. In particular, the predictability of environmental fluctuations, and their impact on the foods which were relied upon by hominids, are the most critical variables. Potts (1998) argues that rather than adapting to any specific climatic change, early hominids were subject to "variability selection," in other words they evolved the behavioral flexibility to adapt to new environments. Some of the physiological adaptations I will discuss below may fall in this category.

Fat Storage

Humans are often cited as being the fattest of primates. People can clearly become extremely obese. However, captive primates can become obese as well. For example, obese pig-tailed macaques average 40.5% body fat (Walike *et al.* 1977). Mean percent body fat across many human societies is roughly 27% in women and 15% in men (Wardle *et al.* 1987; Hattori *et al.* 1991), but estimates range widely between populations. Many of these estimates, however, come from populations living with abundant food resources. People living under more marginal conditions have lower body fat percentages, but, percentages can still be fairly substantial, particularly in females. For example, Howell (1979) calculates that adult !Kung women have a percent body fat of 23.7%. Estimates in New Guinea (cited in Shephard 1991) are 9% in males and 21% in females. Amongst the tribal Maasai, Barac-Nieto (1978) has estimated that men carry 6% body fat. Studies of Western athletes estimate as little as 7-8% body fat in some men (Shephard 1991) and 9% in some women.

How do these figures compare to primates? Unfortunately, the data are extremely slim. One of the only studies to look at this was performed by Altmann *et al.* (1993) on baboons. They report that animals with an abundance of food (those living close to a garbage dump) had a mean body fat percentage of 23.25% compared to 1.9% for wild-feeding baboons. Note that this second figure is much lower than that seen in even the leanest human populations. With the lack of comparative data from the other great apes, we cannot conclusively say that humans are significantly fatter under "natural" conditions. However, the few comparative primate data that exist so far would indicate that this is so.

As I asked in relation to orangutans, do humans have an *enhanced* ability to store fat compared to the other great apes? Do all the great apes equally share the same propensity towards obesity in an over-abundant environment? If so, is this different from that seen in other cattarhines? Conversely, if orangutans and humans do have an enhanced propensity towards fat storage compared to other apes, does this fat storage exist for the same function? Is it of similar origin, a shared trait of hominoids that was lost in the other African apes, or did it arise again in the hominid lineage and, if so, when? Given the emphasis placed on the human ability to store fat and the clear adaptive value of fat storage in orangutans, these are questions that warrant increased comparative study.

The ability to accumulate fat stores has been proffered as a key feature during human evolution, enabling us to survive during food scarce periods, to store enough reserve energy to draw on during pregnancy and lactation (Prentice and Whitehead 1987), and to enable us to grow large brains (R. D. Martin 1981; Aiello and Wheeler 1995). Thus, it is essential to have a better understanding of whether humans differ from other apes in the way we rely on stored energy. Below I describe three ways that fat storage may have been important in human evolution.

Adaptations to Feast and Famine

The fat storage ability of modern humans may indicate that during our evolutionary past we were subjected to periods of feast or famine. As described earlier this argument has been invoked to explain enhanced propensity towards fat storage in particular human populations. These explanations entail both the ability to store fat quickly and efficiently, such as during periods of feasting before long ocean voyages (McGarvey, 1991) and the selective pressure of periods of starvation caused by these ocean voyages or cyclic tropical storms. Such circumstances would have selected for those individuals who had started off with the greatest fat stores. We can see in other extreme examples that pre-existing fat stores can promote survival during unexpected periods of food scarcity. Grayson (1993) has described, for example, how the women of the Donner Party, which were stranded in the Sierra-Nevada mountains of California in 1846, had a rate of survival that was almost twice as great (56.6%) as that of the men (29.4%). Modern hunter-gatherers can also experience prolonged periods of food scarcity. Even if such periods only occurred a few times during an individual's lifespan, they would have exerted a strong selective pressure.

However, as discussed earlier in relation to orangutans, wouldn't all animals be subjected to such periods of low food availability and thus shouldn't there have been equal selection to store fat to survive these episodes in humans compared to other apes? This would depend on the answers to questions that are active areas of research, but for which we still have incomplete answers: What were earlier hominids eating at different stages in their evolution? What were their preferred foods and what were their back-up foods? What was the spatio-temporal distribution of these foods in the environment in which they lived? Were they subject to longer or more unpredictable periods of food shortage than were other

apes? A corollary question is what the cost of fat storage would have been for early hominids. Perhaps they, like orangutans, would have paid a relatively low cost for maintaining these reserves.

Reproduction

In all human populations women store more fat than men (Shephard 1991). For example, average percent body fat in Japanese women is approximately 20.9% compared to 12.4% in men (Hattori *et al.* 1991). Sex differences in body fat are even more pronounced in foragers such as the !Kung (Howell 1979). This has been interpreted by many authors as an adaptive buffer for the energetic burden of reproduction in females. As Pond (1997, p. 159) speculates, "large quantities of adipose tissue ... could be critical to successful reproduction in uncertain or fluctuating seasonal environments with possibilities of severe famine."

The reproductive function of female fat stores is even more apparent during pregnancy when, through several physiological processes, women are able to increase their fat deposits. Prentice and Whitehead (1987) have argued that weight gain in early pregnancy, particularly under marginal nutritional conditions, provides an essential energetic reserve for the later demands of pregnancy and lactation. Even women who are nutritionally stressed are able to decrease their basal metabolic rate to facilitate this fat reserve.

Human females seem to have special adaptations to maintain enough fat reserves to sustain reproduction. But, again, to evaluate whether these adaptations have evolved during human evolution or whether they have been enhanced relative to other apes is still an open question. The finding that some other primate females have larger fat stores than do males suggests that they also are buffering for the high costs of reproduction. Excellent data

along these lines exists from the bioelectrical impedance studies of McFarland (1997) on pig-tailed macaques. She was able to accurately measure body fat levels and found that females who were fatter had shorter interbirth intervals and shorter periods to conception. Fatter females also were more likely to produce surviving offspring. Additionally, the majority of females with surviving offspring had increases in skin-fold thickness during pregnancy. Other studies also suggest that all female mammals gain some fat deposits during pregnancy (Thomson and Hytten 1977). Thus fat storage may be important in both human and non-human reproduction. This is another field of inquiry that warrants specific investigation of the responses of non-human primate females to assess whether and how human reproduction may differ from other species.

Brain Growth

The brain is an energetically expensive organ to produce (R. D. Martin 1981). Thus, it could be argued that the particularly high fat reserves found in human females are needed as an energetic buffer during lactation to fuel the great postnatal growth of the human brain. Developing brains may be particularly vulnerable to caloric and nutrient deprivation. Thus, because of this extended period of post-natal brain development, the importance of having excess fat reserves to combat the possibility of low food availability may be attenuated in humans. Human babies are also particularly fat compared to other primate babies and they can subsist for several days on these fat reserves. Perhaps the consequences of low food availability, especially on the brain development of a juvenile human, are more dire than in other primates, necessitating carrying a back-up energy reserve.

Again, this raises the need for more comparative information. How does milk composition and total milk production in humans compare to other apes? Are human babies more costly energetically to their mothers than other primate, particularly great ape, babies? My initial

observations of suckling frequency in wild orangutans suggest that feeding bouts are fewer than what has been seen in forager populations, but this warrants additional study.

SUMMARY

In sum, fat storage and the mobilization of energy may have been an important adaptation in humans struggling to cope with environmental fluctuations, the needs of costly reproduction, and the growth of large-brained offspring. Fat stores also appear to be an important adaptation in orangutans for coping with low food availability. Studies of other primates suggest that fat is also important in reproduction, but similarly detailed studies have not yet been undertaken in other great apes. The cost of producing a large brain is one human feature that clearly distinguishes us from the other apes, and it may be that this accounts for the particularly high fat deposits seen in modern humans—especially in women and even those living under nutritionally stressful conditions. We can't evaluate fully, though, in what ways humans are different until we know more about the nature, propensity and distribution of fat stores in all the great apes.

Life History

Reproduction

With this study I have tried to extend the ecological models of human reproduction to living orangutans to test whether we find the same type of modulation of ovarian function as has been found in humans. This is important in understanding whether the type of reproductive responses we see in humans are unique adaptations that were acquired

somewhere along the path of hominid evolution, or whether they are shared with other great apes. If they are shared, we can infer that the same processes that are currently seen in humans were operating during both hominoid and hominid evolution. This study suggests that such processes do seem to be shared by orangutans and, I would predict, by other great apes as well.

What does this shared evolutionary history tell us? Reconstructions of hominid evolution tend to focus on food acquisition, ranging patterns, tool use, etc. These are assuredly important variables. Leonard and Robertson (1997), for example, argue that hominid energetic needs increased dramatically with the advent of the genus *Homo*. However, lacking from these descriptions is a discussion of how reproduction, particularly female reproduction, would have been affected by changing energetic status. It tells us that maintaining positive energy balance would have been an important part of the equation, particularly for females. If part of the human adaptation that allowed us to evolve large brains is due to the ability to switch to a lower fiber, higher quality diet (Aiello and Wheeler 1995), it also may have increased the need to maintain positive energy balance in females to nourish these developing human brains. The interaction between food, food acquisition and reproduction may have been particularly important in changing the dynamics of the hominid interbirth interval.

Interbirth Interval

How were reproductive life history patterns of extinct hominids modified in response to a changing environment? Evidence that a major transition in these patterns occurred in human evolution is found in the divergent combination of life history parameters we exhibit compared to other apes. Of the great apes, humans are the most altricial at birth and have the longest maturation period. Curiously, however, our interbirth intervals are shorter than

those of other apes (Galdikas and Wood 1990). In essence, we have been able to lengthen our period of dependency while shortening interbirth interval (Lancaster and Lancaster 1983). This is accomplished by having overlapping, nutritionally dependent offspring.

In this way, an ape mother presents a striking contrast to her human counterpart. Orangutan and chimpanzee females spend most of their time alone with their dependent young. Offspring are reliant on the mother alone for nutrition they cannot acquire on their own. Gorilla mothers remain with a group, but outside of some protection provided by silverback males (Fossey 1983), infants and juveniles receive no direct or indirect paternal care. Food sharing is rare and except for the occasional item that a youngster takes from his or her mother, baby apes must fend for themselves after the end of lactation. Ape mothers must invest in each offspring until they are nutritionally independent. That is, at weaning each offspring must be able to survive without lactational supplementation and must have the cognitive and motor skills sufficient to obtain it's own food. After another offspring is born, juveniles may still accompany their mother, but they no longer nurse or receive other direct nutritional assistance.

Contrast this with a human infant. In all human societies, most males provide at least some direct or indirect care to their offspring. Mothers are dependent on close kin to assist with childcare. Children are still nutritionally dependent on adults long after they have been weaned from the mother's breast. Although they may start helping to obtain food at a relatively young age, they still rely on adults to provide a portion of their food for many years. If a human mother was following the great ape pattern, she would need to nurse until that child was able to obtain sufficient food to feed itself without maternal (or other adult) assistance. Estimates of this age vary, but it is difficult to imagine a human child being a completely competent forager younger than, say, 10 years of age. If the mother was not able to provide any food to this child directly, but could only supplement through

lactation, this would inhibit her ability to invest in future offspring. It is difficult to imagine this being a viable pattern and indeed it is not, since humans have found ways to provide high quality nutrition to offspring outside of lactation.

Thus, I would see human adaptations, such as the sexual division of labor, pair-bonds, tool use, hunting, etc. not for just their effects on survival but for how such adaptations for survival and for more easily procuring higher quality food from the environment allowed humans to shorten their interbirth interval. I would imagine this occurred after the advent of *Homo* when we see more human-like life history features in the fossil record. Ultimately, I believe that it is time to focus more on how such human adaptations affected reproduction and juvenile survival, which are critical, yet often overlooked, components of evolution.

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APPENDIX I — NUTRIENT DATA

Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Anon	13	SD	91	10	78	58	12	9	9	2	0	89	1	88	11	0	52	99
Anon	13	PL	90	19	66	50	16	12	9	6	1	85	11	78	10	1	92	134
Aromadendron		SD	93	37	41	32	18	35	10	2	10	91	33	45	11	11	273	298
Artabotrys		SD	93	4	70	56	17	10	15	1	9	92	0	76	17	10	158	199
Artocarpus		LV	88	21	54	46	25		16	8	1	81	13	67	20	1	136	173
Artocarpus		BK	90	16	59	47	14		6	18	2	75	10	79	8	3	98	141
Artocarpus*		BK	91	0	73	61	31		17	23	1	71	0	103	24	1	105	161
Artocarpus		BK	90	0	60	52	23		8	24	7	68	0	88	11	11	143	190
Artocarpus	5	SD	91	27	45	28	14	8	15	5	9	87	21	51	18	10	244	272
Artocarpus	5	PL	91	47	32	23	5		8	6	7	85	45	38	9	8	290	310
Artocarpus	5	FW	88	20	57	48	27	22	13	7	3	82	11	69	16	3	140	177
Artocarpus	fulvicortex	SD	90	35	41	17	5		18	4	2	86	29	48	20	2	219	245
Artocarpus	fulvicortex	PL	87	60	31	15	2		5	3	2	84	56	37	6	2	264	284

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

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Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Baccaurea		SD	92	41	29	19	9		10	8	13	85	40	34	12	15	341	359
Baccaurea	1	SD	90	37	36	26	11		11	7	9	83	34	43	13	11	284	308
Baccaurea	angulata	SD	90	45	33	24	10		6	7	9	84	42	40	7	11	298	319
Bark		BK	89	30	53	43			10	5	3	85	23	62	12	3	167	201
Bark - red	liana	BK	90	41	46	37	14		3	2	8	89	36	52	3	9	236	264
Bark-light	liana air	BK	91	22	62	47	12		5	10	1	82	18	76	6	1	101	142
Bark-white	liana	BK	90	16	65	51	15		9	10	0	81	8	81	11	0	78	122
Blumeodendron		SD	91	56	26	8	5		12	2	4	90	53	29	13	5	308	324
Blumeodendron		SC	94	14	80	60	26	14	5	1	0	93	9	86	5	0	58	104
Castanopsis		SD	91	67	26	4	2		5	2	0	89	65	29	6	0	284	300
Chaetocarpus		SD	92	4	42	37	30	21	13	3	38	89	0	47	14	43	443	469
Dialium		BK	87	20	64	55			12	4	0	84	9	76	14	0	96	138
Dillenia		FW	91	35	46	40	26	15	11	7	2	85	31	54	13	2	195	224

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV: Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

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Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Dillenia		FB	90	38	49	43	27	16	8	6	0	85	33	57	9	0	172	203
Diospyros	1	PL	88	23	68	80	41	39	4	4	0	85	14	81	5	0	77	121
Diospyros	confertiflora	SD	91	18	70	55	21	34	8	3	0	88	11	80	9	0	81	124
Dipterocarpus	sublamellatus	SD	90	79	11	3	1		5	2	4	89	78	13	5	4	369	376
Drypetes		SD	93	11	29	16	8		15	6	39	87	5	33	18	45	493	511
Drypetes		PL	84	55	33	25	17		8	3	0	81	49	41	10	0	239	261
Durio		PL	89	48	30	23	10		13	6	3	84	45	36	16	4	273	293
Durio		SD	88	41	40	33	23	10	14	4	0	85	36	47	17	1	214	240
Durio	muda	LV	91	21	56	42	18		19	3	1	88	14	63	22	2	157	191
Durio	tua	LV	90	19	57	40	12		12	10	2	81	13	70	14	3	133	172
Epiphyte	wadge	LV	92	19	72	68	9		3	6	1	97	22	74	3	1	111	151
Ficus	delocyce	WF	92	25	65	50	27	23	4	5	0	88	21	74	5	1	106	147
Ficus	dubia	SD	92	13	71	57	38	19	8	3	5	89	6	79	9	6	113	156

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

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Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Ficus	dubia	SK/PL	93	33	44	32	14	18	9	6	8	87	30	51	10	9	243	270
Ficus	punctata	SK/PL	91	32	48	40	18	22	8	8	5	84	28	57	9	6	204	235
Ficus	kerkovenii	SD	92	9	81	62	31	31	5	5	0	88	2	92	6	0	34	84
Ficus	kerkovenii	SK/PL	92	16	69	50	29	21	8	6	1	86	9	80	9	1	83	126
Ficus	sect sycidium	WF	93	20	57	44	21	23	12	7	4	86	15	66	14	4	158	193
Ficus	stupenda	SD	92	20	65	53	35	18	6	6	3	87	15	75	7	3	117	158
Ficus	stupenda	SK/PL	93	30	59	43	17	26	4	6	1	87	26	68	4	2	137	174
Ficus	subgelderi	SD	92	19	68	56	33	23	6	6	2	87	13	78	7	2	99	141
Ficus	subgelderi	SK/PL	93	32	55	44	21	23	5	6	2	87	28	64	6	3	159	194
Ficus	binnendykii	WF	91	20	65	52	32	19	7	8	1	84	14	77	8	1	100	141
Flowers		FW	90	34	50	42	24	16	10	3	3	87	29	57	11	3	188	219
Garcinia		PL/SD	89	50	34	31	21	10	5	2	8	87	45	40	6	9	287	309
Garcinia	Manggis	SD	96	6	34	21	15		4	4	52	92	2	37	4	57	536	556

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

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Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter						
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Garcinia	Manggis	PL	88	84	9	7	4		4	2	1	86	84	10	5	1	367	373
Gnetum	A	SK	93	27	58	47			10	3	1	93	25	63	11	1	157	191
Gnetum	B	SD	93	27	65	53			6	2	1	93	23	70	6	1	126	164
Gnetum	C	PL	92	10	77	62			11	3	0	88	0	87	12	0	54	101
Hoya	besar	LV	92	35	46	40	9		4	13	2	80	34	58	5	3	184	215
Hydnocarpus		PL	79	65	19	14	3		11	4	1	75	59	26	14	1	302	316
Irvingia		SD	88	58	17	7	2	33	9	3	13	86	54	20	11	15	397	408
Koompassia		BK	93	24	65	45			4	6	0	87	20	75	5	0	103	143
Leaves		LV	91	32	45	31	16		18	4	1	87	27	51	20	1	201	229
Lithocarpus		SD	88	21	76	55	28	27	2	1	0	88	11	87	2	0	51	99
Lithocarpus		SD	89	76	19	3	2		3	1	1	88	74	21	4	1	319	331
Microcos		SD	94	12	81	59	23		3	3	2	94	12	86	3	2	77	124
Myristica		LV	92	15	72	63	32		9	2	2	90	8	79	10	2	95	138

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

APPENDIX I — NUTRIENT DATA

Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Neesia		SD	91	36	9				11	5	40	87	32	10	12	46	590	596
Palaquium		PL	92	53	38	18	13	2	4	2	3	90	51	42	4	3	249	272
Palaquium		SD	96	25	18	15	8		5	2	51	94	22	19	5	54	594	605
Pandanus	Besar	PT	92	26	59	55	7		3	10	2	83	23	71	4	2	126	165
Pandanus	Besar	PT	94	28	51	36			6	14	1	80	37	55	7	1	185	215
Pandanus	climbing	PT	71	18	68	46			7	7	1	71	0	95	10	1	51	103
Pandanus	wadge	PT	94	8	82	64			4	5	0	94	8	87	4	0	51	99
Pandanus husk		SK	94	14	82	62	26	21	1	2	0	92	8	90	1	1	43	92
Pandanus seed		SD	92	28	53	39	15		6	4	10	88	22	60	6	11	214	246
Pandanus seed		SD	94	22	51	35	13	11	7	5	15	88	18	57	8	17	255	286
Polyalthia		SD	92	10	79	51	8		6	2	3	90	2	88	7	3	62	110
Pternandra		WF	90	41	50	34	15		4	4	1	86	36	58	5	1	174	206
Rengas		LV	92	27	53	36	19		15	4	1	88	21	60	17	1	165	198

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
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Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Santiria		SD	92	46	43	19	8		6	1	4	90	42	47	7	4	234	260
Scaphium		SD	93	48	24	3	0	3	18	3	7	90	45	27	20	8	331	345
Scaphium		SD	92	40	29	3	1		19	4	9	89	36	33	21	10	318	336
Scuntinanthe		PL	93	47	24	19	7		6	5	18	88	46	27	7	20	390	405
Sindora		SD	91	62	24	17	6		7	1	6	90	59	27	7	7	326	341
Sterculia		SD	92	15	69	55	29		12	3	1	89	8	78	13	2	98	140
Syzygium	1	SK/PL	95	25	68	51	22	29	4	2	0	93	21	74	5	0	106	146
Tetramerista		PL/SD	92	38	54	42	10		4	2	2	90	34	60	4	2	167	200
Unknown		SD	94	9	84	61	23		4	2	1	92	3	91	4	1	42	91
Willughbeia		BK	90	44	44	34			5	2	5	88	38	51	5	6	226	254
Willughbeia	1	PL	90	56	27	14	7	7	8	4	6	86	53	31	9	7	309	326
Willughbeia	1	SD	93	66	28	13	7	7	3	1	1	93	64	31	4	1	284	301
Willughbeia	3	PL	90						6	2	0	89						

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

APPENDIX I — NUTRIENT DATA

Genus/ Description	Species/ Description	Part	Dry Matter	Percentage of Dry Matter								Organic Matter	Percentage of Organic Matter					
				TNC	NDF	ADF	Lignin	Cutin	Crude Protein	Ash	Lipid		TNC	NDF	Crude Protein	Lipid OM	Kcal/100 g	Kcal/100 g with NDF
Willughbeia	3	SD	92						3	1	4	91						
Willughbeia	Big Mature	SD	93	66	28	13	7	7	3	1	1	93	64	31	4	1	284	301

Nutrients: TNC = Total Non-Structural Carbohydrates [100-(NDF + CP + lipid + ash)]; NDF = Neutral Detergent Fiber; ADF = Acid Detergent Fiber
Plant Parts: SD = Seed; SC = Seed Coat; PL = Pulp; SK = Skin/husk; BK = Bark; FW = Flower; FB = Flower bud; LV; Leaves; PT = Pith;
WF = Whole Fruit; Kcal assumes 9 kcal/g lipid, 4 kcal/g CP, 4 kcal/g TNC and NDF x 0.543 Kcal/g; * Values > 100% due to high ash content.

APPENDIX II -
DESICCATION AND ELUTION OF URINE ON FILTER PAPER

Desiccation of urine on filter paper in the field:

1. Prepare five 2.5 cm x 2.5 cm square pieces of filter paper (Schlicker & Schloom Item #16110) by writing on each (in pencil) the date, animal code, sample number and aliquot amount.

2. Aliquot 200 µl of urine on each piece of filter paper using a micropipette.

3. Dry samples flat on parafilm or aluminum foil in a sealed plastic container with fresh silica gel. Drying should take place within 12 hours.

4. After drying, pick up pieces of filter paper with forceps and place in slide sheets. Store slide sheets in another sealed container with silica gel.

Elution of filter paper in the laboratory:

1. Using sterilized forceps, fold and place each piece of dried filter paper individually into a 16 x 100 mm test tube.

2. Under the hood, aliquot 5 ml of methanol into each test tube.

3. Cap tubes and refrigerate overnight.

4. Dry samples down under nitrogen.

5. Remove filter paper from test tube using sterlized forceps by grasping the top edge. Clean forceps between samples with methanol.

6. Remove test tubes from drying block immediately after evaporation.

7. Aliquot 2 ml of Tris Assay buffer into each test tube.

8. Vortex each tube for 2 minutes.

9. Place stoppers in tubes.

APPENDIX III -
URINARY RADIOIMMUNOASSAY
PROTOCOL FOR ESTRONE CONJUGATES

Samples

1. Aliquot 0.1 ml of urine eluted from filter paper into 12 x 75 mm assay tubes.

   (The original volume of urine on the filter paper was 200 µl which was dried down and brought up in 2 ml of buffer. Thus, the aliquoted amount is equal to 0.01 ml of undiluted urine).

2. Aliquot 0.3 ml of Tris buffer.

3. Aliquot 0.1 ml of antiserum - Anti-estrone glucuronide (cross-reacts equally with estrone sulphate and estrone glucuronide) (1:4500. D. Collins, Emory University).

4. Aliquot 0.1 ml of tritiated estrone sulphate (6500 cpm, sp. act. 55 Ci/mmol: New England Nuclear).

5. Incubate overnight at 4°C.

6. Add 0.2 ml of Charcoal-dextran (0.625% charcoal Norite A, 0.0625% in 0.1 M-phosphate buffer pH 7.0).

7. Vortex tubes

8. Incubate tubes for 10 minutes at 4°C.

9. Centrifuge for 10 minutes.

10. Decant supernatant into scintillation vials.

11. Add scintillation fluid. Cap vials. Count each vial for 5 minutes on scintillation counter.

Standards: 50-8000 pg/tube estrone sulphate standard (Sigma Chemicals Co.. St. Louis MO)

Tris assay buffer: pH 8.4 (0.1 m Tris, 0.9% NaCl, 0.1% Na N_3, 0.1% gelatin).

APPENDIX IV -
CREATININE PROTOCOL

1. In first 4 wells (A1-A4) of microtiter plate aliquot 0.1 ml of distilled water

2. In second 4 wells (A5-A8) aliquot 0.1 ml of 0.01 Mg/Ml Cr

3. In third 4 wells (A9-A12) aliquot 0.1 ml of 0.03 Mg/Ml Cr

4. In next row aliquot 0.1 ml of urine pools (diluted 1:10) in triplicate for each pool

5. In rest of wells aliquot (in triplicate) 0.1 ml of urine eluted from filter paper.

   (The original volume of urine on the filter paper was 200 µl which was dried down and brought up in 2 ml of buffer. Thus, the concentration is now equivalent to 0.01 ml of undiluted urine.)

6. Using multiple pipetter, aliquot in all wells:
   50 µl NaOH and
   50 µl of picric acid

7. Count on microtiter counter after 45 minute development time.

Reagents

Picric Acid 0.02 N

NAOH 0.75 N