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By: **Susan Lappan**

Abstract

In mammals with biparental care of offspring, males and females may bear substantial energetic costs of reproduction. Adult strategies to reduce energetic stress include changes in activity patterns, reduced basal metabolic rates, and storage of energy prior to a reproductive attempt. I quantified patterns of behavior in five groups of wild siamangs (*Symphalangus syndactylus*) to detect periods of high energetic investment by adults and to examine the relationships between infant care and adult activity patterns. For females, the estimated costs of lactation peaked at around infant age 4–6 months and were low by infant age 1 year, whereas the estimated costs of infant - carrying peaked between ages 7 and 12 months, and approached zero by age 16 months. There was a transition from primarily female to male care in the second year of life in some groups. Females spent significantly less time feeding during lactation than during the later stages of infant care, suggesting that female siamangs do not use increased food intake to offset the costs of lactation. Female feeding time was highest between infant ages 16 and 21 months, a period of relatively low female investment in the current offspring that coincided with the period of highest male investment in infant care. This suggests that male care may reduce the costs of infant care for females in the later stages of a reproductive attempt. The female energy gain resulting from male care was likely invested in somatic maintenance and future reproduction, rather than the current offspring.

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The Effects of Lactation and Infant Care on Adult Energy Budgets in Wild Siamangs (*Symphalangus syndactylus*)

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ABSTRACT In mammals with biparental care of offspring, males and females may bear substantial energetic costs of reproduction. Adult strategies to reduce energetic stress include changes in activity patterns, reduced basal metabolic rates, and storage of energy prior to a reproductive attempt. I quantified patterns of behavior in five groups of wild siamangs (*Symphalangus syndactylus*) to detect periods of high energetic investment by adults and to examine the relationships between infant care and adult activity patterns. For females, the estimated costs of lactation peaked at around infant age 4–6 months and were low by infant age 1 year, whereas the estimated costs of infant-carrying peaked between ages 7 and 12 months, and approached zero by age 16 months. There was a transition from primarily female to male care in

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For female mammals, the energetic cost of reproduction is high, due to the unavoidable costs of gestation and lactation (Trivers, 1972; Clutton-Brock, 1991). Lactation is the most energetically expensive form of parental investment in mammals, increasing daily energy expenditure by up to 150% (Gittleman and Thompson, 1988; Lee et al., 1991; Lee, 1997). Females may compensate for the costs of lactation by increasing food consumption, mobilizing stored energy, or reducing the energy invested in other activities. Increases in feeding time or food consumption (Altmann, 1980; Sauther and Nash, 1987; Dunbar and Dunbar, 1988; Koenig et al., 1997) or shifts to higher quality foods (Sauther, 1994) during lactation have been reported in many primate studies. Female primates may also lose body mass during lactation (Bercovitch, 1987; Pereira, 1993), suggesting that some of the energetic costs of lactation are met through metabolism of stored energy. Mothers have also been observed reducing their activity levels during lactation to conserve energy (Sauther, 1994; Barrett et al., 2006), or adopting mixed strategies (Roberts et al., 1985; Nievergelt and Martin, 1999). Human females have been reported to increase food consumption, to reduce their basal metabolic rate and physical activity, and to metabolize stored fat during lactation (Prentice and Whitehead, 1987; Doufour and Sauther, 2002).

Other forms of parental care may also be costly in terms of energy and time. Carrying an infant or guarding an infant from predators or hostile conspecifics may reduce the energy and time that the individual can invest in other fitness-enhancing activities. For female mammals, the energetic costs of lactation and infant care may be the primary determinant of the interval between breeding attempts, and may therefore have profound implications for female lifetime reproductive success (Trivers, 1972; Clutton-Brock, 1991; Lee, 1997).

In group-living and biparental species, other individuals may also experience time and energy costs as a result of infant care. Where groups travel cohesively, female activity patterns may constrain and be constrained by the activity patterns of other group members, resulting in a patterning of the group's activities that may not be optimal for any individual. Furthermore, females investing heavily in reproduction may redirect energy to infant care that would otherwise be spent in activities such as territorial defense. This, in turn, may change the costs and benefits of these activities for other group members during some or all stages of infant growth. In species with biparental or alloparental care, other group members may also bear direct costs of infant care. For example, male cotton-top tamarins lose up to 11% of their body weight during the period of most intensive infant care (Sánchez et al., 1999; Achenbach and Snowdon, 2002).

The gibbons (family Hylobatidae) have relatively slow life histories for primates of their body size, reaching maturity late (Brockelman et al., 1998) and having

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inter-birth intervals (IBI) ranging from 2.5–5 years under natural conditions (Mitani, 1990; O'Brien et al., 2003; Barelli et al., 2007). As gibbon gestation periods (189–239 days; Geissmann, 1991) represent only a small fraction of this total interval, prolongation of the period of lactation and infant care is primarily responsible for long gibbon IBIs. However, the underlying pattern of energetic investment in gibbons has not been examined in detail. Here, I examine the behavior of wild siamangs (*Symphalangus syndactylus*), the only gibbon species for which biparental care is common, during the postparturition stages of reproduction (lactation, infant care, and maternal recovery) to assess the effects of infant care on adult activities.

Life history theorists describe two alternative female reproductive strategies: *income breeding*, increasing net food intake during a reproductive attempt to offset the costs of reproduction, and *capital breeding*, the use of stored energy to offset the costs of reproduction (Stearns, 1989; Houston et al., 2007). Although a threshold for the delay between energy intake and energy expenditure distinguishing capital from income breeders has not been established, the underlying concept is nonetheless useful in understanding patterns of energy expenditure during reproduction. Parental care by nonmothers may reduce maternal time and energy costs, which may allow females to increase their investment in the current infant (essentially adding to their net “income”), in future infants (adding to their “capital”), or both. Previous studies suggest that male parental care may permit heavy female investment in the current infant in some small-bodied Neotropical primates while also facilitating rapid reproduction (Garber and Leigh, 1997). However, cross-sectional studies of anthropoid primates report that alloparental care is associated with reduced IBI, but not with increased infant survivorship (Mitani and Watts, 1997; Ross and MacLarnon, 2000), suggesting that female primates often allocate the saved energy to future reproductive attempts.

Male siamangs vary in their contribution to infant care, and higher levels of male care are not associated with increases in the total parental contribution to infant care, but rather with reduced female care (Lappan, 2008). Female nonlactational care for the current infant is a significant predictor of IBI (Lappan, 2008), suggesting that female condition may be an important determinant of the timing of reproductive events. The primary goals of this study were to examine the pattern of energy expenditure by male and female siamangs, to determine whether siamangs are better characterized as income breeders or capital breeders, and to determine whether the female energy savings resulting from male care is directed toward the current or future reproductive attempts.

If siamangs are income breeders, then female food consumption should rise sufficiently to offset the increased female energetic expenditure associated with lactation and infant care, whereas if siamangs are capital breeders, then female food intake should be inadequate to offset the costs of reproduction during the most energetically expensive stages of infant care. I predicted that if siamangs are income breeders then the peak in female energy expenditure associated with reproduction should be temporally associated with the period of highest female feeding time, and used a simple model developed by Altmann (1980) to estimate whether female food intake during lactation is adequate to offset the costs of lactation. I also predicted that if male care permits

increased female investment in the current infant, then the timing of peak male care should be associated with a period of high female energetic investment in the current infant. Alternatively, if male care permits rapid maternal recovery, then the highest male investment in infant care should occur during a period of reduced female energetic investment in the current infant and increased female somatic investment.

METHODS

Study site and animals

The Way Canguk Research Area is located in the Bukit Barisan Selatan National Park in southern Sumatra, Indonesia, and encompasses 900 hectares of primary forest interspersed with forest damaged by drought, wind throws, earthquakes, and fire (Kinnaird and O'Brien, 1998; O'Brien et al., 2003). The research area is run collaboratively by the Wildlife Conservation Society-Indonesia Program (WCS-IP) and the Indonesian Ministry of Forestry's Department of Forestry and Nature Conservation (PHKA). Siamangs at this site have been the subjects of behavioral and demographic studies since 1998 (O'Brien et al., 2003; Lappan, 2005; 2008).

Five groups of siamangs were chosen for the study based on proximity to the research camp and the presence of a young infant in the group (Table 1). All individuals were individually recognizable based on facial and body features. I have described the methods by which individual age-classes were assigned elsewhere (Lappan, 2005; 2007). The infant Chelsea's exact birth date is known. For Arjuna, Frannie, and Ganteng, the interval between the last date on which their mother was observed without a clinging infant and the first date on which she was observed with a clinging infant encompassed ≤ 30 days. I estimated birth dates for these infants as the midpoint of this interval. The interval in which Bambang is known to have been born spanned 56 days. When he was first observed, Bambang was the size of a 2-month-old, had a full hair cover, and lacked the slight pinkish tinge otherwise noted for infants of age ≤ 1 month. He was seen playing off of his mother on the first day in which he was observed, a behavior never otherwise observed in an infant under 2 months old. I assume based on these observations that he was born relatively early in the 56-day interval, and estimated his birth date as 7 days after the last date on which his mother was observed without an infant.

Four of the five study groups contained two adult males (Table 1), and in groups A, B, and C both males copulated with the female and provided care for her infant, whereas in group F, only a single male (Freddie) copulated with the female and carried her infant. Analyses of the effects of infant care on adult activities included all care providers.

Behavioral observations

I collected behavioral data reflecting time budgets, diets, infant care patterns, and daily path lengths from adults in five wild siamang groups from shortly after the birth of an infant to infant age 14–24 months to compare male and female time and energy budgets at different stages of infant development and infant care. Differences in the quality of individuals or territories may confound cross-sectional tests of the relationship between investment in infant care and energetic stress. By following

TABLE 1. Composition of study groups in May 2001

Group	Adult male(s)	Adult female	Subadults	Juveniles	Infants
A	Aming, Amung	Amang			Arjuna (m)
B	Bima, Baron	Bambina		Bram (m), Bim-Bim (m)	Bambang (m)
C	Congo, Cokro	Connie		Combre (m)	Chelsea (f)
F	Freddie, Frank	Frida	Fuli (f)	Fifi (f)	Frannie (f)
G	Gatot	Garwoh	Gadis (f)		Ganteng (?)

the same individuals throughout a reproductive attempt, and including intra-individual as well as inter-individual comparisons, I attempted to minimize these confounding effects.

Behavioral data were collected by a team including myself and three field assistants during sleeping-tree-to-sleeping-tree follows of a focal adult and infant. I selected adults as focal individuals on a rotating basis, and each group was followed until each adult had served as a focal individual for 2 days. The study groups were followed on a rotating basis. A team of 2 observers collected instantaneous samples of behavioral data at 5-minute intervals from a focal adult and infant. Behavioral data collected from focal adults included activity, food type, food species (if feeding), estimated distance from the infant, and interaction with the infant (if any). Activities were classified as resting, feeding (reaching for, handling, chewing, or swallowing food), within-crown movement (movement within a feeding tree), travel (all other types of travel), social activities (e.g., vocalization, social grooming, aggression, social play, copulation), and other (e.g., urination, defecation, drinking). As all types of movement will incur energy costs, I subsequently grouped movement within a feeding tree (often referred to as “foraging”) with other types of travel for analyses. Behavioral data collected from infants included activity, food type (if feeding) and infant social partner (if socializing). Other behaviors of interest were also recorded *ad libitum* if they occurred during the interval, but only the data collected during instantaneous samples were included in the data analyses. One observer paced below the focal animal to estimate daily path lengths (DPL). We initiated behavioral data collection upon the focal adult’s departure from the sleeping site or the observers’ first encounter with the focal adult if sleeping site departure was not observed, and collected data until the focal adult entered the subsequent sleeping site.

Statistical analysis

I estimated the proportion of time that individuals spent engaging in specific activities (e.g., feeding, carrying infants, traveling) as the proportion of instantaneous samples in which they were observed engaging in that activity. For statistical analyses of individual activity data, the units employed were daily means of hourly rates unless otherwise noted. Hours were excluded from analyses if more than 50% of data were missing, and days were excluded if fewer than 6 h of data were available. This resulted in the exclusion of 31 observation days, leaving a data set including 290 days of behavioral data (group A, $N = 55$; group B, $N = 70$; group C, $N = 73$; group F, $N = 52$; group G, $N = 40$) for most variables. When mean values are reported, they represent individual means (\pm SE) unless otherwise noted.

Proportional data were arcsine-square-root transformed prior to the use of parametric statistical tests (Zar, 1996). In analyses of interactions between infant

care variables and adult activity patterns, separate analyses were conducted for each individual or group. Where the results were suggestive, the results of these separate analyses were then combined using the Fisher combined probability method (Sokol and Rohlf, 1981).

Estimation of the costs of infant-carrying

Previous studies in a variety of animals (reviewed in Marsh et al., 2006) found that the proportional increase in the energy cost of movement for an animal carrying a load of moderate size is related to the ratio of the animal’s loaded mass to its unloaded mass. This relationship was expressed by Taylor et al. (1980) as

$$\frac{V_{O^2,L}/V_{O^2}}{m_L/m} \cong 1 \quad (1)$$

where $V_{O^2,L}$ is the energy cost (measured as the volume of oxygen consumed) of travel while loaded, V_{O^2} is the energy cost of travel without a load, m is body mass, and m_L is the loaded mass of the animal (i.e., m + the mass of the load, L). This relationship suggests that the proportional increase in the energy cost of locomotion due to the load is

$$\frac{V_{O^2,L} - V_{O^2}}{V_{O^2}} \cong L/m \quad (2)$$

where L is the mass of the load. I estimated the relative energetic cost of infant-carrying for adults using a simple algebraic model based on this observation. I assumed for the purposes of the model that the energetic cost of carrying a clinging infant was zero when the adult was stationary (although there may still be opportunity costs if infant-carrying interferes with other activities, such as feeding or socializing). While adults may expend some energy carrying infants while stationary if the adult is supporting the infant’s weight through muscular action (e.g., if the adult is hanging with a clinging infant), siamang adults generally sit or recline on a substrate when at rest, so violations of this assumption should have only a minimal impact on the fit of the model. I also assumed that the energetic cost of infant-carrying does not vary with speed, locomotor pattern, or substrate. Siamangs are not sexually dimorphic, and males and females do not provide different types of nonlactational care. Therefore, I assumed that the cost per unit of nonlactational care was equal for males and females. I then calculated a simple index of the relative energy cost of infant-carrying for an adult at time t (I_t) using the equation

$$I_t = T_t L_t / m \quad (3)$$

where m is adult body mass (estimated as 10.6 kg; Smith and Jungers, 1997), L_t is infant body mass at time t , and

T_t is the proportion of adult time spent carrying the infant during travel at time t . The mass of infants of each age was estimated using a body mass at birth of 540 gm (Geissmann and Orgeldinger, 1995) and a growth rate of 4.9 gm/day (Leigh and Shea, 1995).

A previous study of infant-carrying in baboons suggested that the costs of infant-carrying may be more sensitive to the distance traveled than the time spent traveling (Altmann and Samuels, 1992). I was not able to measure the actual distance traveled by individuals carrying infants, so I generated a distance-based estimate of the costs of infant-carrying as follows: First, I estimated the distance traveled while carrying the infant in each hour as the proportion of time that an individual spent carrying the infant during travel in that hour multiplied by the distance that the individual traveled in that hour. Then, I summed the hourly distances to generate the estimated daily distance traveled while carrying the infant (D_c). I then substituted D_c/DPL for T_t in Eq. (3) to estimate the increase in travel costs due to infant-carrying ($I_{t,d}$) as:

$$I_{t,d} = \frac{D_c \cdot L_t}{DPL \cdot m} \quad (4)$$

Evaluation of the effects of lactation on adult behavior

I compared male and female DPL, time of departure from and arrival to the sleeping tree, time budget, and percentage of feeding time eating each plant part using the Mann-Whitney U test with individual means as the dependent variable and sex as the factor. To determine the effects of lactation on adult behavior, I compared behavior across a set of infant age classes roughly corresponding to early lactation (infant age 0–4 months), peak lactation (5–9 months), weaning (10–15 months), and post-lactation (16–21 months). The effects of lactational stage on DPL and times of leaving and entering the sleeping tree were examined for each individual using ANOVA. As elephants (*Elephas maximus*) were present in the study area, and elephant-human conflict results in several human fatalities per year in Sumatra, it was not considered safe to enter the forest under conditions of darkness or heavy rainfall. Therefore, the observers sometimes arrived at the sleeping tree after the siamangs had already departed, especially during the early months of the study, when observers were less familiar with the study area and the siamangs' preferred sleeping sites. As a result, many data on time of departure from the sleeping tree are missing, and the observations are biased toward later departures. However, arrival at the sleeping tree typically occurred ~2 h before sunset, so while some of these data are also missing (e.g., in cases where the focal animal was lost, where observations were interrupted due to the approach of an elephant or heavy rain, etc.), the data should not be biased by the observers' avoidance of night observations. The effect of carrying effort on DPL was examined using linear regression with proportion of time spent carrying the infant as an independent variable and DPL as the dependent variable. DPL data were available for 226 days (group A, $N = 44$; group B, $N = 53$; group C, $N = 58$; group F, $N = 32$; group B, $N = 39$). DPL data were not available for groups A, B, and C before infant age 4 months.

The relationship between lactational stage and adult diets was analyzed using a separate General Linear Model (GLM) using SPSS 11.0 (SPSS, Chicago, Illinois) for each plant part, with the mean proportion of feeding time spent eating the plant part as the dependent variable, lactational stage as a fixed effect, and individual identity as a random effect. To examine the effects of lactational stage on female feeding time, I first tested the hypothesis that there was an effect of lactational stage on female feeding time for each female using the Kruskal-Wallis test. I then used Mann-Whitney U tests to test for differences in mean female feeding time between each pair of lactational stages for each female.

Estimation of the feeding time required to offset the costs of lactation

I used a model developed by Altmann (1980) to estimate the percentage of time that a female needs to spend feeding to offset the costs of lactation at a given infant age as

$$F_t = Am^{0.75} + \frac{A(i_0 + t\Delta i)^{0.75}}{E} \quad (5)$$

where F_t is feeding time at time t , m is the mother's body mass, i_0 is the infant's body mass at birth, $t\Delta i$ is the change in the infant's mass between birth and time t , A is a factor converting energy requirements into feeding time, calculated as the mother's feeding time immediately after birth divided by the sum of maternal and infant mass at the time of birth raised to the 0.75 power, and E is a constant reflecting the efficiency of energy transfer via lactation, estimated as 0.8 (Altmann, 1980; Dewey, 1997). I used published maternal (Smith and Jungers, 1997) and neonatal masses (Geissmann and Orgeldinger, 1995) and growth rates (Leigh and Shea, 1995) and field feeding data to estimate the proportion of time that female siamangs would need to spend eating to offset the costs of lactation.

Evaluation of the effects of infant-carrying on adult activity patterns

To explore the relationship between diet and infant care, I used correlation analysis to examine the relationship between the proportion of feeding time spent eating each food type and the proportion of time spent carrying the infant for each adult. I examined the short-term effects of infant-carrying on adult time budgets by dividing the data into samples in which the focal adult was carrying the infant and samples in which the focal adult was not carrying an infant. I then tested the hypothesis that males and females spent less time feeding while carrying infants than while not carrying infants using one-tailed Wilcoxon signed-rank tests with individual mean proportions of time spent in each activity as the dependent variable and infant-carrying status (i.e., carrying or not) as a factor, with samples paired by individual. I then used regression analysis to determine whether the proportion of time that individual females or males spent carrying infants in a given day was a predictor of the proportion of time that they spent feeding in the same day. For females, longitudinal changes in the energy costs of lactation may be associated with changes in feeding time. Therefore, I conducted separate

analyses for the first year of infant life (lactation) and the second year of infant life (postlactation).

RESULTS

The timing of peak lactation and weaning

The costs of lactation vary over time due to the infant's increasing body mass and changes in the infant's ability to obtain nutrition from other foods. The energy cost of lactation is highest at peak lactation (Altmann, 1980), which occurs immediately prior to the onset of consumption of supplemental foods by the infant, when the energy requirements of the growing infant approach the limit of the female ability to supply energy via lactation (Lee et al., 1991). In this study, infants were first observed consuming solids between ages 3 and 9 months, with a median age at first food consumption of 6 months, which suggests that lactation was an important, and probably the only, source of infant nutrition during the first 6 months of life for most infants.

It was often impossible to ascertain the position of the mouths of young infants. However, for infants >12 months old, the position of the infants' mouths could be consistently determined, so the suckling rate could be estimated. The mouths of infants >12 months old were in contact with the nipple in only $0.46 \pm 0.36\%$ of instantaneous samples (mean of individual means \pm SD), but infants were observed consuming plant food in $15.9 \pm 5.9\%$ of instantaneous samples, which suggests that the contribution of lactation to infant nutrition after age 12 months is unlikely to be substantial. Non-nutritive suckling behavior may persist for social reasons among infants obtaining the majority of their nutrition from supplementary foods (Hayssen, 1993; Cameron, 1998). Accordingly, the estimated costs of lactation for siamang females should peak around infant age 4–6 months, and approach zero by infant age 12–15 months.

Female energy investment in infant-carrying was highest in the first year of infant life, whereas male investment was highest in the second year

Females were generally the sole carriers of infants below the age of 10 months. Most males carried older infants at least sometimes. The quantity and timing of onset of male care varied dramatically among males. In groups A, C, F, and G, a male had become the primary care provider by infant age 15, 18, 13, and 12 months, respectively. However, in group B, the contribution of the males to infant care was negligible throughout the study.

Female mean I_t was substantially higher in the first year of infant life than the second, peaking between infant ages 7 and 12 months and approaching zero by age 2 years (Fig. 1A). However, mean male I_t was higher for older infants (see Fig. 1), reaching a peak between ages 16 and 21 months. The distance-based measure of energy expenditure due to infant-carrying, $I_{t,d}$, produced roughly similar results to the time-based measure, I_t (Fig. 1A,B). While the estimated cost of infant-carrying during the peak period of infant care was generally higher for females than for males, the cost of infant-carrying for the most caring male, Freddie, was higher than that for his pair-mate, Frida (Fig. 1C).

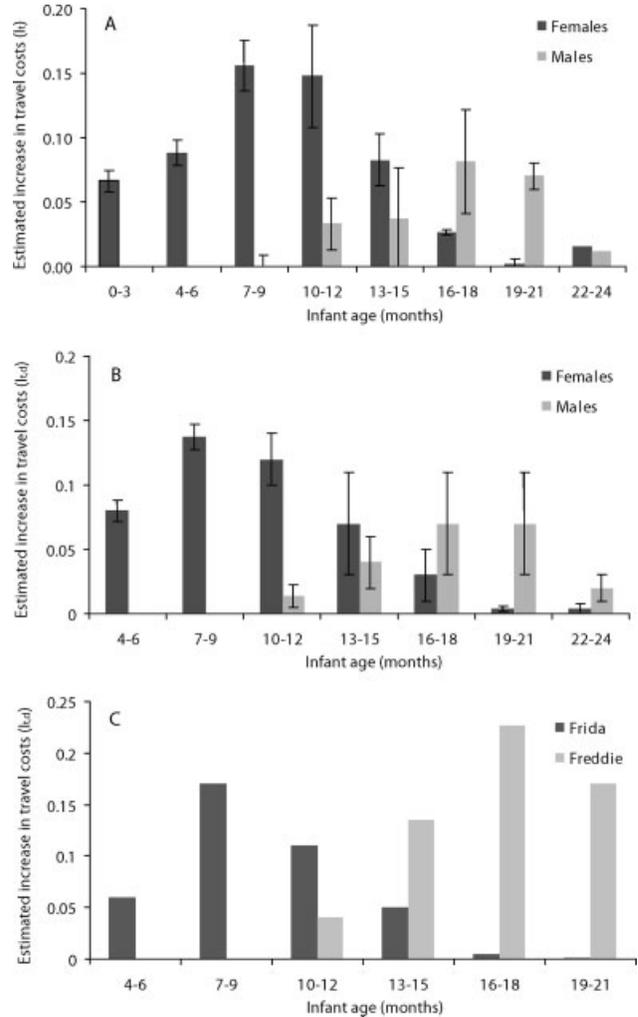


Fig. 1. The estimated relative cost of infant carrying for adult females and males for each three-month infant age class (mean of individual values with SE). (A) Mean values for I_t , a time-based estimate calculated using Equation 3. (B) Mean values of $I_{t,d}$, a distance-based estimate calculated using Equation 4. No distance data were available for the age-class 0–3 months, so only data from ≥ 4 months are presented. (C) Values of $I_{t,d}$ for Freddie, the individual male providing the most infant care, and his pair-mate Frida. Values for the least caring males are zero or close to zero for every infant age class.

DPL did not vary with infant age or adult carrying effort

Mean DPL of the study groups ranged from 1,067 to 1,289 m (Table 2). There was not a significant difference between mean male and female DPL ($U = 22.0$, $N_1 = 5$, $N_2 = 9$, $P = 1.000$). This is not surprising, as male and female siamangs closely coordinate their movements. Therefore, DPL data were grouped for the subsequent analyses. Comparisons of DPL at infant ages 0–4 months, 5–9 months, 10–15 months, and 16–24 months did not detect a significant effect of infant age on DPL for groups A, B, C, and G (group A: $F_{2,43} = 0.395$, $P = 0.676$; group B: $F_{2,51} = 0.488$, $P = 0.617$; group C: $F_{2,54} = 2.702$, $P = 0.077$; group G: $F_{2,38} = 0.415$, $P = 0.663$). Mean DPL differed significantly across infant ages for group F ($F_{2,29} = 7.123$, $P = 0.003$). However, there was

TABLE 2. Mean (\pm SE), minimum, and maximum daily path length (DPL), in meters

Group	Mean DPL	Minimum DPL	Maximum DPL
A ($N = 44$)	1289 \pm 78	396	2933
B ($N = 52$)	1068 \pm 51	402	1927
C ($N = 58$)	1227 \pm 44	482	2114
F ($N = 32$)	1088 \pm 64	457	1800
G ($N = 39$)	1067 \pm 65	441	1915

not a significant effect of carrying effort (estimated as I_t) on adult DPL for any individual (females: Amang: $r = -0.271$, $N = 17$, $P = 0.293$; Bambina: $r = -0.221$, $N = 22$, $P = 0.323$; Connie: $r = 0.099$, $N = 26$, $P = 0.630$; Frida: $r = 0.100$, $N = 13$, $P = 0.745$; Garwoh: $r = 0.252$, $N = 19$, $P = 0.437$; males: Aming: $r = 0.059$, $N = 19$, $P = 0.809$; Amung: $r = -0.589$, $N = 8$, $P = 0.124$; Baron: $r = 0.086$, $N = 13$, $P = 0.780$; Congo: $r = 0.163$, $N = 22$, $P = 0.468$; $P = 0.630$; Freddie: $r = 0.368$, $N = 12$, $P = 0.239$; Gatot: $r = 0.010$, $N = 20$, $P = 0.967$; Cokro and Bima were not recorded carrying infants during travel).

Time of departure from and arrival at the sleeping tree did not vary with lactational stage

The mean time of departure from the sleeping tree for adults was 6:25 \pm 0:01 h (range = 5:40–7:15 h, $N = 181$; females only: 6:25 \pm 0:01 h, range = 5:55–7:00 h, $N = 76$) and the mean time of entrance to the sleeping site was 16:12 \pm 0:02 h. (range = 14:10–17:50 h, $N = 225$; females only: 16:14 \pm 0:03 h, range = 14:10–17:45, $N = 97$). The time of departure from the sleeping site and the time of entrance to the sleeping site did not differ for males and females (departure: $U = 21.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.898$; entrance: $U = 11.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.147$), which is not surprising, as members of a group typically entered and left the sleeping tree within a few minutes of each other. The research station is located <6 degrees of latitude south of the equator, so there is little seasonal variation in sunrise and sunset times. There was not a significant effect of lactational stage on time of departure from the sleeping tree, whether the time of departure was calculated as time of day (Amang: range = $F_{2,5} = 0.453$, $P = 0.659$; Bambina: $F_{2,12} = 1.852$, $P = 0.199$; Connie: range = $F_{2,19} = 1.198$, $P = 0.326$; Frida: $F_{2,9} = 0.596$, $P = 0.577$; Garwoh: $F_{2,14} = 1.909$, $P = 0.191$) or minutes from sunrise (Amang: $F_{2,5} = 0.872$, $P = 0.141$; Bambina: $F_{2,12} = 0.429$, $P = 0.661$; Connie: $F_{2,19} = 0.008$, $P = 0.992$; Frida: $F_{2,9} = 3.318$, $P = 0.097$; Garwoh: $F_{2,14} = 0.032$, $P = 0.745$) for any female. There was also not a significant effect of lactational stage on the time of entrance to the sleeping tree, whether calculated as time of day (Amang: $F_{2,16} = 1.089$, $P = 0.363$; Bambina: $F_{3,23} = 1.051$, $P = 0.392$; Connie: $F_{3,27} = 0.475$, $P = 0.702$; Frida: $F_{3,21} = 1.053$, $P = 0.393$; Garwoh: $F_{2,19} = 0.904$, $P = 0.423$) or minutes before sunset (Amang: $F_{2,16} = 0.476$, $P = 0.631$; Bambina: $F_{3,23} = 1.323$, $P = 0.295$; Connie: $F_{3,27} = 0.393$, $P = 0.759$; Frida: $F_{3,21} = 1.993$, $P = 0.151$; Garwoh: $F_{2,19} = 0.429$, $P = 0.658$) for any female. The total active period (the interval between time of departure from the sleeping tree and time of arrival in the subsequent sleeping tree) did not differ across lactational stages for Amang ($F_{2,5} = 1.032$, $P = 0.422$), Bambina ($F_{2,12} = 1.095$, $P = 0.366$), Connie ($F_{2,17} = 0.659$, $P = 0.530$), or Garwoh ($F_{2,12} = 1.418$, $P = 0.280$). However, the total active period differed across lactational stages for Frida ($F_{2,7} =$

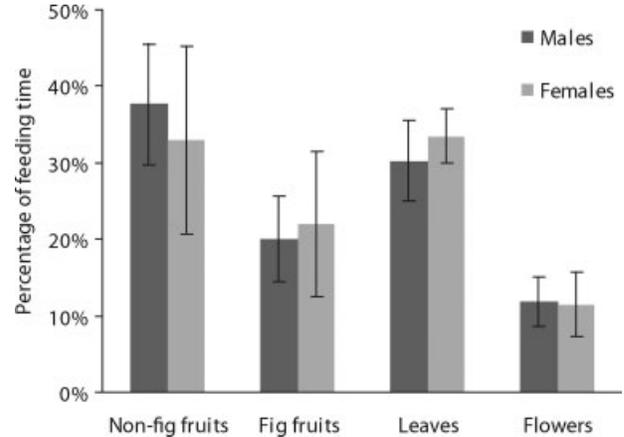


Fig. 2. Adult male and female diets expressed as the mean (\pm SE) of individual mean proportions of feeding time spent feeding on each plant part. The insect component of the diet is not included, as all adults spent <0.01 of their time eating insects.

7.892, $P = 0.016$). Frida had a slightly longer mean active period in the post-weaning stage (10.6 \pm 0.2 h; $N = 4$) than during weaning (9.9 \pm 0.1 h; $N = 5$) or peak lactation (9.3 hours; $N = 1$). However, as the observed differences are small, and not in the direction predicted if females extended the active period during periods of high investment in lactation or infant care, these results do not suggest that females adjust their active periods to compensate for variation in the costs of lactation and infant care across lactational stages.

Male and female diets did not differ

Siamangs spent the vast majority of their feeding time eating fruits, leaves, and flowers. Although siamangs at other sites spend up to 28% of feeding time eating insects (Palombit, 1997), insects comprised a negligible proportion of siamang diets at Way Canguk.

Males and females did not spend significantly different mean percentages of feeding time feeding on any plant part (non-fig fruits: $U = 14.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.298$; fig fruits: $U = 18.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.606$; leaves: $U = 16.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.438$; flowers: $U = 21.0$, $N_1 = 5$, $N_2 = 9$, $P = 0.898$) (see Fig. 2). This is not surprising as males and females typically fed and traveled together throughout the day.

Overall male and female time budgets did not differ

Adult siamangs spent the vast majority of their time feeding, resting, and traveling (Table 3), and males and females in the same group typically ranged together. When all data are included, the difference between mean male and female feeding times did not reach statistical significance ($U = 12$, $N_1 = 5$, $N_2 = 9$, $P = 0.190$). However, female feeding time was slightly higher than male feeding time in four of five groups, and equal to male feeding time in the fifth.

The relationship between lactational stage and female behavioral variables

Female diets did not vary consistently with lactational stage. Siamang diets varied dramatically

TABLE 3. Mean percentage of time that adult siamangs spent in each type of activity (means of individual means \pm SE)

Activity	Males (N = 9)	Females (N = 5)
Feeding	34.0 \pm 1.8	37.3 \pm 1.3
Resting	36.8 \pm 1.8	33.8 \pm 1.4
Traveling	16.8 \pm 0.6	16.9 \pm 0.7
Social	5.2 \pm 0.5	5.4 \pm 0.4
Other	7.3 \pm 0.4	6.6 \pm 0.7

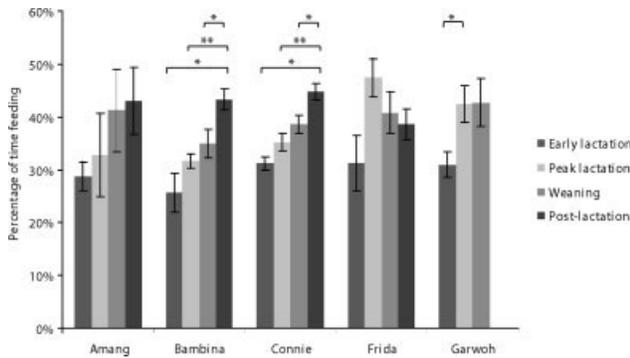


Fig. 3. Mean (\pm SE) proportion of time that each female spent eating during early lactation (0–4 months), peak lactation (infant age 4–9 months), weaning (10–15 months), and post-weaning (16–21 months). * indicates differences that are significant at the $P \leq 0.05$ level. ** indicates differences that are significant at the $P \leq 0.005$ level.

between study months due to variation in the availability of preferred foods. There was not a significant effect of lactational stage on time spent feeding on any type of food (non-fig fruits: $F_{2,7.3} = 0.825$, $P = 0.475$; fig fruits: $F_{2,7.5} = 0.368$, $P = 0.704$; leaves: $F_{2,7.2} = 0.047$, $P = 0.955$; flowers: $F_{2,7.1} = 0.749$, $P = 0.507$). This suggests that females do not use a shift to higher-quality food items to offset their increased energy expenditure during energetically demanding stages of reproduction.

Females spent more time eating during weaning and the postlactational period than during lactation. Females spent a mean (mean of individual means \pm SE) of 29.6 \pm 2.4% of their time feeding in early lactation, 37.9 \pm 3.0% during peak lactation, 39.6 \pm 3.0% during weaning, and 42.4 \pm 2.6% in post-lactation (see Fig. 3). The proportion of female time spent feeding was significantly different at different lactational stages for Amang, Bambina, and Connie (Amang: $X^2 = 12.032$, $df = 3$, $P = 0.007$; Bambina: $X^2 = 7.860$, $df = 3$, $P = 0.049$; Connie: $X^2 = 25.556$, $df = 3$, $P = 0.001$), but not for Frida ($X^2 = 6.991$, $df = 2$, $P = 0.278$) or Garwoh ($X^2 = 0.071$, $df = 2$, $P = 0.965$; Fig. 3).

Results of detailed comparisons among lactational stages for individual females and for all females combined are in Table 4. Individual comparisons did not detect significant differences in the proportion of female time spent feeding at peak lactation and weaning for any female, and the combined result does not suggest that there are significant differences in female feeding time between peak lactation and weaning (Table 4). For comparisons of feeding time between early and peak lactation, the combined result approached, but did not reach significance, although the result was significant for one female (Table 4). However, several individual

TABLE 4. Comparisons of the proportion of female time spent feeding at infant ages 0–4 months (early lactation), 5–9 months (peak lactation), 10–15 months (weaning), and 16–21 months (postlactation)

Infant age class (months)	Female	U	N	P
Early lactation vs. peak lactation	Amang	4	2,7	0.500
	Bambina	11	5,7	0.343
	Connie	4	2,8	0.400
	Frida	5	8,4	0.073
	Garwoh	3	8,4	0.028*
	Combined	$2\sum \ln P = 17.74$		0.059
Early lactation vs. weaning	Amang	3	2,8	0.267
	Bambina	8	5,8	0.093
	Connie	2	2,10	0.121
	Frida	14	8,6	0.228
	Garwoh	14	8,8	0.065
	Combined	$2\sum \ln P = 21.723$		0.017*
Early lactation vs. postweaning	Amang	1	2,7	0.111
	Bambina	1	5,6	0.009*
	Connie	0	2,8	0.044*
	Frida	17	8,6	0.414
	Garwoh	14	4,8	0.002*
	Combined	$2\sum \ln P = 19.110$		0.002*
Peak lactation vs. weaning	Amang	21	7,8	0.463
	Bambina	20	7,8	0.397
	Connie	25	8,10	0.203
	Frida	7	4,6	0.352
	Garwoh	14	4,8	0.808
	Combined	$-2\sum \ln P = 7.883$		0.641
Peak lactation vs. postweaning	Amang	13	7,7	0.165
	Bambina	2	7,6	0.005*
	Connie	4	8,8	0.002*
	Frida	5	4,6	0.171
	Garwoh	14	4,8	0.002*
	Combined	$-2\sum \ln P = 17.764$		0.023*
Weaning vs. postweaning	Amang	22	8,7	0.536
	Bambina	8	8,6	0.043*
	Connie	15	10,8	0.027*
	Frida	14	6,6	0.589
	Garwoh	14	6,6	0.589
	Combined	$-2\sum \ln P = 15.822$		0.045*

* Indicates $P < 0.05$.

results and the combined results suggest that females in this population spent significantly higher mean proportions of time feeding during weaning and post-weaning than during early lactation, and a significantly higher proportion of time feeding postweaning than during weaning or peak lactation (Table 4; Fig. 3).

The positive changes in feeding time displayed by most females in this study as their infants grew older corresponded to negative changes in resting time. As time spent feeding is time not spent resting, however, it is unclear whether the change in female resting time as infants grew older represents a female strategy independent from the change in feeding time.

Female food intake during lactation does not offset the energy costs of lactation

Feeding times for female siamangs in this study in the first 12 months of infant life were consistently lower than the feeding times predicted from Altmann's model (see Fig. 4). However, the differences observed between actual and expected feeding times were small.

The relationship between nonlactational care and adult behavior

Adult diets were not affected by infant care. Results of the correlation analyses are presented in Table 5.

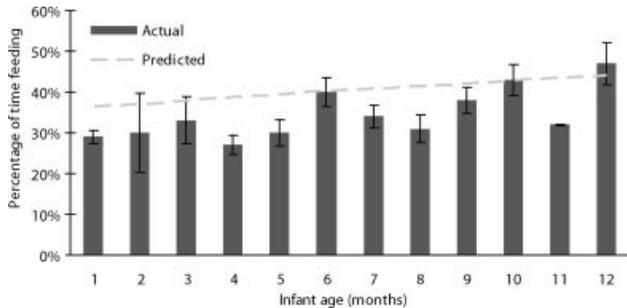


Fig. 4. Comparison of the mean (\pm SE) proportion of time spent feeding by lactating siamang females in this study and the estimated proportion of time that females should spend eating if the costs of lactation are entirely offset by increased feeding time. Calculations followed the model of Altmann (1980), using published mean adult body mass (Smith and Jungers, 1997), neonatal body mass (Geissmann and Orgeldinger, 1995), and growth rate (Leigh and Shea, 1995) estimates.

Although 5 of the 48 individual analyses resulted in significant correlations at the $P < 0.05$ level (slightly more than the 2.5 “significant” results that would be expected by chance given the number of analyses conducted), the slopes were not consistently positive or consistently negative for individuals of the same sex for any food type. These results do not suggest that individuals of either sex shifted their diets to higher-quality foods to offset the costs of infant care.

Nonlactational care is associated with reduced adult feeding time. There were dramatic differences in activity profiles of adults of both sexes when they were carrying infants and not carrying infants (see Fig. 5). Both females and males spent significantly less time feeding (females: $Z = -2.023$, $N = 5$, $P = 0.031$; males: $Z = -2.366$, $N = 7$, $P = 0.008$), and more time traveling (females: $Z = -2.023$, $N = 5$, $P = 0.031$; males: $Z = -2.366$, $N = 7$, $P = 0.008$) while carrying infants than while not carrying infants. As the primary function of infant-carrying is transportation, it is not surprising that adults were more likely to carry infants while traveling than while not traveling. However, if data collected while the adult was traveling are excluded, both females and males still spent less time feeding while carrying infants than while not carrying infants (females: $Z = -2.023$, $N = 5$, $P = 0.031$, males: $Z = -2.201$, $N = 6$, $P = 0.016$). This suggests that infant-carrying may interfere with adult feeding, at least in the short term.

In the first year of infant life, the mean proportion of time that a female spent carrying her infant was not a significant predictor of the mean proportion of time that the same female spent feeding on the same day for Amang, Bambina, Connie, and Frida (Amang: $r = -0.462$, $N = 12$, $P = 0.112$; Bambina: $r = -0.395$, $N = 18$, $P = 0.104$; Connie: $r = -0.184$, $N = 15$, $P = 0.357$; Frida: $r = -0.374$, $N = 12$, $P = 0.215$). However, the mean proportion of time that Garwoh spent carrying her infant was a significant predictor of the mean proportion of time that she spent feeding on the same day ($r = -0.604$, $N = 15$, $P = 0.001$), and the relationship was negative for all five females. The combined result for the five females suggests that the mean proportion of female time spent carrying infants was a significant predictor of female feeding time in the first year of infant life ($-2\ln P = 27.855$, $df = 10$, $P = 0.002$). During the sec-

ond year of infant life, the proportion of female time spent carrying her infant was not a significant predictor of feeding time for any female (Amang: $r = 0.128$, $N = 12$, $P = 0.566$; Bambina: $r = 0.300$, $N = 11$, $P = 0.336$; Connie: $r = -0.208$, $N = 15$, $P = 0.458$; Frida: $r = 0.307$, $N = 9$, $P = 0.964$), and the combined result suggests that the mean proportion of time spent carrying infants was not a significant predictor of female feeding time in the second year of life ($-2\ln P = 4.616$, $df = 8$, $P = 0.797$).

The mean proportion of time that a male spent carrying an infant was not a significant predictor of the mean proportion of time that the male spent feeding on the same day for any male (Aming: $r = 0.075$, $N = 24$, $P = 0.722$; Amung: $r = 0.211$, $N = 9$, $P = 0.586$; Bima: $r = -0.050$, $N = 25$, $P = 0.809$; Baron: $r = 0.164$, $N = 16$, $P = 0.529$; Congo: $r = 0.180$, $N = 30$, $P = 0.334$; Freddie: $r = -0.411$, $N = 21$, $P = 0.057$; Gatot: $r = -0.346$, $N = 20$, $P = 0.135$). However, males differed dramatically in the proportion of time that they spent carrying infants (Lappan, 2008), and it is not surprising that there was not a detectable effect of infant care on the time budgets of males providing little care. If only the results from Freddie and Gatot, the males that spent by far the largest proportions of their time caring for infants (Lappan, 2008) are included, then the combined result suggests that the mean proportion of time males spent carrying infants is a significant predictor of the proportion of male time spent feeding ($-2\ln P = 9.734$, $df = 4$, $P = 0.045$). These results suggest that small quantities of infant care do not disrupt male feeding, but that for males providing extensive care, infant care may result in reduced male feeding time.

DISCUSSION

Lactation is the most energetically expensive component of a reproductive attempt for female mammals. Chivers and Raemaekers (1980) reported that siamangs begin weaning as early as age 3 months, and that weaning is complete by around age 1 year. The results of this study also suggest that infants obtain the vast majority of their nutrients from plant foods after age 1 year (although the effects of night suckling could not be quantified). I estimated that the energy cost of lactation for siamang females peaks around age 4–6 months, and approaches zero by age 1 year. The estimated cost of infant-carrying for females in this study also peaked in the second half of the first year of life. As lactation and infant-carrying are the most energetically expensive components of reproduction for females, the total cost of reproduction should be highest for females between infant ages 6 and 10 months.

Clinging infants may reduce the ability of adults to eat efficiently, both by increasing the costs of foraging movements and by interfering with adult activities through their own movements, especially as the infants grow older and more active. Previous studies have reported a negative effect of infant-carrying on adult feeding efficiency or feeding time in primates (e.g., Altmann, 1980; Goldizen, 1987). In this study, I found that both females and males spent less time feeding while carrying infants than while not carrying infants, even if time spent traveling was excluded. Most females spent more time feeding during weaning and post-lactation than early and peak lactation, and lactating females spent more time resting than other adults did. As

TABLE 5. Results of correlation analyses of the relationship between the proportion of time spent carrying infants and the proportion of feeding time spent eating each type of plant food

	Nonfig fruit		Fig fruit		Leaves		Flowers	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Females								
Amang (<i>N</i> = 26)	-0.076	0.714	0.038	0.853	-0.171	0.404	0.194	0.343
Bambina (<i>N</i> = 30)	0.450	0.013*	-0.493	0.006*	0.178	0.347	-0.321	0.084
Connie (<i>N</i> = 32)	-0.076	0.681	0.102	0.578	0.194	0.287	-0.370	0.037*
Frida (<i>N</i> = 22)	-0.504	0.017*	0.020	0.929	-0.259	0.245	0.636	0.001
Garwoh (<i>N</i> = 20)	0.112	0.637	-0.039	0.870	0.061	0.798	-0.117	0.625
Males								
Aming (<i>N</i> = 24)	-0.073	0.736	-0.111	0.606	0.045	0.835	0.125	0.561
Amung (<i>N</i> = 9)	0.258	0.502	-0.169	0.663	0.314	0.410	-0.322	0.398
Bimo (<i>N</i> = 21)	0.197	0.391	-0.344	0.127	0.064	0.784	0.210	0.362
Baron (<i>N</i> = 16)	-0.162	0.549	0.488	0.055	-0.260	0.331	-0.053	0.845
Congo (<i>N</i> = 31)	0.005	0.980	-0.280	0.127	0.078	0.678	0.167	0.368
Freddie (<i>N</i> = 22)	-0.168	0.455	0.288	0.194	-0.082	0.716	-0.439	0.041*
Gatot (<i>N</i> = 20)	-0.068	0.777	0.225	0.399	-0.347	0.134	-0.099	0.833

* Indicates $P < 0.05$.

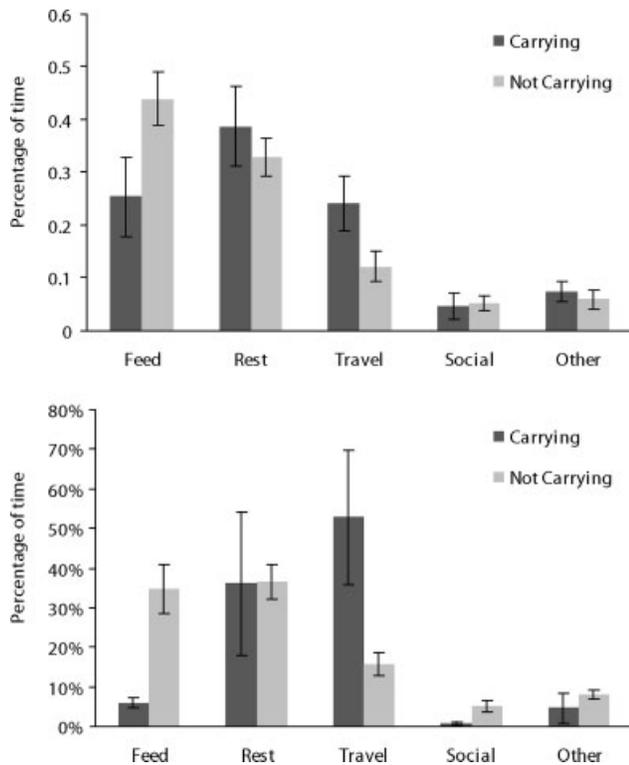


Fig. 5. Comparison of the means (\pm SE) of individual mean proportions of time that females (above) and males (below) spent engaging in each activity while carrying infants and while not carrying infants.

infants are carried by their mothers much of the time during lactation, females may not have been able to compensate behaviorally for the negative effects of infant-carrying on feeding time (e.g., by feeding more while not carrying infants).

Moderate variation in female nutritional status does not affect the volume or nutritional quality of milk produced in humans (Prentice et al., 1983) or other nonhuman primates (Roberts et al., 1985; Nievergelt and Martin, 1999). The results of this study, including both the calculations using Altmann's (1980) model and the fact that female feeding

time was lower during early and peak lactation than post-lactation suggest that female siamangs may have an inadequate food intake during lactation to offset the energy costs of lactation. Females appeared thin in the months after giving birth, although the postpartum loss of substantial quantities of hair on their abdomens may have been a confounding factor. Carpenter (1940) also noted that lactating female white handed gibbons (*Hylobates lar*) were often very lean. This suggests that gibbon females may sometimes sacrifice somatic investment (and therefore future reproduction) to maintain an optimal level of investment in the current reproductive attempt. However, changes in activity patterns and maternal metabolic rates may also offset some of the energetic costs of lactation (Prentice and Whitehead, 1987; Doufour and Sauther, 2002). Furthermore, the difference between predicted and actual feeding times was relatively small ($<10\%$ in every month; Fig. 4) and is likely to have been within the margin of error for Altmann's model. Altmann's model makes a number of simplifying assumptions, including that the rate of nutritional intake per unit of feeding time is constant (i.e., that the quality of food and that the rate of food intake do not differ over time). The rate of food intake was not measured in this study, but a concurrent study involving four of the same groups did not detect a sex difference in siamang food intake rates (A. Roshyd, personnel communication). I found no evidence of a systematic shift in the types of foods included in female diets during any stage of infant growth: all study adults consumed substantial quantities of high-energy non-fig fruits during every stage of reproduction. However, siamang diets do vary over time in response to changes in the availability of preferred plant foods, and different species of plant foods are consumed in different months. Little is known about the nutritional content of most siamang foods. More precise measures of food intake and quantification of the energy content of foods will be required to detect subtle changes in energy intake over time.

The siamangs left their sleeping sites prior to the arrival of observers on a number of occasions, resulting in missing data. Therefore, my estimate of the time of departure from the sleeping tree is biased toward later departures. Furthermore, the strength of this bias varied over time, since the time of the observers' arrival at the sleeping site was affected by weather (departures were often delayed on mornings with heavy rain) and observer

experience (our travel time to the sleeping trees may have decreased as we became more familiar with the research area). Nonetheless, I do not believe that a substantial effect of lactational stage on siamang times of departure from the sleeping site was obscured by the missing data. Reports from other study sites where observers consistently arrived at the sleeping site prior to first light do not suggest pronounced variation in departure times relative to the time of sunrise (Chivers, 1974; Palombit, 1992). Departures from the sleeping tree at other sites typically occurred within a few minutes of sunrise (Chivers, 1974), which suggests that most missed departures in this study were probably missed by only a few minutes, and when siamangs were discovered to have left the sleeping tree prior to the arrival of observers, they were typically located very near to the sleeping tree, which is consistent with this interpretation.

I employed a simple model to estimate the energy costs of infant-carrying, assuming that the costs of travel while carrying an infant are a function of mass alone, disregarding possible effects of speed, substrate, or locomotor pattern, and that there is a linear relationship between the ratio of infant to adult body mass and the costs of infant-carrying. These assumptions are unrealistic, given the complex three-dimensional environments in which gibbons live. Gibbons move by brachiating about 80% of the time (Andrews and Groves, 1976), and the actual energy costs of brachiation are poorly understood and probably vary with substrate and speed of travel (Bertram, 2004). Brachiation has the potential to be an efficient form of locomotion (Preuschoft and Demes, 1984), but the only study actually measuring energy expenditure in brachiating animals reported relatively high energy output (Parsons and Taylor, 1977). Infants may be carried more when the speed of travel is higher (Altmann and Samuels, 1992; Kramer, 1998) confounding the relationship between carrying time or distance and energy expenditure, and changes in load may affect the preferred speed of travel (Wickler et al., 2001), which may in turn affect the cost of travel. Ranging patterns of adults carrying infants may also be constrained by the movements of other party members, particularly juveniles (Pontzer and Wrangham, 2006). Therefore, the relationship between the ratio of infant to adult body mass and energy expenditure is unlikely to be simple. Accordingly, my calculations will provide only a crude index of actual energy expenditure. They should, however, comprise a reasonable approximation of the overall pattern of temporal variation in energy expenditure associated with infant-carrying.

In a careful analysis of the energy costs of self-maintenance, travel, and reproduction for female baboons, Altmann and Samuels (1992) found that baboon mothers carry their infants long distances during rapid travel even after the proportion of time that they spend carrying their infants during travel has declined substantially, which suggests that distance carried, rather than the proportion of time spent carrying infants, may be the best currency for examining the effects of infant-carrying on adult energetics. However, in my study, estimates of the cost of infant-carrying based on a rough approximation of the distance carried did not differ substantially from estimates based on the proportion of time that adults spent carrying the infant.

Altmann and Samuels' (1992) model of maternal and infant energy expenditure predicts a tradeoff between

the cost of lactation and infant-carrying: mothers that carry their infants less (thus reducing the energy costs of locomotion) will incur increased costs of lactation that more than offset the energy savings for as long as their infants are primarily dependent on the mother for nutrition. Similarly, Kramer's (1998) examination of energy expenditure by human mothers suggests that most mothers should carry their infants while walking at the average adult walking speed until infant age 2–3 years, but that the optimal age at which mothers should encourage independent walking by their children declines when the children receive more supplemental nutrition. For siamang mothers, forcing infants to travel independently during the first year of life is probably not an option, as small, uncoordinated infants are probably not capable of brachiating for long distances across the uneven and discontinuous substrate of the forest canopy. However, even if they could do so, it is doubtful that their movement would be sufficiently energy-efficient to benefit their mothers during the period of lactation. Even during the second year of life, infants were frequently carried during long-distance travel, and when traveling independently, sometimes required adult assistance to cross gaps in the canopy.

The contributions of most males in this study to infant care were small, and unlikely to be associated with substantial time and energy costs. However, males spent significantly less time feeding while carrying infants, and analyses of the relationship between infant-carrying and feeding time for the most caring males detected a significant negative relationship between male infant-carrying time and male feeding time, suggesting that infant care can under some sets of circumstances affect male energy budgets. Males also experienced increased costs of locomotion due to the added weight of the growing infant. Therefore, during periods of extensive male care, male daily energy expenditure is likely to have increased, while feeding time decreased. Disruption of maintenance activities (Price, 1992) and weight loss of up to 11% of total body mass (Sánchez et al., 1999) have been reported in captive male cotton-top tamarins (*Saguinus oedipus*) during the period of most extensive infant care. At the age of 1 year, infant siamangs have a body mass approximately 22% of that of adult males, comparable with the ratio of neonate to adult body mass in *Saguinus*. As male siamangs carried infants for a substantially smaller proportion of time than did male tamarins, the total energetic cost of infant care for siamangs should be substantially lower. Nonetheless, the results of this study suggest that the most caring siamang males may experience substantial costs of infant-carrying. Indeed the costs of carrying infants for some males may equal or exceed those for their pair-mates (Fig. 1C).

In most study groups, males started to carry infants during or after weaning. Therefore, any energetic savings that the female experienced as a result of male "help" were likely directed to somatic investment, rather than the current reproductive attempt. Longitudinal female activity profiles are consistent with capital breeding—energy storage prior to conception and partial reliance on stored energy to offset the costs of lactation. There is no evidence of breeding seasonality in siamangs, and IBIs vary among females and populations. Therefore, the timing of conception by siamang females is likely to be determined in large part by body condition, as has been reported in other primate species (e.g., Koenig et al., 1997; Richard et al., 2000; Tardif et al.,

2003) including humans (Doufour and Sauther, 2002; Ellison, 2003).

Siamangs share a set of unusual social features with humans, including pair-bonding and male care of older offspring. Although male parental care is essential for infant survival in most biparental anthropoids, both siamang and human females can successfully rear offspring without substantial direct male assistance, which suggests that alternative mechanisms must have been responsible for the evolution of male parental care in both species. The results of this study suggest such a mechanism: male care may permit females to reduce their energetic expenditure in the current reproductive attempt without compromising offspring fitness, allowing females to produce offspring more rapidly and enhancing the fitness of both parents.

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