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# Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*)

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Mammalian females generally carry the bulk of reproductive costs. They gestate for relatively long periods of time and provide the majority of parental care for dependent offspring. For this reason, many studies have examined how females deal with the energetic costs of reproduction. Here, we examine the influence of reproductive state on activity budgets, diet quality, and sociality in free-living female chimpanzees (*Pan troglodytes*) at Gombe National Park, Tanzania. After controlling for dominance rank, we found that pregnant and lactating females consumed higher quality foods than nonpregnant, nonlactating females. However, pregnant females also traveled less. This result did not reflect differences in sociality, as the pregnant female group sizes included in our analyses were comparable to those in other reproductive categories. *Key words:* chimpanzees, Gombe National Park, lactation, pregnancy, reproductive energetics. *[Behav Ecol]*

Mammalian females must balance the energetic demands of raising offspring with their own survival and future reproductive success. Both gestation and lactation carry significant costs for females, but lactation is more costly (e.g., house mouse: Konig et al. 1988; roe deer: Clutton-Brock et al. 1989). Studies estimate that the amount of energy required (calories consumed) by female mammals increases 20%–30% during gestation and 66%–188% during lactation (Gittleman and Thompson 1988; Clutton-Brock 1991) but primates generally fall on the lower end of that range (Dufour and Sauther 2002). They have longer gestation periods, produce more dilute milk, and have slower postnatal growth rates than other mammals of a similar body size (Martin 1984, 1995; Oftedal and Iverson 1995). These trends reflect primate life history strategy and likely evolved so that individuals can reproduce successfully even when resource availability fluctuates by spreading the costs out over a longer period (Charnov 1993; Aiello and Key 2002). Primate females may therefore have less dramatic daily behavioral changes during reproduction than those observed in other species whose daily costs are much higher. In this study, we examine how female chimpanzee (*Pan troglodytes*) behavior changes during reproductive efforts.

Primate females (including humans) have several adaptations through which they compensate for the energetic demands of reproduction (reviewed in Dufour and Sauther 2002). Increasing caloric intake is a common strategy. Many studies in free-living populations have demonstrated that pregnant and lactating females increase feeding time, particularly during lactation, the most costly part of the reproductive schedule (yellow baboons: Altmann 1980; Barton 1989; ring-tailed lemurs: Sauther 1994). For example, lactating hanuman langurs spent more time feeding than their nonlactating counterparts (Koenig et al. 1997). In other species, females consume higher quality foods during reproductive efforts (squirrel monkeys: Boinski 1988; red-ruffed lemurs: Vasey 2004). Pregnant muriquis spent less time feeding overall but had a better diet typified by consuming more fruits and flowers (Nogueira 1996).

Beyond increasing caloric intake, females can adopt other strategies to offset reproductive costs. Many mammals metabolize fat stores and lose weight during lactation (McFarland 1997). In extreme cases, individuals can rely entirely on fat metabolization. Elephant seals lose about 42% of their body mass during a short 26.2-day lactation period (Costa and Genrty 1986). This is termed a "capital strategy" for reproduction and differs from that often observed in "income breeders" such as rodents in which daily energy intake almost entirely dictates successful lactation (Jönsson 1997). Primates are thought to use a mixed strategy because they have been observed to increase caloric intake as described above but also have a higher adipose deposition than nonprimate species of a similar size. Females can also offset reproductive costs by reducing energy expenditure directly through a lower basal metabolic rate or reduced physical activity. For example, captive lactating baboons on a restricted diet (Roberts et al. 1985) and lactating wild green monkeys (Harrison 1983) were less active. Women may also adopt this strategy under some conditions (Hurtado and Hill 1990; Panter-Brick 1993). A study among the Hiwi in Venezuela similarly found that pregnant and lactating women worked less and acquired less food than their nonreproductive counterparts (Hurtado and Hill 1990). However, it should be noted that human females are different from other nonhuman primates because other individuals can provide supplementary food.

In this study, we investigate reproductive energetics in free-living female chimpanzees at Gombe National Park, Tanzania. East African chimpanzees (*Pan troglodytes schweinfurthii*) exhibit the typical chimpanzee fission–fusion grouping patterns whereby they form temporary subgroups (or "parties") within a permanent community (Goodall 1986). Chimpanzees are ripe-fruit specialists, and party sizes have been tied to resource availability with larger parties forming when food is more

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abundant (e.g., Matsumoto-Oda et al. 1998). The female sexual cycle lasts about 32–36 days (Tutin 1979). Females exhibit conspicuous sexual swellings for about 10–13 days during which they are sexually receptive, and they ovulate when maximally tumescent (Deschner et al. 2003; Emery Thompson 2005). Male chimpanzees do not provide direct parental care. The average interbirth interval for female chimpanzees when the previous infant survives is approximately 5 years (Goodall 1986; Kappeler and Pereira 2003), and lactation lasts approximately 1464 days (Goodall 1986; reviewed in Key 1998). Females spend much of their time alone, ranging in small core areas to which they have high site fidelity (Budongo Forest, Uganda: Fawcett 2000; Gombe: Wrangham and Smuts 1980; Williams, Pusey, et al. 2002; Murray et al. 2007; Kanyawara, Kibale National Park, Uganda: Wrangham et al. 1992; Emery Thompson et al. 2007; and Mahale National Park, Tanzania: Hasegawa 1990). However, it has been well documented that sexually receptive females are more gregarious (Goodall 1986; Williams, Liu, and Pusey 2002) and travel further (Wrangham and Smuts 1980) than nonreceptive females. Pregnant females, in particular, have been shown to be less social (Goodall 1986; Nishida 1990), especially just before parturition (Pusey et al. 2008).

Though several chimpanzee studies have described how female behavior changes with sexual receptivity, fewer have examined behavioral changes when pregnant or lactating. In this study, we analyze 31 years of long-term data to examine how females adjust their behavior to compensate for the energetic demands of reproduction. We test for differences in traveling budgets, feeding time, diet quality, and sociality and compare pregnant, lactating, and nonpregnant, nonlactating (NPNL) females. We hypothesize that behavioral differences will be most pronounced during lactation, which is expected to be the most costly part of the reproductive cycle based on studies in numerous mammalian taxa.

## METHODS

### Study site and study population

Gombe National Park is a small park (35 km$^2$) situated on Lake Tanganyika in western Tanzania. Its habitat ranges from evergreen forests in the valleys to grasslands on the upper ridges (Clutton-Brock and Gillett 1979). This study focuses on females in the Kasekela community, which has been studied continuously since the 1960s. Historically, the community has ranged in size from 38 to 64 individuals, with 11–25 adult females and 6–15 adult males (adult age $>$ 12 years old). It currently contains 64 individuals with 25 adult females and 13 adult males.

### Behavioral data

Tanzanian field assistants and researchers have conducted full-day follows on Kasekela community members since 1973 (Goodall 1986). Full-day follows include tracking one individual from night nest to night nest and recording party composition and location every 15 min. Although the goal is to complete a full day of data collection, some follows are shorter when a target is lost or when field staff search for new individuals. The assistants record feeding data continuously, including bout length and food part (e.g., fruit, leaves, and pith), and dominance interactions throughout the follow. Our analyses spanned 1974–2004 and included 19 080 h of data (2550 h on NPNL, 2890 h on pregnant, and 13 640 h on lactating females) from 2382 follows (337 h on NPNL, 382 h on pregnant, and 1663 h on lactating females).

Dominance ranks were based on the outcome of decided aggressive interactions and the direction of pant grunts, submissive vocalizations that function as reliable indicators of dominance in chimpanzees (Bygott 1979). Categorical ranks (high, middle, and low) have been reported elsewhere for the study period (Pusey et al. 1997; Murray et al. 2006, 2007). Table 1 summarizes our metric of analysis (female year) by reproductive state and dominance rank and also gives the number of different females included in each state/rank combination.

**Table 1**

**Summary of data included in analyses**

| Reproductive state | Dominance rank<br>High | <br>Middle | <br>Low | Total female years |
|---|---|---|---|---|
| NPNL | 6 (4) | 9 (6) | 11 (5) | 26 |
| Pregnant | 10 (4) | 9 (6) | 2 (2) | 21 |
| Lactating | 30 (6) | 42 (12) | 18 (8) | 90 |
| Total female years | 46 | 60 | 31 | 137 |

We give the number of female years (our unit of analysis) by reproductive category and dominance rank. Individual females can appear in the data set more than once, but we control for repeated measures in our analyses. The number of different females in each combination is provided in parentheses.

### Behavioral metrics

To provide a baseline for how female behavior changes with reproductive state, we compared behavioral metrics between NPNL, pregnant, and lactating females. Because we were interested in evaluating the effects of reproductive state only, we excluded follows with the potential confound of sexual state. It has been well documented that sexually receptive females change their social and ranging patterns at Gombe by ranging further and traveling in larger parties (Wrangham and Smuts 1980; Goodall 1986; Williams, Liu, and Pusey 2002). We therefore excluded follows during which a female was maximally tumescent when calculating the metrics described below. We assigned pregnancy by calculating backward from birthdates. We categorized females as lactating from the time they gave birth until the time they resumed cycling.

### Travel budget

We calculated travel budgets as the percentage of 15-min point samples in which the female was traveling. Although cumulative day range would be the most direct way to estimate daily energy expenditure, these data were limited for some females who were infrequently followed for the entire day (particularly low ranking and pregnant individuals). However, we found that the percentage of the follow spent traveling correlated well with day range for follows that were nest-to-nest (simple linear regression of day range on travel budget: $R^2 = 0.35$, $P < 0.00001$). We therefore considered travel budget as a good indicator of cumulative day range and energy expenditure.

### Feeding budget

Because feeding data are collected continuously throughout a follow, the feeding budget was calculated as the percentage of observation time in which the female was feeding.

### Diet quality

Chimpanzees are ripe-fruit specialists. We therefore followed the precedence of other studies (e.g., Conklin-Brittain et al.

1998; Gilby and Wrangham 2007) to estimate diet quality from fruit consumption; more fruit corresponded to a better diet. Diet quality was calculated as the total time spent feeding on fruits divided by the total time spent feeding.

### Sociality

Party size can influence travel and feeding patterns; larger parties travel further and spend less time feeding (Wrangham 2000; Williams, Liu, and Pusey 2002; Murray et al. 2006). We therefore tested for differences in sociality to ensure that significant results did not reflect grouping patterns by reproductive category. We calculated the average party size for a female within a given state and year. Party size was determined for each 15-min point sample and then averaged over the interval of interest.

### Statistical analyses

To account for temporal variation in food availability, we summarized all of our metrics by year because previous analyses on this data set have demonstrated the significance of year (Murray et al. 2006). We thereby calculated our metrics by year and female reproductive state, allowing some individuals to appear in the data set more than once in a given year. For example, one female could be included as pregnant and as lactating at different times in the same year. Her metrics were then calculated within those different states, and we confined analyses to females that were followed at least 30 h in a given state and given year.

We performed all statistical tests with SAS version 9.1 (SAS Institute, Cary, NC). To test for associations between reproductive category and each of our metrics (travel budget, feeding budget, diet quality, and sociality), we used linear mixed models that controlled for repeated measures on the same female in different states and for the potential influence of rank. We also included a year term in these models to account for temporal variation as described above. To illustrate the magnitudes of group differences, we computed model-predicted metrics and standard errors (SEs) for each rank and reproductive category, weighted to reflect the actual population of females. These are reported in the results below.

To estimate effect sizes for significant variables, we relied on a method previously used in similar models (Murray et al. 2006). Effect size was calculated from log-likelihood values as the log likelihood of the full model minus the log likelihood of the reduced model without the predictor of interest, divided by the log likelihood of the reduced model. This gives the relative increase in model fit for the predictor of interest.

## RESULTS

### Influence of reproductive state and rank on behavior

*Travel budget*

We found that travel budgets differed significantly by reproductive state ($F_{2,93} = 3.47$, $P = 0.04$, effect size = 0.024) with the predicted mean travel budget for NPNL, pregnant, and lactating females being 37.7% (SE = ±1.4), 34.5% (SE = ±1.4), and 38.3% (SE = ±0.81), respectively. Post hoc group comparisons revealed significant differences between pregnant versus NPNL and pregnant versus lactating females (Tukey–Kramer adjusted, $P < 0.05$). We also found that travel budgets tended to differ by rank ($F_{2,93} = 2.91$, $P = 0.06$, effect size = 0.028). Low-ranking females spent more time traveling (predicted mean travel budgets: high = 38.9% ± 1.3 SE, middle = 38.1% ± 0.94 SE, low = 39.9% ± 1.3 SE) as is concordant with a previous study demonstrating that lower ranking females had larger core areas (Murray et al. 2007).

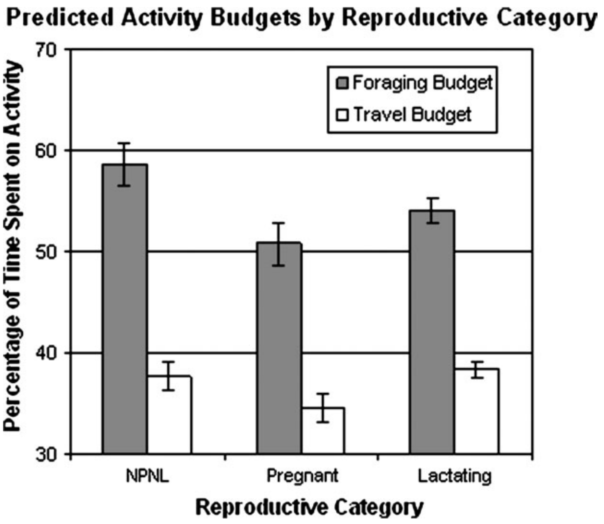

**Figure 1**
Activity budgets by category. The *y* axis gives the percentage of observation time spent traveling or feeding as predicted from our statistical models. The *x* axis categorizes females by reproductive state: pregnant, lactating, and NPNL. SE bars indicated predicated errors.

*Feeding budget*

Feeding budgets differed significantly by reproductive state ($F_{2,93} = 3.89$, $P = 0.02$, effect size = 0.022). NPNL (predicted mean feeding budget = 58.6% ± 2.1 SE) and lactating (predicted mean feeding budget = 54.3% ± 1.3 SE) females spent more time feeding than pregnant (predicted mean feeding budget = 50.7% ± 2.1 SE) females. The difference between pregnant and NPNL females was significant (Tukey–Kramer adjusted, $P < 0.05$). We did not find significant differences by rank ($F_{2,93} = 0.27$, $P = 0.76$). Figure 1 summarizes the effects of reproductive category on activity budgets.

*Diet quality*

We found that diet quality tended to differ by reproductive state ($F_{2,93} = 2.35$, $P = 0.10$, effect size = 0.038). Both lactating (predicted mean diet quality = 61.9% fruit ± 1.4 SE) and pregnant (predicted mean diet quality = 59.0% fruit ± 2.4 SE) females consumed more fruit than NPNL females (predicted mean diet quality = 57.0% fruit ± 2.3 SE). Rank did not significantly correlate to diet quality ($F_{2,93} = 0.16$, $P = 0.85$). Figure 2 gives the predicted means for the percentage of fruit in the diet by reproductive category.

*Sociality*

Average party size tended to differ between reproductive states ($F_{2,93} = 2.46$, $P = 0.09$, effect size = 0.016). The predicted average party size for NPNL, pregnant, and lactating females was 5.9 (SE = 0.41), 5.2 (SE = 0.43), and 5.0 (SE = 0.28) adults, respectively. Post hoc group comparisons demonstrated that the tendency for differences was between NPNL and lactating females. Average party size did not differ by dominance rank ($F_{2,93} = 0.60$, $P = 0.54$).

## DISCUSSION

Female mammals must balance the conflicting demands of their offspring with their own survival and future reproductive success. Many studies have therefore examined how females

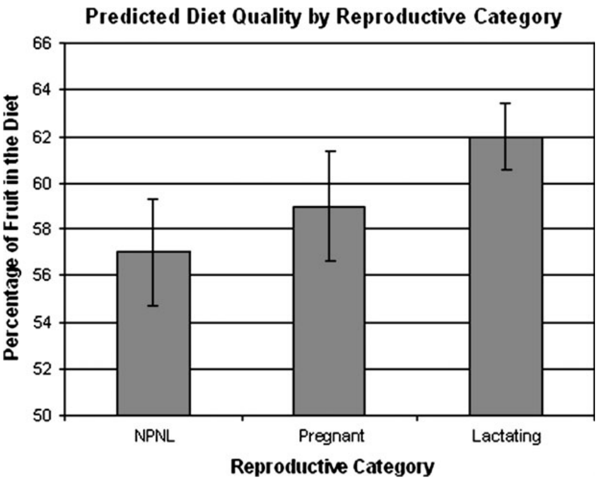

**Figure 2**
Diet quality by category. The *y* axis gives the predicted percentage of fruit in the diet. Because chimpanzees are ripe-fruit specialists, higher percentages correspond to a better quality diet. The *x* axis categorizes females by reproductive state: pregnant, lactating, and NPNL. SE bars were generated from those predicted by the statistical model.

deal with the energetic costs of reproduction (red-ruffed lemurs: Vasey 2005; Egyptian fruit bats: Korine et al. 2004; stellar sea lions: Pitcher et al. 1998). However, few studies have examined how female behavior changes during pregnancy and lactation in free-living great apes, a taxon typified by long lives and slow life histories. Our results demonstrate how female chimpanzees vary their behavior across the reproductive cycle.

Studies in captive and free-living primates have demonstrated that females often compensate for the energetic demands of reproduction by increasing their caloric intake (yellow baboons: Altmann 1980; hanuman langurs: Koenig et al. 1997; squirrel monkeys: Boinski 1988; red-ruffed lemurs: Vasey 2004). The temporary, fission–fusion groupings typical in chimpanzees should theoretically allow a female to forego social activities (e.g., grooming) in order to feed longer. In contrast to studies in other species and somewhat surprisingly, we found that NPNL females fed for longer than pregnant and lactating individuals. It is possible that this reflects other constraints in terms of mobility or the presence of other dependents for multiparous females. Regardless, the decrease in feeding time may be offset by a better quality diet during pregnancy and lactation when females consumed more fruit. Female chimpanzees therefore feed more selectively during reproductive efforts, which may allow them to increase their caloric intake despite feeding less. A similar pattern of consuming better foods during reproductive efforts has been observed in other primate species, including red-ruffed lemurs (Vasey 2004), muriquis (Nogueira 1996), and squirrel monkeys (Boinski 1988). Further insight could be gained in future studies by gathering more detailed data on nutrition and mineral content of specific foods, as well as intake rates.

Pregnant females also reduced their physical activity and spent less time traveling than females in other reproductive states. This energy conservation strategy may allow pregnant females to store fat that can later fuel milk production. This strategy is common in humans and nonhuman primates both of which can deposit substantial fat reserves, to a greater extent than many other mammals. Nonhuman primates, however, rarely do so in the wild presumably because resources are too limited (reviewed in Dufour and Sauther 2002).

It is important to note that the activity budgets presented here may not be typical of pregnant females in general. Studies from Gombe and elsewhere have noted that pregnant females are less gregarious (Nishida 1990; Pusey et al. 2008), particularly around parturition (Pusey et al. 2008). Although we did not detect significant differences between pregnant females and females in the other reproductive states, there is likely a bias in our data toward finding and/or successfully following individuals in larger parties. This bias is not easily overcome given the nature of chimpanzee grouping patterns. Regardless, our results demonstrate clear behavioral differences between females in different reproductive states within similar social conditions. Future studies could focus on following females throughout the course of her pregnancy to test if the data presented here are typical of her behavior in other social environments.

Given the robust literature demonstrating that lactation is the most costly part of the female reproductive schedule, we were somewhat surprised to find that behavioral changes were more pronounced during pregnancy than during lactation though another study reported a similar finding but had a small sample size (Matsumoto-Oda and Oda 2001). In general, primates are buffered from fluctuations in resource availability because they have lower energy content in their milk and because they can metabolize fat reserves (Oftedal and Iverson 1995; Power et al. 2008; Hinde et al. 2009). This may be particularly true for female chimpanzees because they have evolved toward an exceptionally long lactational period (Aiello and Key 2002). Reproductive costs are spread out over a longer period so they may not require dramatic behavioral changes to meet these demands. In addition, mammalian females have multiple strategies to cope with reproductive costs. Although our results clearly demonstrate behavioral changes by reproductive state, there are important aspects of reproductive energetics that are beyond the scope of this paper. A full picture requires compensatory physiological data. It seems very likely that changes in basal metabolic rates and the metabolization of fat reserves compensate for the higher lactation costs.

Future work will investigate the interaction between dominance rank and reproductive category. There are strong theoretical reasons to expect differences based on rank. Previous work at Gombe demonstrated that dominant females have higher reproductive success (Pusey et al. 1997) and a heavier and more constant body mass (Pusey et al. 2005). Subsequent studies suggested that these differences may be mediated by more productive core areas for dominant females (Murray et al. 2006, 2007). Given these differences, we expect that female chimpanzees may adopt a dominance-dependent strategy to deal with the increased costs associated with pregnancy and lactation. Future studies will focus on gathering enough data from low-ranking pregnant females (a subgroup lacking in this data set) to follow up on preliminary analyses supporting this hypothesis.

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