Variability in Population Density Is Paralleled by Large Differences in Foraging Efficiency in Chimpanzees (*Pan troglodytes*)

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Abstract The assumption that population density restricts the foraging efficiency of individuals in the population via increased competition for resources underpins socioecological models of female social relationships in primates. We examined this assumption by comparing quantitative measures of foraging efficiency in two communities of chimpanzees (*Pan troglodytes schweinfurthii*) that inhabit the same contiguous forest in Kibale National Park, Uganda, but differ substantially in size and density. To calculate net caloric gain rates (our measure of foraging efficiency) we obtained data directly from focal follows of individual chimpanzees on 1) residency time in a feeding patch, 2) feeding rate in the patch, 3) the nutrient content of the items fed upon, and 4) the distance walked between feeding patches. We collected foraging efficiency data over 1059 h at Ngogo and 961 h at Kanyawara. We found that individuals in the high-density community (Ngogo) had higher mean foraging efficiency values than those in the low-density community (Kanyawara), and that foraging efficiency varied less over time at Ngogo when assessed over the time scales of individual feeding/traveling bouts and of daily net caloric gain rates. Fluctuation in net caloric gain rates on a monthly time scale was greater at Ngogo than at Kanyawara, but this was likely due to the nutritional effects of a mast fruiting event by one of the most important species at the

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site. These findings suggest that high population density at Ngogo has not precluded high foraging efficiency. The classic view of increased population density inevitably increasing feeding competition and reducing foraging efficiency likely underemphasizes the ability of primates, especially those in rich habitats, to maximize caloric intake.

Introduction

The efficiency with which primates are able to forage for, and extract calories from, food resources bears both directly and indirectly on their survival and reproductive success (Altmann 1998; Barton and Whiten 1993; Boinski 1988; Knott 1998; Murray *et al.* 2009; Pontzer *et al.* 2010; Robinson 1988). In recognition of this, socioecological models developed to explain variation among primate populations and species in female gregariousness, social relationships, and reproductive output make the key assumption that population density and per capita net food intake (caloric intake vs. caloric output, i.e., foraging efficiency) and group size are inversely related. More specifically, these models suggest that animals living at high population density experience more intense competition for food, and ultimately exhibit reduced foraging efficiency and reproductive performance, as a tradeoff for the benefits gained from living in large groups, e.g., reduced per capita predation risk (Isbell 1994; van Schaik 1983). The fitness costs imposed upon females living in groups, in turn, have cascading effects on social behavior and social organization (Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980).

However, this key assumption of inevitable reduction in foraging efficiency with increasing group size is not often fully evaluated quantitatively (Koenig 2002), and studies examining the relationship between population density and per capita resource availability and its fitness consequences have produced conflicting results (Borries *et al.* 2008; Chancellor and Isbell 2009; Robinson 1988; Teichroeb and Sicotte 2009; van Schaik and van Noordwijk 1988). This may be due to the logistical difficulties associated with obtaining the requisite data, including complete assessments of both caloric intakes and caloric outputs of individual animals (Janson and van Schaik 1988). Measurement of caloric intake requires data not only on time spent feeding, but also intake rates (items ingested per unit time), weight of items ingested, and caloric content of these items. Similarly, measurement of caloric output requires data not only on time spent traveling, climbing, etc., but also on mean species- and sex-specific caloric expenditure rates associated with these activities. Finally, foraging efficiency can vary considerably between males and females (Pokempner 2009), among individuals more generally (Fragaszy and Boinski 1995), and among different periods of food availability (Conklin-Brittain *et al.* 2006; Irwin *et al.* 2014). Consequently, with certain notable exceptions (Altmann 1991; Byrne *et al.* 1993; Janson 1988; Muruthi *et al.* 1991; Stacey 1986; Vogel *et al.* 2015; Wright *et al.* 2015), studies linking net caloric intake to fitness and/or population density in primates largely rely on qualitative indices of foraging

efficiency as evidence of this inverse relationship, e.g., the relative amount of time allocated to feeding and resting (Asensio *et al.* 2009; Isbell and Young 1993; Lehmann *et al.* 2007; Riley 2007).

We previously used similar qualitative measures to assess foraging efficiency in two communities of chimpanzees (*Pan troglodytes schweinfurthii*) of the same population inhabiting Kibale National Park, Uganda but differing dramatically in population density (Potts *et al.* 2011). Contrary to patterns found in several other studies (Chapman 1990; Isabirye-Basuta 1988; Stevenson 2006; Teichroeb and Sicotte 2009; Teichroeb *et al.* 2003), in our qualitative approach we found that individuals at Ngogo, where the largest known community of chimpanzees live at an unusually high population density (see Methods for details), exhibit behavior consistent with far higher foraging efficiency than chimpanzees at Kanyawara, a site just 12 km from Ngogo but supporting a community living at a moderate density. These results suggest that increasing group size does not inevitably lead to reduced foraging efficiency, and indeed that individuals in high-density groups may forage more efficiently (perhaps as a consequence of living in a habitat sufficiently rich to support a large group), but quantitative assessments of foraging efficiency are needed to fully evaluate this claim.

Relationships among resource abundance, population density, and foraging efficiency could take several forms (Janson and van Schaik 1988). First, resource abundance may scale positively with both population density and foraging efficiency. In this case, an abundant resource base supports relatively many individuals per unit area and those individuals maintain relatively high net caloric intake rates on timescales relevant to fitness. Because efficient foraging increases an individual's available energy to devote to reproductive efforts (Bårdsen and Tveraa 2012; Bercovitch 1987; Ellison *et al.* 1993; Koenig *et al.* 1997; Lee 1987, 1996; Ward *et al.* 2009), highly efficient foraging may, in turn, lead to higher reproductive outputs, higher infant and juvenile survival rates, and increased population density (Abramsky *et al.* 2002; Ebensperger *et al.* 2012). One could therefore hypothesize that the forest at Ngogo, where chimpanzee density is high, would allow for relatively efficient foraging, because food patch productivity is high and distances between successive patches are short (Potts *et al.* 2009). By extension, foraging efficiency should be higher at this site than at Kanyawara, where chimpanzee density is low. Previous theoretical and empirical evidence support this hypothesis by showing a positive association between group size/density and per capita resource abundance, feeding efficiency, and reproductive success in primate populations characterized by high-potential between-group contest (BGC) competition (especially among those additionally characterized by low intragroup scramble and/or low contest feeding competition; Cheney and Seyfarth 1987; Janson and van Schaik 1988; Robinson 1988; Wrangham 1980). Also, as mentioned earlier, our previous qualitative analysis of differences in feeding ecology between Ngogo and Kanyawara chimpanzees (Potts *et al.* 2011) suggested that individuals at Ngogo forage more efficiently than those at Kanyawara.

Alternatively, because population density and feeding competition may be positively associated for a given level of habitat productivity (Majolo *et al.* 2008), foraging

efficiency may decline with increasing population density (Chapman and Chapman 2000), potentially further limiting any increase in population density by inhibiting reproductive function (Janson and Goldsmith 1995; Roberts and Cords 2013; Whitten 1983). High local population density may engender strong intragroup competition for resources (both in the form of contest and scramble competition), which constrains the ability of group members to procure adequate resources (Chapman and Chapman 2000; Gillespie and Chapman 2001; Janson 1988; Rodriguez-Hidalgo *et al.* 2010; Sterck *et al.* 1997; Stewart *et al.* 2011; Vogel 2005; Wittig and Boesch 2003; Wrangham 1980). Although chimpanzee foraging parties can vary in size and composition to reduce the potential for feeding competition (Anderson *et al.* 2002; Chapman *et al.* 1995; Lehmann *et al.* 2007; Mitani *et al.* 2002; Wakefield 2008; Wittiger and Boesch 2013), individuals in particularly high-density communities may not always be able to avoid such effects. Lehmann *et al.* (2007) modeled the "ecologically tolerable group size" in chimpanzees based on assumed relationships between time budget constraints and group size. The community at Ngogo was an outlier, and the authors thus suggested that it might have surpassed the "ecologically tolerable group size" and may be in the early stages of permanent fission (Lehmann *et al.* 2007). Therefore, an alternative hypothesis is that chimpanzees at Ngogo experience lower foraging efficiency measures than those at Kanyawara due to strong effects of scramble competition.

Several researchers argue that foraging efficiency is usually high even in seemingly suboptimal foraging environments (Cant 1980; Coehlo *et al.* 1976). Chimpanzees show considerable dietary flexibility, despite their propensity to seek out ripe fruit whenever it is available (Watts *et al.* 2012a). Thus, differences in foraging efficiency among populations occupying habitats of different quality may be evident only during times of extremely low fruit abundance. If this is true, only periods of severe resource scarcity, when few or no preferred food items are available and net caloric intake is compromised, act as critical selective forces (Cant 1980; Marshall and Leighton 2006; Marshall and Wrangham 2007; Searle *et al.* 2010; Wiens 1977). During such periods, declining foraging efficiency may induce intense feeding competition among females, thus potentially inhibiting reproductive function and influencing individual life histories (Borries *et al.* 2001; Emery Thompson and Wrangham 2008; Knott 1998; Koenig *et al.* 1997; van Schaik and van Noordwijk 1985; Ziegler *et al.* 2000). Consequently, mean foraging efficiency values pooled across relatively long time periods may be less informative indicators of ecological influences on population density than is the temporal fluctuation in these values. In previous analyses we showed that food availability is more temporally consistent at Ngogo than at Kanyawara, largely because several species that typically fruit when the overall abundance of fruit is relatively low and that show high intraspecific fruiting synchrony are abundant there, but rare or absent at Kanyawara (Potts 2011; Potts *et al.* 2009). It is on this basis that we would predict less intense temporal fluctuations in foraging efficiency, and shorter periods of low foraging efficiency, at Ngogo than at Kanyawara.

To examine these hypotheses, we developed a quantitative measure of foraging efficiency, accounting for both caloric intake and output, and applied it to individuals in the Ngogo and Kanyawara chimpanzee communities to determine how foraging efficiency may be influenced by group size in this population.

Methods

Study Sites

Kibale National Park (795 km^2), located in southwestern Uganda, is classified as a moist evergreen or semideciduous forest transitional between lowland and montane forest (Struhsaker 1997). The park is composed of a mosaic of vegetation formations (58% mature forest, 15% grassland, 6% woodland, 2% lakes and wetlands, and 19% colonizing forest regenerating in areas used in the past for agriculture; Chapman and Lambert 2000; Struhsaker 1997), and its structure and composition vary considerably within and between sites (Chapman *et al.* 1997; Potts 2011; Potts *et al.* 2009). Detailed ecological overviews of both the study sites are provided elsewhere (Butynski 1990; Chapman and Lambert 2000; Ghiglieri 1984; Lwanga *et al.* 2000; Potts 2008; Struhsaker 1997; Wing and Buss 1970).

Chimpanzee community size at Kanyawara (the low-chimpanzee-density site) has varied between 40 and 50 since the onset of habituation in the late 1980s. The community had 11 adult males, 1 subadult male, 15 adult females, 3 nulliparous females, 8 juveniles, and 13 infants during our study (also see Muller and Wrangham 2004), making the density of chimpanzees at Kanyawara *ca.* 1.5 individuals/km^2 (Emery Thompson *et al.* 2007; Wilson 2001; more recently, Wilson *et al.* 2014 provided an estimate of 2.9 individuals/km^2). The chimpanzee community at Ngogo (the high-chimpanzee-density site) is the largest ever observed, with >150 members during the study period (Watts *et al.* 2006; current estimates are close to 200 individuals, *pers. obs.*), including 23–26 adult males, 15 adolescent males, at least 44 adult females, 15 adolescent females, 17 juveniles, and 34 infants, making the population density at Ngogo *ca.* 5.1 individuals/km^2 (the more recent estimate by Wilson *et al.* 2014 is 4.5 individuals/km^2).

We conducted this study for 19 mo, from June 2005 to December 2006. This included at least a full year at each site (Ngogo: 1059 h of focal animal sampling between June 2005 and June 2006; Kanyawara: 961 h between January 2006 and December 2006). However, we were able to simultaneously collect data on both communities only between January 2006 and June 2006 (hereafter referred to as the "overlap" period).

Data Collection

K. Potts or a trained field assistant conducted focal follows of individual chimpanzees at each site. We limited sampling to adults and adolescents. K. Potts collected all of the focal data from Ngogo, while a single field assistant following an identical sampling protocol collected the majority of the data on chimpanzees at Kanyawara. After training, K. Potts occasionally followed chimpanzees at Kanyawara with this assistant and collected data on the same focal chimpanzees at the same time to ensure interobserver reliability. Quantitative tests of interobserver reliability revealed strong concordance between the two observers in determination of feeding rate (see definition in the text that follows), which we considered to be the measure most likely to vary between observers (intraclass correlation coefficient = 0.992, $F = 258$, $P < 0.001$).

During each focal follow, we continuously recorded the behavioral state of the focal animal as either feeding/foraging (defined as ingestion of plant or animal matter uninterrupted by other behaviors for ≥1 min), traveling (sustained movements [>1 min], generally outside of feeding patches and indicating movement between successive patches), resting (any sustained period in which neither feeding nor traveling occurred), hunting, or border patrolling.

We considered feeding bout length to be the total amount of time that the focal individual fed in a given patch. We defined a patch as an aggregation of food items that allowed uninterrupted feeding or foraging movements by individuals or parties (*cf.* Chapman *et al.* 1994). Generally, this was an individual tree or large sapling, but it also included contiguous thickets of terrestrial vegetation or, in the case of species growing in dense groves, e.g., *Uvariopsis congensis* or *Teclea nobilis*, multiple adjacent trees when their crowns overlapped.

Determining Foraging Efficiency

Net caloric intake has long been a standard measure of foraging efficiency (MacArthur and Pianka 1966; Pyke *et al.* 1977; Schoener 1971; *cf.* Raubenheimer *et al.* 2009). We calculated net caloric gain rates on the relatively short timescale of complete feed plus travel bouts, each of which combined a complete feeding bout with the travel bout to the next feeding patch. We assessed efficiency on this scale primarily because of the logistic difficulty of obtaining all of the requisite data on single focal chimpanzees for longer periods. Our net caloric gain rate equation included only complete feeding and traveling bouts. So if our focal chimpanzee feeding in patch A did not then move to patch B, e.g., the individual went on a hunt or border patrol, we did not include that bout. We felt it important not to analyze feeding bouts and travel bouts separately, as it is the combined influence of the feeding bout and its successive travel bout that determines how efficient the foraging bout was. Also, we look at time budgets, including the separate influence of feeding and traveling, and other qualitative indices of foraging efficiency elsewhere (Potts *et al.* 2011). In addition to analyzing foraging efficiency on the temporal scale of each complete combined feeding and traveling bout, we also used daily and monthly mean net caloric gain rates, in which we calculated the mean net caloric gain rates for complete feed plus travel bouts per day and per month as efficiency metrics. Using monthly values is particularly appropriate for chimpanzees because they do not face daily risks of starvation.

We assessed foraging efficiency (φ) using the following equation:

$$\varphi = (\rho\tau\varepsilon\gamma) - (\delta\theta) \tag{1}$$

where ρ = intake rate (items/min) during the feeding bout (see later), τ = time (minutes) spent feeding in the patch, ε = caloric content (kcal/g) of the item being eaten, γ = weight of edible matter (g) per item, δ = distance traveled between successive feeding bouts, and θ = energetic cost (kcal/m) of walking. When focal individuals were in clear view, we made *ad libitum* observations of the number of items ingested in 1 min to calculate intake rates (ρ; items/minute). We did not attempt to record feeding rates

when ingestion by the focal individual could not be directly observed. If only a fraction of the whole item was ingested, we estimated the fraction discarded to avoid inflating total intake values.

We assessed travel distance between successive feeding patches (δ) using either the geo-referenced trail grid system or a handheld GPS unit. We determined the metabolic cost (θ) of walking between successive feeding bouts using the following formula:

$$\theta = \mu\delta \qquad (2)$$

In this equation, δ = distance traveled (meters), as previously, and μ = the age-, sex-, and reproductive class-specific cost of traveling terrestrially 1 m (J/m; the cost of transport; Pontzer et al. 2011). We used data provided in Pontzer et al. (2011) on the cost of transport for Kanyawara males, females without clinging infants, and females with clinging infants.

We considered the caloric costs of all other activities not associated with long-distance locomotion, e.g., grooming, play, to be negligible, and we considered the metabolic demands of resting and thermoregulation to be similar across individuals. This is not an entirely accurate assumption, because basal metabolic rates (kcal/h) scale with body mass to the 0.75 power (Kleiber 1961), but correcting for body mass effects would have had little influence on the results. For example, the cost of thermoregulation for a 33-kg adult female chimpanzee should be ca. 964 kcal (=$70 \times (33)^{0.75}$), while that for a 42-kg adult male should be ca. 1154 kcal (=$70 \times (42)^{0.75}$), a difference of 190 kcal. This is roughly equivalent to the mean number of calories obtained during just 8 min of feeding by a noncycling female at Ngogo (see Results).

Although we did not include the energetic costs of climbing in the equation, these costs were estimated to be similar for chimpanzees at the two sites. If we assume that the energetic cost of climbing is a function of the mechanical work performed, which in turn is a function of the climber's body mass and the height climbed (Pontzer and Wrangham 2004; Pontzer et al. 2011), then we expect climbing costs to be roughly similar in our Ngogo and Kanyawara datasets. Ngogo chimpanzees climbed a mean of 4.9 trees/day, whereas Kanyawara chimpanzees climbed 4.8 trees/day. In addition, any attempts at estimating tree heights would likely have been imprecise and inaccurate. Thus, although estimates of energy expenditure using only terrestrial locomotion probably underestimate true values, the overall intersite differences would likely remain even if climbing were included. However, in the Discussion section we speculate on the possible implications of omitting data on climbing.

Plant Sample Collection and Phytochemical Analysis

We collected samples of immature and mature fruits, young leaves, seeds, and piths eaten by chimpanzees to estimate caloric intake of focal individuals. Because considerable information on the nutrient content of foods eaten by chimpanzees at Kanyawara already exists (Conklin and Wrangham 1994; Conklin-Brittain et al. 1998, 2006; Wrangham et al. 1991, 1993a; Wrangham et al. 1998), we collected and analyzed samples only from Ngogo (Table I).

We attempted to collect samples from individual trees, hemiepiphytic figs, terrestrial herb patches, or saplings that had been used by chimpanzees. Whenever possible, we

Table I Digestible energy values for food items included in foraging efficiency analyses for chimpanzees at Ngogo and Kanyawara in Kibale National Park, Uganda from June 2005 to December 2006

Plant species	Digestible energy at Ngogo (kcal/g)	Digestible energy at Kanyawara (kcal/g)
***Celtis africana* young leaves**	**2.08**	**2.72**
Chrysophyllum albidum ripe fruit	3.76	
***Ficus capensis* ripe fruit**	**2.60**	**2.55**
Ficus exasperata ripe fruit		2.90
Ficus exasperata unripe fruit		2.99
Ficus exasperata young leaves		2.65
Ficus natalensis ripe fruit		2.36
Ficus mucuso ripe fruit	2.83	
***Ficus sansibarica* ripe fruit**	**2.96**	**3.05**
***Ficus sausureana* ripe fruit**	**2.59**	**2.60**
***Mimusops bagshawei* ripe fruit**	**2.89**	**2.93**
Pouteria altissima ripe fruit	3.92	
Pseudospondias microcarpa ripe fruit	3.05	
Pterygota mildbraedii unripe fruit and seed	2.82	
Pterygota mildbraedii young leaves	2.88	
***Uvariopsis congensis* ripe fruit**	**2.68**	**2.60**
Warburgia ugandensis ripe fruit	3.14	

Data for Ngogo samples were obtained as described in the text, and those for Kanyawara samples are from Conklin-Brittain *et al.* (2006). Items listed in bold are those that were included in foraging efficiency analyses for both Ngogo and Kanyawara

collected samples from feeding patches while the focal individual fed in them. When this was impossible, we collected a sample either from the same feeding patch after the focal individual left, or from a patch similar in size and phenophase. We collected 44 samples of foods representing >80% of focal individual feeding time. Most samples were made up of intact items that fell to the ground incidentally as chimpanzees moved through a feeding tree (we avoided collecting dropped items that were clearly discarded by a feeding chimpanzee, as their nutritional content likely differs from that of selected items). We took other samples directly from feeding trees/patches. We collected samples in plastic bags in the forest, brought them back to camp within a few hours, and weighed the items as soon as possible. Prior to performing chemical analyses, we processed the food items so that they included only the parts eaten by chimpanzees, e.g., the meso- and exocarp of fruits, then reweighed the samples. To prevent mold- or bacterial-induced changes in the chemical content of fresh material, we stored the samples in liquid nitrogen or in a freezer.

We freeze-dried and ground all samples prior to analysis. We conducted all nutritional assays of plant samples at the Leibniz Institute for Zoo and Wildlife Research (Berlin, Germany) using the same methodology as Hohmann *et al.* (2010). We determined dry matter content by drying a portion of the sample at 105°C overnight, and crude ash by burning a portion of the sample in a muffle furnace at 550°C for 6 h.

We assessed crude protein using Dumas combustion. Dumas combustion measures the nitrogen liberated from a sample entirely combusted at extremely high temperatures. Total nitrogen (N) provided an estimate of crude protein (CP) (protein level = N × 6.25). We determined crude lipids by petroleum ether extraction (Soxhlett). We performed detergent fiber analysis following van Soest (1994), which included a rapid stepwise procedure for determining soluble cellular components as well as the insoluble cell wall matrix and its major subcomponents: hemicellulose, cellulose, and lignin. We estimated cell contents and soluble components by boiling the sample in neutral detergent solution. The residue neutral detergent fiber (NDF) contained hemicellulose, cellulose, and lignin. We extracted hemicellulose by boiling the sample in acid detergent solution. The residue acid detergent fiber (ADF) contained only cellulose and lignin. The last step extracts cellulose by acid hydrolysis and burns the sample to ash at 550°C. The residue acid detergent lignin (ADL) contained only lignin. We calculated hemicellulose and cellulose contents by weighing and subtracting residues, with hemicellulose = NDF–ADF and cellulose = ADF–ADL. The 6.25 correction factor applied to the nitrogen content likely overestimates available crude protein levels because it does not account for the lignin-bound fraction of crude protein, which is entirely indigestible (Conklin-Brittain *et al.* 1999). However, it is the same value used by Conklin-Brittain *et al.* (2006) in analyzing the Kanyawara samples, and we therefore use it here to facilitate comparisons.

We converted the nutrient values determined by these assays into total digestible energy (DE) using the equation given in Conklin-Brittain *et al.* (2006) that assumes a high capacity of chimpanzees to ferment neutral detergent fibers (NDF; based on the digestion coefficient for fibers of 0.543 given by Milton and Demment 1988):

$$DE = (4 \times \%TNC) + (4 \times \%CP) + (9 \times \%lipid) + (1.6 \times \%NDF) \quad (3)$$

In equation 3, TNC refers to total nonstructural carbohydrates, which we calculated as:

$$\%TNC = 100 - \%lipid - \%CP - \%total\ ash - \%NDF \quad (4)$$

The values derived from equation 3 are in units of kilocalories/100 g of dried (lyophilized) organic matter (OM). To convert this value into a more meaningful kcal/g of fresh OM, we corrected the value obtained from equation 3 for the percent organic matter present in the fresh sample. Resulting values obtained using these derivations are directly comparable to those for foods eaten by Kanyawara chimpanzees given in Conklin-Brittain *et al.* (2006).

Estimates of net caloric gain might have been biased because the digestible energy equation (equation 3) assumes a high capacity to ferment structural carbohydrates (Conklin-Brittain *et al.* 2006). Although chimpanzees can extract energy from these fibers via hindgut fermentation (Conklin and Wrangham 1994), the coefficient used may overestimate this capacity (Conklin-Brittain *et al.* 2006). However, the equation was applied to the data from each site, so the bias would have disproportionately affected one site or the other only if there was a strong disparity in the fiber fraction of the foods used to calculate foraging efficiency scores. There is no indication that such a disparity exists (Conklin-Brittain *et al.* 2006; Hohmann *et al.* 2010).

Data Analysis

To quantify the extent to which chimpanzees at our two sites differed in foraging efficiency measures, we generated a mixed-effects model that included site, sex, and food class as fixed predictor variables and ID (focal chimpanzee ID) as a random variable. Food class refers to food items that are more readily available during times of high food abundance vs. those more commonly available during times of low food abundance (Bortolamiol *et al.* 2014; Potts *et al.* 2009). We employed a Satterthwaite's approximation to estimate the denominator degrees of freedom for each parameter, making our model a slightly conservative test of the predictive power of each factor.

We assessed the differences between the sites in temporal patterns of foraging efficiency by quantifying intersite differences in coefficients of variation (CV) using Levene's test for equality of variance (Schultz 1985). We set significance levels for all models and parameters within models at $\alpha = 0.05$, and conducted each as a two-tailed test. We used the R programming environment (R Core Team 2015) for all of our analyses.

Ethical Note

We conducted this research noninvasively and avoided disturbance of focal animals to the fullest extent possible. The plant samples we collected largely consisted of dropped fruit, so it is unlikely that the removal of these items from the forest would constitute the loss of a major food source for chimpanzees or other frugivores. The proper Ugandan authorities fully approved of our research as described here.

Results

We obtained data on 210 complete feeding/traveling bouts at Ngogo, of which 155 were from males and 55 were from females. At Kanyawara we obtained data on 163 complete feeding/traveling bouts, with 72 on males and 91 on females. Both site (generalized linear model: $F = 24.21$, df = 1, $P < 0.001$) and food class ($F = 14.75$, df = 2, $P < 0.001$) strongly influenced variability in net caloric gain rates. Sex received virtually no support as a significant predictor ($F = 0.054$, df = 1, $P = 0.817$).

Ngogo chimpanzees had higher mean net caloric gain rates than did Kanyawara chimpanzees, whether we calculated this value at the level of individual feeding/traveling bouts (Ngogo = 71.88 kcal/min feeding, Kanyawara = 44.97 kcal/min feeding; independent samples *t*-test, $t = 32.97$, df = 371, $P < 0.001$), daily means (Ngogo = 79.47 kcal/min feeding, Kanyawara = 46.72 kcal/min feeding; $t = 29.13$, df = 136, $P < 0.001$), or monthly means (Ngogo = 82.21 kcal/min feeding, Kanyawara = 42.36 kcal/min feeding; $t = 14.81$, df = 21, $P < 0.001$). In 7 out of 11 mo of study at Kanyawara, net caloric gain rates did not even reach the lowest recorded monthly net caloric gain rate at Ngogo. Notably, monthly net caloric gain rates were higher at Ngogo than at Kanyawara during every month of the overlap period.

Net caloric gain rates exhibited significantly greater variability among feeding/traveling bouts at Kanyawara than at Ngogo ($CV_{Kanyawara} = 0.873$, $CV_{Ngogo} = 0.676$; Levene's test for homogeneity of variances: $F = 7.251$, $P = 0.007$). Similarly, mean daily net caloric gain rates showed greater temporal variability at Kanyawara ($CV_{Kanyawara} = 0.631$, $CV_{Ngogo} = 0.503$; $F = 12.167$, $P < 0.001$; Fig. 1). However, mean monthly net caloric gain rates fluctuated more at Ngogo than at Kanyawara ($CV_{Kanyawara} = 0.250$, $CV_{Ngogo} = 0.399$; $F = 11.267$, $P = 0.003$; Fig. 2). This was very likely due to the effects of a mast fruiting event involving *Chryophyllum albidum*. This is among the most common species at Ngogo (Potts and Lwanga 2014) and tends to produce massive quantities of fruit in a supra-annual mast-like fashion (Watts *et al.* 2012b). If we remove mast months for *Chrysophyllum* (July–September 2005) from the monthly analysis at Ngogo, the significantly higher fluctuation in monthly net caloric gain rates disappears (recalculated $CV_{Ngogo} = 0.302$; $F = 2.64$, $P = 0.122$).

At Kanyawara, net caloric gain rates varied more on days of high caloric gain (defined as falling above the overall mean for daily caloric gain rates) than on other days (Levene's test for equality of variance comparing coefficients of variation above vs. below mean daily net caloric gain rates: $CV_{above} = 0.458$, $CV_{below} = 0.326$, $F = 21.160$, $P < 0.001$). Net caloric gain rates at Ngogo varied more on days of low caloric gain ($CV_{above} = 0.212$, $CV_{below} = 0.337$, $F = 4.484$, $P = 0.0370$). Net caloric gain rates on days of low caloric gain were, on average, lower and less variable at Kanyawara than at Ngogo ($\mu_{Kanyawara} = 26.66$, $\mu_{Ngogo} = 45.01$; Levene's test comparing Ngogo CV_{below} and Kanyawara CV_{below}: $F = 7.720$, $P = 0.007$). On days of high caloric gain, net caloric gain rates were lower at Kanyawara than at Ngogo, and variability in net caloric gain rates was similar between the two sites ($\mu_{Kanyawara} = 78.41$, $\mu_{Ngogo} = 116.18$; Levene's test comparing Ngogo CV_{above} and Kanyawara CV_{above}: $F = 1.432$, $P = 0.236$).
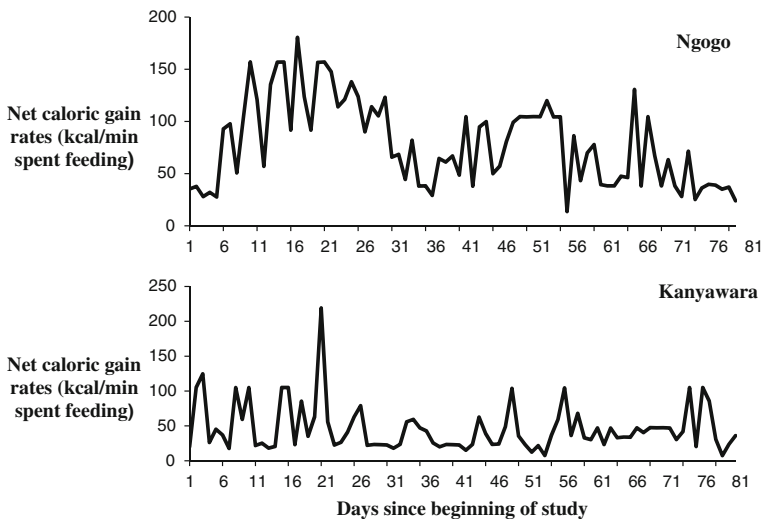
Fig. 1 Net caloric gain rates for chimpanzees at Ngogo (top) and Kanyawara (Kanyawara) in Kibale National Park, Uganda between June 2005 and December 2006. Each time series begins on the first day of study at the respective site.
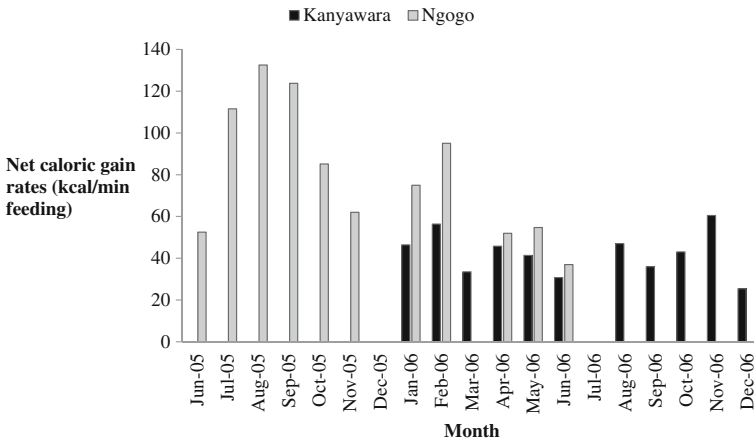
Fig. 2 Net caloric gain rates across months for chimpanzees at Kanyawara and Ngogo in Kibale National Park, Uganda between June 2005 and December 2006.

Discussion

Relationships Among Foraging Efficiency, Food Abundance, and Population Density

Mean net caloric intake values were higher at Ngogo for individual feeding/traveling bouts and at the scales of daily and monthly net caloric gain rates. This supports the prediction that the forest at Ngogo is a higher quality foraging environment than that at Kanyawara and argues against the notion that scramble competition effects are prohibitively high at Ngogo. Further, this contradicts previous suggestions that the Ngogo community is unsustainably large, has grown beyond carrying capacity, and must be in the early stages of permanent fission (Lehmann et al. 2007). Rather, the resource base appears to be productive enough to support the high population density, and feeding competition appears to be minimal enough as not to affect foraging efficiency.

We have shown elsewhere that pregnant and lactating females at Ngogo have relatively high foraging efficiency indices when feeding on items that are either extremely rare or absent entirely from Kanyawara, and items that are common to the diet of chimpanzees at both sites provide higher net caloric returns to Ngogo chimpanzees than to Kanyawara chimpanzees (Potts 2013). Furthermore, months during which the disparity in foraging efficiency quantified in this study was most apparent between the sites corresponded to periods during which Ngogo chimpanzees fed heavily on fruits of Chrysophyllum albidum (July–September 2005) and Ficus mucuso (January and February 2006), two species that are calorie rich and extremely abundant at Ngogo but are essentially absent from Kanyawara (Potts et al. 2009, 2011).

The efficiency with which long-lived individuals with slow life histories procure calories over long time scales should be an indicator of fitness and, potentially, of future population dynamics (Sæther et al. 1996). Suboptimal foraging prolonged over weeks and months is likely to affect female reproductive ecology (Bårdsen and Tveraa 2012; Emery Thompson 2013; Knott 1998; Potts 2013; Ward et al. 2009). Ngogo chimpanzee foraging had lower temporal variation and consistently higher net caloric gain rate

values compared to Kanyawara. Although variability in mean monthly net caloric gain rates was higher at Ngogo than at Kanyawara, this seemed to be driven by a mast fruiting of *Chrysophyllum*, and thus by the intense spike in caloric gains afforded by this event. This relatively invariant (and high) net caloric gain rate among Ngogo chimpanzees, punctuated by periodic masts of *Chrysophyllum*, would be expected to translate into higher reproductive rates and, by extension, higher intrinsic community growth rates than among Kanyawara chimpanzees (assuming that mortality rates are not unusually high at Ngogo). This is supported by previous studies indicating that interbirth intervals at Kanyawara are longer than at any other site for which comparable data are available (Emery Thompson 2013; Emery Thompson *et al.* 2007) and that intervals are relatively short and survivorship is relatively high at Ngogo (Watts 2012).

Kanyawara chimpanzees apparently experienced relatively more intense periods of low food abundance (LFA) than did Ngogo chimpanzees, as evidenced by the overall low (relative to Ngogo) and relatively invariant net caloric gain rates exhibited during times of low caloric gain. Also, despite showing relatively intense fluctuations among days, net caloric gain rates among days of high caloric gain at Kanyawara were lower, on average, than at Ngogo. These pieces of evidence suggest that foraging efficiency of chimpanzees at Kanyawara is uniformly low, and that relatively intense fluctuations during times of high caloric gain (likely related the periodic fruiting of preferred species such as *Mimusops bagshawei*; Conklin-Brittain *et al.* 2006) may be insufficient to entirely make up for the relative caloric deficit experienced during times of low caloric gain. Resources providing fruit, and producing fruit synchronously among individual stems, during times of low habitat-wide fruit abundance are far more abundant at Ngogo than at Kanyawara (Potts *et al.* 2009), and the relative temporal consistency of the resource base created by the abundance of these foods buffers Ngogo chimpanzees against periods of fruit scarcity to an extent not seen at Kanyawara.

Methodological Constraints and Assumptions

We incorporated several assumptions into the estimates of net caloric intake, each of which might have introduced a bias into the results. One possible bias comes from estimates of ingestion rates, which were occasionally based on rough approximations of the proportion of an item consumed, e.g., figs, which were generally consumed by "wadging." We attempted to reduce this bias by performing trials with field assistants in which two or more of us observed the same chimpanzee for the same 1-min period and compared our estimated intake rates. We performed these comparison trials throughout the feeding bout until our scored intake rates were equivalent, and it was thus likely that the rates we recorded accurately represented the amount of ingested material. Also, we often observed a focal chimpanzee drop the discarded portion of an otherwise ingested item to the ground, or to eat a portion of it on the ground, and then could better estimate the proportion left uneaten. Still, such biases were possible, and are generally difficult to avoid.

Another potential bias stems from our assumption that the items we collected for weighing and nutrient analysis adequately represent the weight and chemical composition of those eaten by chimpanzees. The weight and nutritional quality of plant parts can vary tremendously even within a single crown (Houle *et al.* 2007), and thus we might have wrongly estimated both the fresh weight ingested and the caloric content

per gram of fresh food. However, we tried to avoid this bias by collecting items of varying size and by collecting those that fell to the ground as chimpanzees foraged.

Finally, in measuring energy expenditure, we assumed that costs associated with all activities other than sustained travel were negligible relative to travel costs, and thus did not include them in the analyses. Although this is may be an accurate assumption for particular activities, such as thermoregulation and social activities, e.g., grooming, other behaviors (climbing, in particular) are undoubtedly metabolically expensive, and future studies should focus on how best to incorporate these activities in measures of foraging efficiency over multiple timescales (see Pontzer *et al.* 2011).

Implications for Socioecological Models

The notion that scramble competition for food inevitably restricts group size or population density is well engrained and generally supported by various lines of evidence (Chapman and Chapman 2000; Gillespie and Chapman 2001; Izar 2004; Janson and Goldsmith 1995; Wittiger and Boesch 2013; Wrangham *et al.* 1993b). Several socioecological models predicting female social relationships in primates (Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980) are predicated on the assumption that the competitive costs, and fitness consequences, of increasing group size determine the form and extent of female dominance hierarchies (or lack thereof). However, it is becoming apparent that scramble competition, even if demonstrably present, does not necessarily entail fitness costs (Gogarten *et al.* 2014) or even a reduction in population density (Milich *et al.* 2014). These more recent studies suggest that primates exhibit a perhaps underappreciated flexibility in behaviors related to maximizing caloric intake. Our study supports this idea, and indeed goes a step further to show that not only is the predicted negative relationship between population density and foraging efficiency not always present, but in fact that the opposite relationship may prevail in certain exceptionally rich habitats. This furthermore highlights the likely possibility that optimal group sizes, particularly in environments with an abundant resource base, may be determined by factors not directly related to food limitation, e.g., infanticide risk (Steenbeek and van Schaik 2001).

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