Energetic Responses to Variation in Food Availability in the Two Mountain Gorilla Populations (*Gorilla beringei beringei*)

Edward Wright,[1]* Cyril C. Grueter,[2] Nicole Seiler,[1] Didier Abavandimwe,[3] Tara S. Stoinski,[4] Sylvia Ortmann,[5] and Martha M. Robbins[1]

[1]*Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany*
[2]*School of Anatomy, Physiology and Human Biology, The University of Western Australia, Crawley, Perth, WA 6009, Australia*
[3]*Karisoke Research Center, The Dian Fossey Gorilla Fund International, Musanze, North Province, Rwanda*
[4]*The Dian Fossey Gorilla Fund International, Atlanta, GA 30315, USA*
[5]*Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany*

ABSTRACT

Objective: Here, we compare food availability and relate this to differences in energy intake rates, time spent feeding, and daily travel distance of gorillas in the two populations.

Comparative intraspecific studies investigating spatiotemporal variation in food availability can help us understand the complex relationships between ecology, behavior, and life history in primates and are relevant to understanding hominin evolution. Differences in several variables have been documented between the two mountain gorilla populations in the Virunga Massif and Bwindi Impenetrable National Park, but few direct comparisons that link ecological conditions to feeding behavior have been made.

Materials and Methods: Using similar data collection protocols we conducted vegetation sampling and nutritional analysis on important foods to estimate food availability. Detailed observations of feeding behavior were used to compute energy intake rates and daily travel distance was estimated through GPS readings.

Results: Food availability was overall lower and had greater temporal variability in Bwindi than in the Virungas. Energy intake rates and time spent feeding were similar in both populations, but energy intake rates were significantly higher in Bwindi during the period of high fruit consumption. Daily travel distances were significantly shorter in the Virungas.

Conclusions: Overall, despite the differences in food availability, we did not find large differences in the energetics of gorillas in the two populations, although further work is needed to more precisely quantify energy expenditure and energy balance. These results emphasize that even species with high food availability can exhibit behavioral and energetic responses to variable ecological conditions, which are likely to affect growth, reproduction, and survival. Am J Phys Anthropol 158:487–500, 2015.   © 2015 Wiley Periodicals, Inc.

Spatiotemporal variation in ecological conditions for a species can influence a number of factors such as energy intake and expenditure (Knott, 1998, 2005), grouping patterns (Wrangham, 1980; Koenig et al., 2013), life-history characteristics (Altmann and Alberts, 2003), reproductive performance (Knott, 2001), mortality (Gogarten et al., 2012), and population density (Chapman and Chapman, 1999; Marshall and Leighton, 2006). Energy balance (energy intake minus energy expenditure) is intrinsically linked to food availability, which influences the amount of energy available for growth, reproduction, and survival. Despite its relevance for understanding the evolution of life-history strategies in hominins and other primates (Brockman, 2005; Kuzawa and Bragg, 2012), few studies have collected quantitative data to examine how variation in food availability influences energy budgets, especially in great apes (but see: Knott, 2005). The goal of this paper is to quantify the differences in food availability between the two mountain gorilla populations and to investigate how such differences relate to some components of energy balance, specifically energy intake rates, time spent feeding, and daily travel distance of these two populations.

Spatial variation in food availability has been shown to elicit considerable variability in feeding ecology, growth patterns, and reproductive rates in primates. Captive primates are an extreme example of how increased energy intake and decreased energy

expenditure result in earlier maturation and faster reproduction rates compared to wild individuals (reviewed in: Pusey, 2012). Provisioned wild primates, which have greater food availability, spend less time feeding, more time resting, and have shorter daily travel distances than their nonprovisioned counterparts, resulting in faster growth rates, earlier maturation, higher infant survival, and shorter interbirth intervals (Altmann and Muruthi, 1988; Altmann and Alberts, 2003). In both wild chimpanzees (*Pan troglodytes)* and orangutans (genus *Pongo*), higher food availability has been linked to shorter interbirth intervals (summarized in: Knott et al., 2009; Potts et al., 2009; Watts, 2012; Thompson, 2013). Intergroup variation among small-scale human societies also follows the expected pattern of better environmental conditions correlating with faster growth and earlier puberty (Walker et al., 2006; Kuzawa and Bragg, 2012).

In addition to overall food availability, seasonal fluctuations in food availability are predicted to influence fertility, growth, and mortality. Species that experience large and unpredictable seasonal variation in food availability tend to grow and reproduce at slower rates than species with more predictable environments (e.g., Barret et al., 2006), which is thought to buffer them against the risk of starvation during periods of low food availability (Janson and van Schaik, 1993). This "risk aversion hypothesis" may also help explain why frugivorous species, which are more prone to unpredictable periods of food availability, have slower life-histories than folivorous species (Janson and van Schaik, 1993; Leigh, 1994). Even though this relationship has been contested (Lee and Kappeler, 2003), great apes seem to fit within this framework, with predominantly folivorous mountain gorillas having faster life-histories than the more frugivorous chimpanzees and bonobos, while orangutans have the slowest life-histories and the greatest reliance on ripe fruit of all extant apes (e.g., Wich et al., 2004).

Gorillas live in a wide variety of ecological conditions (summarized in Robbins, 2011), and comparisons between mountain and western gorillas (*Gorilla gorilla gorilla*) provide support for the predictions that spatiotemporal variation in food availability influences activity budgets, ranging patterns, and life-history characteristics. A lower density of terrestrial herbaceous vegetation (fibrous foods) combined with a greater reliance on seasonally available fruit is thought to explain why western gorillas have longer daily travel distances and larger home range sizes than mountain gorillas (Doran et al., 2002; Robbins, 2011), which may contribute to the differences in some life-history characteristics between these two species. Mountain gorillas mature faster and are weaned at an earlier age, leading to shorter interbirth intervals than western gorillas (Breuer et al., 2009; Stoinski et al., 2013). The slower life-history of western gorillas may be an adaptation to the potentially higher ecological risks they face due to higher spatial and temporal variability of food (Breuer et al., 2009; Stoinski et al., 2013).

Variation in food availability and feeding ecology have also been observed within and between the two mountain gorilla populations located only 25 km apart (Watts, 1984; McNeilage, 2001; Ganas et al., 2004, 2009a; Robbins, 2011). The ecological differences are likely driven by considerable variation in elevation (2,227–4,507 m in the Virungas vs. 1,160–2,607 m in Bwindi) (Robbins et al., 2006). Both populations rely heavily on terrestrial herbaceous vegetation that is available year-round (Watts,

1984, 1998; Ganas et al., 2009a). Bamboo shoots are the main seasonally available food consumed by Virunga gorillas, but do not occur where most of the Bwindi gorillas range (Vedder, 1984; McNeilage, 1995; Robbins et al., 2006). Moreover, fruit availability and therefore fruit consumption is negligible in the Virungas, whereas fruit is seasonally available and forms an important part of the gorillas' diet in Bwindi (Watts, 1984; Ganas et al., 2004; Robbins, 2008; Wright et al., 2014). The degree to which seasonal fruit availability in Bwindi may lead to greater overall increase in food availability than the seasonal increase caused by bamboo shoots in the Virungas has not been quantified. Additionally, overall biomass of terrestrial herbaceous vegetation appears to be higher in the Virungas than in Bwindi but no direct statistical comparisons have been made (Ganas et al., 2004; Grueter et al., 2013). Furthermore, a comparison of total biomass may not reflect a "gorilla's eye" view of the habitat, as it does not reflect the importance of particular food items in the gorillas' diet (Watts, 1984; Ganas et al., 2008). For example, one of the most abundant plants in Bwindi, *Mimulopsis solmsii*, accounts for only a small proportion of their diet (Ganas et al., 2008). Moreover, the nutrient concentrations of staple foods in both populations have been shown to be similar (with the exception of fruit) (Rothman et al., 2007; Wright et al., 2014), but comparing only the nutritional values of foods in the absence of a measure of food availability provides an incomplete picture of the quality and density of the food resources.

Ecological variation within and between the Virungas and Bwindi seemingly leads to different behavioral responses. Interbirth intervals are shorter in the Virungas than they are in Bwindi (4 vs. 5 years; Robbins et al., 2009). Virunga gorillas appear to have shorter daily travel distances (Watts, 1991; Ganas and Robbins, 2005) and smaller home ranges than Bwindi gorillas (Vedder, 1984; Watts, 1991; Robbins and McNeilage, 2003; Caillaud et al., 2014). These differences in habitat utilization may be due to the proposed higher densities of terrestrial herbaceous vegetation and the near absence of frugivory in the Virunga gorillas, but differences in methodology used may also contribute to the variation. In addition, female Virunga gorillas had significantly higher C-peptide levels, an indication of energy balance, during the bamboo season compared to outside this period (Grueter et al., 2014). Virunga gorillas are expected to decrease both the time spent feeding and daily travel distance when bamboo is available, but this has yet to be empirically tested (Vedder, 1984; Watts, 1988). In Bwindi, seasonally available fruit provides higher rates of energy return than terrestrial herbaceous vegetation and consequently gorillas spend less time feeding but have longer daily travel distances during periods of high fruit consumption (Ganas and Robbins, 2005; Wright et al., 2014). It remains unclear whether the influence of these two seasonal food types (bamboo and fruit) on gorilla energy budgets is expected to be stronger in one of the populations.

The aim of this study is to directly compare food availability in the two mountain gorilla populations and relate this to variability in energy intake rates, time spent feeding, and daily travel distance as a first step to understanding the ecological causes of variation in energy balance and life-histories between the two populations. First, we predicted higher food availability in the Virungas than in Bwindi. Instead of overall food availability, we used a measure of energy density

comprised of the most important dietary items by considering only foods that cumulatively contributed to over 90% of the total energy ingested by each population. We also compared the seasonal increase in food availability caused by bamboo shoots in the Virungas and by fruit in Bwindi. Next, we compared energy intake rates, time spent feeding, and daily travel distance of each population. We use these results to discuss the link between ecology, energetics, and life-history in mountain gorillas and other primates.

METHODS

Study sites

The study was conducted in the Karisoke region of the Volcanoes National Park, Rwanda, and in Bwindi Impenetrable National Park, Uganda (Fig. 1). Both sites are characterized by two dry seasons (June–August and December–February) and two wet seasons (March–May and September–November). Annual rainfall outside Volcanoes National Park (elevation 2400 m) for the current study period was 2066 mm (recorded by staff of the Dian Fossey Gorilla Fund International's Karisoke Research Center) and daily temperatures within the Karisoke area typically ranging between 3.9 and 14.5°C (Vedder, 1984). Annual rainfall in Ruhija in Bwindi (elevation 2400 m) is on average 1176 mm a year and average daily temperatures range between 13.5 and 19.4°C (Ganas et al., 2009b).

Data collection

Following the regulations of the Rwanda Development Board and the Uganda Wildlife Authority, daily observations on the habituated gorillas were limited to 4 h/day and were conducted at similar times (median observation times: 09:31–13:10 in the Virungas; 09:20–13:15 in Bwindi). Detailed feeding behavior, activity budgets, and daily travel distance were recorded on three groups from the Karisoke Research Center, Pablo (PAB), Bwenge (BWE), Ntambara (NTA), between October 2009 and September 2010, and the Kyagurilo group (KYA) in Bwindi Impenetrable National Park, between September 2010 and August 2011. Daily travel distance was recorded on an additional two Karisoke groups [Kuryama (KUY) and Inshuti (INS); henceforth, the five groups are referred to as Virunga groups], during the same study period as above, and on 12 additional groups habituated for tourism from Bwindi Impenetrable National Park (henceforth Bwindi groups), between May 2012 and June 2013. Membership of the groups remained relatively stable throughout the study periods, although some variation was present due to normal life-history events such as births, deaths, and transfers (see Supporting Information for group size). In the following analyses, we included the number of weaned individuals per group as a control variable, which has been shown to influence the ranging patterns in both populations (Watts, 1991; Ganas and Robbins, 2005; Caillaud et al., 2014).

In the analyses that used individual females as data points, we included dominance rank as a control variable. Dominance hierarchies were based on the direction of displacements (approach and retreat interactions) and determined using a normalized David's score (de Vries et al., 2006). A statistically significant dominance hierarchy was found for all groups (all $P < 0.004$). We also
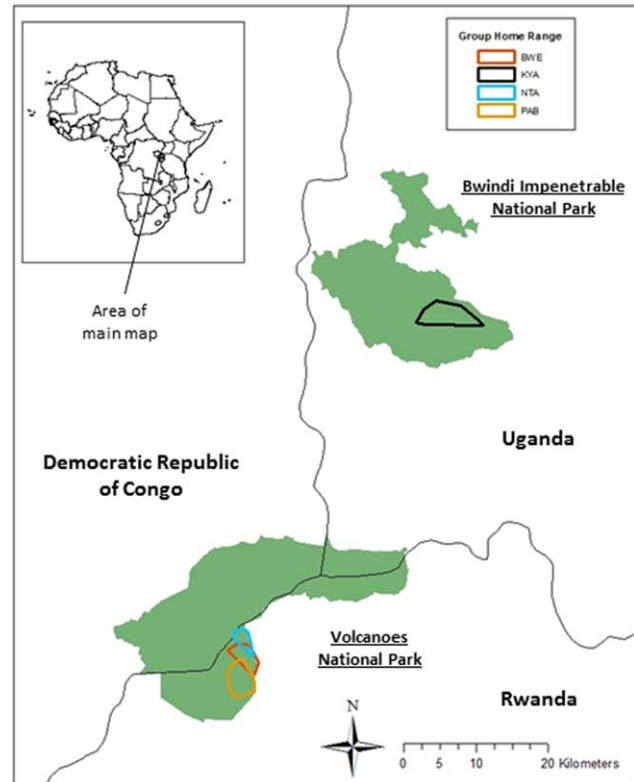

Fig. 1. The two mountain gorilla populations found in the Virunga massif of Rwanda, Democratic Republic of Congo and Uganda and Bwindi Impenetrable National Park, Uganda. Home ranges are displayed for the three Virunga groups (BWE, NTA, and PAB) and one Bwindi group (KYA), estimated via minimum convex polygon. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

included reproductive state (cycling, gestation, or lactation) of each focal female as a control variable. We considered females to be gestating for 8.5 months backdated from the birth of an infant. Females were assumed to be lactating following the birth of an infant for 3 years in the Virungas and for 4 years in Bwindi (Robbins et al., 2009).

Food availability

Our measure of food availability was based on the energy density of the most important foods for each population, which we defined as foods that cumulatively contributed to over 90% (range: 91–98%) of the total energy ingested over the study period. Energy density, a "common currency" which can be easily compared with other studies (Knott, 2005), was estimated by multiplying the dry biomass (g DW/m²) of the most important foods by the energy concentration of each food item (see *Energy intake* below). When the gorillas fed on multiple plant parts of the same species (bark and leaves for example), the energy concentration was weighted according to the proportion of each part in the total energy ingested. Because the biomass for terrestrial herbaceous vegetation does not show significant variation over the year in either site (Watts, 1984, 1998; Ganas et al., 2009a), we used values from one sampling period. The methods for estimating biomass in the Virungas are detailed in Grueter et al. (2013). Briefly, vegetation

sampling was conducted in 473 circular plots ["extended area" in Grueter et al. (2013)] and the stem length, number of leaves, or whole plants were counted for each species. A similar method was employed for the Bwindi group, using 166 vegetation plots, between May 2012 and June 2013 (Seiler et al. in prep). Biomass availability was estimated for each group by considering only vegetation plots in each group's home range (vegetation plots that were located 250 m or less from both the sleeping sites and where the observers left the gorillas at the end of the daily observation periods). To obtain dry biomass estimates (g DW/m^2), we used phytometric regression equations (mathematical functions that relate dry biomass as a function of a single or a combination of known plant dimensions) by extrapolating the plant dimensions collected during the vegetation sampling (as per Grueter et al., 2013). Phytometric regression equations have been published for the Virunga gorilla foods by Plumptre (1991) and by Ganas et al. (2009a) for Bwindi gorilla foods (with the exception of *Urera hypselodendron;* Seiler et al. in prep). Lastly, it was not feasible to estimate the biomass for the fruit of *Rubus runssorensis* shrub in the Virunga vegetation plots (thought not to be seasonal), so we did not fully account for this in the energy density estimates.

Temporal availability

Bamboo shoots (*Yushania alpina*) are the only seasonal food in the Virungas (Vedder, 1984; Watts, 1984, 1998). Because of the difficulties in estimating the biomass of the shoots, we used the biomass estimate of 2.11 g/m^2 calculated in a previous study (McNeilage, 1995). In the absence of phenology data on shoot availability, we relied on when the gorillas fed on bamboo shoots as an approximate indication of availability, using instantaneous scan sampling (presence/absence of bamboo consumption per group per month).

Among the important foods consumed by the Bwindi group, two were seasonal fruits *Chrysophyllum albidium* and *Myrianthus holstii*. In the absence of the precise number of fruits for these two species, we roughly estimated the fruit dry weight in an average sized tree for each species (see Supporting Information). We monitored fruit trees on a monthly basis to qualitatively record fruit abundance [0% = no fruit; 25%, 50%, and 100% = tree crown full of fruit (Ganas et al., 2009a)], which we applied to the total fruit dry weight estimate; food availability was therefore a monthly value. We used the period of fruit consumption by the gorillas as an indication of fruit availability. During the study period, fruit consumption showed one large peak during 3 months of the year (referred to as the period of high fruit consumption), while the rest of the year was characterized as low fruit consumption.

Energy intake

Feeding behavior of adult females was recorded using focal animal sampling (Altmann, 1974) for 30 min periods in the Virungas and 15–60 min periods in Bwindi (variation was due to the dense understory vegetation in Bwindi that made it difficult to follow individuals for extended periods of time). Priority was given to the individual with the least focal time so as to obtain a similar amount of focal time on each adult female. We recorded 242 focal feeding hours in total (27 h BWE; 26 h NTA; 69 h PAB; 120 h KYA). The methods to record energy

intake were the same in both sites and are detailed in Wright et al. (2014) and Grueter et al. (in review). Briefly, we estimated the wet weight ingested by the focal female based on the number of food units consumed for each species (food units were pre-defined as being a handful of leaves, one fruit or a certain length of bark, for example). This was then converted into organic matter. Plant samples were collected for nutritional analysis in the Virungas between October 2009 and September 2010 (Grueter et al. in review) and in Bwindi by Ganas et al. (2008) and Wright et al. (2014). We assumed that energy concentration of the foods did not vary significantly, although we do acknowledge that nutritional content can vary over time (Chapman et al., 2003; Worman and Chapman, 2005; Rothman et al., 2012). Nutritional analysis of the plant samples were conducted in the same laboratory (Leibniz Institute for Zoo and Wildlife Research in Berlin) by SO. The energy concentration of each food (predicted metabolic energy) was based on the amount of crude protein (CP), total nonstructural carbohydrates (TNC), lipids (L), and neutral detergent fiber (NDF) present, using the following conversion factors: 4 kcal/g CP; 4 kcal/g TNC; 9 kcal/g L; 1.6 kcal/g NDF [as per Conklin-Brittain et al. (2006)]. TNC was calculated by difference: %TNC = 100- %L- %CP- %TA- %NDF (Conklin-Brittain et al., 2006). The predicted metabolic energy (PME) per gram of organic matter of each food was calculated using the following formula as per N'guessan et al. (2009): PME (kcal/g) = (4*%CP + 4*%TNC + 9*%L + 1.6*%NDF)/100. The total organic matter ingested was then multiplied by the PME of each food item to obtain energy intake.

Time spent feeding

Instantaneous scan sampling was conducted every 10 min in the Virungas and every 5 min in Bwindi throughout the daily observation period to record the activity that most of the individuals in view were doing at the time of the scan (feeding, resting, or travelling), referred to as group activity.

Daily travel distance

Using GPS readings at 30 s intervals, we recorded the distance each group travelled between consecutive night nesting sites by following the main trail that the majority of the group travelled. For the Virunga groups, a team backtracked from the most recent nest site to older nest sites. For the Bwindi groups, part of the nest to nest track was recorded by following gorilla trail and part was recorded during the daily gorilla observation period. Because considerable error is sometimes obtained when repeated GPS readings are taken from roughly the same location (or individuals spend relatively little time travelling; see Janmaat et al., 2013 for discussion and similar approach), the daily travel distances were cleaned to remove large "knots" in the GPS recordings (daily travel distance when the group was stationary) using a program developed in R (R Core Team, 2013) by Roger Mundry to smooth the daily travel distance and obtain more reliable travel distances.

Food availability analysis

To examine whether food availability varied significantly among the groups, we conducted a Kruskal–Wallis H-test and Welch two sample T-tests to test the

significance between each pair of groups. An F-test for equality of variance was used to test whether food availability had significantly higher variance in the Bwindi group than the Virunga groups.

Models used in the analysis

To test our predictions, we developed six mixed models. Their structure with regard to the key predictors is described in the following.

Energy intake rates

To examine the relationship between energy intake rates and food availability in the two populations, we ran a linear mixed model (LMM) (Baayen, 2008). The response variable was the total energy ingested (kcal) in each focal period per day. The response variable was not a rate (i.e., the total energy ingested per focal period was not divided by the feeding duration), instead we included feeding duration as a control variable (Wright et al., 2014). The analysis used a separate data point for each female that was observed on a given day. The test predictors (variables of interest) were population (Virunga and Bwindi), food availability, and the interaction between these two variables, as we wanted to specifically test whether an increased food availability influenced energy intake rate differently depending on the population. The following variables were included as control variables: dominance rank, the interaction between dominance rank and population (assuming that dominance rank could have influenced energy intake rates differently depending on the population), reproductive state, group size, day time and day time squared (to account for a potential nonlinear relationship between day time and energy intake rate), and feeding duration. We included random effects for focal female, group ID, and date. To keep type 1 error rates at the required level of 5%, we included random slope terms to allow for food availability, reproductive state, time and time squared to vary in their relationship to group, food availability, group size, time and time squared to vary in their relationship to focal and rank to vary in its relationship to date as well as the correlation parameters between the random slope terms and random intercepts (Schielzeth and Forstmeier, 2009; Barr et al., 2013).

In addition to the above model, we ran a further two LMMs to compare the energy intake rates between the two populations, specifically testing whether energy intake rates were a) overall higher and b) varied more in one of the populations. We did not include a measure of food availability in these two models, as we wanted an overall comparison over the entire year, irrespective of variation in food availability. The response variable was the mean energy intake rate per female over the entire study period in the first model and the standard deviation in energy intake rate per female in the second model. We thus had one data point per individual in each model. We included group size, dominance rank, and reproductive state as control variables in both models and included group ID as a random variable. Because of small sample size, we did not test for a possible interaction between rank and population, nor did we calculate random slopes.

Proportion of time spent feeding

To test whether the two populations spent different proportions of time feeding, we ran a LMM. The response variable was the proportion of time that the group spent feeding calculated from the instantaneous scan samples of group activity. The analysis used a separate data point for each group per month. As test predictors we included population and food availability and the interaction between these two variables to examine whether the influence of food availability on the proportion of time spent feeding depended on the population. We included group size as a control predictor and group ID as a random effect as well as random slope terms to allow for food availability and group size to vary in their relationship to group ID. We excluded 5 group-months because they had fewer than 50 scans each. We recorded a total of 56,613 group scans (6,093 BWE; 8,454 NTA; 13,431 PAB; and 28,635 KYA). Although we did not use full-day observations, the comparison of the proportion of time spent feeding is likely to be valid, because our times of observation were similar, the gorillas in the two populations become active at similar times, and they have comparable cycles of feeding and resting throughout the day (M. Robbins, personal observation).

Daily travel distance

To test the prediction that Virunga gorillas have shorter daily travel distances than Bwindi gorillas, we ran two LMMs. In the first of these, we included the travel distances of three Virunga groups (PAB, BWE, and NTA) and the one Bwindi group (KYA) as well as term for food availability. We recorded a total of 508 daily travel distances (75 BWE; 84 NTA; 80 PAB; 269 KYA). In the second model, we included a total of 2123 daily travel distances from the 5 Virunga groups and 13 Bwindi groups, but we did not include a term for food availability because it was not available for all groups. The response variable for both of these models was daily travel distance. In the first model, we included the interaction between population and food availability, to test whether daily travel distance was influenced differently by food availability depending on the population. We included group size as a control variable and included group ID as a random effect in both models. We included random slope terms to allow for food availability and group size to vary in their relationship to group ID in the first of these models and group size to vary in its relationship to group ID in the second model.

Data analysis

The models were fitted in R (R Core Team, version 3.11, 2014) and run with Gaussian error structure and identity link. The models were implemented using the function "lmer" of the "lme4" package (Bates et al., 2014). We accounted for temporal autocorrelation (data points close in time being more similar to each other than data points further away in time) in all the models, with the exception of the two models which had one data point per female. This variable was derived by first obtaining the residuals of each model. Then for each data point, we averaged the residuals of all the other data points in the data set (considering only data points of the same individual or group in the case of the proportion of time feeding and daily travel distance models), whereby the contribution of the other data points to this

average was dependent on the temporal distance between the two data points [see Fürtbauer et al. (2011) for more detailed explanation]. This variable was then included in the models as a control predictor. We z-transformed (to a mean of 0 and a standard deviation of 1) all quantitative predictor variables. We checked for the assumptions of normally distributed and homogenous residuals by visually inspecting q–q plots and the residuals plotted against fitted values and found no violations. We checked for model stability by excluding each level of the random effects one at a time from the data and comparing the estimates of each predictor to the estimates obtained from a model with the full data set; no influential cases were found. Variance inflation factors (VIF; Field, 2005) were derived using the function "vif" of the "car" package (Fox and Weisberg, 2011) based on a standard linear model excluding random effects and interactions and no collinearity issues were found. Before interpreting the results of each model, we com-

pared the full model to a corresponding null model (a model without test predictors) using a likelihood ratio test (R function ANOVA with argument test set to "Chisq"), and only when this comparison was significant we inspected the significance of each individual predictor variable. This was done using likelihood ratio tests comparing the full models with respective reduced models, using the R function "drop1".

RESULTS

Food availability

There was a significant difference in food availability among the four groups, defined as the amount of energy (kcal/m^2) of the most commonly consumed foods in each groups' home range (Kruskal–Wallis H test: $\chi^2 = 37.31$, df = 3, $P < 0.001$; Table 1; Fig. 2). The Bwindi group (KYA) had the lowest food availability, followed by PAB, BWE, and NTA (post hoc pairwise comparisons using

TABLE 1. *The most important food species for each population (species which cumulatively contributed to over 90% of the total energy ingested by each population) for the three Virunga groups (BWE, NTA, and PAB) and one Bwindi group (KYA)*

Group	Species	Dietary importance	Cumulative	Biomass density (g DW/m^2)	Weighted energy concentration (kcal/g)	Energy density (kcal/m^2)	Seasonal
NTA	*Galium* sp.	45.7%	45.7%	0.7	2.4	1.7	n
NTA	*Carduus nyassanus*	16.4%	62.1%	4.5	2.4	10.9	n
NTA	*Yushania alpina*	11.1%	73.3%	2.1	2.4	5.0	y
NTA	*Droguetia iners*	10.8%	84.1%	1.5	2.6	3.9	n
NTA	*Peucedanum linderi*	6.4%	90.4%	33.9	2.0	66.4	n
NTA	*Rubus runssorensis*[a]	4.1%	94.5%	2.1	2.8	5.9	n
NTA	*Laportea alatipes*	3.8%	98.3%	24.5	2.4	57.5	n
Total				69.3		151.3	
BWE	*Galium* sp.	43.6%	43.6%	0.7	2.4	1.6	n
BWE	*Carduus nyassanus*	15.8%	59.4%	5.1	2.4	12.0	n
BWE	*Yushania alpina*	14.4%	73.8%	2.1	2.3	4.9	y
BWE	*Rubus runssorensis*[a]	7.4%	81.2%	2.6	2.7	7.2	n
BWE	*Laportea alatipes*	5.6%	86.8%	40.5	2.3	95.2	n
BWE	*Droguetia iners*	3.1%	90.0%	1.9	2.6	4.9	n
BWE	*Peucedanum linderi*	2.5%	92.5%	7.7	2.0	15.1	n
Total				60.5		140.8	
PAB	*Rubus runssorensis*[a]	34.8%	34.8%	12.2	2.9	35.4	n
PAB	*Galium* sp.	33.6%	68.5%	1.6	2.4	3.8	n
PAB	*Carduus nyassanus*	17.9%	86.4%	11.1	2.3	25.2	n
PAB	*Peucedanum linderi*	4.0%	90.4%	10.2	2.0	19.9	n
PAB	*Laportea alatipes*	1.0%	91.3%	13.1	2.4	30.8	n
PAB	*Droguetia iners*	0.3%	91.6%	0.6	2.6	1.5	n
PAB	*Yushania alpina*	0.1%	91.8%	2.1	2.2	4.7	y
Total				50.8		121.4	
KYA	*Urera hypselodendron*	22.7%	22.7%	3.0	2.3	7.0	n
KYA	*Triumfetta sp*	14.4%	37.0%	0.6	2.4	1.5	n
KYA	*Ipomoea involucrata*	13.7%	50.7%	3.3	2.9	9.3	n
KYA	*Chrysophyllum albidium*	13.6%	64.3%	3.1	3.7	11.6	y
KYA	*Momordica foetida*	10.3%	74.6%	3.0	2.9	8.6	n
KYA	*Mimulopsis solmsii*	6.5%	81.1%	14.5	2.1	30.3	n
KYA	*Myrianthus holstii*	3.7%	84.8%	0.7	2.4	1.3	y
KYA	*Rubus* sp.	3.6%	88.4%	5.9	2.7	16.0	n
KYA	*Basella alba*	2.9%	91.3%	0.6	2.7	1.6	n
Total				34.7		87.2	

Dietary importance was measured by the proportion of energy each food contributed to the total amount of energy ingested by each group over the study period. Biomass density (g DW/m^2) was calculated separately for each group by considering only vegetation plots which were within each group's home range. When the gorillas fed on multiple parts of the same species, the energy concentrations (kcal/g) of the species was weighted by the individual contribution of energy of each part. Energy density (kcal/m^2) is biomass density (g DW/m^2) multiplied by the weighted energy concentration (kcal/g) of each food. For seasonal species (y = yes, n = no), the energy density was added to the corresponding months of availability (the energy density value displayed in the table for *Chrysophyllum albidium* and *Myrianthus holstii* is averaged across the 12-month period).
[a] The fruit of *Rubus runssorensis* was not considered in the biomass estimates, therefore the biomass estimate is likely to be higher than what is shown.

Welch two sample t tests, all $P < 0.002$). Food availability for the three Virunga groups was 50–100% higher than for the Bwindi group. Food availability for PAB group would likely had been more similar to that of BWE and NTA group if we had been able to include a measure of availability for *Rubus runssorensis* fruit that is common in PAB's home range (Table 1; see Supporting Information for further discussion). Fruit availability lead to a more pronounced increase in food availability

in Bwindi compared to the availability of bamboo shoots in the Virungas (F-test for equality of variance: $F = 3.03$, $df_{num} = 11$, $df_{denom} = 35$, $P = 0.012$; Fig. 2). Mountain gorillas from both populations heavily relied on relatively few plant species (Table 1). Between four and six species accounted for over 90% of the total energy consumed by the Virunga groups, whereas the Bwindi group relied on nine.

Energy intake rates

The rate of increase in energy intake rates with increasing food availability was the same in the two populations (nonsignificant interaction between food availability and population; Table 2), but due to the greater overall increase in food availability during the period of high fruit consumption in Bwindi, energy intake rates in this population increased to higher overall levels than those in the Virungas. During the period of high fruit consumption, Bwindi gorillas had over double the energy intake rates of the Virunga gorillas (Fig. 3). Outside this period, energy intake rates were comparable between the two populations. Of the seven control variables, group size and feeding duration had a positive influence on energy intake rates. Dominance rank was positively correlated to energy intake rates in Bwindi, but not in the Virunga groups (Wright et al., 2014; Table 2).

The additional model, which compared overall energy intake rates between the two populations with one data point per female and which did not consider differences in food availability, confirmed the finding that energy intake rates were overall higher in Bwindi (Table 3; Fig. 4). This was exclusively caused by the months of fruit feeding, as a model without the 3 months of high fruit consumption did not reveal a significant difference between the two populations (full vs. null model comparison, without the three high fruit consumption months; $\chi^2 = 0.01$, $df = 1$, $P = 0.936$).

The model which compared the variance in energy intake rates between the two populations and that did not include food availability revealed that Virunga gorillas had significantly lower variance in energy intake rates over the year than Bwindi gorillas (Table 4; Fig. 5). Of the three control variables, only group size had a
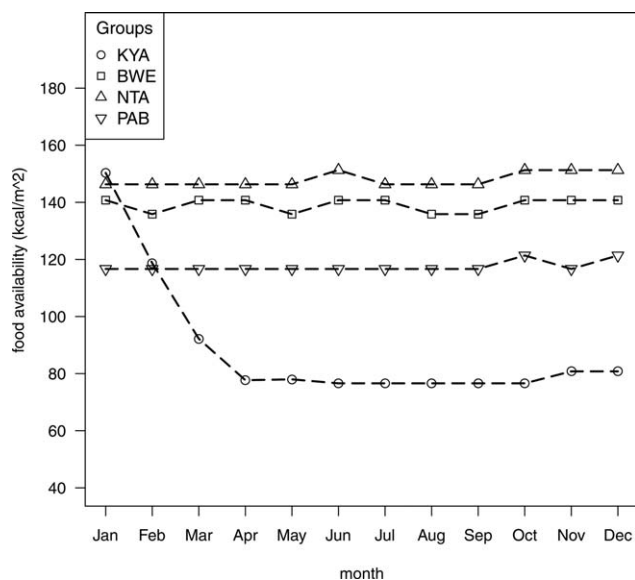

Fig. 2. Food availability, measured via energy density (kcal/m^2) per calendar month for the three Virunga groups (BWE, NTA, and PAB) and one Bwindi group (KYA). *Rubus runssorensis* fruit was not taken into account in the biomass estimates, which would likely result in an increase in food availability for the three Virunga groups, but particularly for PAB, because this shrub was considerably more abundant in its home range compared to the other groups. Bamboo shoots only marginally increased food availability in the Virungas, while fruit considerably increased food availability in Bwindi. Additional very small fluctuations were also apparent in Bwindi, caused by the non-seasonal availability of *Myrianthus holstii* fruit occurring at very low density.

TABLE 2. *The influence of population, food availability, and other variables on energy intake rates.*

Full vs. null model Data points = 1090	$\chi^2 = 20.67$; df = 5; $P < 0.001$				
	Estimate	Std. error	χ^2	df	P
Intercept	7.16	0.11			
Population	−0.44	0.29			
Food availability	0.31	0.06	10.52	1	0.001
Dominance rank	0.14	0.04			
Group size	0.05	0.10	5.39	1	0.020
Reproductive state—lactating	−0.02	0.07	0.36	2	0.83
Reproductive state—gestating	0.02	0.07			
Day time	0.06	0.02			
Day time^2	−0.00	0.02	0.06	1	0.81
Feeding duration	1.05	0.02	1261.81	1	<0.001
Temporal autocorrelation	0.05	0.02	6.18	1	0.013
Interaction population and rank	−0.20	0.06	7.78	1	0.005

The estimate and standard error for population is in relation to Bwindi, while the reproductive state lactation and gestation are in relation to cycling. The interaction between population and food availability was not significant (estimate = −0.26, standard error = 0.24, $\chi^2 = 1.18$, df = 1, $P = 0.277$) and therefore removed from the model. Blank cells are given when values would not be meaningful, i.e., when the variables are included in interactions or when an equivalent squared term is present in the model. Quantitative predictor variables were z-transformed
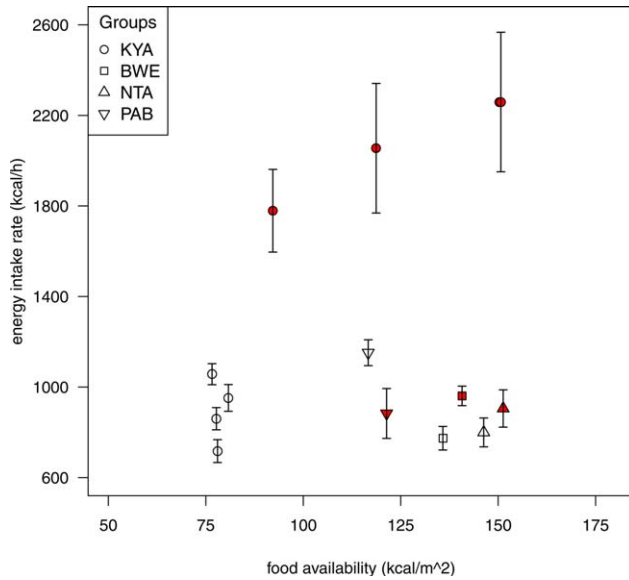
Fig. 3. The relationship between energy intake rate (kcal/h) and food availability for the three Virunga groups (BWE, NTA, and PAB) and one Bwindi group (KYA). The energy intake rate for each food availability value is displayed (due to monthly variation in food availability, the Bwindi group had seven separate food availability values, whereas the Virunga groups had two). The periods of high fruit and bamboo shoot consumption are denoted in red. Indicated are means (points) with standard error bars. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE 3. *A comparison of overall energy intake rates between the two populations, using the one data point per female approach, which did not include a term for food availability.*

Full vs. null model	$\chi^2 = 9.37$; df = 1; $P = 0.002$				
Data points = 27	Estimate	Std. Error	χ^2	df	P
Intercept	1280.57	65.17			
Population	−312.35	74.50	7.51	1	0.006
Dominance rank	−6.41	33.04	0.03	1	0.852
Group size	69.47	31.35	0.58	1	0.446
Reproductive state	−31.16	33.24	0.90	1	0.342

The estimate and standard error for population is in relation to Bwindi. Quantitative predictor variables were *z*-transformed

significant positive influence on the variance in energy intake rates (Table 4).

Proportion of time spent feeding

The combined influence of population and food availability only marginally influenced the proportion of time spent feeding (full vs. null model comparison: $\chi^2 = 7.64$; df = 3; $P = 0.054$; Table 5). Both populations spent similar proportions of time feeding (fitted values for the proportion of time spent feeding were 0.49 and 0.51 for the Virunga and Biwndi gorillas, respectively). Furthermore, both populations significantly decreased the proportion of time spent feeding during periods of either high fruit or bamboo shoot consumption periods (nonsignificant interaction between population and food availability; Table 5). Against expectations, group size was negatively correlated with the proportion of time spent feeding, with larger groups spending a lower proportion of time feeding than smaller groups (Table 5).
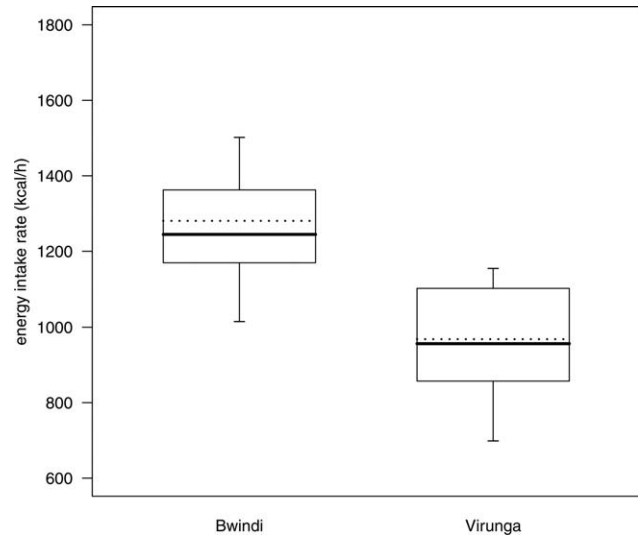

Fig. 4. The relationship between overall energy intake rates (kcal/h) for each population, using the one data point per female approach and without considering changes in food availability. Solid lines represent median values, dotted lines are fitted values, boxes depict quartiles, and vertical lines quantiles (2.5% and 95%).

TABLE 4. *A comparison of the variance in energy intake rates between the two populations, from a model which did not include a term for food availability.*

Full vs. null model	$\chi^2 = 10.83$; df = 1; $P = 0.001$				
Data points = 27	Estimate	Std. error	χ^2	df	P
Intercept	735.92	55.04			
Population	−300.93	62.91	10.83	1	0.001
Dominance rank	−37.71	25.86	2.05	1	0.153
Group size	80.33	27.43	6.45	1	0.011
Reproductive state	0.52	26.68	0.00	1	0.980

The estimate and standard error for population is in relation to Bwindi. Quantitative predictor variables were *z*-transformed
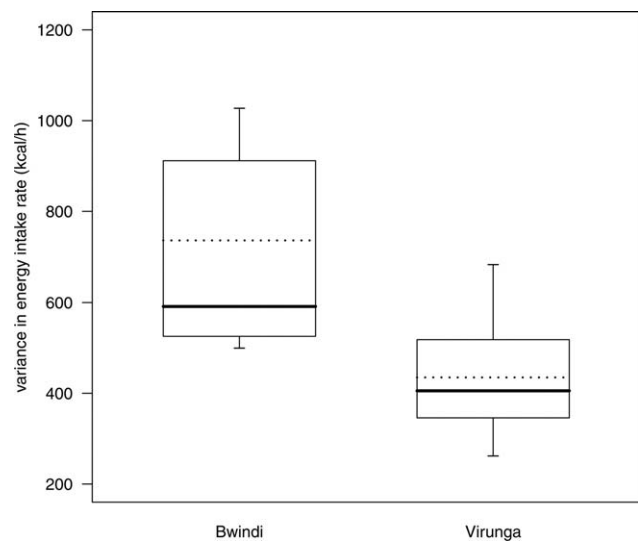

Fig. 5. The variance in energy intake rates (kcal/h) for each population, without considering changes in food availability. Solid lines represent median values, dotted lines are fitted values, boxes depict quartiles, and vertical lines quantiles (2.5% and 95%).

TABLE 5. *The influence of population, food availability and group size on the proportion of time spent feeding.*

Full vs. null model	$\chi^2 = 7.64$; df = 3; $P = 0.054$				
Data points = 43	Estimate	Std. error	χ^2	df	P
Intercept	0.51	0.04			
Population	−0.02	0.05	0.21	1	0.645
Food availability	−0.06	0.02	6.03	1	0.014
Group size	−0.04	0.01	5.24	1	0.022

The estimate and standard error for population is in relation to Bwindi. The estimate for temporal autocorrelation was negative, therefore it was removed from the model. The interaction between population and food availability was not significant (estimate=0.02, standard error = 0.07, χ^2 = 0.12, df = 1, P = 0.732) and therefore removed from the model. Quantitative predictor variables were z-transformed
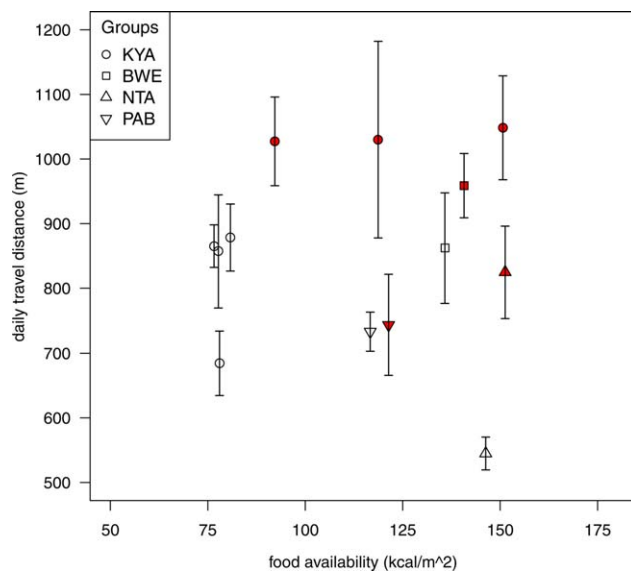

Fig. 6. The relationship between daily travel distance (m) and food availability for the three Virunga groups (BWE, NTA, and PAB) and one Bwindi group (KYA). The mean daily travel distance for each food availability value is displayed (due to monthly variation in food availability, the Bwindi group had seven separate food availability values, whereas the Virunga groups had two). The period of high fruit and bamboo shoot consumption are denoted in red. Indicated are means (points) with standard error bars. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Daily travel distance

Overall, Bwindi gorillas had longer daily travel distances than Virunga gorillas, particularly during periods of high fruit consumption (Fig. 6). However, contrary to our prediction, Virunga gorillas had longer, not shorter daily travel distances during the bamboo period. In fact, the rate of increase in daily travel distances was significantly steeper for the Virunga gorillas during the bamboo period than it was for the Bwindi gorillas during the period of high fruit consumption (significant interaction between population and food availability; Table 6). There was a trend for larger groups to travel further than smaller groups (Table 6).

The model with the additional groups and consequently many more daily travel distances, but without a term for

TABLE 6. *The influence of population, food availability and other variables on daily travel distance in three Virunga groups and one Bwindi group.*

Full vs. null model	$\chi^2 = 11.28$; df = 3; $P = 0.010$				
Data points = 508	Estimate	Std. error	χ^2	df	P
Intercept	6.98	0.18			
Population	−0.77	0.49			
Food availability	0.09	0.03			
Group size	0.66	0.61	3.45	1	0.063
Temporal autocorrelation	0.10	0.02	35.16	1	<0.001
Interaction population and food availability	0.63	0.34	7.05	1	0.008

The estimate and standard error for population is in relation to Bwindi. Blank cells are given when values would not be meaningful, i.e., when the variables are included in an interaction. Quantitative predictor variables were z-transformed

TABLE 7. *The influence of population, food availability, and other variables on daily travel distance in five Virunga groups and 13 Bwindi groups; the model does not include a term for food availability.*

Full vs. null model	$\chi^2 = 6.36$; df = 2; $P = 0.042$				
Data points = 2123	Estimate	Std. error	χ^2	df	P
Intercept	6.70	0.05			
Population	−0.27	0.10	5.84	1	0.016
Group size	0.04	0.04	1.23	1	0.267
Temporal autocorrelation	0.19	0.01	288.99	1	<0.001

The estimate and standard error for population is in relation to Bwindi. Quantitative predictor variables were z-transformed

food availability, confirmed that Bwindi gorillas have longer daily travel distances than Virunga gorillas (the fitted value for daily travel distance was 815 and 625 m for Bwindi and the Virunga gorillas, respectively; Table 7; Fig. 7). However, there was significant overlap in daily travel distance both between and within the two populations.

DISCUSSION

Food availability

Rather than using a measure of overall food availability, our study used a refined measure, combining the biomass and energy concentrations of the most commonly consumed foods to obtain the energy density (kcal) per square meter (Knott, 2005). Bwindi gorillas have a lower overall amount and greater temporal variability of food availability than Virunga gorillas. Food availability was 50–100% higher for the Virunga groups than for the Bwindi group, which was due to higher biomass of important terrestrial herbaceous vegetation species in the Virungas than in Bwindi, as there was no significant difference in the nutritional content of foods in the two sites (Rothman et al., 2007; unpublished data). Previous studies have shown intrapopulation variation in overall biomass of foods consumed by gorillas both in the Virungas and in Bwindi (Watts, 1984; McNeilage, 2001; Ganas et al., 2004, 2009a). We also found significant variation in food availability of important foods among the three Virunga groups (Fig. 2), but we could not examine within-population variability in Bwindi because we had only one study group. However, it is likely that even if
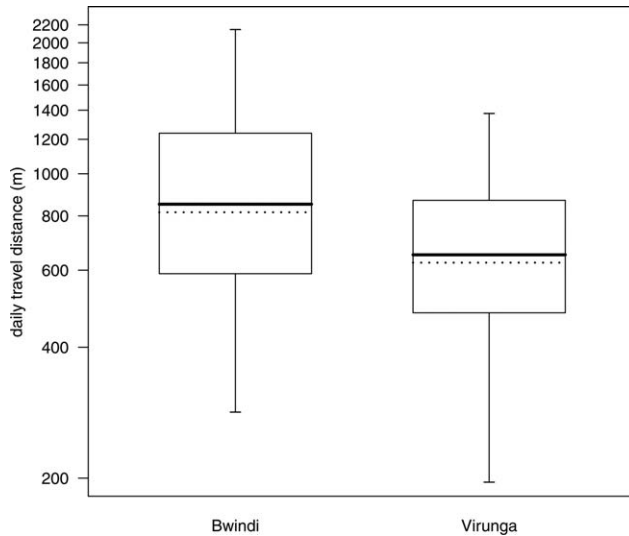
Fig. 7. The relationship between daily travel distance (m), presented on a log-transformed scale, and population (Virungas = 5 groups; Bwindi = 13 groups) from a model not comprising a term for food availability. Solid lines represent median values, dashed lines are the fitted values (accounting for differences in group size), boxes depict quartiles, and vertical lines quantiles (2.5% and 95%).

we had included additional areas in Bwindi we would have found lower food availability than in the Virungas because previous studies in Bwindi found a higher biomass of gorilla foods in the area used in this study compared to other areas (Ganas et al., 2004, 2009b; Nkurunungi et al., 2004). Given the importance of terrestrial herbaceous vegetation in the diet of all apes (Wrangham et al., 1991; Harrison et al., 2010; Harrison and Marshall, 2011) and the fact that they are selective feeders (Ganas et al., 2008; Hohmann et al., 2010), we stress the importance of going beyond Knott's (2005) suggestion of presenting data on only the energy density of fruit, but to also incorporate the energy density of terrestrial herbaceous vegetation, to better examine the relationship between food availability and variation in behavior and life-history parameters at both the intraspecific and interspecific level.

Mountain gorillas from both the Virungas and Bwindi are somewhat unique among primates, as they do not appear to have a period of low food availability. On the contrary, one could argue that seasonal availability of fruit in Bwindi and bamboo in the Virungas provides times of even greater food availability against a background of constant high availability of terrestrial herbaceous vegetation. Fruit availability in Bwindi had a much larger influence on food availability than bamboo shoots in the Virungas. During 2 of the 3 months of high fruit availability, food availability in Bwindi rose to values comparable to those in the Virungas, whereas the availability of bamboo shoots only marginally increased food availability in the Virungas. The greater variability, combined with the lower overall amount, of food availability in Bwindi suggests that Bwindi gorillas live in a more ecological complex environment than Virunga gorillas. However, the higher density of terrestrial herbaceous vegetation in Bwindi compared to western gorilla habitat makes it unlikely that Bwindi gorillas

need to follow a risk aversion strategy. The seasonal availability of fruit represents a major increase in food availability for Bwindi gorillas and for the vast majority of other primate populations (Brockman, 2005); however, it remains unclear to what extent it plays a role in the life-history evolution of this population.

Energy intake rates and time spent feeding

Energy intake rates of gorillas in the two populations were similar for most of the year, which is unsurprising given that the nutritional content of the majority of foods is similar (Rothman et al., 2007). These results also suggest that ingestion rates and processing times also were similar. However, the more pronounced increase in food availability in Bwindi compared to the Virungas lead to energy intake rates in Bwindi being over double the values for the Virungas during the period of high fruit consumption. Fruit-related increases in energy intake rates has also been shown in several other species including western gorillas (Masi, 2008), orangutans (Knott, 1998; Harrison et al., 2010), and Assamese macaques (*Macaca assamensis*) (Heesen et al., 2013). However, seasonal availability in leaves and other nonreproductive plant parts may also lead to changes in energy intake (Koenig, 2000; Harris et al., 2009). The smaller increase in food availability in the Virungas during the period of bamboo shoot consumption also increased energy intake rates in this population but to a smaller extent.

No significant difference was found in the time spent feeding between the two populations, which could be due to the lack of differences in both energy concentration of foods and intake rates. It should be noted that as the gorillas were observed for only four hours per day in this study, we may not have captured the variability in the total time spent feeding. However, the hours of observation were similar for both populations so the activity budgets were likely to be comparable during this time window. Nonetheless, the gorillas may also be constrained by time needed for digestion ["enforced resting" (McFarland et al., 2014)] and they could be feeding for the maximum possible time. Mountain gorillas spend a higher proportion of their time resting compared to western gorillas, which may be due to the increased time needed for digesting a more fibrous diet (Masi et al., 2009). Interestingly, Potts et al. (2011) also did not find significant differences in feeding time between neighboring chimpanzee communities living in different quality habitats.

Gorillas at both sites spent significantly less time feeding during times of higher food availability, which is consistent with findings in western gorillas (Masi et al., 2009) and is a common strategy in many primates species that is most likely due to increased energy intake rates (Knott, 2005). Against expectation, larger groups had higher energy intake rates and spent less time feeding than smaller groups, which may be due to the intriguing possibility that larger groups have better quality diets and home ranges, but this remains to be tested (Seiler et al., in prep).

Daily travel distance

The average daily travel distance of the Bwindi groups was nearly 25% longer (625 vs. 815 m) than those of the Virunga groups (Fig.7). Whether this represents a significant increase in energy expenditure is difficult to say

without more precise measurements of locomotor energetics which at present can only be roughly estimated (Knott et al., 2009). Using Taylor's et al. (1982) equation for energy expended in primates and assuming an average body mass of 85 kg and a walking speed of 0.5 m/s (Wright et al., 2014), the extra 190 m walked per day by Bwindi gorillas would incur a further cost of 37 kcal per day, which seems inconsequential as it would take Bwindi gorillas an extra 2 min of feeding to achieve this extra cost. At the same time, Bwindi gorillas are expected to expend more energy on climbing than Virunga gorillas due to their considerable higher degree of arboreality. Climbing is estimated to be over twice as expensive compared to walking in large primates (Pontzer and Wrangham, 2004).

The increased daily travel distance by Bwindi gorillas may reflect the lower densities of important terrestrial herbaceous vegetation species or the increased travel distances associated with feeding on fruit. Similarly, a community of chimpanzees with lower density of important foods was thought to expend more energy on travel than a nearby community with higher densities of important foods (Potts et al., 2009). However, primates in general have almost 50% lower total energy expenditure relative to their body size compared to other mammals and interestingly wild primates do not necessarily expend more energy than captive primates, which suggests activity patterns may not always be a good indication of energy expenditure (Pontzer et al., 2014).

A common pattern in primates is to increase the daily travel distances during periods of higher food availability (and vice versa) (Hemingway and Bynum, 2005). Bwindi gorillas increased daily travel distance during the period of high fruit consumption which is in agreement with the previous findings in this population (Ganas and Robbins, 2005), and similar to findings in western gorillas (Goldsmith, 1999; Masi et al., 2009) and Bornean orangutans (Knott, 1999). Interestingly, Virunga gorillas significantly increased daily travel distance during the bamboo period, which was against predictions because of the clumped nature of bamboo shoots. Overall, the relationship between ranging patterns and food availability is complex, and is likely to be influenced by factors such as the spatial distribution and quality of foods (Ganas and Robbins, 2005; Hemingway and Bynum, 2005).

Energetics and life history

Gorillas from the two populations did not differ in energy intake rates and time spent feeding for most of the study period, but daily travel distance was overall greater in Bwindi than the Virungas. This would suggest that Virunga gorillas may have more positive energy budgets than Bwindi gorillas for most of the year, but we acknowledge that additional research using more refined estimates of energy expenditure and energy balance is necessary to further substantiate this finding. For example, energy balance can be assessed using urinary C-peptide, an indicator of insulin levels (Knott et al., 2009). Positive correlations between food availability (or ripe fruit consumption) and C-peptide levels have been shown in chimpanzees (Emery Thompson et al., 2009) and orangutans (Emery Thompson and Knott, 2008). Interestingly, the same Virunga gorillas as in this study had higher levels of C-peptide and therefore energy balance during the bamboo period (Grueter et al., 2014). The higher energy intake rates during this period likely contributes to more positive energy balance, even though they had to travel further to obtain it.

One potentially important factor mediating energy expenditure (and energy balance) that we did not measure is the cost of thermoregulation. Though extremely challenging to measure in the wild, it is a considerable cost for some primates such as Japanese macaques (*Macaca fuscata*), geladas (*Theropithecus gelada*), and some baboon species (genus *Papio*) (Dunbar, 1992; Hill et al., 2000; Hanya et al., 2004). For example, geladas residing at higher altitudes spend more time feeding than populations at lower altitudes and those living at temperature extremes had longer interbirth intervals than those living in more temperate regions, which is thought to be reflective of the cost of thermoregulation (Dunbar, 1992; Hill et al., 2000). Due to the lower average daily minimum temperature in the Virungas (3.9°C compared to 13.5°C in Bwindi) energy expenditure for maintaining stable body temperature is likely to be noticeably higher for Virunga gorillas, so future studies should attempt to measure this variable.

This study provides another example of how primate populations can respond to differing environmental conditions despite being in close geographic proximity (Chapman and Chapman, 1999; Potts et al., 2011). Such variation in ecological parameters has been linked to reproductive parameters (Pusey, 2012; Thompson, 2013). Further study is needed to better elucidate whether the energy used for thermoregulation combined with the energy used for locomotion, including climbing, significantly contribute to differences in energy balance between the two populations, which may explain the longer interbirth intervals in Bwindi compared to the Virungas (Robbins et al., 2009). To better understand how variation in ecology drives diversity in behavioral and life-history patterns within species, future studies would benefit from documenting the precise energetic responses to spatiotemporal variation in food availability (Borries et al., 2001; Strier, 2009).

ACKNOWLEDGMENTS

International, and the Swiss National Science Foundation/Schweizerischer Nationalfonds (PBZHP3-128152).

LITERATURE CITED

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Altmann J, Alberts SC. 2003. Variability in reproductive success viewed from a life-history perspective in baboons. Am J Hum Biol 15:401–409.

Altmann J, Alberts SC. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol 57:490–501.

Altmann J, Muruthi P. 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. Am J Primatol 15:213–221.

Baayen RH. 2008. Analyzing linguistic data: a practical introduction to statistics using R, 1st ed. Cambridge: Cambridge University Press.

Barr DJ, Levy R, Scheepers C, Tily HJ. 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang 68:255–278.

Barret L, Henzi P, Lyccet J. 2006. Whose life is it anyway? Maternal investment, developmental trajectories, and life history strategies in baboons. In: Swedell L, Leigh S, editors. Reproduction and fitness in baboons. University of Chicago, Chicago, Illinois: Springer. p 199–224.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4.

Borries C, Koenig A, Winkler P. 2001. Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). Behav Ecol Sociobiol 50:391–402.

Breuer T, Hockemba MB-N, Olejniczak C, Parnell RJ, Stokes EJ. 2009. Physical maturation, life-history classes and age estimates of free-ranging western gorillas—insights from Mbeli Bai, Republic of Congo. Am J Primatol 71:106–119.

Brockman DK. 2005. What do studies of seasonality in primates tell us about human evolution? In: Brockman DK, van Schaik CP, editors. Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 543–570.

Caillaud D, Ndagijimana F, Giarrusso AJ, Vecellio V, Stoinski TS. 2014. Mountain gorilla ranging patterns: Influence of group size and group dynamics. Am J Primatol 730–746.

Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. Primates 40:215–231.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. 2003. Variation in the nutritional value of primate foods: among trees, time periods, and areas. Int J Primatol 24:317–333.

Conklin-Brittain NL, Knott CD, Wrangham R. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects. Cambridge: Cambridge University Press. p 445–471.

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. Am J Primatol 58:91–116.

Dunbar RIM. 1992. Time: a hidden constraint on the behavioural ecology of baboons. Behav Ecol Sociobiol 31:35–49.

Emery Thompson M, Knott CD. 2008. Urinary C-peptide of insulin as a non-invasive marker of energy balance in wild orangutans. Horm Behav 53:526–535.

Emery Thompson M, Muller MN, Wrangham RW, Lwanga JS, Potts KB. 2009. Urinary C-peptide tracks seasonal and individual variation in energy balance in wild chimpanzees. Horm Behav 55:299–305.

Field AP. 2005. Discovering statistics using SPSS. London: SAGE Publications.

Fox J, Weisberg S. 2011. An {R} companion to applied regression. Sage: Thousand Oaks.

Fürtbauer I, Mundry R, Heistermann M, Schülke O, Ostner J. 2011. You mate, I mate: macaque females synchronize sex not cycles. PLoS ONE 6:e26144.

Ganas J, Nkurunungi JB, Robbins MM. 2009a. A preliminary study of the temporal and spatial biomass patterns of herbaceous vegetation consumed by mountain gorillas in an Afromontane rain forest. Biotropica 41:37–46.

Ganas J, Ortmann S, Robbins MM. 2008. Food preferences of wild mountain gorillas. Am J Primatol 70:927–938.

Ganas J, Ortmann S, Robbins MM. 2009b. Food choices of the mountain gorilla in Bwindi Impenetrable National Park, Uganda: the influence of nutrients, phenolics and availability. J Trop Ecol 25:123.

Ganas J, Robbins MM. 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. Behav Ecol Sociobiol 58:277–288.

Ganas J, Robbins MM, Nkurunungi J, Kaplin BA, McNeilage A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 25:1043–1072.

Gogarten JF, Brown LM, Chapman CA, Cords M, Doran-Sheehy D, Fedigan LM, Grine FE Perry S, Pusey AE, Sterck EHM, Wich SA Wright PC. 2012. Seasonal mortality patterns in non-human primates: implications for variation in selection pressures across environments. Evolution 66:3252–3266.

Goldsmith ML. 1999. Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. Int J Primatol 20:1–23.

Grueter CC, Deschner T, Behringer V, Fawcett K, Robbins MM. 2014. Socioecological correlates of energy balance using urinary C-peptide measurements in wild female mountain gorillas. Physiol Behav 127:13–19.

Grueter CC, Ndamiyabo F, Plumptre AJ, Abavandimwe D, Mundry R, Fawcett KA, Robbins MM. 2013. Long-term temporal and spatial dynamics of food availability for endangered mountain gorillas in Volcanoes National Park, Rwanda. Am J Primatol 75:267–280.

Hanya G, Yoshihiro S, Zamma K, Matsubara H, Ohtake M, Kubo R, Noma N, Agetsuma N, Takahata Y. 2004. Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. Ecol Res 19:485–493.

Harrison ME, Marshall AJ. 2011. Strategies for the use of fallback foods in Apes. Int J Primatol 32:531–565.

Harrison ME, Morrogh-Bernard HC, Chivers DJ. 2010. Orangutan energetics and the influence of fruit availability in the nonmasting peat-swamp Forest of Sabangau, Indonesian Borneo. Int J Primatol 31:585–607.

Harris TR, Chapman CA, Monfort SL. 2009. Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. Behav Ecol 21:46–56.

Heesen M, Rogahn S, Ostner J, Schülke O. 2013. Food abundance affects energy intake and reproduction in frugivorous female Assamese macaques. Behav Ecol Sociobiol 67:1053–1066.

Hemingway CA, Bynum N. 2005. The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP, editors. Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 57–104.

Hill RA, Lycett JE, Dunbar RIM. 2000. Ecological and social determinants of birth intervals in baboons. Behav Ecol 11:560–564.

Hohmann G, Potts K, N'Guessan A, Fowler A, Mundry R, Ganzhorn JU, Ortmann S. 2010. Plant foods consumed by Pan: exploring the variation of nutritional ecology across Africa. Am J Phys Anthropol 141:476–485.

Janmaat KRL, Ban SD, Boesch C. 2013. Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Anim Behav 86:1183–1205.

Janson CH, van Schaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 57–74.

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079.

Knott CD. 1999. Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability.

Knott CD. 2001. Female reproductive ecology of the apes: implications for human evolution. In: Ellison PT, editor. Reproductive ecology and human evolution. New York: Aldine de Gruyter. p 429–463.

Knott CD. 2005. Energetic responses to food availability in the great apes: implications of hominin evolution. In: Brockman DK, van Schaik CP, editors. Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 351–378.

Knott CD, Emery Thompson M, Wich SA. 2009. The ecology of female reproduction in wild orangutans. In: Wich SA, Utami SS, Setia TM, van Schaik CP, editors. Orangutans compared: ecology, evolution, behavior and conservation. Oxford: Oxford University Press. p 171–188.

Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behav Ecol Sociobiol 48:93–109.

Koenig A, Scarry CJ, Wheeler BC, Borries C. 2013. Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Phil Trans R Soc 368:20120348.

Kuzawa C, Bragg J. 2012. Plasticity in human life history strategy: implications for contemporary human variation and the evolution of genus Homo. Curr Anthropol 53:S369–S382..

Lee P, Kappeler P. 2003. Socioecological correlates of phenotypic plasticity of primate life histories. In: Primate life histories and socioecology. Chicago and London: The University of Chicago Press. p 41–65.

Leigh SR. 1994. Ontogenetic correlates of diet in anthropoid primates. Am J Phys Anthropol 94:499–522.

Marshall A, Leighton M. 2006. How does food availability limit the population density of white-bearded gibbons? In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects. Cambridge: Cambridge University Press. p 311–333.

Masi S. 2008. Social influence on foraging strategies, activity and energy budgets, of western lowland gorillas (*Gorilla gorilla gorilla*). Central African Republic.

Masi S, Cipolletta C, Robbins MM. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. Am J Primatol 71:91–100.

McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP. 2014. Behavioral flexibility of vervet monkeys in response to climatic and social variability. Am J Phys Anthropol 154:357–364.

McNeilage A. 1995. Mountain gorillas in the Virungas Volcanoes: ecology and carrying capacity.

McNeilage A. 2001. Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins MM, Sicotte P, Stewart KJ, editors. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 265–292.

N'guessan AK, Ortmann S, Boesch C. 2009. Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. Int J Primatol 30:481–496.

Nkurunungi JB, Ganas J, Robbins MM, Stanford CB. 2004. A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda. Afr J Ecol 42:289–297.

Plumptre A. 1991. Plant-herbivore dynamics in the Birungas.

Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, Muldoon KM, Dunsworth HM, Wood BM, Isler K, Burkart J, Irwin M, Shumaker RW, Lonsdorf EV

Ross SR. 2014. Primate energy expenditure and life history. Proc Natl Acad Sci USA 111:1433–1437.

Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. J Hum Evol 46:315–333.

Potts KB, Chapman CA, Lwanga JS. 2009. Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. J Anim Ecol 78:1269–1277.

Potts KB, Watts DP, Wrangham RW. 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. Int J Primatol 32:669–690.

Pusey A. 2012. Magnitude and sources of variation in female reproductive performance. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 343–366.

R Core Team. 2013. A Laguage and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org.

Robbins MM. 2008. Feeding competition and agonistic relationships among Bwindi *Gorilla beringei*. Int J Primatol 29:999–1018.

Robbins MM. 2011. Gorillas: diversity in ecology and behavior. In: Campbell CJ, Fuentes A, MacKinnon K, Bearder S, Stumpf R, editors. Primates in perspective. New York: Oxford University Press. p 326–339.

Robbins MM, Gray M, Kagoda E, Robbins AM. 2009. Population dynamics of the Bwindi mountain gorillas. Biol Cons 142:2886–2895.

Robbins MM, McNeilage A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 24:467–491.

Robbins MM, Nkurunungi JB, McNeilage A. 2006. Variability of the feeding ecology of eastern gorillas. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects. Cambridge: Cambridge University Press. p 25–47.

Rothman JM, Chapman CA, Soest PJV. 2012. Methods in primate nutritional ecology: a user's guide. Int J Primatol 33:542–566.

Rothman JM, Plumptre AJ, Dierenfeld ES, Pell AN. 2007. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. J Trop Ecol 23:673–682.

Van Schaik CP, Brockman DK. 2005. Seasonality in primate ecology, reproduction, and life history: an overview. In: Brockman DK, van Schaik CP, editors. Seasonality in primates: Studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 3–20.

Schielzeth H, Forstmeier W. 2009. Conclusions beyond support: overconfident estimates in mixed models. Behav Ecol 20:416–420.

Stoinski TS, Perdue B, Breuer T, Hoff MP. 2013. Variability in the developmental life history of the genus gorilla. Am J Phys Anthropol 165–172.

Strier KB. 2009. Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. Curr Anthropol 50:213–228.

Taylor CR, Heglund NC, Maloiy GM. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. J Exp Biol 97:1–21.

Thompson EM. 2013. Reproductive ecology of female chimpanzees. Am J Primatol 75:222–237.

Vedder AL. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. Am J Primatol 7:73–88.

De Vries H, Stevens JMG, Vervaecke H. 2006. Measuring and testing the steepness of dominance hierarchies. Anim Behav 71:585–592.

Walker R, Gurven M, Hill K, Migliano A, Chagnon N, De Souza R, Djurovic G, Hames R, Hurtado AM, Kaplan H, Kramer K, Oliver WJ, Valeggia C, Yamauchi T. 2006. Growth rates and

life histories in twenty-two small-scale societies. Am J Hum Biol 18:295–311.

Watts D. 1988. Environmental influences on mountain gorilla time budgets. Am J Primatol 15:195–211.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the Central Virungas. Am J Primatol 7:323–356.

Watts DP. 1991. Strategies of habitat use by mountain gorillas. Folia Primatol 56:1–16.

Watts DP. 1998. Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). Int J Primatol 19: 929–948.

Watts DP. 2012. Long-term research on chimpanzee behavioral ecology in Kibale National Park, Uganda. In: Kappeler PM, Watts DP, editors. London: Springer Heidelberg Dordrecht. p 313–338.

Wich SA, Utami-Atmoko SS, Setia TM Rijksen HD, Schürmann C van Hooff JARAM van Schaik CP. 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). J Hum Evol 47:385–398.

Worman CO, Chapman CA. 2005. Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. J Trop Ecol 21:689.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300.

Wrangham RW, Conklin NL, Chapman CA, Hunt KD. 1991. The significance of fibrous foods for Kibale forest chimpanzees. Phil Trans R Soc 334:171–178.

Wright E, Robbins AM, Robbins MM. 2014. Dominance rank differences in the energy intake and expenditure of female Bwindi mountain gorillas. Behav Ecol Sociobiol 68:957–970.