

Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity

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The influence of diet and food distribution on the socioecology of group-living species has long been debated, particularly for primates. It has typically been assumed that folivorous primates experience relatively little feeding competition due to the abundant, widespread nature of their food, freeing them to form large groups in response to predation, to disperse with relative ease, and to have egalitarian female social relationships. Recent studies, however, have come to different conclusions about the extent to which folivorous primates are limited by food and experience food competition and how these factors affect folivore socioecology. To better understand the selective pressures that diet places on folivores, we investigated how 2 small highly folivorous groups of colobus monkeys (*Colobus guereza*) in Kibale National Park, Uganda, responded behaviorally and physiologically to a steep reduction in availability of their most important foods. The monkeys decreased their reliance on their 2 most frequently eaten food species and increased their daily path length, number of feeding patches visited/day, size of individual feeding areas, percentage of time spent feeding, and dietary diversity. They also showed evidence of physiological costs, in that lactating females' urinary C-peptide levels (i.e., insulin production) declined as top foods became scarce, and parasite loads slightly, but significantly, increased in 2 of 3 adult females examined. These results suggest that highly folivorous primates, even in very small groups, may experience behavioral and physiological effects of food limitation, within-group scramble competition for food, and possibly substantial selective pressures during periods of food scarcity. *Key words:* black and white colobus monkeys, feeding competition, folivores, food availability, group size, primates. [*Behav Ecol* 21:46–56 (2010)]

Behavioral ecologists have long sought to understand how and to what extent diet and the dispersion of food resources influence mammalian socioecology (Crook and Gartlan 1966; Eisenberg et al. 1972; Clutton-Brock 1974; Jarman 1974; Bradbury and Vehrencamp 1976; Macdonald 1983). For primates, diet has been suggested to influence levels and types of feeding competition and consequently social relationships, group size, dispersal patterns, ranging behavior, and numerous other traits (Wrangham 1980; van Schaik 1989; Isbell 1991; Janson and Goldsmith 1995). The impact of a folivorous diet on these traits in primates is of considerable debate (reviewed in Saj et al. 2007 and in Snaith and Chapman 2007).

Because leaves are ever-present and abundant in many moist tropical forests, it has typically been assumed that folivorous primates should experience relatively little feeding competition, freeing them to form large groups as a response to predation, to disperse with relative ease, and to have relatively egalitarian social relationships (Wrangham 1980; Isbell 1991). Although there is some supporting evidence (e.g., western red colobus monkeys, *Procolobus badius*: Korstjens et al. 2002; mountain gorillas, *Gorilla beringei*: Robbins et al. 2007; ursine colobus monkeys, *Colobus vellerosus*: Saj et al. 2007), other studies have noted

behavioral and ecological patterns inconsistent with these ideas (reviewed in Saj et al. 2007; Snaith and Chapman 2007).

At the heart of this debate is whether folivores are limited by food and feeding competition in ways similar to those of frugivores (Isbell 1991; Snaith and Chapman 2007). In particular, numerous researchers have questioned why some folivorous primates form small groups, when a relative lack of feeding competition should theoretically free them to form large groups to better evade predation (Snaith and Chapman 2007). It has been suggested that greater infanticide risk in large groups may explain these primates' small groups (Janson and Goldsmith 1995; Crockett and Janson 2000; Steenbeek and van Schaik 2001), but it is unclear whether this applies to a select group of species or if it is widespread. Alternatively, it has been suggested that folivores may be food-limited and experience group size limiting within-group scramble competition in the same ways as many frugivores (Snaith and Chapman 2007). Evidence both for and against this hypothesis has been presented (Snaith and Chapman 2007).

Timing of research studies is potentially one reason why studies have come to different conclusions about the extent to which folivores are limited by food and experience feeding competition. Even though leaves tend to be ever-present and abundant in many tropical forests, there can be substantial fluctuations in the availability of young leaves (van Schaik and Pfannes 2005), which many folivores prefer to eat (Milton 1979). Furthermore, there is ample evidence that folivores are selective in the species on which they feed (Milton 1980; Glander 1982; Ganzhorn 1992; Koenig et al. 1998; Chapman

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et al. 2004). Studies that take place when the plant parts of preferred species are abundant may be much less likely to find evidence of food limitation and feeding competition. Food scarcity, on the other hand, may impose substantial selective pressures on consumers (van Schaik et al. 1993). Selective pressures on features such as group size, if related to feeding competition, should be greatest when food is exceptionally scarce. Longitudinal studies that investigate the behavioral and physiological effects of severe reductions in top folivore food resources may provide valuable insights about the selective pressures that diet places on folivorous primates.

Most studies of feeding competition in folivorous primates have also only investigated its behavioral indicators, such as increasing daily path length (a proposed effect of increasing within-group scramble competition), rather than measuring its ultimate effects—net energy gain and reproductive success (Koenig 2002). Because these effects are difficult to measure in wild, long-lived primates, in this study, we consider 2 alternative measures of the costs of feeding competition: urinary C-peptide and parasite loads. Urinary C-peptide levels track changes in energy balance and body mass in great apes and thus offer a potentially useful way to measure net energy gain in wild nonhuman primates (Sherry and Ellison 2007; Deschner et al. 2008; Emery Thompson and Knott 2008; Emery Thompson et al. 2009). Parasite loads may indicate the physiological costs of food stress (Chapman et al. 2006), with reduced food availability potentially leading to declines in immune systems (Ilmonen et al. 1999) and increases in parasite infection (Coop and Holmes 1996).

Black and white colobus monkeys (*Colobus guereza*, “guerezas”) in Kibale National Park, Uganda, are ideal for this type of study because they are highly folivorous and occur in very small groups (Oates 1977a, 1997b; Harris and Chapman 2007), despite facing predation pressure from crowned hawk-eagles, *Stephanoaetus coronatus*, and chimpanzees, *Pan troglodytes* (Oates 1974, 1977b; Struhsaker and Leakey 1990; Tappen and Wrangham 2000; Mitani et al. 2001; Watts and Mitani 2002). Their main food resources have been well documented and are known to be seasonally available (Oates 1977b; Struhsaker 1997; Harris and Chapman 2007). Lastly, the relatively open forest structure in which they often occur facilitates observation of all group members and biological sample collection.

Here, we investigate whether 2 highly folivorous, small guereza groups show behavioral and physiological evidence of food limitation during a longitudinal seasonal reduction in the availability of top foods. If the availability of these top foods, and potentially resulting within-group scramble competition, exerts a substantial influence on groups in this population and influences fitness, we predict that one or more of the following behavioral modifications will occur as the availability of top food items declines (reviewed in Hemingway and Bynum 2005): 1) daily path length will increase, after controlling for other factors that can greatly influence daily travel; 2) the number of feeding patches visited per day will increase; 3) individuals will spread out during feeding such that each feeding individual has a greater amount of space in which to feed; 4) the percentage of time groups devote to feeding will increase; and/or 5) guerezas will switch food resources—relying less on the small set of foods that typically compose most of their diet and instead relying on an increasingly diverse set of foods less typically ingested and presumably less preferred.

Additionally, we predict that the following physiological changes will occur as the availability of top food items declines (i.e., as the result of scramble competition): 1) urinary C-peptide levels, particularly in energetically stressed lactating females, will decline; and 2) parasite loads will increase.

MATERIALS AND METHODS

Study species, subjects, and site

We conducted this study in Kibale National Park, Uganda, which consists mostly of “medium altitude tropical moist forest” (Wing and Buss 1970; Kasenene 1987). The Kanyawara study site at which we worked is located near the edge of the park (0.13–0.41°N and 30.19–30.32°E) and has been logged to varying degrees (Kasenene 1987; Struhsaker 1997; Chapman and Lambert 2000). Struhsaker (1997) detailed Kanyawara’s location, climate, soil chemistry, flora, and logging history.

Guerezas are medium-sized arboreal primates that occur throughout sub-Saharan Africa (Oates et al. 1994). They form small groups with variable compositions, typically consisting of 1–5 adult males, 1–4 adult females, and their offspring (Fashing 2007). In Kibale, total group size typically ranges from 4–11 and leaves form most of the diet (88%, on average; Harris and Chapman 2007). As with other colobine monkeys, guerezas are foregut fermenters, with complex chambered stomachs (Kay and Davies 1994). They are described as energy minimizers, in that they are inactive for a large proportion of the day, have relatively small home ranges, and short daily travel distances (Oates 1977a; Fashing 2001).

We simultaneously collected data on 2 guereza groups for 16 weeks between February and June 2006. Both groups, “Kasembo” and “Basaija,” were part of a long-term project on guereza behavioral ecology and their home ranges and diets have been described previously (Harris and Chapman 2007). At the time of study, Kasembo group consisted of 8 individuals: 3 adult females, 2 adult males, 1 subadult male, 2 juvenile males, and 1 infant; Basaija group contained 5 individuals: 1 adult female, 2 adult males, 1 juvenile female, and 1 infant. All study subjects were individually recognizable using facial markings, tail shape, body size, and sex differences in coat coloration near the genital region.

Although the main purpose of our study was to examine both study groups longitudinally, we compared their home ranges in 2006 using previously described methods (Harris 2006; Harris and Chapman 2007). Kasembo group’s home range size (17.24 ha, using the minimum convex polygon method; 10.10 ha using the 95% kernel method) was double that of Basaija group’s (9.10 ha, using minimum convex polygon method; 4.77 ha using 95% kernel method). The overall basal area of 14 important foods for Kasembo and Basaija groups’ core areas (15.10 and 11.76 m²/forested ha, respectively) was comparable, particularly relative to previous years (Harris 2006).

Phenology data

From February–June 2006, a single observer collected phenology data on *Celtis durandii*, *Celtis africana*, *Albizia grandibracteata*, and *Prunus africana* trees, rating production of young and mature leaves on a scale of 0–4 (cf., Harris and Chapman 2007) and scoring the presence/absence of ripe and unripe fruit. Ten trees per species within each group’s home range were inspected approximately every 2 weeks. We chose the above species because they were the top 4 species consumed by guerezas at Kanyawara in 2002–2003 (Harris 2005), constituting 56.6% of the diet. However, given our focus on the main food species and plant parts (young leaves) guerezas ate, we later narrowed the phenology data set to just *C. durandii* and *A. grandibracteata*. The groups rarely ate *C. africana* in 2006 (0.2% and 0.7% of Kasembo and Basaija groups’ diets, respectively) and readily ate all plant parts and phenophases of *P. africana*, including mature leaves when young leaves were available. During the study, *C. durandii* and *A. grandibracteata*

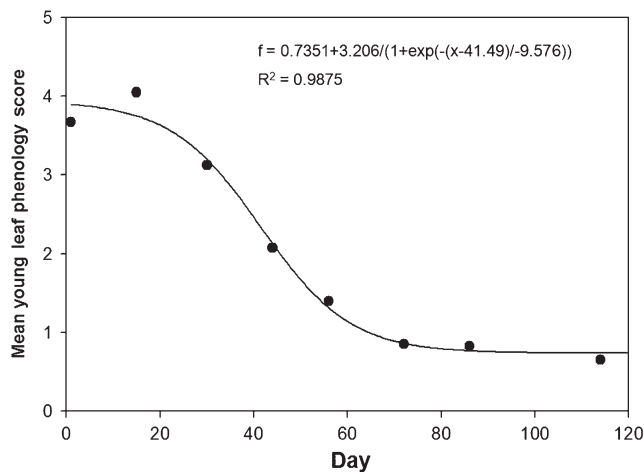


Figure 1
Mean young leaf phenology scores for *C. durandii* and *A. grandibracteata* trees over time (starting 24 February, 2006) and fitted sigmoidal curve.

plant parts composed 70.2% and 74.9% of Kasembo and Basaija groups' diets, respectively, based on 30-min scan sampling (see Harris and Chapman 2007 for a description of methods). Guerezas typically selected young leaves of these species (Harris 2005; Harris and Chapman 2007), presumably due to their higher nutritional quality (Chapman CA, Chapman LJ, Bjorndal, and Onderdonk 2002).

For each date on which we collected phenology data, we averaged young leaf scores for *C. durandii* and *A. grandibracteata* for both groups. Because the phenology data for the 2 guereza groups were nearly identical (2-tailed Spearman rank correlation: $r_s = 0.932$, $N = 9$, $P < 0.001$), we combined the raw data and calculated overall means. Graphing these data revealed a dramatic decrease in the availability of these top 2 foods over time, with a sigmoidal curve that described these data well (Figure 1). We used the formula ($f = 0.7351 + 3.206 / [1 + \exp\{-(x-41.49)/-9.576\}]$) for this best-fit curve (as determined using SigmaPlot software) to obtain predicted young leaf phenology scores in analyses below.

Daily path length data and number of feeding patches visited/day

For each group, we chose a single focal adult female for collecting data on daily path length and number of feeding patches visited per day. Guereza groups in Kibale National Park tended to be very cohesive (group spread was typically 10–15 m; Harris TR, unpublished data), so the data we collected for a given female were generally representative of that for the group. We collected data on these females on a near-daily basis from 20 Feb 2006 to 14 June 2006 (84 days for female Mr, Kasembo group; 92 days for female Nk, Basaija group), which roughly corresponded to the beginning and end of the phenology data set. For each female, we recorded the tree number (each feeding tree was given a number and set of GPS coordinates as part of a long-term study of the monkeys' ecology) and/or GPS coordinates for every feeding and resting stop she made from dawn to dusk. We recorded 11.5 ± 0.4 ($X \pm$ standard error [SE]) feeding and resting stops/day for female Nk (range: 3–22; with 3 stops recorded on a day that she visited only 2 nearby trees the entire day) and 16.4 ± 0.5 feeding and resting stops/day for female Mr (range: 7–30). The mean distance between stops was 24.0 ± 0.5 m. We used

the GPS coordinates of each feeding and resting stop to calculate daily path length. We also used the feeding stop data to calculate the number of different feeding patches each female visited per day. We defined a feeding patch as a single tree or other food location in which continuous feeding on the food item was possible within a bounded area.

Factors other than food availability and feeding competition may affect daily path length. Because guerezas are typically inactive during and even after moderate to heavy rain (Oates 1974; Harris TR, personal observation), we recorded presence/absence of rain during 30-min activity scan samples for both groups. We created a nominal (0/1) variable, "rainy," and coded a given day as rainy (i.e., "1") if we recorded moderate to heavy rain during >1 scan that day.

Because guereza groups at Kanyawara frequently engage in aggressive encounters with other groups, many of which involve lengthy chases (Oates 1977a; Harris 2006), we considered participation in these events as a factor potentially increasing daily path length. Groups also tended to travel relatively long distances to feed on high-sodium resources, such as eucalyptus trees (Harris and Chapman 2007). Thus, we created a nominal variable, "encounter/eucalyptus" and coded it as "1" if the study group either participated in a highly aggressive (i.e., involving chasing) intergroup encounter that day and/or traveled toward and eventually fed within eucalyptus plantation areas; we coded it as "0" if neither of these activities occurred that day.

For each of the 2 females, we used multiple linear regression to predict daily path length. We initially used "predicted young leaf phenology score" as the independent variable. However, because plots of daily path length over time appeared to have a linear, nonsigmoidal relationship and data could not be normalized by transformation, we used "day" as the independent variable. We also entered the "rainy" and "encounter/eucalyptus" variables as predictors to control for their effects. Low variance inflation factors and condition indices for both regression models indicated that there were no multicollinearity problems.

For each female, we also used linear regression to test for a relationship between the number of different feeding patches she visited per day and the predicted young leaf phenology score for that day. These and all other tests below were one-tailed unless stated otherwise because all the hypotheses we made were directional (Table 1) and P values for each hypothesis test were subsequently combined using an omnibus test (Sokal and Rohlf 1995; Table 1), which requires one-tailed P values to make conclusions about directionality of the relationship.

Per capita feeding area

If groups spread out during feeding, each feeding individual should have a greater amount of space in which to feed (i.e., per capita feeding area). To test this hypothesis, we collected feeding data 4–7 days/week from 8:30 AM (typically before groups left their sleeping trees) to dusk using 30-min scan samples. For each scan, we recorded which noninfant individuals fed, the species/item and part consumed, the tree diameter at breast height (DBH) if applicable, and the number of individuals that fed on the same tree/shrub/vine or other item (i.e., "food patch"). Because both groups were small and highly visible, we usually located all members (Basaija: mean 3.9 of 4 noninfant individuals seen/scan; Kasembo: mean 7.7 of 8 noninfant individuals seen/scan).

To investigate the spacing of individuals during feeding, we only examined scans during which multiple individuals fed on trees (i.e., food items for which we could not record DBH were excluded). From these data, we calculated a "per capita

Table 1
Summary of predictions and results

Variable	Predicted relationship with decreasing <i>C. durandii</i> and <i>A. grandibracteata</i> young leaf availability	Test performed	Number of tests performed	Number of tests significant in the expected direction	Combined <i>P</i> value ^b
Daily path length	Increasing ^a	Multiple linear regression	2	2	<0.001
Feeding patches visited/day	Increasing	Linear regression	2	2	<0.001
Per capita feeding area	Increasing	Spearman rank correlation	2	1	0.012
Percentage of time spent feeding	Increasing	Spearman rank correlation	2	2	<0.001
Reliance on <i>C. durandii</i> and <i>A. grandibracteata</i> relative to other foods	Decreasing reliance on top 2 foods, increasing dietary diversity	Spearman rank correlation	4	4	<0.001
Urinary C-peptide (lactating females)	Decreasing	Spearman rank correlation	2	2	0.005
Parasite (<i>Trichuris</i>) load	Increasing	Spearman rank correlation	3	2	0.004

^a “Day,” rather than young leaf availability, was used as the independent variable; see MATERIALS AND METHODS for full explanation.

^b *P* values are one-tailed.

feeding area score” for each scan—the total basal area of items fed on divided by the number of individuals feeding (i.e., an estimate of the sizes of individual feeding areas). We then square root transformed the data because they were right-skewed due to occasional feeding on very large trees and calculated the weekly mean and calculated the weekly mean. For each group, we used Spearman rank correlation to test for a relationship between the weekly mean per capita feeding area index and predicted mean young leaf phenology score.

Percentage of time spent feeding

Using the feeding data from the scan samples, we estimated the percentage of time groups spent feeding by calculating the weekly percentage of individuals observed that were engaged in feeding. For scans that were interrupted by heavy rain, we assumed that individuals were not feeding because guerezas are typically immobile during such weather (Oates 1974; Harris TR, personal observation). For each group, we used Spearman rank correlation to test for a relationship between the weekly percentage of time spent feeding and predicted mean young leaf phenology score.

Resource switching and diversity

Using the feeding data from the scan samples, we calculated the weekly percentage of the diet composed by *C. durandii* and *A. grandibracteata*—the top 2 species consumed overall. For each group, we used Spearman rank correlation to test for a relationship between reliance on these species and their mean predicted young leaf phenology score.

We used the Shannon diversity index (H') to measure the diversity of food items that guereza groups consumed each week. For this analysis, we considered not only different species as separate food items but also different plant parts from the same species because these plant parts of the same species often have very different nutritional values. For example, the petioles of leaves are often higher in specific minerals, particularly sodium, than any other part of the leaf (Rode et al. 2003). From the feeding scans, we calculated the number of different food items a group fed on during a given week and the number of times each food item was recorded as being consumed. We calculated the diversity index using the formula,

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

with p_i as the proportion of feeding records devoted that week to a given food item and S as the number of different food items recorded that week. For each group, we used Spearman correlation to test for a relationship between H' and mean predicted young leaf phenology score.

Urinary C-peptide

C-peptide is a molecule that is cleaved from proinsulin, is produced in a 1:1 ratio with insulin, and is excreted in urine. It is effectively, therefore, a measure of insulin, which is secreted by the pancreas in response to food ingestion and is also a long-term signal of food intake and energy balance (reviewed in Havel 2001).

We collected urine on aluminum foil pans every approximately 3–4 days, between 24 February 2006 and 26 May 2006, from females that were lactating during the entire period: Nk from Basajja group (18 samples) and Kb from Kasembo group (21 samples). Each female had a single 2–3 month old infant at the start of the study. Both infants increasingly consumed leaves during weeks 11–16 of this study (of a total 16 weeks). We focused on lactating females because they presumably experienced the greatest energy demands (Pond 1977); thus, scramble competition was predicted to have impacted their energy balance, and consequently, C-peptide values. Samples were pipetted into plastic tubes and kept on ice packs until placed in a freezer at dusk.

We collected samples at different times of day, during daylight hours. Other studies have collected early morning samples to obtain baseline C-peptide values (Sherry and Ellison 2007; Emery Thompson and Knott 2008), but we did not attempt this because colobus monkeys' foregut-fermenting digestive systems pool and retain food for long periods of time (estimated as ~14 h: Kay and Davies 1994), making it likely that no samples are at baseline, or “fasting” levels. Visual inspection of a plot of sample collection time versus date indicated that samples were essentially collected at random times across the study period. There was no linear relationship between urinary C-peptide levels and time of day for either female (linear regression, Nk: $F = 0.755$, $N = 18$,

$R^2 = 0.045$, 2-tailed $P = 0.398$; Kb: $F = 0.797$, $N = 21$, $R^2 = 0.083$, 2-tailed $P = 0.383$) and visual inspection of plots indicated no nonlinear relationships.

All C-peptide concentrations (which were nonzero, positive values) were indexed by creatinine (Cr) concentrations (Taussky 1954) and expressed as ng C-peptide/mg Cr excreted. Creatinine concentrations averaged 0.56 ± 0.03 mg/ml ($X \pm SE$). We analyzed urinary C-peptide using Diagnostic Systems Laboratories radioimmunoassay kits (DSL-7000), using the provided protocol but with urine samples diluted from 1:5–1:20 for different samples. A parallel displacement curve was obtained by comparing serial dilutions (1:2–1:256) of pooled guereza urine. Recovery of known amounts of C-peptide (range: 0.1–18.0 ng/mL) added to pools of diluted guereza urine was $92.8 \pm 14.8\%$ ($y = 0.018 + 0.930x$, $r^2 = 0.995$). Interassay coefficients of variation for 2 separate internal controls were 12.9% at 68.9% binding and 9.1% at 22.2% binding. Intraassay coefficients of variation averaged $4.2 \pm 0.4\%$.

There was no evidence of autocorrelation among urinary C-peptide values, in that the number of days between consecutive samples was unrelated to the absolute difference in C-peptide values between those samples (linear regression, Nk: $F = 0.231$, $N = 17$, $R^2 = 0.015$, 2-tailed $P = 0.637$; Kb: $F = 2.595$, $N = 20$, $R^2 = 0.126$, 2-tailed $P = 0.125$). For each female, we used Spearman rank correlation tests to investigate the relationship between urinary C-peptide and predicted young leaf phenology score for the date on which the sample was collected.

Parasite loads

To investigate the relationship between parasite infections and reduced food availability, we collected fecal samples approximately every week, from 18 February 2006 to 9 June 2006, from adult females Kb and Mr in Kasembo group and Nk in Basaija group. We stored a portion of each sample individually in 10% formalin and processed samples using concentration by sodium nitrate flotation and faecal sedimentation (Sloss et al. 1994). Eggs and larvae of parasites were counted and identified on the basis of egg color, shape, contents, and size. Coprocultures and necropsies were used to match parasite eggs to larvae for positive identification.

No confirmed protozoans were found in the fecal samples we investigated. This agrees with Freeland (1979), but we view that this is not conclusive because slides were not subject to a variety of stains, which are required to identify smaller protozoans (Chapman CA, unpublished data). We used a Spearman rank correlation test, for each female, to investigate the relationship between *Trichuris* load and predicted young leaf phenology score for the date on which the sample was collected.

RESULTS

Daily path length

Daily path length, measured for one adult female per group, increased significantly over time for both groups as food availability declined (multiple linear regression, controlling for the occurrence of rain, high-level intergroup aggression, and travel to high-sodium resources; Figure 2; Table 1). Mean daily path length was 305 ± 14 m ($X \pm SE$) for female Nk of Basaija group and 298 ± 13 m for female Mr of Kasembo group.

Feeding patches visited/day

The number of different feeding patches visited/day (square root transformed) by females Nk of Basaija group and Mr of Kasembo group was inversely related to the predicted young

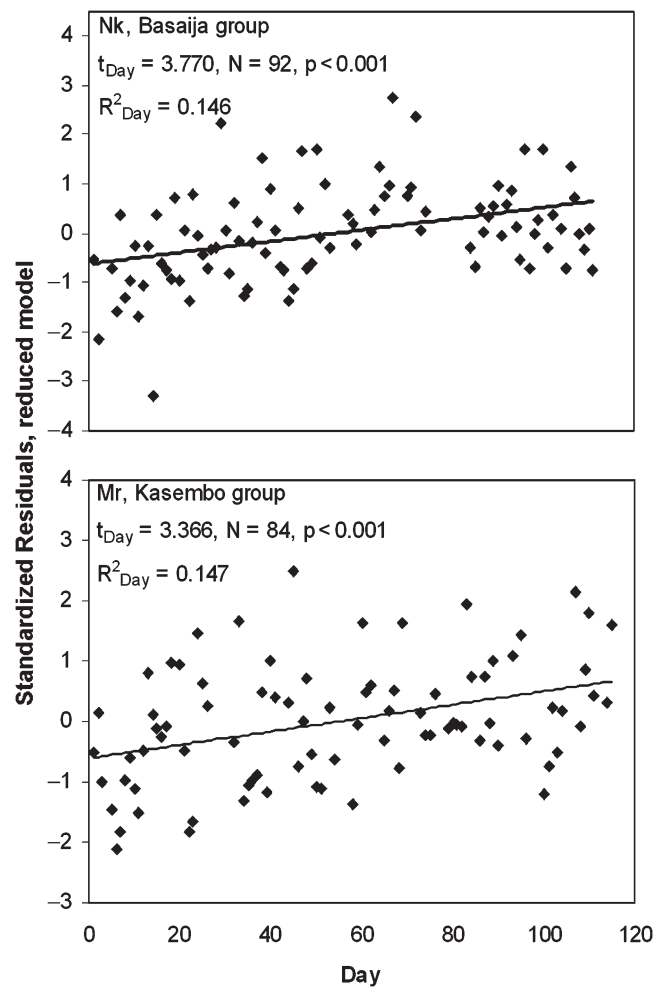


Figure 2

Daily path length (residuals of reduced model) over time as the decline in food availability persisted. The full model (multiple linear regression) included “day” as a predictor of daily path length (square root transformed) and controlled for the occurrence of rain, high-level aggression, and travel to high-sodium resources. Model R^2 was 0.305 for female Mr and 0.173 for Nk.

leaf phenology score (Figure 3; Table 1), indicating that they visited more feeding patches/day when food availability was low. Mean number of feeding patches visited/day was 6.8 ± 0.3 ($X \pm SE$) for female Nk and 8.3 ± 0.4 for female Mr.

Per capita feeding area

For Basaija group, the weekly mean per capita feeding area index (total basal area of items fed on per scan, divided by the number of individuals feeding, and square-root transformed; for scans with multiple feeders) was inversely related to the weekly mean predicted young leaf phenology score (Figure 4; Table 1), indicating that feeding individuals were less clumped and had greater areas in which to feed when food availability was low. For the larger group, Kasembo, these 2 variables were unrelated (Figure 4; Table 1), but the combined P value for both groups was significant (Table 1). The median estimated feeding area (basal area) occupied by each feeding individual in a scan (i.e., the per capita feeding area index) ranged from 179 cm² (week 4) to 714 cm² (week 16) for Basaija group and from 162 cm² (week 12) to 780 cm² (week 1) for Kasembo group.

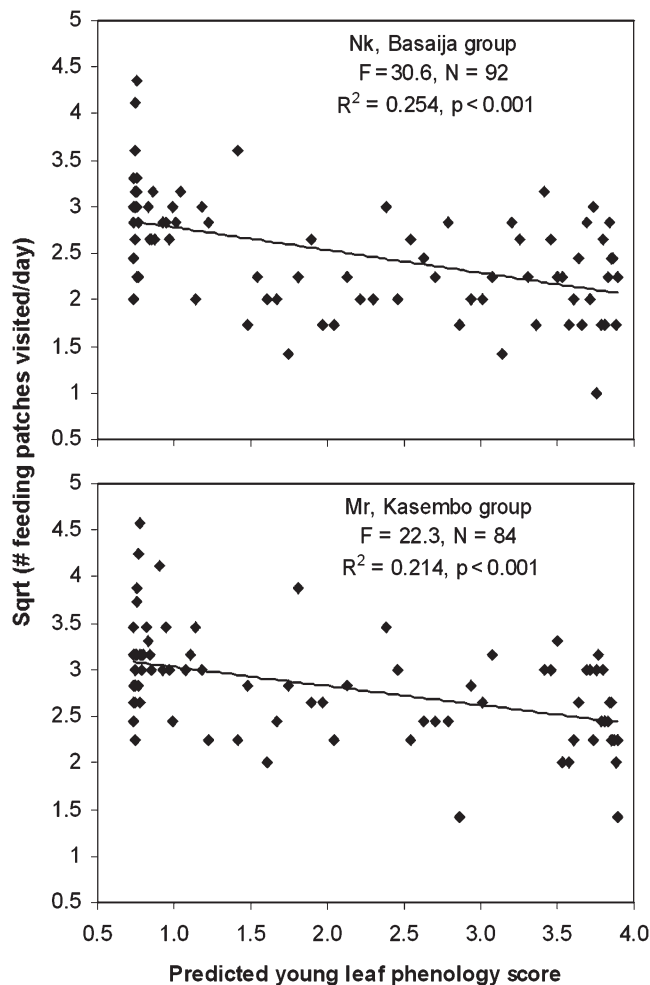


Figure 3
Number of feeding patches visited/day (square root transformed) versus predicted young leaf phenology score. Results reported are for linear regression.

Percentage of time spent feeding

For both groups, the weekly estimated time spent feeding during the day was inversely related to the mean predicted young leaf phenology score (Figure 5; Table 1), indicating that groups spent more time feeding when food availability was low. Basaija group spent the lowest percentage of time (16.6%) feeding in week 2 and the highest (25.0%) in week 15. The larger of the 2 groups, Kasembo, spent 17.5% of its time feeding at the start of the study (week 1) and increased its feeding time to 29.9% by week 15.

Resource switching and food diversity

Consumption of the top 2 food species, *A. grandibracteata* and *C. durandii*, was highly related to the availability of their young leaves (Figure 6; Table 1), in that both groups reduced consumption of these species as the food decline persisted. During week 1, when young leaves were abundant, these species constituted 82.1% of Basaija's and 92.8% of Kasembo's diets; during the final week (16) when their availability was low, these plant species constituted 41.4% of Basaija's and 39.4% of Kasembo's diets. For both groups, weekly *H'* (food diversity index) was inversely related to the mean predicted young leaf phenology score (Figure 7; Table 1), indicating that groups

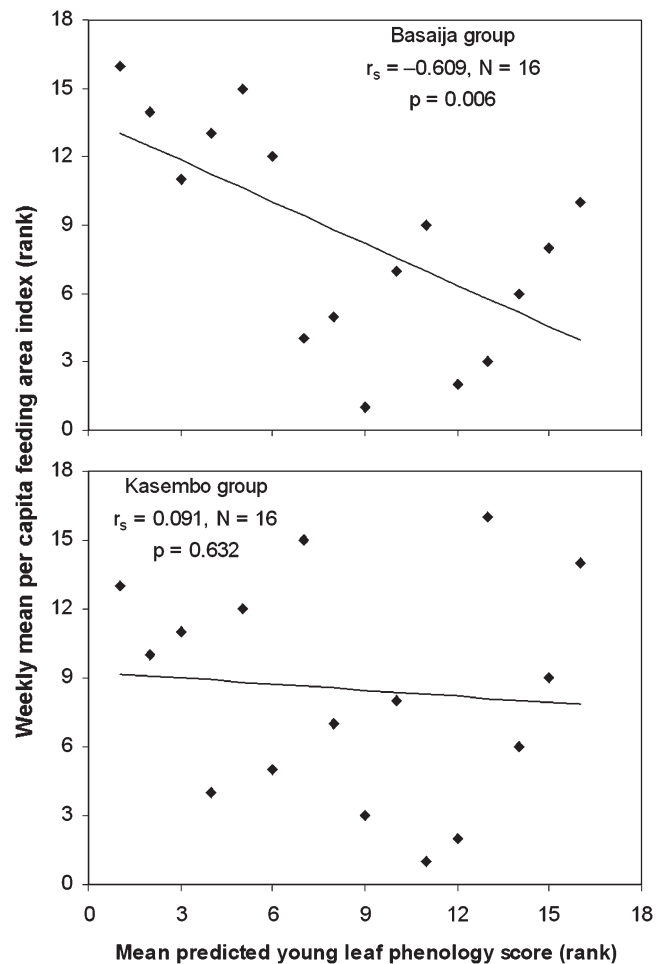


Figure 4
Weekly mean per capita feeding area index versus mean predicted young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

consumed a greater diversity of food items when the availability of *A. grandibracteata* and *C. durandii* was low. Overall, leaves constituted 94.9% and 93.7% of Basaija and Kasembo groups' diets, respectively. The total number of food items consumed during scans (all vines were combined, as were all shrubs, due to difficulties with species identification; different plant parts counted as separate food items) was 37 and 57 for Basaija and Kasembo groups, respectively.

Urinary C-peptide

Urinary C-peptide values for lactating females Nk (Basaija group) and Kb (Kasembo group) were positively related to the predicted young leaf phenology score on the day of sample collection (Figure 8; Table 1), indicating that C-peptide decreased along with food availability. Urinary C-peptide values for female Nk ranged from 3.4 ng/mg Cr (week 11) to 227.6 ng/mg Cr (week 4) and for female Kb ranged from 8.7 ng/mg Cr (week 7) to 124.0 ng/mg Cr (week 4).

Parasite loads

Females Nk (Basaija group), Kb (Kasembo group), and Mr (Kasembo group) had low mean *Trichuris* loads (1.4 ± 0.4 , 1.7 ± 0.6 , and 1.5 ± 0.6 eggs/g, respectively) and no

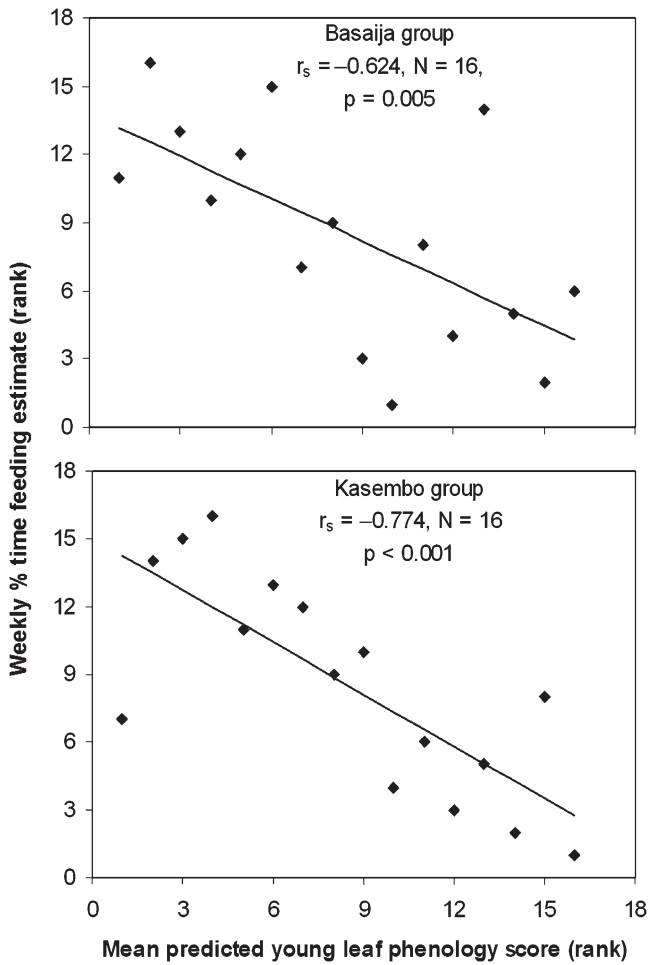


Figure 5
Estimated weekly percentage of time spent feeding versus mean predicted young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

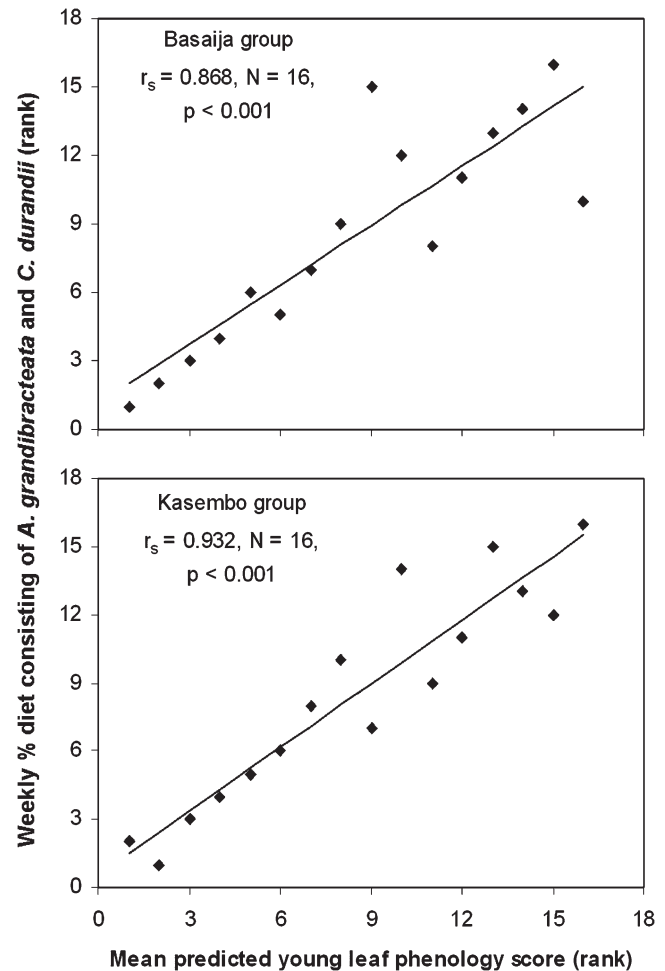


Figure 6
Weekly percentage of the diet consisting of *C. durandii* and *A. grandibracteata* plant parts versus mean predicted young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

protozoans were detected. The number of *Trichuris* eggs/gram of sample (load) for Nk and Mr was inversely related to predicted young leaf phenology scores (Figure 9; Table 1), indicating that *Trichuris* load was higher when food availability was low. For female Kb, these 2 variables were not related in the expected direction (Figure 9; Table 1), but the combined P value for the 3 tests (assuming an inverse relationship) was significant (Table 1).

DISCUSSION

Our results provide evidence that highly folivorous guerezas in 2 small groups exhibited substantial behavioral and physiological effects of a steep reduction in the availability of their top 2 foods. The monkeys decreased their reliance on their top 2 food species and increased their daily path length, the number of feeding patches visited/day, spread during feeding, percentage of time spent feeding, and dietary diversity. They also showed evidence of associated physiological costs, in that lactating females' urinary C-peptide levels (i.e., insulin production) declined as top foods became scarce, and parasite loads slightly, but significantly, increased in 2 of 3 adult females examined.

These findings are consistent with the idea that guerezas experienced increasing within-group scramble competition for

food as a result of decreasing food availability. This type of feeding competition occurs when individuals cannot monopolize food resources and results in reduced foraging efficiency for all individuals. It is also the primary type of feeding competition thought to limit group size (reviewed in Koenig 2002 and in Snaith and Chapman 2007). Increasing within-group scramble competition for food is thought to lead to quicker depletion of food patches. As a result, individuals in larger groups must compensate behaviorally (e.g., traveling longer distances per day to find food and/or increasing group spread during feeding) and/or physiologically (e.g., by having reduced energy available for somatic maintenance and/or reproduction) (reviewed in Koenig 2002 and in Snaith and Chapman 2007). It could be argued that solitary individuals might have experienced behavioral and physiological effects of reduced food availability similar to those we found here for the guerezas. However, our finding that feeding was less clumped, with individuals having larger areas in which to feed (a sign of greater feeding spread), when young leaves were scarce points to group living and competition as a likely driving mechanism.

The behavioral and physiological changes we documented are striking given the small sizes of the study groups (5 and 8 individuals) and the extreme degree of folivory they

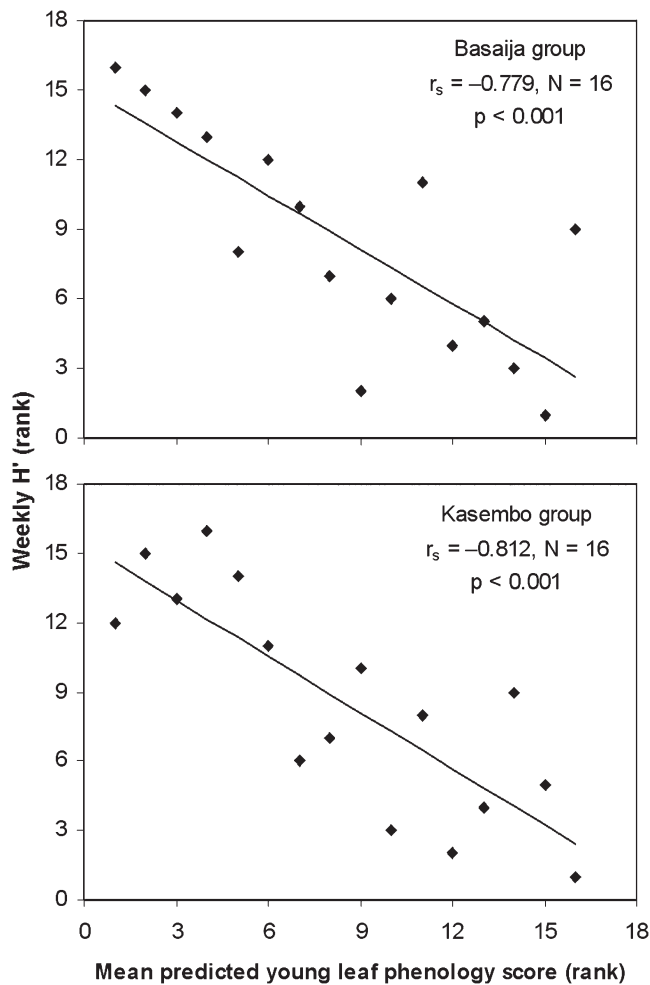


Figure 7
Weekly H' (food diversity index) versus weekly predicted mean young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

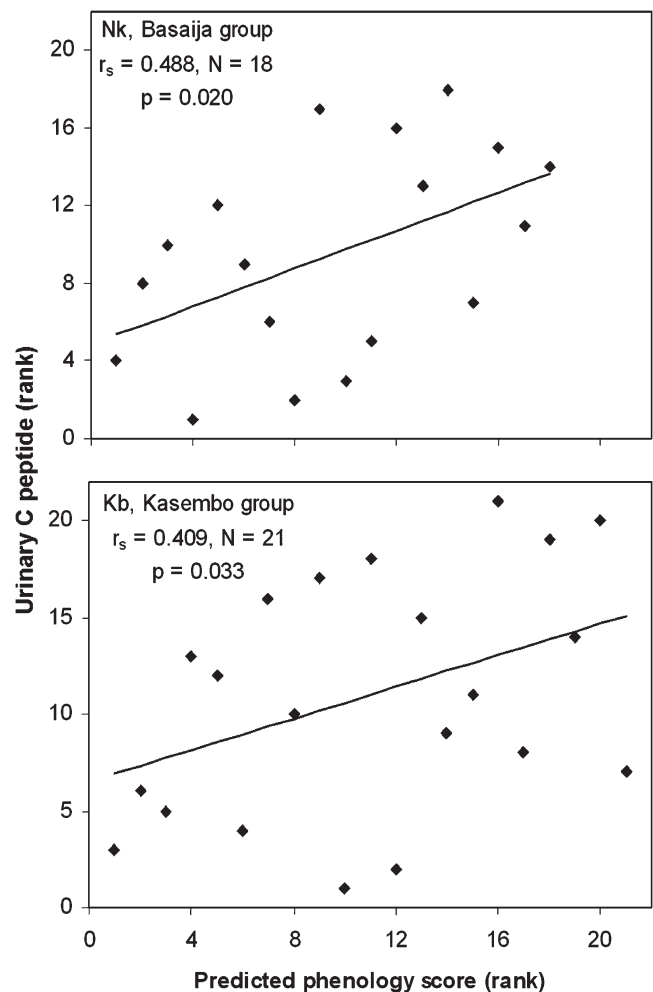


Figure 8
Urinary C-peptide (initially ng/mg Cr but converted to ranks) versus predicted young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

exhibited (94.9% and 93.7% of Basaija and Kasembo groups' diets, respectively, consisted of leaves). Although we have not compared levels of feeding competition across species (as in Janson and Goldsmith 1995), this research nevertheless suggests that at least some folivores may be food-limited and experience potentially group size limiting within-group scramble competition in ways similar to that of frugivores. Recent studies have come to similar conclusions, but for less folivorous primates, or those with larger group sizes (Ganas and Robbins 2005; Snaith and Chapman 2005; Borries et al. 2008; Snaith and Chapman 2008; Teichroeb and Sicotte 2008).

Furthermore, this study improves on previous research by investigating the physiological costs that may accompany reduced food availability and/or increased feeding competition. This study is one of the first to use urinary C-peptide as a proxy for net energy gain, and we found it to be a potentially useful tool, in that it tracked young leaf availability in the most energy-limited individuals—lactating females. This finding provides insights about how selective pressures associated with food scarcity might operate on reproductive success. Other research suggests that the ability of folivorous lemurs to survive seasonal food shortages may depend less on the quantity of food available during such periods than the quality of available

foods (Ganzhorn 1992). Further studies will be necessary to understand how and to what extent steep declines in food availability affect fitness in highly folivorous primates.

We also found that 2 of 3 adult females we tested had higher loads of *Trichuris* parasites as young leaf availability decreased. Overall, however, these loads were relatively low, particularly compared with levels reported for guerezas living in forest fragments outside Kibale National Park (Chapman et al. 2005). Thus, it is unclear whether this increase in parasite loads over time has an influence on fitness.

This study also points out that, though leaves are often abundant and ever-present in many tropical forests, such as the one at our study site, highly folivorous primate populations can sometimes be very selective and reliant on a small number of food species (e.g., our study groups had ~90% reliance on 2 species at the beginning of the study). Though they have the flexibility to switch resources, changes in the availability of these select species' young leaves can have important consequences for their behavior and potentially even their fitness. In this sense, the nature of folivore food resources does not seem so different from that of frugivorous species.

One particularly interesting question that remains is why red colobus monkeys and guerezas (black and white colobus

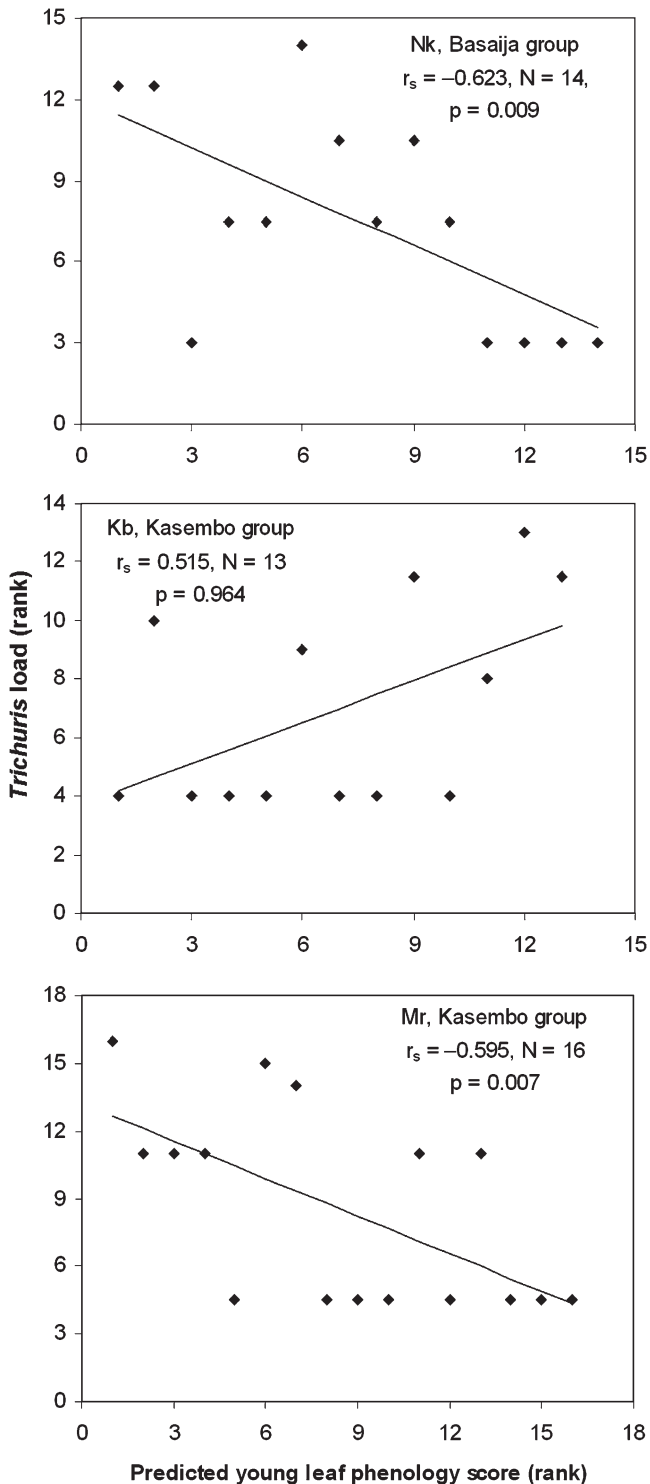


Figure 9
Trichuris load (initially eggs/g but converted to ranks) versus predicted young leaf phenology score. Results reported are for Spearman correlation; trendline is for demonstration purposes only.

monkeys), which inhabit the same areas in Kibale National Park and have very similar diets (Chapman CA, Chapman LJ, and Gillespie 2002; Rode et al. 2003; Chapman and Pavelka 2005), are so different from one another. Red colobus groups in Kibale are multimale, whereas a majority of guereza groups are unimale, and red colobus groups are much larger,

ranging in size from 12 to 127 individuals (Struhsaker 1975; Snaith and Chapman 2008). Red colobus are much more active than guerezas, spending much more time feeding (Fashing 2007), and have much more overlapping home ranges with neighboring groups (Struhsaker 1975; Harris 2006; Snaith and Chapman 2008). Grooming in red colobus is typically male-centered (Struhsaker and Leland 1979), as opposed to female-centered in guerezas (Oates 1977a), and natal female dispersal is far more common in red colobus (Struhsaker and Leland 1987) than in guerezas (Harris et al. 2009).

Simply examining the difference in group size between these species, one possibility is that despite their phylogenetic closeness, they use or process energy differently (Korstjens and Dunbar 2007), with guerezas being more energy constrained than red colobus. For example, behavioral observations suggest that guerezas engage in thermoregulation, by sunbathing before moving in the mornings and after rainstorms and by the huddled positions in which they rest when it is cold (Oates 1974; Fashing 2001; Harris TR, personal observation). These behaviors are rarely seen in red colobus monkeys in the same habitat. Another possibility is that different levels of predation risk and/or different strategies for evading predation have led to larger group sizes in red colobus. Red colobus tend to face greater predation by chimpanzees in Kibale than do guerezas (Watts and Mitani 2002). Also, red colobus are typically vocal throughout the day, attracting attention, whereas guereza groups are typically silent, except for the loud roars they perform during morning choruses (and occasionally at predators). It is possible that the “selfish herd” characterizes the red colobus antipredation strategy, leading these monkeys to form large groups, whereas guerezas more often rely on a cryptic strategy that is enhanced by small group size (see Janson 1998 for a review of strategies). Lastly, it is possible that interactions between infanticide levels and group size differ for the 2 species (Chapman and Pavelka 2005). Sorting out these nonmutually exclusive hypotheses will require further testing.

Diet clearly is not a straightforward predictor of behavior or grouping patterns in primates (Clutton-Brock 1974), and further studies will be needed to understand the factors influencing behavior and grouping patterns among folivores. More studies that investigate the physiological and fitness effects of feeding competition in folivorous primates (e.g., Borries et al. 2008) will also be important. Importantly, though, this study demonstrates that even highly folivorous primates in very small groups may be food-limited, experiencing both behavioral and physiological effects when top resources become scarce, most likely due to increasing within-group scramble competition for food. Periods of food scarcity may thus exert substantial selective pressures on folivores, potentially affecting important aspects of socioecology (e.g., group size), warranting further study.

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