



Comparative Feeding Ecology of Two Communities of Chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda

Kevin B. Potts · David P. Watts ·
Richard W. Wrangham

Received: 21 March 2010 / Accepted: 29 August 2010 / Published online: 2 February 2011
© Springer Science+Business Media, LLC 2011

Abstract Several recent studies have documented considerable intraspecific and intrapopulation ecological variation in primates. However, we generally lack an understanding of how such variability may be linked to concomitant demographic variation among groups or populations of the same species, particularly in regard to large-bodied and wide-ranging species with high ecological flexibility, such as chimpanzees (*Pan troglodytes*). We compared the feeding ecology of chimpanzees inhabiting 2 sites in Kibale National Park, Uganda that differ 3-fold in chimpanzee density and support notably different plant communities. Chimpanzees at Ngogo, a site with the largest known chimpanzee community and unusually high chimpanzee density, spent a significantly lower percentage of time resting (and pregnant and lactating females spent more time feeding), incorporated higher percentages of ripe fruit in their diet, had lower dietary diversity values, and had shorter and less variable average patch residency times than did their counterparts at the nearby Kanyawara site, which supports a relatively low density of chimpanzees. In addition, feeding party size was significantly and positively related to feeding patch size at Ngogo, but not at Kanyawara. Together these findings aid in explaining the noted disparity in chimpanzee community size and density between Ngogo and Kanyawara by suggesting that the diet of Ngogo chimpanzees is of higher overall quality than that of Kanyawara chimpanzees. They also highlight the potentially profound influence of even small-scale habitat heterogeneity on the ecology of primates. Researchers must take such influences into account when attempting to draw conclusions about species- or population-level characteristics.

K. B. Potts (✉) · D. P. Watts
Department of Anthropology, Yale University, New Haven, CT 06520, USA
e-mail: kbpotts1@gmail.com

R. W. Wrangham
Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

Present Address:

K. B. Potts
Department of Biology, Augsburg College, Minneapolis, MN 55454, USA

Keywords Chimpanzee · Feeding ecology · Foraging efficiency · Population density

Introduction

Recent studies of feeding ecology in primates have documented considerable intraspecific dietary variation in several species, e.g., *Gorilla gorilla beringei*: Watts (1996); *Procolobus tephrosceles*: Chapman and Chapman (1999); *Cercopithecus* spp.: Glenn and Cords (2002); *Colobus guereza*: Harris and Chapman (2007). Despite the increased awareness of ecological variability at the species level (Strier 2009), we generally lack sufficient information on how variation in diet and habitat use within species is tied to intraspecific differences in group size and gregariousness. Based on the limited data that are available, it is clear that noteworthy variation in diet and habitat use in primates exists not only between populations of the same species, but also among social groups of the same population, e.g., *Colobus guereza* (Harris and Chapman 2007) and *Cercopithecus mitis* (Butynski 1990) in Kibale National Park, Uganda; *Gorilla beringei beringei* in Bwindi National Park, Uganda (Ganas *et al.* 2004), *Hapalemur griseus* in Ranomafana National Park, Madagascar (Grassi 2006), particularly in highly heterogeneous environments, e.g., *Lemur catta* in Beza Mahafaly, Madagascar (Yamashita 2002). While data indicate that feeding ecology and habitat use of chimpanzees (*Pan troglodytes*) vary considerably across populations, e.g., Gombe: Wrangham (1977); Lopé: Tutin *et al.* (1991); Bossou: Yamakoshi (1998); Budongo: Newton-Fisher (1999); Kibale: Wrangham (2000); Kahuzi-Biega: Basabose (2002), few comparative data exist regarding the extent of diversity within populations, and how such diversity may be tied to differences among communities in size and density. Our goal in this study was to compare the feeding ecology of 2 well-habituated study communities in Kibale National Park, Uganda to assess intraspecific ecological diversity in chimpanzees on a finer scale than is generally possible, and examine how ecological variability between these communities may be tied to noted disparities in chimpanzee density between the sites.

The 2 well-habituated chimpanzee focal communities in Kibale National Park (Ngogo and Kanyawara) differ dramatically in overall size, density, and composition. The Ngogo community is the largest ever known, with *ca.* 155 individuals (Mitani and Watts 1999; Watts 1998; Watts and Mitani 2002). In contrast, the much smaller community at Kanyawara, located 10 km from Ngogo in the same forest, has an overall size (*ca.* 45–50 individuals) and demographic composition comparable to the average for many study sites (Muller 2002; Wrangham *et al.* 1992). Kibale is composed of a mosaic of habitats that vary both within and between sites in vegetation composition, canopy structure, elevation, and human impact (Chapman *et al.* 1997; Lwanga *et al.* 2000; Struhsaker 1997; Wing and Buss 1970). Extensive botanical analyses conducted at both sites indicate that the spatiotemporal availability of key classes of food resources is notably higher at Ngogo than at Kanyawara (Chapman *et al.* 1997; Potts *et al.* 2009). Previous research on the feeding ecology of the Kanyawara community (Isabirye-Basuta 1987, 1988; Conklin-Brittain *et al.* 1998; Wrangham *et al.* 1998), more limited analysis on the ecology of the Ngogo community (Ghiglieri 1984; Mitani *et al.* 2002), and general

comparisons of the dietary profiles of the 2 communities (Wrangham *et al.* 1991), combined with the botanical differences noted in the preceding text, suggest that the Kibale population provides a unique opportunity to address the extent to which chimpanzee ecology may vary over small spatial scales.

Based on the botanical evidence of a higher-quality resource base at Ngogo compared to Kanyawara (Chapman *et al.* 1997; Potts *et al.* 2009), combined with the markedly higher density of chimpanzees at Ngogo, we hypothesize that the diet of chimpanzees at Ngogo is of overall higher quality than is that of Kanyawara chimpanzees. We present data here on the activity budgets, diets, food patch characteristics and patterns of patch use, and feeding party sizes from both Kanyawara and Ngogo collected during overlapping time periods as qualitative indicators of dietary quality and foraging efficiency in these communities. We specifically predict that Ngogo chimpanzees: 1) incorporate a higher percentage of ripe fruit in their diet, 2) spend less time feeding and more time resting, 3) have lower dietary diversity values, and 4) remain in feeding patches for shorter periods than Kanyawara chimpanzees. We also predict that the relationship between feeding party size and feeding patch size is more strongly positive at Ngogo than at Kanyawara. Elsewhere (Potts *et al.*, in preparation) we present data on quantitative measures of foraging efficiency in the same two communities, incorporating values of food wet weights, ingestion rates, and energetic costs associated with travel between feeding sites. Also, see Potts (2008) for a discussion of the differences between these sites in other variables not directly related to feeding ecology, e.g., anthropogenic disturbance, predation, disease risk, and how they might be impacting density differences between the 2 communities.

Methods

Focal Communities

Isabirye-Basuta (1988) was the first to study intensively the chimpanzees at Kanyawara between 1983 and 1985. Wrangham and colleagues began to habituate the community in the late 1980s and early 1990s, and now conduct all-day follows of focal chimpanzees (though before August 2009 all-day follows focused on parties rather than individuals; Conklin-Brittain *et al.* 1998; Emery Thompson *et al.* 2007; Muller *et al.* 2007; Wrangham *et al.* 1991, 1996, 1998). Community size at Kanyawara has varied between 39 and 52 since the onset of habituation. The community had 11 adult males, 1 adolescent male, 15 adult females, 3 nulliparous females, 8 juveniles, and 13 infants during our study (Potts 2008). The density of chimpanzees at Kanyawara was *ca.* 1.4 individuals/km².

Ghiglieri (1984) conducted the first study of the chimpanzee community at Ngogo in the late 1970s and early 1980s. Wrangham *et al.* (1991) briefly studied chimpanzees there in the late 1980s and 1990, and B. Grieser-Johns worked on habituation of the community in the early 1990s. However, intensive research and habituation at Ngogo by D. P. Watts and J. C. Mitani did not commence until 1995. Researchers have continuously observed the community since then (Mitani and Watts 1999, 2005; Watts 1998; Watts and Mitani 2001; Watts *et al.* 2006). It is the

largest ever observed, with >150 members. At the time of this study, 23–26 adult males, 15 adolescent males, ≥ 44 adult females, 15 adolescent females, 17 juveniles, and 34 infants resided within the community. The density of chimpanzees at Ngogo was *ca.* 5.1 individuals/km².

We conducted this study over 19 mo, from June 2005 to December 2006, but we were able to conduct simultaneous data collection on both communities only between January and June 2006 (hereafter referred to as the overlap period). In all, we observed Ngogo chimpanzees between June 2005 and June 2006 and Kanyawara chimpanzees between January and December 2006. The data we present here came from 1059 and 961 h of focal animal sampling at Ngogo and Kanyawara, respectively. Detailed ecological overviews of Kibale and of both the study sites can be found in Butynski (1990), Chapman and Lambert (2000), Ghiglieri (1984), Lwanga *et al.* (2000), Potts (2008), Struhsaker (1997), and Wing and Buss (1970).

Data Collection

K. B. Potts or a trained field assistant conducted focal follows of individual chimpanzees at both sites. K. B. Potts collected all of the focal data from Ngogo, while a single field assistant following an identical sampling protocol collected the majority of the data on chimpanzees at Kanyawara. After a period of intensive training in the data collection protocol, K. B. Potts occasionally followed chimpanzees at Kanyawara with this assistant and collected data on the same focal chimpanzees at the same time to ensure interobserver reliability.

The length of each focal follow varied, but ideally lasted for 1 full feeding bout and 1 full travel bout between consecutive feeding patches, *i.e.*, we observed the subject enter a feeding patch, forage and ingest or chew food items within it, leave the patch, travel to a new patch, and enter it. We then designated a new individual to follow, and began focal observation of the individual as soon as it began its next feeding bout. We chose the first adult or adolescent chimpanzee encountered in the morning as our first focal individual of the day, and subsequently rotated focal effort among individuals present in the party. We occasionally left a party to find others if we completed focal follows on all members of the current party, but usually remained with the same party of chimpanzees throughout the day.

During each focal follow, we continuously recorded the behavioral state of the focal individual as either feeding/foraging (defined as ingestion or chewing of plant or animal matter uninterrupted by other behaviors for ≥ 1 min), traveling (defined as sustained movements [>1 min], generally occurring outside of feeding patches and involving movement between successive patches), resting (defined as any sustained period in which neither feeding nor traveling occurred [this included time spent grooming]), hunting (defined as in Mitani and Watts 1999), or border patrolling (as in Goodall 1986 and Watts and Mitani 2001). To make intersite comparisons of activity budgets, we used data pooled across all individuals at each site and also compared data on adult males, on cycling females, and on pregnant and lactating females separately.

We defined feeding bout length as the total amount of time that the focal individual fed in a given patch. We defined a patch as an aggregation of food items that allowed uninterrupted feeding or foraging movements by individuals or parties (*cf.* Chapman *et al.* 1994). Generally, this was a single tree or large sapling, but it also included

multiple adjacent stems of terrestrial vegetation and, for species growing in dense groves, e.g., *Uvariopsis congensis* or *Teclea nobilis*, multiple adjacent trees when their crowns overlapped sufficiently to allow direct tree-to-tree travel. We indexed the size of a feeding patch as its diameter at breast height (DBH), in the case of single trees, or as the sum total of the DBH of each tree used within a single grove. For strangler figs, we visually assessed the diameter of the fig stem just above the point at which the stem branched from its host tree (the presumed germination point). We did not assess patch size in the case of patches consisting of terrestrial herbaceous vegetation.

With the aid of field assistants, we noted the number and age/sex class of all independently traveling chimpanzees present in the same party as the focal individual on first encounter. We then assessed party membership continuously, considering individuals to have joined the party when we first noted their presence and to have left if they had not been seen in >1 h. Assessing party membership over this time scale reduced the possibility of omitting individuals that were present in the party but temporarily (<1 h) out of view (Chapman *et al.* 1993). We also recorded the location of the focal individual at each feeding and resting site using known crossings of the trail grid system or, if the individual was not within the trail system, using a GPS unit. We often searched for individuals of particular age/sex classes that might otherwise have been underrepresented in sampling, e.g., adult females often forage in small, inconspicuous parties and tend to be more difficult to locate than adult males, which are often in large parties.

This methodology allowed for straightforward assessment and intersite comparisons of monthly activity budgets (the total percentage of time each month individuals devoted to feeding, resting, traveling, hunting, or border patrolling), diet composition and diversity, food patch size, feeding party size (the maximum number of independently feeding chimpanzees, including the focal individual, cofeeding in a given patch during a particular feeding bout), and patch occupancy times. To assess feeding patch productivity, we multiplied the DBH of the feeding tree by the phenology score for the patch (indexed as 0–4, with 0 indicating no fruit in the crown and 4 indicating maximum fruit concentration within the crown). To ensure precision in the assignment of phenology scores to feeding patches, only one of us (K. B. Potts) assigned scores at Ngogo, while the same field assistant conducting behavioral sampling at Kanyawara assigned scores to feeding patches there. K. B. Potts conducted extensive interobserver reliability tests with this field assistant and randomly spot-checked scored feeding patches to ensure that assignment of phenology scores was consistent between sites. We used the Shannon-Wiener diversity index ($H' = -\sum [P_i \log P_i]$, where P_i is the proportion of species i in the sample area) to estimate dietary diversity (Pielou 1974), and Hill's index ($J = H'/x$, where x is the total number of species sampled) to estimate dietary evenness (Hill 1973; Pielou 1974). Larger H' values indicate higher diversity, with a minimum score of 0. J ranges from 0 to 1, with a score of 1 indicating maximum equitability of feeding time among all items included in the diet.

Data Analysis

We used parametric procedures whenever possible and used ln-transformed values (or arcsine transformed values for percentages) when the data did not meet the assumptions

Fig. 1 Proportional contribution of various plant parts to the diet of chimpanzees. **a** All monthly values for each site. **b** Average of monthly values from the overlap period only. RF=ripe fruit; UF=unripe fruit; YL=young leaves.

of parametric statistics. For most comparisons of feeding ecology variables between the sites, we used independent samples *t*-tests; we used Mann-Whitney *U* tests if the data could not be transformed to meet the assumptions of a *t*-test. For specific comparisons of monthly values during the overlap period, we assessed differences between the sites using paired samples *t*-tests or, when necessary, Wilcoxon signed rank tests. We assessed the differences between the sites in coefficients of variation (CV) using Levene's test for equality of variance (Schultz 1985; Sokal and Braumann 1980). Significance was set at $\alpha=0.05$ for all tests.

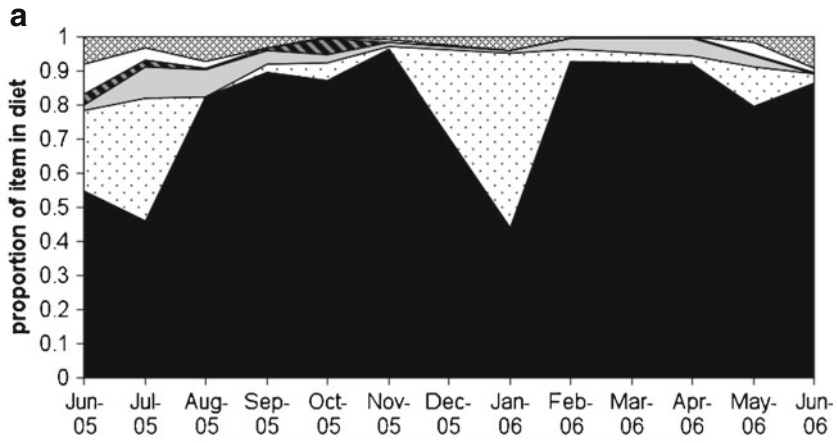
Results

Diet

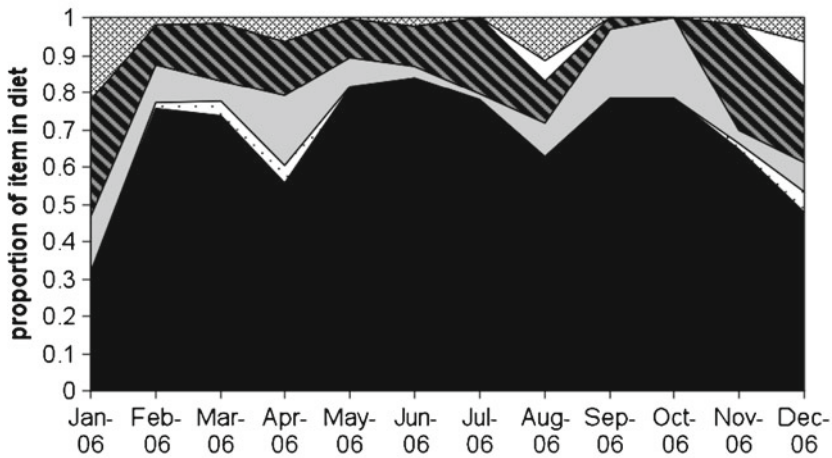
Chimpanzees at Ngogo devoted proportionally more of their feeding time to ripe fruit than did chimpanzees at Kanyawara (80.5% vs. 64.4%; Mann-Whitney *U* based on monthly averages: $N_{\text{Ngogo}}=11$, $N_{\text{Kanyawara}}=12$, $U=35.0$, $p=0.05$; Fig. 1a). Of the time spent feeding on ripe fruit, 70.6% and 46.6% was spent feeding on figs at Kanyawara and Ngogo, respectively. Kanyawara chimpanzees ate relatively more pith and stems of terrestrial vegetation ($K=17.4\%$, $N=1.0\%$ of total feeding time; $U=11.5$, $p=0.001$), whereas Ngogo chimpanzees ate more unripe fruit ($K=2.0\%$, $N=11.7\%$ of feeding time; $U=24.0$, $p=0.009$). These differences were apparent during both the overlap and nonoverlap periods (Fig. 1b).

Ngogo and Kanyawara chimpanzees shared only 8 items among those that were the top 20 dietary items for each community (40%; Tables I and II), and only 4 out of the top 10. These 8 common items made up 25.4% of the diet at Ngogo and 51.87% of the diet at Kanyawara. There was no difference between the communities in the proportion of feeding time devoted to these common species (paired samples *t*-test; $t=-1.311$, $N=8$, $p=0.231$) or to the top 20 items considered together (Mann-Whitney *U* test; $U=229.0$, $N=20$, $p=0.441$). In total, 40% (24/60) of all items included in the diet of Ngogo chimpanzees were also included in the Kanyawara chimpanzee diet, whereas 37.5% (24/64) of items eaten by Kanyawara chimpanzees were also eaten by Ngogo chimpanzees. Further, of the 12 food items included in the top 20 at Ngogo that were not common to the top 20 at Kanyawara, 10 (83%) were from species that are locally absent from or rare at Kanyawara (defined as <3 stems appearing in botanical plot sampling summarized in Potts 2008). Thus much of the intersite difference in diet composition was apparently due to heterogeneity in floral composition within Kibale. Conversely, none of the top 20 items at Kanyawara were from species that are absent from or rare at Ngogo.

Diet diversity was low at both sites (Shannon-Wiener diversity index [*H'*]; Ngogo: monthly mean=1.553, Kanyawara: monthly mean=1.781). The average monthly equitability index (*J'*) was 0.58 (range: 0.36–0.74) and 0.70 (range: 0.51–0.86) at Ngogo and Kanyawara, respectively. Over the entire study period, monthly dietary diversity did



Ngogo



Kanyawara

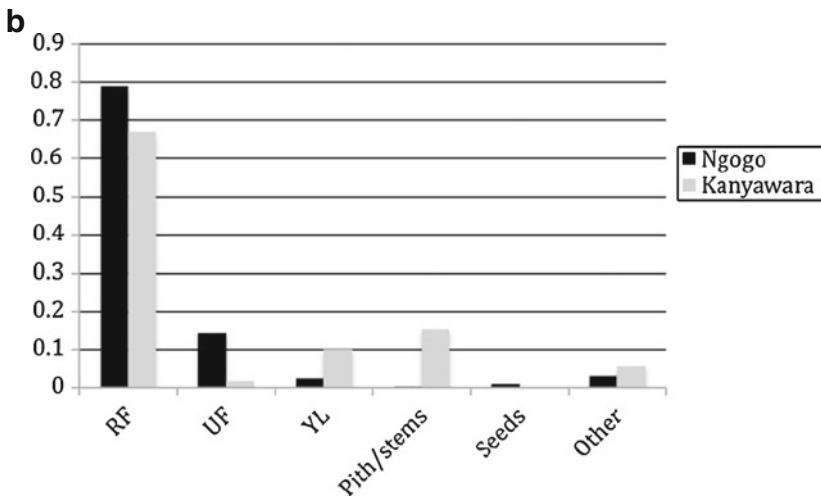
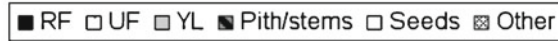


Table 1 Plant items in the diet of chimpanzees at Ngogo and Kanyawara, and the percent contribution of each item

Ngogo			Kanyawara		
Species	Part	% of feeding time	Species	Part	% of feeding time
<i>Ficus mucuso</i>	RF	34.11	<i>Ficus natalensis</i>	RF	17.90
<i>Uvariopsis congensis</i>	RF	11.16	<i>F. sansibarica</i>	RF	13.75
<i>Chrysophyllum albidum</i>	RF	9.84	<i>Mimusops bagshawei</i>	RF	8.31
<i>Pterygota mildbraedii</i>	UF/SD	5.91	Unknown spp.	Pith/stems/ YL	5.42
<i>Teclea nobilis</i>	RF	5.46	<i>Acanthus arborescens</i>	Pith	5.33
<i>Mimusops bagshawei</i>	RF	5.05	<i>F. capensis</i>	RF	4.94
<i>F. sausureana</i>	RF	3.68	<i>Celtis africana</i>	YL	4.88
<i>Morus mesozygia</i>	RF	2.62	<i>F. exasperata</i>	RF	4.62
<i>Pouteria altissima</i>	RF	2.16	<i>Uvariopsis congensis</i>	RF	3.94
<i>F. sansibarica</i>	RF	1.77	<i>Aframomum</i> spp.	Pith	2.87
<i>Treulia africana</i>	RF	1.24	<i>F. exasperata</i>	YL	2.07
<i>Pseudospondias microcarpa</i>	RF	1.16	<i>Celtis africana</i>	LB	2.00
<i>Pterygota mildbraedii</i>	YL	1.07	<i>Lepistemon</i> spp.	Pith	1.80
<i>Cassine buechananii</i>	RF	1.03	<i>Pennisetum purpureum</i>	Pith	1.62
<i>F. exasperata</i>	YL	0.98	<i>Ensete</i> spp.	Pith	1.27
<i>Cordia millenii</i>	RF	0.98	<i>Cordia abyssinica</i>	RF	1.17
<i>F. natalensis</i>	RF	0.96	<i>F. sausureana</i>	RF	1.39
<i>Monodora myristica</i>	RF	0.95	<i>Pseudospondias microcarpa</i>	RF	1.14
<i>F. capensis</i>	RF	0.72	<i>Linociera johnsonii</i>	RF	1.04
<i>Cola gigantea</i>	RF	0.68	<i>Cyperus papyrus</i>	Pith	0.96
<i>Neoboutonia macrocalyx</i>	Roots	0.60	<i>F. exasperata</i>	UF	0.95
<i>Celtis africana</i>	YL	0.46	<i>Brilliantasia</i> spp.	Seeds	0.80
<i>F. variifolia</i>	RF	0.46	Unknown Ulmaceae	YL	0.70
<i>F. exasperata</i>	UF	0.41	<i>Phytolacca dodecandra</i>	RF	0.62
<i>Aframomum</i> spp.	PITH	0.38	<i>Marantochloa leucantha</i>	Pith	0.60
<i>Acanthus arborescens</i>	PITH	0.36	<i>Prunus africana</i>	RF	0.58
<i>F. cyathistipula</i>	UF	0.35	<i>F. urceolaris</i>	YL	0.57
<i>Morus mesozygia</i>	FL	0.35	<i>F. cyathistipula</i>	RF	0.52
<i>Celtis durandii</i>	RF	0.35	<i>F. thoningii</i>	RF	0.50
<i>Iligeria pentaphylla</i>	FL	0.34	<i>Monodora myristica</i>	RF	0.48
<i>Warburgia ugandensis</i>	RF	0.34	<i>Rubia cordifolia</i>	YL	0.46
<i>Antiaris toxicaria</i>	UF	0.29	<i>Chaetacme aristata</i>	YL	0.44
Unknown spp. bark	Cambium	0.29	<i>Triumphetta</i> spp.	Pith	0.37
<i>F. variifolia</i>	YL	0.23	unk climber	UF	0.36
<i>Baquertiodendron oblancoelatum</i>	RF	0.20	<i>Uretia</i> spp.	RF	0.30

Table I (continued)

Ngogo			Kanyawara		
Species	Part	% of feeding time	Species	Part	% of feeding time
<i>Pseudospondias microcarpa</i>	UF	0.20	<i>Acalypha</i> spp.	Pith	0.28
<i>Cyperus papyrus</i>	Pith	0.18	<i>Treculia africana</i>	RF	0.25
<i>Phytolacca dodeandra</i>	RF	0.17	<i>Todaria</i> spp.	RF	0.25
<i>Hoslundia opposita</i>	RF	0.15	<i>Trichilia drageana</i>	YL	0.24
<i>Chaetacme aristata</i>	YL	0.15	<i>Neoboutonia macrocalyx</i>	Dead wood	0.24
Honeycomb	Honey	0.15	<i>Aphania senegalensis</i>	RF	0.19
<i>Allophyllus abyssinicus</i>	RF	0.15	<i>F. sansibarica</i>	UF	0.17
<i>Iligera pentaphylla</i>	SD	0.14	<i>Olea capensis</i>	RF	0.16
<i>Celtis durandii</i>	YL	0.13	<i>F. vallis-choudae</i>	UF	0.14
Unknown spp.	YL	0.13	<i>Cordia abyssinica</i>	YL	0.14
<i>F. thoningii</i>	RF	0.13	<i>Celtis durandii</i>	RF	0.12
<i>Cordia millenii</i>	FL	0.11	<i>F. natalensis</i>	UF	0.10
Unknown spp.	Bryophyte	0.11	<i>Iligera pentaphylla</i>	Seeds	0.10
<i>Celtis mildbraedii</i>	YL	0.11	Unknown vine	RF	0.09
Unknown spp.	Wood	0.10	<i>Bridelia</i> spp.	RF	0.08
<i>F. brachylepis</i>	UF	0.10	<i>F. sansibarica</i>	Cambium	0.08
<i>Piper capense</i>	Pith	0.10	<i>F. stipulifera</i>	RF	0.07
<i>Pennisetum purpureum</i>	Reeds	0.09	<i>Pancovia turbinata</i>	RF	0.06
<i>F. vallis-choudae</i>	RF	0.09	<i>Piper capense</i>	Pith	0.06
Unknown vine	YL	0.08	Unknown spp.	Wood	0.06
Unknown spp.	Larvae	0.06	<i>Antiaris toxicaria</i>	YL	0.06
<i>Trichilia drageana</i>	YL	0.06	Honeycomb	Honey	0.06
<i>Zanha golungensis</i>	RF	0.06	<i>Trichilia drageana</i>	RF	0.05
<i>F. cyathistipula</i>	YL	0.05	<i>Markhamia platycalyx</i>	Cambium	0.04
<i>Cola gigantea</i>	YL	0.05	<i>Myrianthus holstii</i>	RF	0.03
<i>Morus mesozygia</i>	YL	0.05	Unknown fern	YL	0.03
<i>F. congensis</i>	UF	0.04	<i>Bridelia</i> spp.	UF	0.02
Unknown spp.	Pith	0.02	<i>Jasmina</i> spp.	YL	0.01
Unknown spp.	Wood	0.02	<i>Lantana</i> spp.	RF	0.01
<i>Celtis durandii</i>	Cambium	0.02	Soil	Soil	0.01
<i>Antiaris toxicaria</i>	YL	0.01	<i>F. urceolaris</i>	RF	0.004
<i>Phoenix reclinata</i>	Frond	0.01			
<i>Teclea nobilis</i>	YL	0.01			

RF=ripe fruit; UF=unripe fruit; SD=seed; YL=young leaves; LB=leaf buds.

not differ between Ngogo and Kanyawara (independent samples *t*-test; $N_{\text{Kanyawara}}=12$, $N_{\text{Ngogo}}=11$, $t_{1,21}=1.253$, $p=0.224$). However, during the overlap period, dietary diversity at Kanyawara (mean=2.003) was higher than at Ngogo (mean=1.330; $t=-6.998$, $N=4$, $p=0.002$). Monthly variation in dietary diversity was similar at Kanyawara (CV=

Table II The 20 most common items in the diet of chimpanzees at Ngogo and Kanyawara

Ngogo	% of feeding time	Kanyawara	% of feeding time
<i>Ficus mucuso</i> RF	34.00	<i>Ficus natalensis</i> RF	17.90
<i>Uvariopsis congensis</i> RF	11.10	<i>Ficus sansibarica</i> RF	16.10
<i>Chrysophyllum albidum</i> RF	9.80	<i>Mimusops bagshawei</i> RF	8.30
<i>Pterygota mildbraedii</i> UF/SD	5.90	<i>Celtis africana</i> YL/LB	6.90
<i>Teclea nobilis</i> RF	5.50	Unknown THV pith/stems/YL	5.40
<i>Mimusops bagshawei</i> RF	5.10	<i>Acanthus arborescens</i> pith	5.30
<i>Ficus saussureana</i> RF	3.70	<i>Ficus capensis</i> RF	4.90
<i>Morus mesozygia</i> RF	2.60	<i>Ficus exasperata</i> RF	4.60
<i>Pouteria altissima</i> RF	2.20	<i>Uvariopsis congensis</i> RF	3.90
<i>Ficus sansibarica</i> RF	1.70	<i>Aframomum</i> spp. pith	2.90
<i>Treulia africana</i> RF	1.24	<i>Ficus exasperata</i> YL	2.07
<i>Pseudospondias microcarpa</i> RF	1.15	<i>Lepistemon</i> spp. pith/YL	1.80
<i>Pterygota mildbraedii</i> YL	1.07	<i>Pennisetum purpureum</i> reeds	1.62
<i>Cassine buchananii</i> RF	1.03	<i>Ficus saussureana</i> RF	1.40
<i>Ficus exasperata</i> YL	0.98	<i>Ensete</i> spp. Pith	1.27
<i>Cordia millenii</i> RF	0.98	<i>Cordia abyssinica</i> RF	1.17
<i>Ficus natalensis</i> RF	0.96	<i>Pseudospondias microcarpa</i> RF	1.14
<i>Monodora myristica</i> RF	0.95	<i>Linociera johnsonii</i> RF	1.05
<i>Ficus capensis</i> RF	0.72	<i>Cyperus papyrus</i> pith	0.96
<i>Cola gigantea</i> RF	0.70	<i>Ficus exasperata</i> UF	0.95
Total %	91.49	Total %	89.50

Items in bold were included in the top 20 at both sites. RF=ripe fruit, UF=unripe fruit, SD=seed, YL=young leaves; LB=leaf buds.

0.275) and Ngogo ($CV=0.237$; $F=0.699$, $p=0.413$). The top 20 items in the diet accounted for 91.5% and 89.1% of all feeding time at Ngogo and Kanyawara, respectively.

Activity Budgets

Pooling data for all individuals revealed that the activity budgets of chimpanzees at the 2 sites were roughly similar (Fig. 2). The primary difference between the 2 communities was that chimpanzees at Kanyawara devoted a relatively large proportion of time to resting, at the expense of feeding, traveling, and energetically costly hunting and border patrolling. This was the only significant difference between the sites (monthly means: Ngogo=34.0%, Kanyawara=44.8%; independent samples t -test, $t=-3.511$, $N_{\text{Ngogo}}=12$, $N_{\text{Kanyawara}}=12$, $p=0.002$; all other $p>0.05$).

Differences between the 2 communities were more apparent when males and females were considered separately (Fig. 3). Ngogo and Kanyawara cycling females and males had broadly similar activity budgets, though males at Kanyawara spent more time resting. However, the activity budgets of pregnant/lactating females diverged considerably between the sites. Those at Ngogo devoted more time to feeding and less time to resting than did those at Kanyawara (Fig. 3).

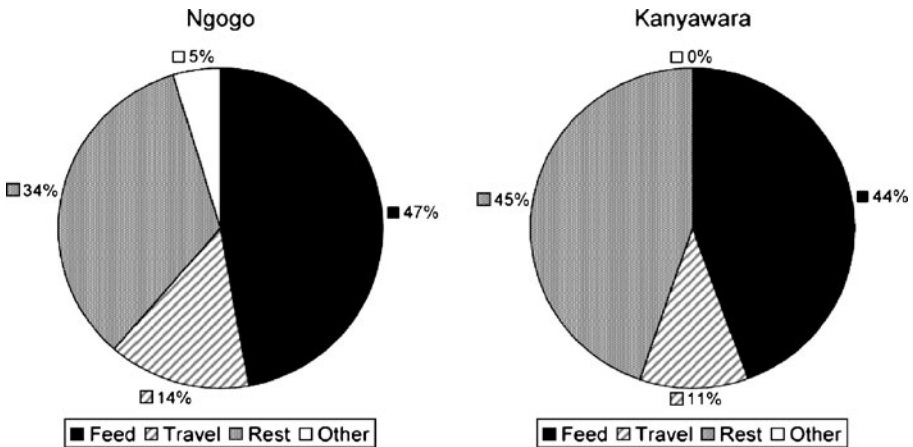
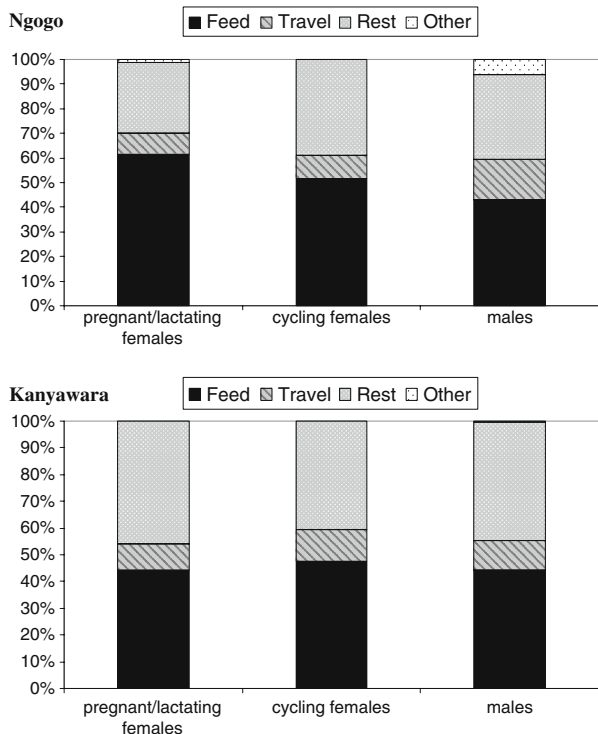


Fig. 2 Activity budgets of all individuals (pooled percentages) at Ngogo and Kanyawara. See text for explanations of each behavioral category. Only time spent resting differed significantly between the sites.

Food Patch Characteristics and Patch Use

Chimpanzees at Kanyawara and Ngogo used food patches of roughly the same size (66.87 vs. 63.38 cm DBH, respectively; independent samples *t*-test: $t=1.209$, $p=0.102$). However, at both sites >20% of food patches used by chimpanzees were of

Fig. 3 Activity budgets of pregnant/lactating females, cycling females, and males at Ngogo (top) and Kanyawara (bottom). See text for explanations of each behavioral category.



growth forms other than trees (Table III), and thus the size of the patch could not be meaningfully assessed or quantified by the measure used here.

Chimpanzees at Kanyawara occupied feeding patches (including both arboreal [trees and figs] and terrestrial patches) for longer periods than Ngogo chimpanzees (46.2 vs. 27.0 min/patch/visit; MWU test, $Z=-9.188$, $n_{\text{Ngogo}}=348$, $n_{\text{Kanyawara}}=317$; $p<0.001$). Patch occupancy times also varied less at Kanyawara ($CV=0.94$) than at Ngogo ($CV=1.32$; $F=6.24$, $p=0.013$). After controlling for the number of individuals cofeeding in the patch, focal chimpanzees at Kanyawara fed longer than those at Ngogo in patches of the same species and similar productivity (tree/fig size \times phenology score) in 4 out of 7 cases (Table IV). In no case was mean patch residency longer at Ngogo, suggesting that *per capita* patch exploitation levels were more intense at Kanyawara than at Ngogo.

Feeding Party Size

On average, feeding party size (FPS) was higher at Kanyawara ($x=8.39$, range=1–32) than at Ngogo ($x=7.29$, range=1–40; MWU, $Z=-4.680$, $p<0.001$). There was no difference in the variability in FPS among feeding bouts between the 2 sites (CV in FPS; Kanyawara=0.836, Ngogo=1.01; $F=0.010$, $p=0.920$).

At Ngogo, FPS was positively related to the size (DBH) of the food patch, which explained 80% of the variance in FPS (simple linear regression with ln-transformed data, $R^2=0.801$, $p<0.001$). The relationship between these variables was similar, but far weaker, at Kanyawara, where DBH explained only 22.7% of the variance in FPS ($R^2=0.227$, $p<0.001$; Fig. 4).

Discussion

Dietary Quality

The most frequently consumed dietary items at Ngogo and Kanyawara overlapped relatively little. This is at first surprising, especially considering the close proximity

Table III Percentage contribution of various food patch types in the diet of chimpanzees at Ngogo and Kanyawara

Form	Ngogo	Kanyawara
Trees	58.0	29.0
Free-standing figs	14.2	17.1
Strangler figs	4.8	32.2
Herbs	2.1	13.7
Vines	1.0	1.5
Dropped fruits	8.1	0.13
Shrubs	1.1	1.2
Saplings	8.7	3.1
Other	2.0	2.1
Total nontree or nonfig	23.0	21.6

Table IV Average per capita patch residency times (number of minutes spent feeding in a patch corrected for the feeding party size) at each site for the same tree species and roughly the same productivity score (phenology score multiplied by tree size [DBH])

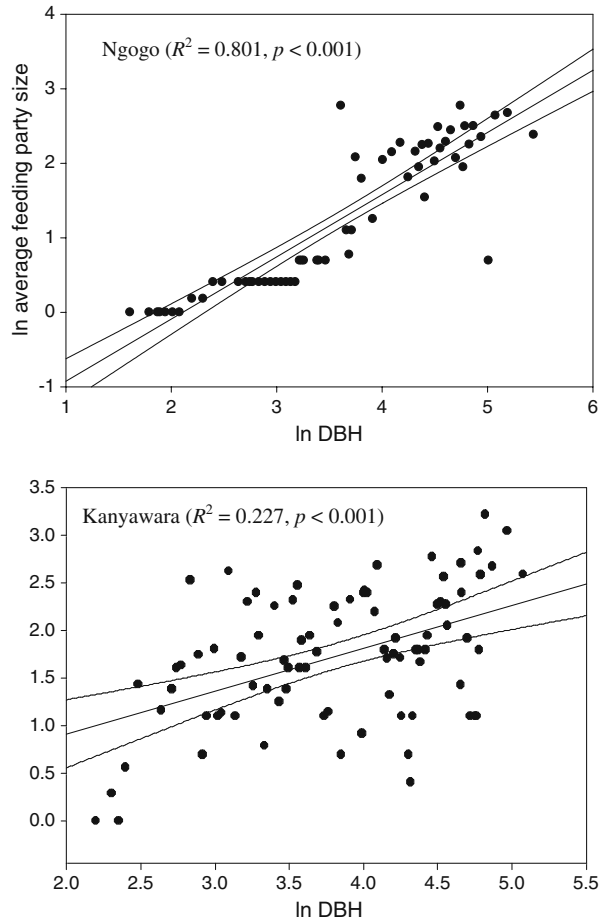
	Productivity score (phenology score × DBH)	Ngogo	Kanyawara	
<i>Uvariopsis congensis</i>	10–40	12	23.5	K>N (U=667.5, p=0.048)
	>40	3.315	3.743	K=N (U=655.5, p=0.232)
<i>Pseudospondias microcarpa</i>	0–200	2.77	2.07	K=N (U=425.0, p=0.142)
	>200	1.39	5.88	K>N (U=100.0, p=0.010)
<i>Ficus saussureana</i>	All	2.57	3.27	K=N (U=440.5, p=0.690)
<i>F. sansibarica</i>	All	2.27	8.27	K>N (U=1923.5, p<0.001)
<i>F. natalensis</i>	All	3.75	5.87	K>N (U=1572.0, p=0.048)

Bold text in the last column indicates a significant difference between the sites.

of the sites, but most of the important items in the Ngogo diet that were not also among the most important items in the Kanyawara diet were from species absent or locally rare at Kanyawara. This contrast highlights the potentially profound influence of habitat heterogeneity at this scale on the ecology of primate populations (Butynski 1990; Chapman and Chapman 1999; Ganas *et al.* 2004; Harris and Chapman 2007; Kool 1993; Watts 1984).

Perhaps related to this intersite floristic heterogeneity, the proportion of ripe fruit in the diet (a putative indicator of dietary quality for frugivores; Wrangham *et al.* 1998) was higher at Ngogo than at Kanyawara, whereas the Kanyawara chimpanzee diet included a higher percentage of young leaves and pith. In addition, all of the top 10, and 18 of the top 20, most important items in the Ngogo diet were fruit (including unripe fruit of *Pterygota mildbraedii*), whereas at Kanyawara, only 6 of the top 10, and 11 of the top 20, were fruit. Finally, figs accounted for a considerably higher proportion of the ripe fruit component of the diet at Kanyawara than at Ngogo. The water-soluble carbohydrate concentrations in figs are generally lower than in similarly sized nonfig ripe fruits eaten by Kibale chimpanzees (Conklin and Wrangham 1994), and large-bodied frugivores typically prefer nonfig drupes over figs (Leighton 1993; Wrangham *et al.* 1996; though figs often provide a balanced supply of different macronutrients (Felton *et al.* 2009a). Thus the Ngogo chimpanzee diet apparently included a higher proportion of readily digestible sugars than the Kanyawara diet. However, it is also noteworthy that the most common item in the Ngogo diet was ripe figs of *Ficus mucuso*, a species important in promoting large parties due to its unusually large crown (Potts 2008). Also, it is clear that equating the percentage of ripe fruit in the diet with dietary quality is an oversimplification (Raubenheimer *et al.* 2009). The nutritional goal of omnivores is to achieve a balanced intake of necessary macronutrients (proteins, lipids, carbohydrates, etc.), rather than to necessarily maximize the intake of any single food type (Felton *et al.* 2009b). By this rationale, ripe fruit alone may not adequately index diet quality, as it is assumed that only through the incorporation of other food types, e.g., leaves and pith, are chimpanzees able to maintain macronutrient balance. However, to some extent this simplification is warranted in the case of chimpanzees in Kibale. For

Fig. 4 Regression of feeding party size vs. feeding patch size (DBH; both ln-transformed). See text for details.



example, intake of lipids and carbohydrates by Kanyawara chimpanzees correlates positively with ripe fruit abundance (Conklin-Brittain *et al.* 1998), and fruit mesocarp eaten by chimpanzees at Ngogo appears to be unusually high in protein concentration (Hohmann *et al.* 2010, Watts *et al.*, in prep). Kibale chimpanzees may therefore achieve macronutrient balancing primarily through a fruit-based diet, as shown in spider monkeys (*Ateles chamek*) feeding on figs (Felton *et al.* 2009a). We nonetheless acknowledge that using dietary ripe fruit component as primary proxy of dietary quality is largely based on energy optimization principles (Emlen 1966) that are beginning to fall out of favor with nutritional ecologists (Felton *et al.* 2009b; Raubenheimer *et al.* 2009).

Dietary Diversity

At all sites where they have been intensively studied, chimpanzees show high preference and selectivity for a small number of foods (Newton-Fisher 1999; Wrangham *et al.* 1996), and both Ngogo and Kanyawara conform to this pattern. In

fact, the dietary diversity of Kibale chimpanzees is relatively low compared to that of some populations of other large-bodied ripe fruit specialists with similar dietary niches, e.g., *Lagothrix lagotricha poeppigii* in Yasuñi National Park, Ecuador (Di Fiore 2004). For example, monthly dietary diversity (H') indices ranged from 1.8 to 3.6 and 1.9 to 3.0 for gibbons (*Hylobates muelleri* × *agilis*) in Kalimantan (McConkey *et al.* 2003) and mangabeys (*Lophocebus albigena*) in Cameroon (Poulsen *et al.* 2001), respectively. However, dietary diversity at Ngogo and Kanyawara was similar to that of other frugivorous great ape populations, including populations of chimpanzees (Budongo: Newton-Fisher 1999; Kahuzi-Biega, DRC: Basabose 2002; Goualougo Triangle, Republic of Congo: Morgan and Sanz 2006; Gashaka, Nigeria: Hohmann *et al.* 2006), bonobos [*Pan paniscus*] Lomako, DRC: Badrian *et al.* 1981; White 1998; Wamba, DRC: Kano and Mulavwa 1984; LuiKotal, Salonga, DRC: Hohmann *et al.* 2006), western lowland gorillas ([*Gorilla gorilla gorilla*] Lopé Reserve, Gabon: Rogers *et al.* 1990; Tutin and Fernandez 1993; Williamson *et al.* 1990; Bai Hokou, Central African Republic: Masi 2007), and orangutans ([*Pongo* spp.] Kutai National Park, East Kalimantan, Borneo: Rodman 1977; Leighton 1993; Tanjung Puting, Central Kalimantan: Galdikas 1988).

The higher dietary diversity and equitability indices at Kanyawara than at Ngogo, particularly during the overlap period, have numerous potential explanations. Low-diversity diets could result from a relative lack of available high-quality resources (Simmen *et al.* 2003). In a species-poor environment, few alternative dietary options may be available for frugivores, and thus dietary diversity would be low. Alternatively, diversity could be low in situations in which high-quality resources are abundant (Isabirye-Basuta 1988; Murray *et al.* 2006; Poulsen *et al.* 2001; Terborgh 1983). If widespread and abundant crops of a small number of species are available, there might be little need for frugivores to maintain a high-diversity diet. This is in accordance with the principles of optimal foraging theory (OFT; MacArthur and Pianka 1966; Pyke *et al.* 1977; Schoener 1971), which predict that, as habitat productivity increases, the number of species or items incorporated into the diet should decrease. Such a principle best explains the relatively low dietary diversity and equitability values at Ngogo. Although the number of species enumerated in botanical plots at Ngogo and Kanyawara by Potts (2008) was roughly similar, a higher proportion of the tree community provides fruit at any given time at Ngogo than at Kanyawara. Chapman *et al.* (1997) found that, on average, 878 stems/km²/mo bore fruit at Kanyawara, whereas at Ngogo the figure was 1748 stems/km²/mo. Thus chimpanzees at Kanyawara are limited in the extent to which they can incorporate a higher diversity of ripe fruit into their diets. Moreover, during this study, ripe fruit made up a much higher percentage of the diet at Ngogo, and Kanyawara chimpanzees' greater use of pith and stems of herbaceous vegetation largely determined the intersite differences in dietary diversity values. Low dietary diversity at Ngogo may thus be a reflection of a relatively high abundance and low temporal variability of preferred resources (Potts *et al.* 2009).

Activity Budgets

Individuals inhabiting home ranges with high abundances of important foods should more easily satisfy caloric and other nutritional requirements than those inhabiting

lower-quality ranges. More immediate access to essential resources, in turn, should reduce the time engaged in feeding and foraging, including traveling between patches, and allow more time for resting, socializing, or energetically costly behaviors, as found in several studies of wild primates, e.g., female *Papio cynocephalus*: Altmann (1980); female *Theropithecus gelada*: Dunbar and Dunbar (1988), and supported by theoretical time budget models, e.g., *Papio* spp.: Dunbar (1992); *Ateles* spp.: Korstjens *et al.* (2006); and colobines: Korstjens and Dunbar (2007). By this logic, time budget data given in the preceding text would suggest that chimpanzees at Kanyawara have a higher quality home range and feed more efficiently than those at Ngogo, because Kanyawara chimpanzees spent slightly less time feeding and traveling and considerably more resting. Further, pregnant and lactating females, which have particularly high energetic demands (Gittleman and Thompson 1988; Oftedal 1991), spent far more time feeding, at the expense of resting, at Ngogo than at Kanyawara.

The problem with this comparison of gross activity budgets is that it obscures important differences in diet composition between the 2 communities, specifically the greater contribution of ripe fruit to the diet at Ngogo. Ripe fruit typically is quantitatively the major component of chimpanzee diets (Basabose 2002; Nishida and Uehara 1983; Potts 2008; Tutin *et al.* 1991; Wrangham 1977; Wrangham *et al.* 1996, 1998), and it is likely their predominant source of metabolizable energy (Conklin-Brittain *et al.* 1998). Thus, although Kanyawara chimpanzees spent less time feeding and more time resting than Ngogo chimpanzees, they did not necessarily meet their caloric requirements more easily. Rather, they minimized the cost portion of their energy budgets by devoting more time to resting. The relatively low frequency of energetically costly border patrolling and hunting at Kanyawara was also consistent with a cost-minimization strategy, whereas these activities constituted 4.6% of the Ngogo activity budget. Moreover, the rise in feeding time during pregnancy and lactation among Ngogo females may reflect a reproductive strategy, whereby female caloric intake spikes when energetic demands are highest due to pregnancy and lactation (Bercovitch 1987; Lee 1987; Ross 1998), thereby increasing energy accumulation and probability of successful parturition and weaning. Similar reproductive strategies—akin to income breeding strategies (Stearns 1989)—have been documented in other primates (*Cercopithecus mitis*: Butynski 1988; *Presbytis entellus*: Koenig *et al.* 1997). The activity budgets and diet composition of Kanyawara females suggest they cannot use such a strategy as efficiently as Ngogo females. This notable difference in feeding ecology may help to explain the differences in overall density of chimpanzees at the 2 sites, if such a strategy results in higher fecundity and offspring survival at Ngogo, which preliminary data suggest is the case (Watts *et al.*, *unpubl. data*).

Food Patch Characteristics, Patch Occupancy Times, and Feeding Party Size

Despite overall similarity in feeding party size and patch size between the 2 communities, chimpanzees adjusted their feeding efforts according to prevailing ecological conditions, e.g., patch size and per capita productivity, more readily at Ngogo. To the extent that a fission–fusion dynamic allows individuals to minimize the costs of feeding competition, the higher coefficient of variation in feeding party size at Ngogo and the higher percentage of variation in feeding party size explained

by feeding tree patch size there suggest that feeding competition costs were lower there than at Kanyawara. Chapman *et al.* (1995) suggested that a strong positive relationship between feeding party size and patch size should exist in habitats with abundant alternative feeding sources in relatively close proximity, e.g., contagiously distributed fruiting trees, whereas in habitats in which high-quality patches are rare or sparsely distributed or widely scattered, no such relationship may exist. This is because when travel costs do not prohibit the formation of large groups, large patches will promote large foraging subgroups (*Ateles belzebuth*: Klein and Klein 1977; *A. paniscus*: Symington 1988; *Brachyteles arachnoides*: Strier 1989; *Pongo pygmaeus*: Utami *et al.* 1997). However, high travel costs between successive patches can constrain the ability of individuals to form large groups even in large patches (Chapman *et al.* 1995). The difference in R^2 values relating foraging party size to patch size at the 2 sites suggests that Ngogo chimpanzees more frequently had access to a high density of relatively evenly distributed food sources.

Increased intragroup feeding competition can lead to increased mortality, e.g., *Macaca sinica* (Dittus 1979) and decreased reproductive output, e.g., *Cercopithecus aethiops* (Whitten 1983) and *Theropithecus gelada* (Dunbar and Dunbar 1988). Ngogo chimpanzees therefore are able to avoid these fitness consequences more readily than Kanyawara chimpanzees. Similarly, Symington (1988) found that agonistic interactions among female black spider monkeys (*Ateles paniscus*) occurred substantially more often within a fruit patch when the feeding party size was larger than average for a patch of that size. Presumably as a consequence of food-related aggression, low-ranking females had longer interbirth intervals than high-ranking females (Symington 1988).

After controlling for the number of cofeeding individuals, residency times were longer for feeding patches of the same species, size, and phenophase at Kanyawara. This could indicate that 1) Ngogo chimpanzees more efficiently harvested items within patches, and thus required less foraging effort per patch, or 2) giving-up densities (resource levels at which a patch ceases to be efficiently exploitable [Brown 1988, 1989]) were lower at Kanyawara, or both. Ngogo chimpanzees might have ended feeding bouts and moved to alternative patches before or at the point at which current patches were functionally depleted (Chapman 1988), whereas Kanyawara chimpanzees might have more frequently reached or surpassed this point.

The first option is improbable, because it is unlikely that individuals at one site are inherently better able to forage for items within patches than conspecifics at another site (*cf.* Muruthi *et al.* 1991). However, the second option is supported by theoretical expectations. Notably, giving-up densities can differ among groups of the same species when habitat-wide mean energy harvest rates vary (Bowers *et al.* 1993; Brown 1988; Houle *et al.* 2006). According to optimal foraging theory (MacArthur and Levins 1967; Stephens and Krebs 1986), animals foraging in a heterogeneous environment composed of depletable patches should abandon a patch at the point at which the opportunity or energetic costs associated with remaining there rather than moving to a new patch begin to outweigh the caloric benefits accrued from continuing to forage in it, although this requires a certain degree of knowledge about the location of alternative food sources (Hancock and Milner-Gulland 2006). Thus, all else equal, patch residence times should be longer in habitats with fewer or more widely spaced resource patches because of relatively high interpatch travel costs (McNair 1982). Kanyawara has a lower basal area

per hectare of important food species, on average, than Ngogo (Potts *et al.* 2009). Longer patch occupancy times at Kanyawara thus likely result from the lower average density of alternative high-quality food patches at this site and from the lower marginal value (Charnov 1976) of food patches there. Similarly, if the resource base is of generally lower quality at Kanyawara than at Ngogo, chimpanzees at Kanyawara might require longer patch residencies to extract sufficient nutrients from a given patch (see also Hanya 2004 for a similar relationship between food availability and time devoted to feeding in Japanese macaques [*Macaca fuscata*]).

Further, under equivalent patch conditions, i.e., same species, size/productivity, and number of cofeeding individuals, Ngogo and Kanyawara chimpanzees should require approximately the same foraging effort to deplete a patch. If so, and if Ngogo chimpanzees abandoned patches near the point of functional depletion (Chapman *et al.* 1995), then it follows that Kanyawara chimpanzees foraged suboptimally on certain occasions by overexploiting resource patches.

Conclusion

This study documents considerable ecological diversity within a single population of chimpanzees inhabiting Kibale National Park, Uganda. The evidence presented here suggests that chimpanzees at Ngogo, a site of unusually high chimpanzee density, have notably higher-quality diets and forage more efficiently than chimpanzees at Kanyawara, a site of average chimpanzee density located just 12 km from Ngogo. It is likely that this variability relates to the 3-fold difference in density of chimpanzees at the Kanyawara and Ngogo sites, but data from chimpanzees at other Kibale sites are necessary to substantiate fully the link between feeding ecology and population density. This study adds to the growing body of research documenting noteworthy variation in ecology among distinct social groups of a single primate population (Chapman and Chapman 1999; Ganas *et al.* 2004; Grassi 2006; Harris and Chapman 2007), particularly for populations inhabiting highly heterogeneous landscapes. Based on these results, it is clear that caution is warranted in drawing conclusions about species- and population-level characteristics in primates without simultaneously accounting for the potential range of variation within populations.

Acknowledgments We thank the Uganda Wildlife Authority, Uganda National Council of Science and Technology, and the Makerere University Biological Field Station for granting us permission to conduct research in Kibale. We thank Colin Chapman, Eric Sargis, Tara Harris, and 2 anonymous reviewers for helpful comments on earlier versions of this manuscript, and special thanks to Sunday John for invaluable assistance in data collection at Kanyawara. K. B. Potts thanks the LSB Leakey Foundation, Wenner Gren Foundation, the American Society of Primatologists, and Yale University for generous financial support for his fieldwork.

References

- Altmann, J. (1980). *Baboon mothers and infants*. Chicago: University of Chicago Press.
- Badrian, N., Badrian, A., & Susman, R. L. (1981). Preliminary observations on the feeding behavior of *Pan paniscus* in the Lomako Forest of central Zaire. *Primates*, 22, 173–181.

- Basabose, K. (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology*, *58*, 1–21.
- Bercovitch, F. B. (1987). Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *American Journal of Primatology*, *12*, 189–195.
- Bowers, M. A., Jefferson, J. L., & Kuebler, M. G. (1993). Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos*, *66*, 229–236.
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, *22*, 37–47.
- Brown, J. S. (1989). Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs*, *59*, 1–20.
- Butynski, T. M. (1988). Guenon birth seasons and correlates with rainfall and food. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & Kingdon (Eds.), *A primate radiation: Evolutionary biology of the African guenons* (pp. 284–322). Cambridge: Cambridge University Press.
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecological Monographs*, *60*, 1–26.
- Chapman, C. A. (1988). Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour*, *105*, 99–116.
- Chapman, C. A., & Chapman, L. J. (1999). Implications of small-scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, *40*, 215–231.
- Chapman, C. A., & Lambert, J. A. (2000). Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *American Journal of Primatology*, *50*, 169–185.
- Chapman, C. A., White, F. J., & Wrangham, R. W. (1993). Defining subgroup size in fission-fusion societies. *Folia Primatologica*, *61*, 31–34.
- Chapman, C. A., White, F. J., & Wrangham, R. W. (1994). Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 41–58). Cambridge, MA: Harvard University Press.
- Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*, 59–70.
- Chapman, C. A., Chapman, L. J., Basuta, G. I., & Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology*, *35*, 287–302.
- Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136.
- Conklin, N. L., & Wrangham, R. W. (1994). The value of figs to a hindgut fermenting frugivore: a nutritional analysis. *Biochemical Systematics and Ecology*, *22*, 137–151.
- Conklin-Brittain, N. L., Wrangham, R. W., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance II: macronutrients. *International Journal of Primatology*, *19*, 971–998.
- Di Fiore, A. (2004). Diet and feeding ecology of woolly monkeys in a western Amazonian forest. *International Journal of Primatology*, *25*, 767–801.
- Dittus, W. (1979). The evolution of behaviours regulating population density and age-specific sex ratios in a primate population. *Behaviour*, *69*, 265–301.
- Dunbar, R. I. M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, *31*, 35–49.
- Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, *36*, 970–980.
- Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, *73*, 501–512.
- Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., Wallis, I. R., et al. (2009a). Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choices. *International Journal of Primatology*, *30*, 675–696.
- Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009b). Nutritional goals of wild primates. *Functional Ecology*, *23*, 70–78.
- Galdikas, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, *9*, 1–35.
- Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A., & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, *25*, 1043–1072.

- Ghiglieri, M. P. (1984). *The chimpanzees of the Kibale Forest: A field study of ecology and social structure*. New York: Columbia University Press.
- Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*, 863–875.
- Glenn, M. E., & Cords, M. (Eds.). (2002). *The guenons: Diversity and adaptation in African monkeys*. New York: Kluwer Academic/Plenum Press.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Grassi, C. (2006). Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, *131*, 50–63.
- Hancock, P. A., & Milner-Gulland, E. G. (2006). Optimal movement strategies for social foragers in unpredictable environments. *Ecology*, *87*, 2094–2102.
- Hanya, G. (2004). Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. *American Journal of Primatology*, *63*, 165–177.
- Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, *48*, 208–221.
- Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, *54*, 427–432.
- Hohmann, G., Fowler, A., Sommer, V., & Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 123–160). Cambridge: Cambridge University Press.
- Hohmann, G., Potts, K., N'Guessan, A., Fowler, A., Sommer, V., Mundry, R., et al. (2010). Plant foods consumed by *Pan*: exploring the variation of nutritional quality across Africa. *American Journal of Physical Anthropology*, *141*, 476–485.
- Houle, A., Vickery, W. L., & Chapman, C. A. (2006). Testing mechanisms of coexistence among two species of frugivorous primates. *Journal of Animal Ecology*, *75*, 1034–1044.
- Isabirye-Basuta, G. (1987). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In P. Heltne & L. Marquant (Eds.), *Understanding chimpanzees*. Cambridge, MA: Harvard University Press.
- Isabirye-Basuta, G. (1988). Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest. *Behaviour*, *105*, 135–147.
- Kano, T., & Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In R. L. Susman (Ed.), *The pygmy chimpanzee* (pp. 233–274). New York: Plenum Press.
- Klein, L. L., & Klein, D. B. (1977). Feeding behaviour of the Colombian spider monkey. In T. Clutton-Brock (Ed.), *Primate ecology* (pp. 153–181). London: Academic Press.
- Koenig, A., Borries, C., Chalisse, M. K., & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology, London*, *243*, 215–235.
- Kool, K. M. (1993). The diet and feeding behavior of the silver leaf monkey (*Trachypitecus auratus sondaicus*) in Indonesia. *International Journal of Primatology*, *14*, 667–700.
- Korstjens, A. H., & Dunbar, R. I. M. (2007). Time constraints limit group sizes and distribution in red and black-and-white colobus. *International Journal of Primatology*, *28*, 551–575.
- Korstjens, A. H., Verhoeck, I. L., & Dunbar, R. I. M. (2006). Time as a constraint on group size in spider monkeys. *Behavioral Ecology and Sociobiology*, *60*, 683–694.
- Lee, P. C. (1987). Nutrition, fertility, and maternal investment in primates. *Journal of Zoology*, *213*, 409–422.
- Leighton, M. (1993). Modeling dietary selectivity of Bornean orangutans: evidence for integration of multiple criteria. *International Journal of Primatology*, *14*, 257–313.
- Lwanga, J. S., Butynski, T. M., & Struhsaker, T. T. (2000). Tree population dynamics in Kibale National Park, Uganda 1975–1998. *African Journal of Ecology*, *38*, 238–247.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of apathy environment. *The American Naturalist*, *100*, 603–609.
- MacArthur, R. H., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*, 377–385.
- Masi, S. (2007). *Seasonal influence on foraging strategies, activity and energy budgets of western lowland gorillas (Gorilla gorilla gorilla) in Bai Hokou, Central African Republic*. Ph.D. thesis, Università di Roma, La Sapienza.
- McConkey, K. R., Arrio, A., Aldy, F., & Chivers, D. J. (2003). Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan. *International Journal of Primatology*, *24*, 19–32.
- McNair, J. N. (1982). Optimal giving-up times and the marginal value theorem. *The American Naturalist*, *119*, 511–529.

- Mitani, J. C., & Watts, D. P. (1999). Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology*, *109*, 439–454.
- Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*, 1079–1086.
- Mitani, J. C., Watts, D. P., & Lwanga, J. S. (2002). Ecological and social correlates of chimpanzee party size and composition. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 102–111). Cambridge: Cambridge University Press.
- Morgan, D., & Sanz, C. (2006). Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goulougo Triangle, Republic of Congo. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 97–122). Cambridge: Cambridge University Press.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press.
- Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *274*, 1009–1014.
- Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*, *17*, 1020–1028.
- Muruthi, P., Altmann, J., & Altmann, S. (1991). Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia*, *87*, 467–472.
- Newton-Fisher, N. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology*, *37*, 344–354.
- Nishida, T., & Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from Mahale Mountains, Tanzania. *African Study Monographs*, *3*, 109–130.
- Oftedal, O. T. (1991). The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *334*, 161–170.
- Pielou, E. C. (1974). *Population and community ecology: Principles and methods*. New York: Gordon and Breach.
- Potts, K. B. (2008). *Habitat heterogeneity on multiple spatial scales in Kibale National Park, Uganda: implications for chimpanzee population ecology and grouping patterns*. Ph.D. dissertation. Yale University, New Haven, CT.
- Potts, K. B., Chapman, C. A., & Lwanga, J. S. (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. *Journal of Animal Ecology*, *78*, 1269–1277.
- Poulsen, J. R., Clark, C. J., & Smith, T. B. (2001). Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*, *54*, 901–105.
- Pyke, G., Pulliam, H. R., & Charnov, E. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, *52*, 137–154.
- Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology, and nutritional ecology: towards an integrated framework. *Functional Ecology*, *23*, 4–16.
- Rodman, P. S. (1977). Feeding behavior of orangutans in the Kutai Reserve, East Kalimantan. In T. Clutton-Brock (Ed.), *Primate ecology*. London: Academic Press.
- Rogers, M. E., Maisels, F., Williamson, E. A., Fernandez, M., & Tutin, C. E. G. (1990). Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia*, *84*, 326–339.
- Ross, C. (1998). Primate life histories. *Evolutionary Anthropology*, *6*, 54–63.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, *2*, 369–404.
- Schultz, B. B. (1985). Levene's test for relative variation. *Systematic Zoology*, *34*, 449–456.
- Simmen, B., Hladik, A., & Ramasiarisoa, P. (2003). Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. *International Journal of Primatology*, *24*, 949–968.
- Sokal, R. R., & Braumann, C. A. (1980). Significance tests for coefficients of variation and variability profiles. *Systematic Zoology*, *29*, 50–66.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*, 259–268.
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Strier, K. B. (1989). Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). *Folia Primatologica*, *52*, 70–77.

- Strier, K. B. (2009). Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. *Current Anthropology*, *50*, 213–228.
- Struhsaker, T. T. (1997). *Ecology of an African rainforest*. Gainesville: University of Florida Press.
- Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, *105*, 117–132.
- Terborgh, J. (1983). *Five New World primates: A study in comparative ecology*. Princeton, NJ: Princeton University Press.
- Tutin, C., Fernandez, M., Rogers, E., Williamson, E., & McGrew, W. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *334*, 179–185.
- Tutin, C., & Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology*, *30*, 195–211.
- Utami, S. S., Wich, S. A., Sterck, E. H. M., & van Hooft, J. A. R. A. M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology*, *18*, 909–927.
- Watts, D. P. (1984). Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology*, *7*, 323–356.
- Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*, 43–55.
- Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*, 299–327.
- Watts, D. P., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *23*, 1–28.
- Watts, D. P., Muller, M. N., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*, 161–180.
- White, F. J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology*, *19*, 1013–1027.
- Whitten, P. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, *5*, 139–159.
- Williamson, E. A., Tutin, C. E. G., Rogers, M. E., & Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lopé, Gabon. *American Journal of Primatology*, *21*, 265–277.
- Wing, L. D., & Buss, I. O. (1970). Elephants and forests. *Wildlife Monographs*, *19*, 3–92.
- Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In T. Clutton-Brock (Ed.), *Primate ecology* (pp. 504–538). London: Academic Press.
- Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. M. Kappeler (Ed.), *Primate males* (pp. 248–258). Cambridge: Cambridge University Press.
- Wrangham, R. W., Conklin, N. L., Chapman, C. A., & Hunt, K. D. (1991). The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *334*, 171–178.
- Wrangham, R. W., Clark, A. P., & Isabirye-Basuta, G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In T. Nishida, W. McGrew, P. Marler, M. Pickford, & F. DeWaal (Eds.), *Topics in primatology, Vol. 1: Human origins* (pp. 81–98). Tokyo: University of Tokyo.
- Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the cost of great ape groups. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45–57). Cambridge: Cambridge University Press.
- Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance I: antifeedants. *International Journal of Primatology*, *19*, 949–970.
- Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for importance of tool use. *American Journal of Physical Anthropology*, *106*, 283–295.
- Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, *23*, 1025–1051.