

# Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate

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## Summary

1. Despite a long history of research on the influence of fruit availability on the population density of large-bodied vertebrate frugivores, operational understanding of the factors regulating density in these taxa remains elusive. We propose that fruit resources can be distinguished from one another on the basis of their functional role for the animals in question, and that such a classification system can aid in identifying the most influential determinants of frugivore density.
2. We compared the availability of several resource classes between two sites in Kibale National Park, Uganda separated by only 12 km yet differing threefold in density of chimpanzees (*Pan troglodytes*).
3. We categorized plant species used for fruit by chimpanzees according to their availability relative to habitat-wide fruit productivity, and by their tendency towards inter-individual fruiting synchrony. We predicted that the site of high chimpanzee density would support a higher density of food plant species tending to produce crops during periods of high habitat-wide productivity [high fruit abundance (HFA foods)] and of those tending to fruit synchronously among individuals during times of low habitat-wide availability (sLFA foods). The first food class should provide chimpanzees with a high nutrient density (and thus promote population growth), whereas the second should provide stable subsistence during lean periods and thus a temporally consistent resource base.
4. Counter to our prediction, only sLFA resources were more abundant at the site of high chimpanzee density than at the site of low density. We suggest that sLFA resources are most important in influencing density of large-bodied frugivores.

**Key-words:** animal density, chimpanzee, food availability, population regulation.

## Introduction

Factors regulating the density of consumer populations include both top-down (predation effects and disease) and bottom-up (resource availability and quality) components. Although the relative influence of each component is widely debated (e.g. Polis & Strong 1996; Schmitz, Hambäck & Beckerman 2000; Terborgh *et al.* 2001), it is likely that top-down and bottom-up processes play synergistic roles in limiting consumers (Krebs *et al.* 1995). Disentangling the relative effects of predators vs. resources ultimately requires either eliminating or controlling for one of these variables, thereby assessing the impact of the other (Moen & Oksanen 1998).

Similarly, bottom-up and top-down regulatory factors may exert both spatial and temporal influences on consumers, and a complete understanding of how the environment limits populations requires examination of both factors. For example, Brown, Mehlman & Stevens (1995) found that the spatial distribution of abundance within North American bird species was well explained by concomitant spatial environmental variability that was relatively fixed over time. However, Ives & Klopfer (1997), building on Brown *et al.*'s (1995) work, suggested that similar spatial patterning could be created from temporal environmental variation without a fixed spatial component.

Tropical forests are ideal sites in which to simultaneously incorporate both spatial and temporal components in understanding the determinants of density in vertebrates,

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particularly frugivorous species, as such ecosystems generally exhibit considerable spatiotemporal variability in fruiting phenology (van Schaik, Terborgh & Wright 1993; Condit *et al.* 2002; Cannon *et al.* 2007). Furthermore, the great apes (family Hominidae), the vast majority of which inhabit tropical forests (Campbell *et al.* 2007), represent a model taxon in which to address the role of bottom-up processes in regulating vertebrate frugivores. With some exceptions, most great apes are not subject to notable mortality risk from natural predators (Miller & Treves 2007), thus removing (or at least diminishing) the effect of top-down processes.

We assessed which fine-scale ecological characteristics are potentially limiting the density of chimpanzees (*Pan troglodytes* Blumenbach, 1799) by comparing the spatiotemporal availability of resources between the home ranges of two communities of known size inhabiting Kibale National Park (KNP), Uganda. Chimpanzees are large-bodied, wide-ranging frugivorous apes with home ranges of *c.* 8–40 km<sup>2</sup>. The two communities included in this study are separated by only 12 km (or approximately one to three home ranges), and that at Ngogo (hereafter referred to as the ‘high-chimpanzee-density’ site) is the largest and most densely populated chimpanzee community currently known, with over 155 members (5.1 individuals km<sup>-2</sup>; Mitani & Watts 2005; Potts 2008), compared to *c.* 50 chimpanzees (1.5 individuals km<sup>-2</sup>) at Kanyawara (hereafter referred to as the ‘low-chimpanzee-density’ site; Muller & Wrangham 2004). Detailed long-term observations from this population suggest that other extrinsic variables (both top-down and bottom-up factors) not explicitly dealt with here, including disease, inter-specific niche overlap, predation, and/or non-fruit resource availability have played relatively limited roles in influencing spatial variations in chimpanzee density in KNP (Potts 2008). This population therefore presents an ideal model for isolating the effects of fruit resource availability in both space and time on the population ecology of large-bodied tropical frugivores.

Several studies attest to the importance of bottom-up processes, most notably temporal fluctuations in fruit production, in limiting vertebrate frugivores in tropical forests (e.g. Wright *et al.* 1999; Wong *et al.* 2005). Although it is generally agreed that similar bottom-up factors regulate many, if not most, primate populations (Cant 1980; Oates *et al.* 1990; Marshall 2004), the exact nature of these limiting factors remains ambiguous (Chapman & Chapman 1999). We suggest this ambiguity may stem from two non-mutually exclusive sources. First, primates, more so than perhaps any other large-bodied mammalian taxon, show considerable intra-specific and intra-population variation in ecology (Chapman, Chapman & Gillespie 2002; Ganas *et al.* 2004; Harris & Chapman 2007). The majority of studies attempting to relate habitat variables to primate density among locations rely on comparisons of populations separated by large distances, which may obscure relevant intra-specific variation (Chapman & Fedigan 1990; Chapman *et al.* 2002). Comparison of ecology and population density at the within-population level (the level at which this study was conducted) is more

likely to distinguish which variables most strongly influence spatial variation in primate density, as this level of analysis largely controls for the influence of unmeasured abiotic and biotic variables (Chapman & Chapman 1999; Chapman *et al.* 2002) and removes any potential influence of phylogeny. Second, as noted by Ives & Klopfer (1997) and discussed above, both spatial and temporal components of environmental variability must be incorporated into studies of factors limiting populations. We develop a resource classification scheme here that attempts to account for the potentially simultaneous influence of both spatial and temporal variability on tropical frugivores.

#### WHAT CLASSES OF RESOURCES LIMIT LARGE-BODIED TROPICAL FRUGIVORES?

The general assumption that the availability of fruit resources limits the density of large-bodied frugivores in the tropics, although likely accurate, implicitly treats all fruit-providing plant species as functionally equivalent – each provides fruit for consumers, and thus each plays the same role. In so doing, it ignores the potentially great temporal fluctuations in fruit availability characteristic of the tropical forests (van Schaik *et al.* 1993; Brockman & van Schaik 2005). A species providing fruit during times of high fruit abundance (HFA), in which a wide diversity of alternative fruit sources may be available, cannot be considered functionally equivalent (from the perspective of a frugivore) to one providing fruit during an extended period in which no other species are fruiting – the second is critical to survival, whereas the first is likely not. For these reasons, species can usefully be classified by common fruiting strategies, or other shared characteristics, that make them similarly important for a given animal species. Using such operational (or ‘functional’) categories as units of comparison among sites provides a straightforward assessment of differences in resource availability from a perspective relevant to frugivore ecology (also see Marshall 2004). A particularly relevant functional distinction is between resources available during times of food abundance vs. those available during times of scarcity, as discussed below.

During times of HFA in tropical forests, both the overall density of fruiting stems and the diversity of fruiting taxa tend to increase relative to times of low fruit abundance (LFA; Lieberman 1982; Kinnaird 1992; White 1994). Although fruiting patterns are in many cases not easily predictable, plant species in tropical forests are generally divisible into those tending to fruit more often during HFA than during LFA, and those fruiting more often during LFA (Lieberman 1982; White 1994). A further distinction, most relevant (from the perspective of consumers) for LFA plants, exists between those with high intra-specific fruiting synchrony, which thus may be capable of sustaining a frugivore population during LFA, and those that fruit less synchronously or asynchronously, which likely are incapable of solely sustaining an entire frugivore population.

### High and low fruit abundance foods

Species producing large fruit crops during periods that overlap with the production of large crops of other species face considerable inter-specific competition to attract seed dispersers (Snow 1965; Smythe 1970; Stiles 1980). An ecological consequence of the diverse array and relatively high density of items available during HFA is that frugivores can show high selectivity for preferred items (Julliot 1996), as has been described, for example, in Sumatran gibbons (*Hylobates muelleri x agilis*; McConkey *et al.* 2003), Mediterranean frugivorous warblers (*Sylvia* spp.; Jordano 1988), and in Costa Rican tanagers and manakins (Levey, Moermond & Denslow 1984). For chimpanzees, which are the subjects of this study, this implies that foods eaten during these periods (high food abundance, or 'HFA' foods) should be those most preferred and thus rich in readily-digestible carbohydrates and low in structural carbohydrates and tannins (Reynolds *et al.* 1998; Remis 2002). As a result these foods likely provide the bulk of energy and nutrients necessary for growth and reproduction (Sherry 2002).

Because by definition fewer dietary options are available to frugivores during LFA than during HFA, selectivity may be reduced. As a result, the species chosen for fruit by frugivores during these periods (LFA foods) are likely to be less preferred and to provide inferior caloric returns compared to those chosen during HFA (Stiles 1980; Jordano 1988; Leighton 1993). Crops available during LFA may be insufficient to promote energetically costly activities such as reproduction (Knott 1998), but nonetheless presumably are critical for somatic maintenance (Terborgh 1986, Wrangham *et al.* 1996).

We define two classes of LFA foods, distinguished by their degrees of inter-individual fruiting synchrony: those with low fruiting synchrony (asynchronous LFA or, aLFA, resources) and those with high synchrony (synchronous LFA, or sLFA, resources). This distinguishes resources that are capable of producing adequate resources to sustain a frugivore population during a given LFA period (sLFA foods, provided they are sufficiently abundant in the habitat; Chapman *et al.* 2005) from those that provide a near constant, but relatively low, supply of food at a given time (aLFA).

### Hypotheses

We test three non-mutually-exclusive hypotheses relating potential bottom-up regulatory factors to the density of chimpanzees at the two KNP sites: the basal areas of the most common fruit-providing species – regardless of functional class – at each site (Hypothesis 1), of HFA foods (Hypothesis 2), and of sLFA foods (Hypothesis 3) are higher at the high-chimpanzee-density site than at the low-chimpanzee-density site.

## Materials and methods

### STUDY SITES

Kibale National Park (795 km<sup>2</sup>), located in southwestern Uganda (Fig. 1), is classified as a moist evergreen or semi-deciduous forest transitional between lowland and montane forest (Struhsaker 1997).

The park comprises a mosaic of vegetation formations (58% mature forest, 15% grassland, 6% woodland, 2% lakes and wetlands and 19% colonizing forest regenerating in areas used in the past for agriculture; Struhsaker 1997; Chapman & Lambert 2000), and its structure and composition vary considerably within and between sites (Chapman *et al.* 1997).

Kanyawara, the low-chimpanzee-density site, is in the northern sector of Kibale (Fig. 1) at an average altitude of ~1500 m and is classified by foresters as *Parinari* forest (Skorupa 1988). Ngogo, the high-chimpanzee-density site, is about 12 km southeast of the low-chimpanzee-density site (Fig. 1), and is at a slightly lower elevation (1350 m). Floristic composition there differs distinctly from that at the low-chimpanzee-density site (Chapman *et al.* 1997), and is more consistent with lowland than montane forest (see Potts 2008). In contrast to the low-chimpanzee-density site, the forest at the high-chimpanzee-density site has never been commercially logged (Struhsaker 1997), but the site has a history of human habitation, perhaps as recently as the 1930s (Wing & Buss 1970; Lwanga 2006). As a result, the site is currently composed of heterogeneous forest types, including large tracts of old growth stands adjacent to colonizing forests, swamp forest and, on hill-tops, anthropogenic grasslands maintained by burning (Lwanga, Butynski & Struhsaker 2000; Lwanga 2003).

### ASSESSING SPATIAL VARIATION IN FOOD AVAILABILITY

To determine the extent of floristic heterogeneity within and between sites, we enumerated and measured woody stems in 104 botanical plots covering an equal area at both sites ( $n = 52$  plots/site; see details below). We determined plot locations using a stratified random placement technique (Greig Smith 1983), such that the number of plots placed in a given habitat subtype was directly proportional to its percentage representation in the habitat as a whole. Habitat subtypes included primary forest, early- to mid-stage regenerating forest, wet (valley bottom) forest, swamp forest and grassland (see Wing & Buss 1970 and Potts 2008 for detailed descriptions).

Plots were constructed at the intersection of pre-existing trails, or were located using a GPS unit if no trail existed in the sampling area. Each plot ran 50 m along a single midline. We used nested strip widths of 50, 25 and 5 m to enumerate and measure stems of different size classes and growth forms within each plot. Within each large plot (50 × 50 m), we identified and measured all trees and free-standing figs (*Ficus* spp.) that had diameters at breast height (d.b.h.) of > 80 cm and all strangler figs with d.b.h. ≥ 10 cm. This methodology was repeated for both the intermediate-sized (25 × 50 m) and small (5 × 50 m) plots, except that only tree and free-standing fig stems of 30 <  $x$  < 80 cm and 10 <  $x$  < 30 cm diameter, respectively, were included in these plots. This sampling regime resulted in 26.0 ha sampled for large stems and strangler figs (13.0 ha/site), 13.0 ha for intermediate-size stems (6.5 ha/site), 2.6 ha sampled for small stems (1.3 ha/site). We restricted all analyses to enumerated stems that were adult size and thus capable of fruiting.

### ASSESSING TEMPORAL VARIATION IN FOOD AVAILABILITY

To assess temporal fluctuations in the availability of fruits important in the diet of chimpanzees, we analysed long-term data obtained from permanent phenology trails established independently at each site. These trails focus on species known to be important in the diets of primates in KNP ( $N_{\text{Ngogo}} = 717$  stems,  $N_{\text{Kanyawara}} = 309$  stems). Each trail was walked once monthly by field assistants and/or researchers (data presented here come from 82 months of monitoring

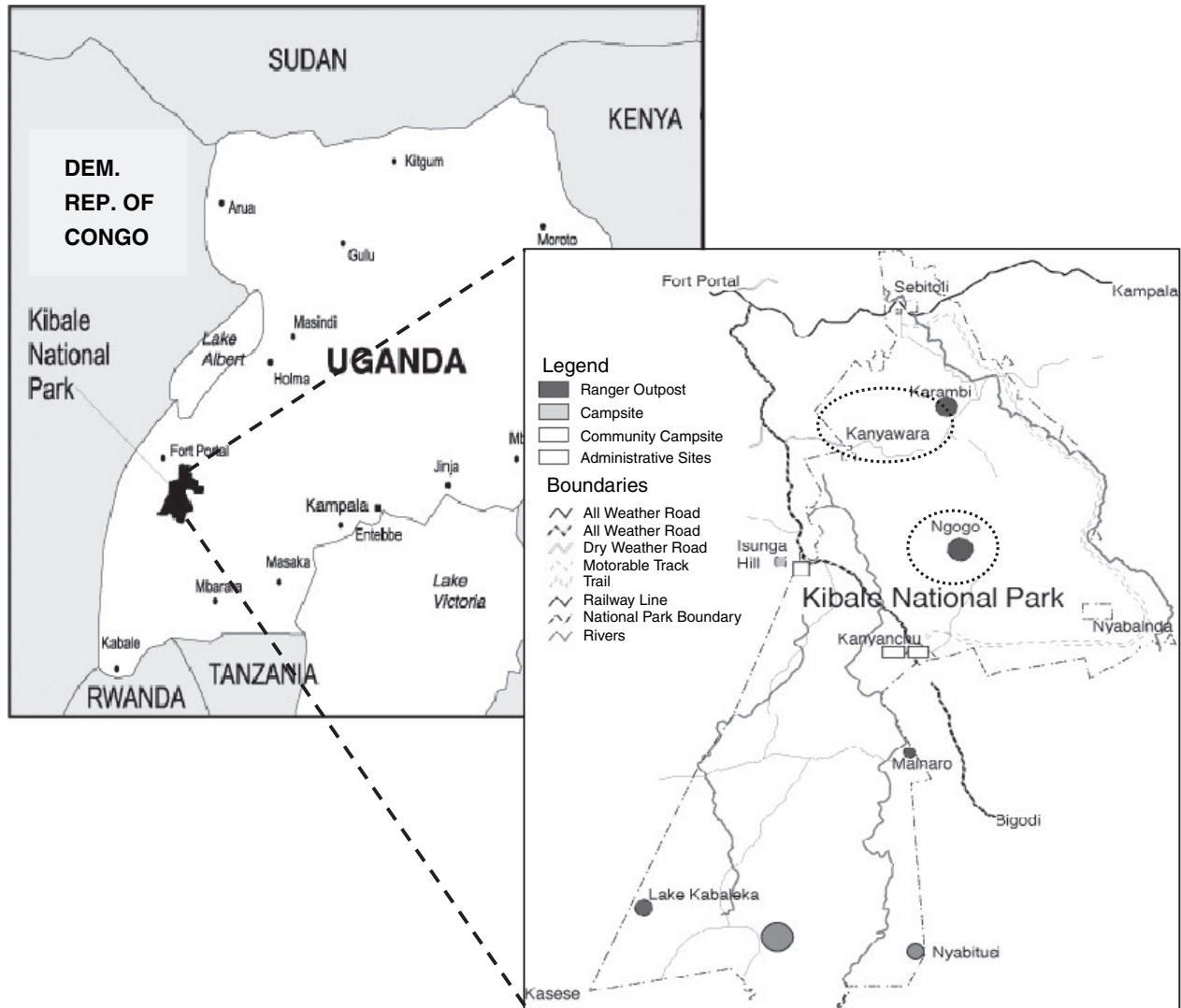


Fig. 1. Map of Uganda highlighting the location of Kibale National Park, in the southwest of the country. Within Kibale, the low-chimpanzee-density site is located in the northwest part of the park, and the high-chimpanzee-density site is 12 km to the southeast (both sites are circled in the inset map of Kibale).

between January 1999 and October 2005). For each tree or hemi-epiphytic fig on the phenology trail, the observers noted the presence or absence of fruits in the canopy (Chapman *et al.* 2005). A d.b.h. measurement was taken once for all free-standing stems on the trail.

In subsequent analyses of food availability, we included only individuals of species sampled that *a priori* were considered to be potential sources of fruit for chimpanzees, based on long-term feeding data from each site (see below). We assessed temporal fluctuations in monthly fruit availability at each site using a 'fruiting basal area/ha' method (as in Cannon *et al.* 2007):

$$FAI = \sum N_{xm} B_x$$

In this equation, FAI is the monthly fruit availability index for month  $m$ ,  $N_{xm}$  is the number of stems of species  $X$  on the phenology trail bearing fruit,  $B_x$  is the basal area per ha of species  $X$  (determined with the botanical plot data), and  $S$  is the total number of food species included in the analysis.

For the 82 months for which data were available from each site, we classified fruit abundance scores in the lowest 25th percentile of

all monthly indices for a given site as 'low' (LFA). Months with scores that fell between the 25th and 75th percentiles were 'intermediate' (IFA). Those with scores above the 75th percentile were 'high' (HFA; also see Marshall 2004).

#### DETERMINING FOOD ITEMS TO INCLUDE IN COMPARATIVE ANALYSES

Chimpanzees continue to seek fruit even when it is scarce (Tutin *et al.* 1991; Wrangham, Conklin-Brittain & Hunt 1998; Potts 2008), thus we examined between-site differences in food availability by focusing on species from which chimpanzees ate fruit. Based on long-term data from the high-chimpanzee-density site (D. P. Watts, J. S. Lwanga & K. B. Potts, unpublished data, Potts 2008), published data from the low-chimpanzee-density site (Basuta 1988; Wrangham *et al.* 1998; Conklin-Brittain, Wrangham & Hunt 1998; Conklin-Brittain, Knott & Wrangham 2006), and our own observations, we generated a list of 18 species at each site that produce fruit that contributed to more than 1% of chimpanzee feeding records (Table 1).

Wrangham *et al.* (1996) noted that seven species (species in bold print in Table 1) accounted for 60–80% of chimpanzee feeding time

**Table 1.** The total measured basal areas and classifications of the top 18 fruit-providing species (those making up > 1% of feeding time) for chimpanzees at the low-chimpanzee-density site and the high-chimpanzee-density site

Kanyawara (low-chimpanzee-density site)	Total BA (cm <sup>2</sup> )	Classification	Ngogo (high-chimpanzee-density site)	Total BA (cm <sup>2</sup> )	Classification
<b><i>Ficus natalensis</i></b> (+)	15 330.2	aLFA	<b><i>Ficus mucuso</i></b>	44 394.6	aLFA
<b><i>Ficus sansibarica</i></b> (–)	10 426.2	aLFA	<b><i>Uvariopsis congensis</i></b> (+)	40 202.3	HFA
<b><i>Uvariopsis congensis</i></b> (–)	13 168.9	HFA	<b><i>Pseudospondias microcarpa</i></b> (–)	15 875.1	HFA
<b><i>Pseudospondias microcarpa</i></b> (+)	19 757.3	HFA	<b><i>Cordia melleni</i></b>	33 366.1	HFA
<b><i>Mimusops bagshawei</i></b> (–)	65 673.2	HFA*	<b><i>Chrysophyllum albidum</i></b>	166 870.7	HFA
<b><i>Ficus exasperata</i></b>	27 453.2	aLFA	<b><i>Pterygota mildbraedii</i></b>	284 277.1	sLFA
<b><i>Ficus saussureana</i></b> (+)	16 353.6	HFA	<b><i>Monodora myristica</i></b> (+)	26 867.7	sLFA
<b><i>Pouteria altissima</i></b> (+)	44 028.2	HFA	<b><i>Ficus saussureana</i></b> (–)	314.2	HFA
<b><i>Ficus capensis</i></b>	1802.0	aLFA	<b><i>Ficus natalensis</i></b> (–)	702.1	aLFA
<b><i>Teclea nobilis</i></b> (–)	3456.3	HFA*	<b><i>Pouteria altissima</i></b> (–)	7088.2	HFA
<b><i>Celtis durandii</i></b> (+)	198 975.8	HFA*	<b><i>Mimusops bagshawei</i></b> (+)	171 428.3	sLFA*
<b><i>Celtis africana</i></b>	72 884.9	sLFA	<b><i>Morus lactea</i></b>	—	sLFA
<b><i>Chaetacme aristata</i></b>	2408.2	sLFA	<b><i>Ficus sansibarica</i></b> (+)	12 612.1	aLFA
<b><i>Ficus cyathistipula</i></b>	96.7	aLFA	<b><i>Treulia africana</i></b>	—	HFA
<b><i>Ficus stipulifera</i></b>	530.9	aLFA	<b><i>Teclea nobilis</i></b> (+)	5663.3	sLFA*
<b><i>Cordia abyssinica</i></b>	3225.3	HFA	<b><i>Celtis durandii</i></b> (–)	159 209.9	sLFA*
<b><i>Tabernaemontana holstii</i></b>	1695.3	aLFA	<b><i>Zhana golungensis</i></b>	8128.7	HFA
<b><i>Monodora myristica</i></b> (–)	3452.4	sLFA	<b><i>Aphania senegalensis</i></b>	18 300.7	HFA

In bold are the top seven species from each site (those making up c. 75% of monthly feeding time). An asterisk following the classification (HFA, sLFA or aLFA) indicates that the classification of the given species differs between the sites. A minus sign (–) or a plus sign (+) following a species name indicates that the species is included among the top 18 fruit items in the diet of chimpanzees at both sites, and that the species is less (–) or more (+) abundant, respectively, at the given site.

and 78–94% of time eating fruit over a 3-year period at the low-chimpanzee-density site. The equivalent top seven species at the high-chimpanzee-density site (Table 1) make up c. 75% of average monthly feeding time (Watts *et al.*, unpublished data) and likely play a similarly strong role in driving foraging behaviour of chimpanzees. We therefore conducted separate between-site analyses using only the basal area of these species at each site.

#### CLASSIFYING IMPORTANT FRUIT ITEMS BY FUNCTIONAL TYPE

To determine spatial heterogeneity in the availability of functional resource classes, we first derived operational criteria for placing each of the food species into the functional categories HFA, aLFA, or sLFA. For each species, we calculated the proportion of fruiting events falling within HFA months and LFA months weighted by the proportion of stems bearing fruit. A fruiting event was defined as a month in which at least one stem belonging to the species in question bore ripe fruit. The only exception was *Pterygota mildbraedii* at the high-chimpanzee-density site. Because chimpanzees almost exclusively use unripe fruits of this species (Potts 2008), we considered a fruiting event for *P. mildbraedii* as a month in which at least a single stem bore unripe fruit.

For a given species exhibiting completely random fruiting, 25% of all fruiting events should fall in HFA months, 25% in LFA months, and 50% in IFA months, based on our definitions of HFA, LFA and IFA months (see above). However, by definition more species should fruit, and at a higher intensity, in HFA months than in LFA months. We therefore defined HFA foods as those for which > 30% of all weighted fruiting events took place during HFA months and not more than 20% occurred during LFA, and LFA foods as those for which > 20% of all weighted fruiting events took place during LFA months and not more than 30% occurred during HFA. In some of the species sampled, the vast majority of fruiting took place during IFA months, thus less than 30% of fruiting occurred during HFA

and less than 20% occurred during LFA. For each of these species, we compared the weighted percentage of fruiting events confined to HFA (and LFA) to the mean percentage of fruiting events during HFA (and LFA) for all species. If the species in question had a higher than average percentage of fruiting events confined to HFA and a lower than average percentage confined to LFA relative to all sampled species, then we classified the species as HFA (and vice versa for LFA species).

We used data on the synchrony of fruiting events measured with Green's index of dispersion (Green 1966; Ludwig & Reynolds 1988) to subdivide LFA species into synchronous and asynchronous fruit producers. This index detects the degree to which the monthly per cent of stems bearing fruit deviates from a random distribution, and ranges from  $-1/(N-1)$  (where  $N$  is the total number of individuals in the sample) to 1, with larger GI values indicating higher contagion. We also used the maximum percentage of stems bearing fruit in any month as an index of fruiting intensity for each LFA species. Those species with Green's indices above the mean for all analysed species and with a monthly maximum of at least 50% of all stems bearing fruit were classified as 'synchronous'; those with GI values below the community-wide mean and with a monthly maximum of less than 50% of all stems bearing fruit were classified as 'asynchronous'.

We used published data from the low-chimpanzee-density site (Balcomb & Chapman 2003; Chapman *et al.* 2005) to categorize four remaining species from this site for which we lacked sufficient phenology data. This resulted in nine and eight HFA foods; three and seven aLFA foods; and six and three sLFA foods at the high-chimpanzee-density site and the low-chimpanzee-density site respectively (Table 1).

#### STATISTICAL ANALYSES

We tested each of the hypotheses using the basal area of stems in each botanical plot as the unit of analysis. We conducted non-parametric

Mann–Whitney *U*-tests (and report *Z*-scores here) and used Monte–Carlo simulations with 10 000 iterations (Manly 1997) to reduce the effect of tied observations among sampling units (see Potts 2008 for details). Because the hypotheses together constitute a more general hypothesis (namely, that the resource base at the high-chimpanzee-density site is of higher quality than that at the low-chimpanzee-density site), it was necessary to correct the significance level of the associated *P*-values to account for multiple testing. To do so, we applied the false discovery rate (FDR) test developed by Benjamini & Hochberg (1995) and expanded upon by Verhoeven, Simonsen & McIntyre (2005). The FDR test uses the number of hypotheses tested under a more ‘global’ hypothesis to determine the *P*-value at which the proportion of type I errors (erroneous rejection of  $H_0$ ) among significant tests does not exceed the 5% value expected by  $\alpha = 0.05$  (Benjamini & Hochberg 1995). This resulted in a significant level of  $P < 0.024$  for all tests.

## Results

### HYPOTHESIS 1

The overall basal area of the top seven food species ( $N_1 = N_2 = 52$ ,  $Z = -4.335$ ,  $P < 0.001$ ) was significantly higher at the high-chimpanzee-density site, as were the basal areas of intermediate-sized ( $30 < x < 80$  cm d.b.h.;  $Z = -5.272$ ,  $P < 0.001$ ) and small ( $Z = -4.818$ ,  $P < 0.001$ ) stems considered separately. The basal area of large trees ( $> 80$  cm d.b.h.) and strangler figs ( $\geq 10$  cm d.b.h.) was marginally higher at the high-chimpanzee-density site ( $Z = -2.212$ ,  $P = 0.026$ ; Table 2). Hypothesis 1 was therefore supported.

### HYPOTHESIS 2

The basal area of HFA species did not significantly differ between the high- and low-chimpanzee-density sites ( $Z = -1.483$ ,  $P = 0.138$ ; Table 2). Hypothesis 2 was therefore not supported.

### HYPOTHESIS 3

The overall basal area of LFA synchronous (sLFA) resources was significantly higher at the high-chimpanzee-density site than at the low-chimpanzee-density sites ( $Z = -6.126$ ,  $P < 0.001$ ), as were the basal areas of large ( $Z = -4.162$ ,  $P < 0.001$ ), intermediate-sized ( $Z = -4.994$ ,  $P < 0.001$ ) and small ( $Z = -2.991$ ,  $P = 0.003$ ) sLFA stems considered separately (Table 2). Hypothesis 3 was therefore supported.

## Discussion

By establishing a resource classification scheme that accounted for the simultaneous influence of both spatial and temporal components of bottom-up regulatory factors, we were able to isolate the variables most likely limiting chimpanzee communities in KNP. Contrary to our predictions, only the top seven most important fruit-providing species and sLFA species significantly differed between the two

home ranges. Although other extrinsic variables not dealt with here appear to play relatively minor roles in limiting chimpanzees in KNP (see above), it is nonetheless possible that other factors are importantly influencing the differences in density between the Ngogo and Kanyawara sites. Similar analyses from other KNP sites (thus increasing our sample size) would therefore be greatly beneficial to further validate these results.

### HYPOTHESIS 1

The basal area of the top seven fruit-providing species for chimpanzees was higher at Ngogo (the high-chimpanzee-density site) than at Kanyawara (the low-chimpanzee-density site). Chimpanzees typically devote the majority of their feeding time to fruit of a few select species (Wrangham *et al.* 1996; Newton-Fisher 1999; Potts 2008). Because of the preponderance of relatively few items in their diet, these few important food species should be more abundant in the home ranges of chimpanzees living at high densities than in those of chimpanzees living at low densities. The higher basal area of these important food species at the high-chimpanzee-density site implies that chimpanzees here may encounter important food items at a high frequency and can obtain most of their dietary needs with lower travel costs than can chimpanzees at the low-chimpanzee-density site. Quantitative data on foraging efficiency in the two KNP chimpanzee communities (Potts 2008) support this claim, in that chimpanzees at the high-chimpanzee-density site had consistently higher foraging efficiency measures that varied less over time than those from the low-chimpanzee-density site.

### HYPOTHESIS 2

Females of large-bodied and long-lived frugivore species, who face high energy demands associated with gestation and lactation, may obtain most of the excess calories required for reproduction during relatively infrequent ‘pulses’ of high food abundance and may then store the surpluses for future reproduction (Lee 1987; Knott 1998). Similar mechanisms exist in many non-primate, non-frugivorous mammals [e.g. grey seals (*Halichoerus grypus*); Sparling, Speakman & Fedak 2006] that can be considered capital breeders (Stearns 1992). Significant relationships have been found between primate abundance or biomass and the density of preferred resources (e.g. colobines, Oates *et al.* 1990; Wasserman & Chapman 2003; Chapman *et al.* 2002), suggesting that population density in these species may be regulated by the availability of resources during times of high overall food abundance. Spatial variation in the abundance of HFA species may contribute to differences among groups in per capita birth rates and, by extension, in group size and density (assuming that mortality and/or emigration rates are not unusually high). However, this does not appear to be the case in this population of chimpanzees.

**Table 2.** Summary of Mann–Whitney *U*-tests of basal area differences in various resource class abundances between the high-chimpanzee-density site (high chimpanzee density) and the low-chimpanzee-density site (low chimpanzee density)

Food class	Category	Ngogo (high-chimpanzee-density site)			Kanyawara (low-chimpanzee-density site)			Z-score (MWU test)	<i>P</i> -value	Direction
		Mean BA/ha (cm <sup>2</sup> ha <sup>-1</sup> )	median BA/ha (cm <sup>2</sup> ha <sup>-1</sup> )	SE	Mean BA/ha (cm <sup>2</sup> ha <sup>-1</sup> )	Median BA/ha (cm <sup>2</sup> ha <sup>-1</sup> )	SE			
Top 18 food species	Overall	157 875.2	132 622.4	16 511.7	83 752.5	74 038.4	8409.3	2.46	0.015	N
	Large trees/strangler figs	39 919.0	22 698.0	8461.0	14 807.7	0.0	3989.7	2.01	0.045	—(N)
	Intermediate-sized stems	57 128.6	43 568.5	6156.8	43 181.9	32 114.3	5037.4	1.68	0.094	—
	Small stems	60 827.6	52 400.2	6422.4	25 763.0	20 998.5	4140.0	4.37	< 0.001	N
Top seven food species	Overall	104 763.9	88 911.3	13 462.7	25 567.5	1836.2	6390.6	4.34	< 0.001	N
	Large trees/strangler figs	26 213.3	0.0	5769.5	9039.6	0.0	2561.0	2.21	0.026	—(N)
	Intermediate-sized stems	32 620.2	20 434.2	4655.9	5476.5	0.0	1905.9	5.27	< 0.001	N
	Small stems	45 930.5	27 354.3	6733.2	11 051.3	0.0	3568.9	4.82	< 0.001	N
HFA	Overall	72 055.3	65 737.5	9489.5	62 455.8	58 738.3	7412.0	1.48	0.138	—
	Large trees/strangler figs	5677.9	0.0	2072.4	10 214.1	0.0	3913.7	0.42	0.627	—
	Intermediate-sized stems	20 447.0	8073.9	3751.2	33 014.3	21 384.9	4305.7	2.66	0.008	K
	Small stems	45 930.5	27 354.3	6733.2	19 227.4	5291.2	4031.5	2.88	0.004	N
sLFA	Overall	81 380.7	73 868.2	9644.8	14 498.7	7228.3	2433.6	6.13	< 0.0001	N
	Large trees/strangler figs	29 802.0	0.0	7894.4	1691.0	0.0	959.4	4.16	< 0.0001	N
	Intermediate-sized stems	36 681.6	33 560.2	4367.1	7714.0	0.0	1553.4	4.99	< 0.0001	N
	Small stems	14 897.1	6372.4	2745.9	5093.8	0.0	1283.5	2.99	0.003	N
aLFA	Overall	4439.1	0.0	1924.2	6798.0	0.0	1811.8	2.25	0.024	K
	Large trees/strangler figs	4439.1	0.0	1924.2	2902.5	0.0	964.3	0.58	0.561	—
	Intermediate-sized stems	0.0	0.0	0.0	2453.6	0.0	1065.6	2.51	0.03	—(K)
	Small stems	0.0	0.0	0.0	1441.8	0.0	574.1	2.93	0.005	K

For significant differences, the site with the higher basal area is indicated. A '—' followed by a site name in parentheses indicates a trend towards a higher basal area at that site ( $0.24 < P < 0.05$ ).

### HYPOTHESIS 3

In theory, long-lived, slow-reproducing species, including most primates (and particularly frugivorous primates; Charnov & Berrigan 1993), cannot directly track short-term fluctuations in resources by modulating reproductive efforts. This has led many to conclude that the population dynamics of frugivores may be primarily regulated by the availability and quality of LFA resources (Cant 1980; Terborgh 1983; Tutin *et al.* 1997). Our results are consistent with this conclusion in that only sLFA species (among the classes we considered potentially limiting) were significantly more abundant at the high-chimpanzee-density site. Habitats rich in plant species that provide synchronous fruit crops during times of habitat-wide scarcity may therefore be higher quality for chimpanzees and other large-bodied tropical frugivores than habitats rich in HFA or aLFA foods (although the designation of plant species as sLFA,

aLFA, and HFA will differ depending on the animal consumer in question).

### *How does spatiotemporal variation in food availability limit tropical frugivores?*

Resource classification schemes similar to that developed here can likely improve our understanding of the processes regulating density in other large-bodied tropical frugivores. For example, Chiarello (1999) attributed differences in frugivorous mammal density among small, intermediate and large forest fragments in Brazil to bottom-up factors (food availability), while differences between fragments of the same size class were attributed to top-down effects (hunting pressure). Classification of the resource base at these sites according to both spatial and temporal availability may help to resolve whether hunting pressure is acting alone in limiting the density of frugivores in otherwise

high-quality habitat, or if patterns of resource availability may play a synergistic role.

Classification of the resource base according to functional traits of fruit-providing species may shed light on bottom-up processes regulating non-mammalian tropical frugivores, as well. For example, Levey (1988) found that the breeding season of frugivorous birds at La Selva, Costa Rica corresponds to the period of lowest fruit abundance, which is also the period of lowest temporal fluctuation in food availability. In essence, the species producing fruit during the low-food-abundance period in Levey's (1988) study are therefore analogous to our sLFA designation, in that they provide a component of temporal reliability to the resource base even during LFA. Explicit recognition of the functional role played by different fruit-providing species can thus aid in identifying bottom-up effects most directly influencing frugivores.

## Conclusion

Despite considerable attention given to the question of what factors limit the population density of large-bodied vertebrates, few operational conclusions have been drawn. Primates, owing to considerable intra-specific ecological variation among groups and populations in close proximity, are an ideal taxon in which to isolate these limiting factors. In general, it is thought that a complex interplay of per capita resource abundance, predation pressure, and disease impact constrain primate population density. However, more specific information regarding the relative importance of each factor, which is necessary for testing basic hypotheses about determinants of population density in primates, is relatively rare. Explicit recognition of the simultaneous role of spatial and temporal resource availability in influencing population dynamics can aid in improving the precision of such information (Marshall 2004). In this study, we took advantage of the notable ecological heterogeneity and chimpanzee population density differences between two sites in Kibale National Park to develop and test hypotheses about the role of resources in influencing chimpanzee density. Using this framework, as well as that of similar studies (Marshall 2004; Marshall & Leighton 2006), generalized hypotheses relating population density of large-bodied vertebrates to operationally-defined resource classes can be generated and tested, and our knowledge of the fundamental bases of vertebrate population ecology can be further enhanced.

## Acknowledgements

We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology for permission to work in Uganda, and Drs John Kasenene and Gilbert Isabirye-Basuta for access to the field sites in Kibale National Park. KBP thanks Magambo Norris for assistance in vegetation sampling and the many field assistants at Ngogo and Kanyawara that have assisted in phenology sampling. Many thanks to David Watts, Eric Sargis, and Tara Harris for comments on previous drafts of this paper. KBP was supported by the LSB Leakey Foundation, the Wenner-Gren Foundation, and the American Society of Primatologists.

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Received 18 November 2008; accepted 18 May 2009  
Handling Editor: Chris Thomas