

Intratree vertical variation of fruit density and the nature of contest competition in frugivores

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Abstract Recently, we demonstrated that the highest densities of fruit pulp are located in the uppermost zones of tree crowns. Since heterogeneous distributions of depletable food is theorized to foster contest competition, we tested three hypotheses involving rank differences among species of arboreal frugivores: (1) In the absence of competitors, species tend to feed in higher strata of tree crowns; (2) interspecific contest competition occurs through monopolization and usurpation of feeding sites in these higher strata; and (3) subordinate species decrease their feeding height and ingestion rate when

dominants enter the food patch. To test these hypotheses, we observed chimpanzees (*Pan troglodytes*), red-tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), and gray-cheeked mangabeys (*Lophocebus albigena*) in Kibale National Park, Uganda. We found that: (1) all four primates fed preferentially in upper tree crowns when alone, (2) dominant species monopolized and aggressively usurped the upper crown when co-feeding with subordinates and the latter retreated below the middle of tree crowns, (3) in the presence of dominant species, subordinate species showed lower standardized feeding height and modified their food intake rates, while dominants were not affected by the subordinate species, (4) subordinates moved down at the arrival of and up at the departure of dominants, and (5) the presence of folivores in the tree did not affect the feeding height of a frugivore, even through folivores were socially dominant. Contrary to expectations, we found that red-tailed monkeys decreased their movements between successive fruits that they ate in the presence of blue monkeys compared to when they were feeding alone, perhaps to avoid disturbing dominants and attracting aggression or because they ingested more semi-ripe and green unripe fruits, i.e., more food of lower quality.

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Introduction

The quantity, distribution, and quality of food are theorized to affect the social relationships and organization of animals (van Schaik 1989; Isbell and Young 2002; Koenig 2002)

and the coexistence of species (Houle et al. 2006). This paper focuses on how food availability and distribution combine with social dominance (particularly through contest competition) do affect access to food by comparing the foraging behaviors of four species of frugivorous primate when feeding alone versus co-feeding with a competitor.

Social dominance has mostly been studied intraspecifically and has been shown to allow individuals to secure food resources in vertebrates, including primates (Whitten 1983; Janson 1985; Sterck and Steenbeek 1997; Wittig and Boesch 2003; Vogel 2005), elephants (Archie et al. 2006), birds (Woodrey 1991), and fish (Marsh and Ribbink 1985). This foraging advantage could explain the relationship between dominance and reproductive success often found in many species of mammals such as primates (Whitten 1983; Pusey et al. 1997; Altmann 1998; van Noordwijk and van Schaik 1999; Charpentier et al. 2005; Boesch et al. 2006), hyenas (Holekamp et al. 1996) and reindeer (Hirota 1994), although this is not always the case (Takahata et al. 1999; Marvan et al. 2006). For arboreal species of frugivores, it is possible that securing the best fruit production zones in the canopy results in increased foraging gains and thus increased fitness.

Little is known about how contest competition in frugivores varies within tree crowns. Observers have noted that food sometimes occurs in localized patches that dominants may monopolize (Pollock 1977; Whitten 1983; Goodall 1986; Wittig and Boesch 2003). However, researchers have not clearly identified what determines the location of these sites. As a result, it is currently unclear whether there are consistent advantages for feeding in specific areas of tree crowns and, if so, how such advantages to being dominant emerge. Dominant species and individuals within foraging groups may profit by excluding competitors from the best feeding sites (portions of tree-crowns) or from the whole food patch (the tree itself).

We have previously shown in Kibale National Park, Uganda that the highest densities of edible fruit pulp were predictably located in the uppermost zones of tree crowns for 16 out of 17 tree species (Houle et al. 2007). We argued that this distribution is predictable from forest structure since lower levels of tree crowns receive less sunlight and represent therefore less favorable sites for plant growth. Many botanical studies support the relation between light availability and nutrient allocation within tree crowns through increases of photosynthetic rates, photosynthate production, dry matter allocation, chloroplast size, and mean stomatal densities (Brady 1987; Lynch and Gonzalez 1993; Mehrotra et al. 1998; Taiz and Zeiger 1998; Proietti et al. 2000; Sellin and Kupper 2005). Because heterogeneous distributions of food is theorized to foster contest

competition and given that the vertical stratification of the fruit within tree crowns is a predictable phenomenon (Houle et al. 2007), we predict that higher ranking species or individuals of a foraging group will monopolize and aggressively usurp the upper zones of the canopy and thus will feed better (e.g., higher nutrient ingestion rates) and at a lower cost (e.g., less movement per fruit eaten) than lower ranking competitors. Specifically, we test the following hypotheses involving rank differences between species of arboreal frugivorous primates: (1) In the absence of competitors, species will feed in higher strata of tree crowns, (2) contest competition will occur through monopolization (physical presence) and usurpation (aggression) of feeding sites in these higher strata, and (3) subordinate but not dominant species will modify their feeding height and ingestion rates and will also move more per fruit eaten relative to dominant species in the same food patch (a tree crown).

Materials and methods

We observed four frugivorous primates (chimpanzees, *Pan troglodytes*; gray-cheeked mangabeys, *Lophocebus albigena*; blue monkeys, *Cercopithecus mitis*; and red-tailed monkeys, *Cercopithecus ascanius*) in Kibale National Park, Uganda (see Struhsaker 1997 for habitat description). We determined interspecific dominance ranks based on the outcome of agonistic interactions (Table 1). Aggressions were considered at four levels of increasing intensity: (1) slow displacement, (2) chasing quickly with no vocalization, (3) chasing quickly with vocalization, and (4) physical contact (pushing, kicking, biting, jumping over, and pulling the hair). Submissions included three levels of intensity: (1) leaves the aggressor slowly and calmly, (2) flees quickly away from the aggressor without vocalization, and (3) flees and screams.

We used two observation methods. First, from dawn to dusk, we watched specific trees in which large crops of fruit were ripening (tree sampling method) and collected data on feeding animals. This provided 262 h of primate data ($n=562$ feeding sessions, i.e., the time between the first individual's entry and the last one's departure, per tree species) over 1,381 h of tree watching. Second, we followed focal groups of the four primates from dawn to dusk (5,908 hours of focal observation, 2099 feeding sessions). We quantified foraging behaviors (Table 2) during 1-min focal sampling periods, and these feeding bouts were averaged per feeding sessions (Fig. 2, Tables 3 and 4; red-tailed monkeys, 1,260 h of focal observation, 5,119 1-min focal follows, 738 feeding sessions, in four social groups; blue monkeys, 1,219 h, 3,657 1-min focal follows, 443 feeding sessions, in three social groups; chimpanzees,

Table 1 Social dominance matrix of four species of primate frugivores in Kibale National Park, Uganda (Oct 1999–Nov 2000)

	Recipient (primate frugivores)				Total
	CH	MG	BL	RT	
Actor					
Chimpanzee (CH)		4/0	5/0	7/0	16/0
Mangabey (MG)	0/3		57/12	70/0	127/15
Blue monkey (BL)	0/8	12/56		365/18	377/82
Red-tailed monkey (RT)	0/9	0/70	20/366		20/445
Total	0/20	16/126	82/378	442/18	540/542

Aggression by the actor: left of slash; submission by the actor: right of slash. In the table, x/y represents the behavior of the actor (aggression/submission) versus a given recipient. For instance, blue monkeys directed 365 aggressions and 18 submissions towards red-tailed monkeys, while the latter directed 20 aggressions and 366 submissions towards the former. Blue and red-tailed monkey data were derived from 2,479 focal observation hours, while all other data came from ad libitum sampling method (262 h of primate observation data over 1381 h of tree watching). No interspecific aggressions were observed between June 2004 and June 2005 while we focal followed the chimpanzee.

3,341 h, 5,724 1-min focal follows, 799 feeding sessions, in one community; mangabeys, 88 h of focal observation, 1,196 1-min focal follows, 119 feeding sessions, in one social group). Although the sample size for mangabeys was small, it was sufficiently large to determine a clear interspecific dominance hierarchy and provided enough values for statistical testing in some tree species. From October 1999 to November 2000, blue and red-tailed monkeys were observed alternately every 4 days, while from June 2004 to June 2005, the chimpanzee was followed almost every day; in both cases, observations were collected from 6:00 A.M. to 7:30 P.M.. Focal animals were chosen randomly, alternating between individuals of different age–sex classes; should the animal disappear behind vegetation or otherwise, the observation was canceled and another one taken; should a conflict arise among any visible individuals while observing foraging behaviors, the latter observation was canceled and we focused our attention to the conflict, given the scarcity of aggressive interactions.

Groups of primates were monitored with local experienced field assistants. We saw no evidence of observer effects on monkey or chimpanzee behavior, including during the presence of a human observer in the canopy (no physical contact with the animals). All monkeys were classified by age–sex classes (AM, AF, SAM, SAF, JUV, and INF), while chimpanzees were individually identified. Group size for red-tailed monkey social groups varied from 31, 42, 54 to 69 individuals, in which 2, 1, 3, and 5, respectively, were adult males, and 13, 20, 25, and 28 were adult females. Group size for blue monkey social groups

varied from 16, 18 to 25 individuals, in which only one adult male led each group, and 7, 6, and 13, respectively, were adult females. The only followed gray-cheeked mangabey social group contained 15 individuals, from which three adult males and six adult females could be recognized. Finally, the only community of chimpanzee in Kanyawara was composed of 47 individuals, including ten adult males and 13 adult females. From June 2004 to June 2005, eight chimpanzee females gave birth and one female was carrying a newborn at the onset of our observations.

We standardized the feeding height by dividing the height of the focal animal above the crown base by the crown height (values ranged from 0 to 1). Because the feeding height is a critical measure in the present study and because data collection involved four different observers (AH and three field assistants), the trees were climbed to the uppermost zones of the crowns and their height measured to the nearest meter. Crown height was defined as the vertical length between the top of the tree crown and its base thus excluded the trunk. Flag tapes were attached to strategic branches to increase accuracy and inter-observer reliability in the measure of the animal's feeding height. Feeding benefits were defined in two ways: (1) feeding rate (number of fruit put in the mouth per minute) and (2) pulp ingestion rate (gram of dry pulp ingested per minute). Feeding costs in a tree crown were defined as the distance (to the nearest meter) moved between two fruit ingested sequentially.

A feeding record was measured during a 1-min focal follow or during a 5-min scan and was used to obtain the average feeding record. Behavior data were analyzed per tree species to control for variation in fruit size and pulp availability (cf. handling and processing times). Tree species are listed in the figures and tables. Species were chosen because they were important food sources and because we could collect fruit and measure fruit density *before* primates or other frugivores exploited them. Because pulp biomass per fruit varies vertically across ripening categories within tree crowns (Houle et al. 2007), semi-ripe and ripe fruit ingestion rates were paired to the animal's standardized feeding height when estimating pulp ingestion rates.

To estimate fruit density and pulp mass per crown layer, we collected fruit from the canopy of 56 trees from 12 species and classified them by ripeness category (unripe, 100% of skin was green; semi-ripe, between 25% and 75% of skin showed the ripe color; ripe, 95–100% of skin showed the ripe color; fruit showing intermediate color patterns were discarded). We measured their mass within 3 hours of collection and fruits were kept in a refrigerator while being processed to minimize evaporation.

Most sampled trees ($n=46$ trees from nine species) were divided into two vertical layers of equal height (Fig. 1a; we did not compare the outermost versus the innermost zones of the crown). The upper half of the crown is referred to as

Table 2 Standardized feeding height (height at which a focal animal feeds above the base of a tree crown divided by the height of that tree crown) as a function of competitive feeding status among four species of primate frugivores living in Kibale forest

Standardized feeding height		Social dominance = CH > MG > BL > RT																
Red-tailed monkeys (RT)—females 2.9 kg, males 3.7 kg																		
Tree species	RT feeding alone	RT co-feeding with BL	RT co-feeding with MG	RT when aggression from BL	RT when aggression from BL	RT after aggression from BL	RT when aggression from MG	RT after aggression from MG	RT after aggression from tree	RT after BL left								
	x	SD	n	x	SD	n	x	SD	n	x	SD	n	x	SD	n			
<i>C. africana</i>	0.67	0.34	60	0.36	0.20	5	0.22	0.00	2	Left tree	x	1	x	SD	n			
<i>C. durandii</i>	0.52	0.34	88	0.27	0.25	14	0.25	0.50	4	Left tree	x	10	Left tree	2	0.61	0.48	4	
<i>D. abyssinica</i>	0.53	0.39	563	0.37	0.28	174	0.58	0.31	12	Left tree	x	32	Left tree	6	0.72	0.31	35	
<i>F. angolensis</i>	0.57	0.34	86	0.45	0.35	37	0.17	–	1	0.58	0.00	2	0.48	0.26	6	0.66	0.32	203
<i>F. exasperata</i>	0.66	0.31	1554	0.58	0.33	294	0.50	0.37	70	0.41	0.27	42	0.79	0.21	6	0.66	0.32	203
<i>F. natalensis</i>	0.71	0.21	52	0.68	0.27	3	0.45	0.13	8	0.40	0.28	2	Left tree	1	0.67	0.22	5	
<i>F. samsibarica</i>	0.63	0.24	96	0.47	0.19	32	0.60	0.28	2	Left tree	x	1	Left tree	1	0.67	0.22	5	
<i>F. saussureana</i>	0.56	0.28	10															
<i>F. sur</i>				0.57	0.00	6				Left tree	x	1	Left tree	1				
<i>F. africana</i>	0.54	0.31	44							Left tree	x	1	Left tree	1				
<i>L. johnsonii</i>	0.84	0.22	55							Left tree	x	1	Left tree	1				
<i>Macaranga</i> spp.	0.85	0.23	17							Left tree	x	4	Left tree	3				
<i>M. bagshawei</i>	0.49	0.25	24							Left tree	x	4	Left tree	3				
<i>M. myristica</i>	0.29	0.20	6	0.38	0.17	5				Left tree	x	3	Left tree	1				
<i>S. mitis</i>	0.57	0.24	696	0.48	0.29	144	0.29	0.00	4	0.51	0.21	8	Left tree	1	0.62	0.33	58	
<i>U. congensis</i>	0.62	0.32	1085	0.48	0.27	35	0.88	0.00	2	0.25	0.00	2	Left tree	1	0.45	0.28	19	
Blue monkeys (BL)—females 4.3 kg, males 7.9 kg																		
Tree species	BL feeding alone	BL co-feeding with RT	BL co-feeding with MG	BL when aggression from RT	BL when aggression from RT	BL after aggression from RT	BL when aggression from MG	BL after aggression from MG	BL when aggression from tree	BL after aggression from tree								
	x	SD	n	x	SD	n	x	SD	n	x	SD	n	x	SD	n			
<i>C. africana</i>	0.62	0.35	26	0.87	0.03	4												
<i>C. durandii</i>	0.51	0.37	140	0.58	0.30	31	0.29	0.26	17	Aggressions from red-tailed to blue monkeys were rare, and when they did occur, often involved a large adult male red-tailed against a small juvenile or subadult blue.	Left tree	1	0.32	0.34	6			
<i>C. millenii</i>	0.63	0.29	16															
<i>D. abyssinica</i>	0.72	0.33	430	0.75	0.31	156	0.50	0.36	18									
<i>F. angolensis</i>	0.94	0.17	16	0.77	0.28	42	0.58	–	1									
<i>F. exasperata</i>	0.71	0.27	1249	0.73	0.30	330	0.49	0.37	61	0.75	0.35	2	0.67	0.22	6	0.72	0.25	37
<i>F. natalensis</i>				1.00	0.00	3	0.67	0.27	4									

<i>F. samsibarica</i>	0.54	0.25	194	0.57	0.19	35	0.39	0.18	25												0.53	0.10	9		
<i>F. sur</i>	0.81	0.00	4	0.78	0.09	7																			
<i>F. africana</i>	0.56	0.27	65	0.91	0.14	34																			
<i>M. myristica</i>				0.68	0.19	7	0.50	0.00	3																
<i>S. mitis</i>	0.52	0.34	252	0.62	0.30	175	0.89	0.15	2																
<i>U. congensis</i>	0.56	0.33	406	0.60	0.32	39	0.14	–	1																
Gray-cheeked mangabeys (MG)—female 6.0 kg, male 8.3 kg																									
Tree species	MG feeding alone	x	SD	n	MG co-feeding with RT	x	SD	n	MG co-feeding with BL	x	SD	n	MG when aggression from RT	MG after aggression from RT	MG when aggression from BL	x	SD	n	MG after aggression from BL	x	SD	n	RT after MG left tree		
<i>C. africana</i>					0.78	0.00	2																		
<i>C. durandii</i>	0.50	0.25	8	1.00	–	1	0.57	0.28	15																
<i>D. abyssinica</i>	0.74	0.34	168	1.00	0.00	18	0.77	0.32	11														1.00	0.00	2
<i>F. angolensis</i>	1.00	0.00	3	1.00	0.00	8	1.00	0.00	8																
<i>F. exasperata</i>	0.75	0.25	339	0.73	0.32	39	0.75	0.30	68																
<i>F. natalensis</i>	0.75	0.25	96	0.76	0.24	12	0.73	0.28	5																
<i>F. samsibarica</i>	0.86	0.15	31				0.66	0.11	21																
<i>M. myristica</i>				0.70	0.17	5	0.81	0.00	3																
<i>S. mitis</i>	0.71	0.32	240	0.95	0.14	7	0.92	0.03	9																
<i>U. congensis</i>	0.55	0.34	87																						
Red-tailed monkeys have not been observed to aggress gray-cheeked mangabeys.																									
Chimpanzees (CH)—female 33.7 kg, male 42.7 kg																									
Tree species	CH feeding alone	x	SD	n	CH co-feeding with MG	x	SD	n	MG co-feeding with CH	x	SD	n	CH co-feeding with RT and BL	CH when aggression from MG	CH after aggression from MG	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree	MG after CH left tree
<i>P. altissima</i>					0.84	0.17	78																		
<i>C. africana</i>	0.75	0.23	332																						
<i>C. durandii</i>	0.75	0.21	92																						
<i>C. abyssinica</i>	0.78	0.21	254																						
<i>L. johnsonii</i>	0.65	0.25	48																						
<i>M. bagshawei</i>	0.78	0.20	2140																						
<i>P. microcarpa</i>	0.75	0.21	148																						
<i>U. congensis</i>	0.79	0.19	40																						
<i>F. exasperata</i>	0.74	0.20	420																						
<i>F. natalensis</i>	0.73	0.19	1185	0.55	0.33	41	0.60	0.23	25																
Blue and red-tailed monkeys were never seen co-feeding with chimpanzees.																									
Gray-cheeked mangabeys have not been observed to aggress chimpanzees.																									

Table 2 (continued)

Standardized feeding height	
Social dominance=CH>MG>BL>RT	
<i>F. samsbarica</i>	0.76 0.20 406
<i>F. sur</i>	0.62 0.17 380
Other spp.	0.64 0.28 201

Monkey data were collected in 1999–2000 and chimpanzee data in 2004–2005. We compare the feeding height of the animal before versus after it was aggressed (middle columns), and most aggressions were sampled ad libitum. It was not possible to get agonistic data for each tree species; in such cases, we provide when available the frequencies the aggressed left the fruit tree altogether (rather than moving down the tree crown) after the aggression. We also compared the feeding height of frugivores when the very last member of a competing species left the fruit tree (last column to the right). Body weight from Fleagle 1999
 x average standardized feeding height, SD standard deviation, n number of feeding records, i.e., feeding height measured at the end of a 1-min focal follow or during a 5-min scan

“upper crown” and the lower half as “lower crown.” After we gained more experience at climbing the trees, we evaluated the vertical stratification of the fruit in some additional trees, most of them emergent ($n=10$ trees from six species; range, 8–50 m). Because tree crowns of these emergent trees were high (range, 6–24 m), we decided to divide these crowns into three vertical layers of equal height, with the objective to evaluate the relative quality of the middle crown feeding site (Fig. 1b). These emergent trees were chosen on the basis that they produced a particularly large fruit crop and that at least one primate species fed in the tree. All fruit counts were obtained throughout the fruiting cycle.

Fruit densities were calculated for each canopy layer as the product of (1) the number of fruit of a given ripeness stage in a predetermined volume (on average 1/40th of the layer) and (2) the number of predetermined volumes of this size that filled the canopy layer, as determined visually while in the tree and based on the mean of four counts. The predetermined volume was defined so as to contain between 500 and 1,000 fruits. Above that range, counting became difficult due to eye fatigue and confusion as to which individual fruit had been counted or not. Below that range, we found an increased probability that the predetermined volume was not representative of the canopy layer. Repeated counts in zones containing between 500 and 1,000 fruits yielded the smallest margin of error, i.e., 4.8% ($n=10$ trees; Houle et al. 2007).

We used paired t tests on log-transformed data to compare dry pulp density variation in two-layered trees and ANOVA for repeated measures also on log-transformed data in three-layered trees, with the tree being the unit that repeats. In both cases, sample sizes represent the number of individual trees. We used MatMan® to quantify the strength of dominance hierarchies among the species (Table 1). To minimize pseudoreplication of foraging data, we averaged feeding records of focal species per feeding session per tree species, and we applied statistics to these sessions (average feeding sessions per tree species, 158; median, 63; range, 10–692). However, similar results were obtained with data analyzed per individual tree. We executed statistics per tree species to control for variation in handling and processing times. We applied one-sample t tests to determine if species fed higher than an expected standardized feeding height of 0.5. We used multiple non-parametric Mann–Whitney tests to contrast interspecific foraging data (Table 3) because many samples were not normally distributed and variances differed between samples, even after transformations. We applied a G test for independent samples to measure the interaction between interspecific co-feeding status (co-feeding with dominants versus subordinates) and whether the focal species foraging behaviors were affected (Table 3). We added a value of 1 to all cells to avoid a “zero cell” when using Bonferroni corrected tests $[(1-(1-\alpha)^{1/n})]$, a procedure similar to avoiding negative values when log-

Table 3 Mann–Whitney analyses testing the effect of interspecific social dominance on foraging behaviors among four species of primates feeding alone in fruit trees versus feeding with subordinate or dominant co-feeders

Tree species	Standardized height (0–1)	Feeding rate (n/min)	Semi-ripe pulp ingestion rate (g/min)	Ripe pulp ingestion rate (g/min)	Distance moved (m/fruit)
Red-tailed monkey: Feeding alone versus co-feeding with dominant species (blue and mangabey)					
<i>D. abyssinica</i> (131)	<i>0.001*</i> (–)	0.774	nd	0.957	0.695
<i>F. exasperata</i> (232)	<i>0.001*</i> (–)	<i>0.001*</i> (+)	<i>0.040</i> (+)	<i>0.001*</i> (+)	<i>0.043</i> (–)
<i>S. mitis</i> (159)	0.433	<i>0.037</i> (–)	not eaten	0.092	0.109
<i>U. congensis</i> (242)	<i>0.048</i> (–)	0.664	0.608	0.426	<i>0.001*</i> (–)
Blue monkey: Feeding alone versus co-feeding with subordinate species (red-tailed monkey)					
<i>D. abyssinica</i> (115)	0.471	0.793	nd	0.988	0.209
<i>F. exasperata</i> (197)	0.052	0.591	0.222	0.311	0.409
<i>S. mitis</i> (94)	0.189	0.912	not eaten	0.808	0.211
<i>U. congensis</i> (100)	0.711	0.411	0.086	0.730	0.457
Blue monkey: Feeding alone versus co-feeding with dominant species (mangabey)					
<i>F. exasperata</i> (175)	<i>0.035</i> (–)	nd	nd	nd	nd
Mangabey: Feeding alone versus co-feeding with subordinate species (red-tailed and blue monkeys)					
<i>F. exasperata</i> (72)	0.107	0.252	0.800	0.168	0.254
Mangabey: Feeding alone versus co-feeding with dominant species (chimpanzee)					
<i>F. natalensis</i> (15)	<i>0.045</i> (–)	nd	nd	nd	nd
Chimpanzee: Feeding alone versus co-feeding with subordinate species (mangabey)					
<i>F. natalensis</i> (32)	0.647	0.594	0.412	0.113	0.506

Data were based on feeding sessions (the time between the first individual's entry and the last one's departure). We first averaged feeding records of focal species (Table 2) per feeding session per tree species, and we applied statistics to these sessions. Numbers in cells represent the probability, based on a Mann–Whitney test, that foraging behavior was the same when alone as it was when co-feeding with another species. The (–) or (+) sign after the probabilities indicates whether the focal species was negatively or positively affected by the presence of a competitor in the same fruit tree. Note how subordinate species were often affected when co-feeding with dominant species. By contrast, dominant species were never affected by the presence of subordinate species. Numbers after tree species names represent frequencies of feeding sessions (derived from 9,229 1-min scan feeding records from five tree species). Only the ripe fruit of *S. mitis* was eaten by all three species of monkeys (unripe and semi-ripe fruit were avoided), while chimpanzees avoided this fruit completely. Probabilities of significant differences are shown in italics, and differences that are still significant after Bonferroni corrections are identified with stars (Sokal and Rohlf 1981)

nd no data

transforming (Sokal and Rohlf 1981). We used paired *t* tests to contrast the feeding height of species before and after an aggressive interaction (n =the number of conflicts) and to compare the height of the focal species before the arrival of, during co-feeding sessions with, and after the departure of a competitor. All tests were two-tailed (alpha, 0.05) and were computed with SPSS 16.0.

Results

Intratree variation in food production

We quantified intratree fruit production before exploitation by frugivores (8,196 fruits were counted; Fig. 1). Among

two-layered trees, the upper crown produced higher dry pulp densities than the lower crown ($t_{45}=2.91$, $p=0.006$; upper crown, 42.7 g dry pulp per cubic meter, range 0.001–244.6; lower crown, 11.9 g/m³, range 0.001–136.6; Fig. 1a). There were no interactions between canopy layers and tree species ($F_{1,8}=0.192$, $p=0.990$). Among three-layered trees, higher crown layers also produced larger dry pulp densities than lower crown layers ($F_{1,5}=55.36$, $p=0.002$; upper crown, 32.9 g dry pulp per cubic meter, range 0.47–117.7; middle crown, 6.3 g/m³, range 0.64–21.1; lower crown, 2.4, range 0.08–9.3; Fig. 1b). We detected no significant interaction between canopy layers and tree species ($F_{1,5}=5.11$, $p=0.07$), even after removing *Ficus sur* ($F_{1,4}=1.98$, $p=0.262$). This tree species was the only one in which the middle crown produced higher pulp

Table 4 Standardized feeding height before a competing species entered the tree (feeding alone) versus after the competing species entered the same tree (co-feeding status) during the same feeding session (paired samples)

Averaged standardized feeding height of focal species per competitive feeding status, during the same feeding session			
Social dominance=(red colobus or black and white colobus or mangabey)>blue>red-tailed			
Primate frugivores tested against other frugivores			
RT before BL enters tree $x=0.62$; $SD=0.25$; $n=26$ $t_{25}=3.27$, $p=0.003$	RT after BL enters tree $x=0.47$; $SD=0.24$; $n=26$	BL before RT enters tree $x=0.67$; $SD=0.24$; $n=52$ $t_{51}=-1.37$, $p=0.176$	BL after RT enters tree $x=0.72$; $SD=0.24$; $n=52$
(RT or BL) before MG enters $x=0.74$; $SD=0.24$; $n=12$ $t_{11}=2.94$, $p=0.014$	(RT or BL) after MG enters $x=0.50$; $SD=0.33$; $n=12$	MG before (RT or BL) enters $x=0.63$; $SD=0.23$; $n=7$ $t_6=-1.59$, $p=0.162$	MG after (RT or BL) enters $x=0.78$; $SD=0.20$; $n=7$
Primate frugivores pooled per social dominance rank			
Subordinate before dominant enters tree $x=0.66$; $SD=0.25$; $n=39$ $t_{38}=4.40$, $p<0.001$	Subordinate after dominant enters tree $x=0.49$; $SD=0.27$; $n=39$	Dominant before subordinate enters tree $x=0.66$; $SD=0.24$; $n=62$ $t_{61}=-1.71$, $p=0.092$	Dominant after subordinate enters tree $x=0.71$; $SD=0.24$; $n=62$
Primate frugivores tested against primate folivores			
RT before (RC or BW) enters tree $x=0.64$; $SD=0.20$; $n=8$ $t_7=-0.15$, $p=0.886$	RT after (RC or BW) enters tree $x=0.65$; $SD=0.65$; $n=8$	BL before (RC or BW) enters tree $x=0.64$; $SD=0.14$; $n=9$ $t_8=1.50$, $p=0.173$	BL after (RC or BW) enters tree $x=0.57$; $SD=0.22$; $n=9$

Cells represent the averaged standardized feeding height based on feeding sessions. We contrasted the averaged value of all feeding height records when feeding alone in the tree against the averaged value of all records when co-feeding with a competitor, during the very same feeding session (paired samples). RT, BL, and MG are frugivores; RC and BW are folivores. Sample size for RT against MG and BL against MG were too small to be tested separately, so RT and BL data were pooled and contrasted to MG. Note that folivorous BW and RC each socially dominated both frugivorous RT and BL (see text). Averaged body weight: frugivores, MG 7.2 kg; BL 6.1 kg; RT 3.3 kg; folivores, BW 11.4 kg; RC 8.3 kg (body weight data from Fleagle 1999).

RT red-tailed monkey, BL blue monkey, MG gray-cheeked mangabey, RC red colobus monkey, BW black-and-white colobus monkey

densities (3.50 g/m^3) than the high crown (0.47 g/m^3) and the low crown (1.97 g/m^3). Some trees ($n=11$) produced enough fruit for the primates to exploit them over many consecutive days allowing us to measure food depletion per canopy layer over time. We found that the uppermost canopy layers produced higher densities of dry pulp not only at the onset of the fruit cycle ($t_{10}=3.74$, $p=0.004$; upper, 93.9 g/m^3 against lower, 18.6 g/m^3) but also towards the end ($t_{10}=2.57$, $p=0.028$; upper, 28.6 g/m^3 against 9.9 g/m^3). This result suggested that the uppermost layers of tree crowns were profitable at all times compared to lowermost layers (see Houle et al. 2007).

Dominance hierarchy

We found a linear and transitive dominance hierarchy among the four species corresponding to body weight (Table 1). The chimpanzee (female, 33.7 kg; male, 42.7 kg) dominated all three monkeys, including the gray-cheeked mangabey (female, 6.0 kg; male, 8.3 kg), who dominated the two smaller monkeys, and the blue monkey (female, 4.3 kg; male, 7.9 kg) dominated the red-tailed monkey (female, 2.9 kg; male, 3.7 kg; body weight data after Fleagle

1999). Although social groups of red-tailed monkeys were larger and contained 2.5 times as many individuals and three times as many adult males as groups of blue monkeys, the latter won 98.4% (377/383) of conflicts.

Feeding height preferences within tree crowns and the consequences of contest competition

We found that, when alone, each foraging group fed higher in trees than an expected standardized feeding height if they fed indiscriminately with respect to height (one-sample t test, test value, 0.5; group of red-tailed monkeys, $t=12.71$, $p<0.001$, $n=738$ feeding sessions; group of blue monkeys, $t_{442}=11.17$, $p<0.001$; group of mangabeys, $t_{118}=9.47$, $p<0.001$; party of chimpanzees, $t_{798}=43.6$, $p<0.000$; Fig. 2). Interestingly, we found a negative relationship between mean group size and mean feeding height when feeding alone (average group size for red-tailed, 49; blue, 19.7; mangabey, 15; chimpanzee mean party size, 4.5; Spearman's $\rho=-1.00$, $p<0.001$, $n=4$ primate species). Mean group size was also negatively related to species body weight of females (Spearman's $\rho=-1.00$, $p<0.001$), suggesting a confounding effect of group size and body weight as a possible explanation of the

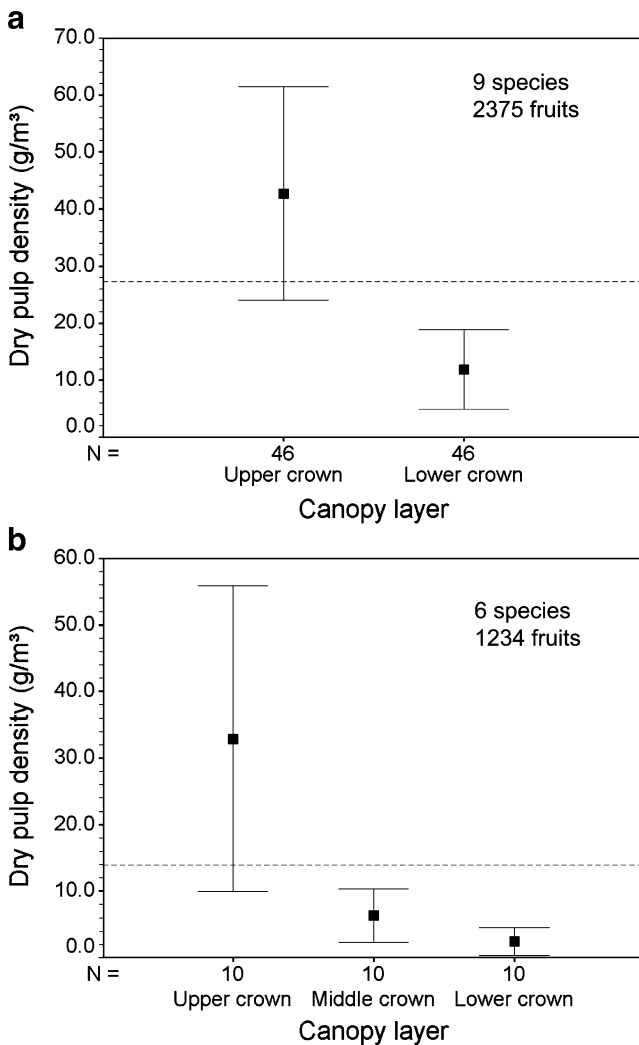


Fig. 1 Intratree variation in dry pulp density of 56 trees from 12 species exploited by four species of primate frugivores in Kibale National Park, Uganda. See Houle et al. (2007) for data per tree species. Trees were originally divided into two vertical canopy layers of equal volumes (**a** upper graph; mean DBH, 59.6 cm) and subsequently into three layers of equal heights (**b** lower graph; mean DBH, 115.6 cm). Sample size (N) represents the number of trees; dotted lines average dry pulp density for the entire tree crown of all sampled trees; squares and bars mean \pm 2 SEM. Tree species in **a**: *Clauseana anisata*, *Diospyros abyssinica*, *Ficus exasperata*, *Ficus natalensis*, *Ficus sansibarica* (formerly *brachylepis*), *Strychnos mitis*, *Linociera johnsonii*, *Pseudospondias microcarpa*, *Uvariopsis congensis*, *Cordia abyssinica*, *Cordia millenii*, *Tabernaemontana* sp. (likely *johnstonii*). Tree species in **b**: *F. natalensis*, *F. sansibarica*, *Ficus vallis-choudae*, *Mimusops bagshawei*, *Ficus sur* (formerly *capensis*), *Pouteria altissima* (formerly *Aningeria*)

vertical distribution of foragers in tree crowns. More species are needed to clarify this situation.

Based on feeding sessions, subordinate species showed lower standardized feeding height (five tests out of six) when they fed with a dominant species compared to when they fed alone (Table 3). Competing monkeys co-fed at the same height in *Strychnos mitis* understory trees only (mean

tree height, 15 m; mean crown height, 8 m; mean DBH, 41 cm, $n=5$ trees; Houle et al. 2007).

We found contradictory results regarding feeding rates and semi-ripe and ripe pulp ingestion rates. Subordinate species modified their food ingestion rates (six tests out of ten) when they co-fed with a dominant species compared to when they fed alone (Table 3). Red-tailed monkeys fed more quickly in *Ficus exasperata* and more slowly in *S. mitis* when co-feeding with blue monkeys compared to when the former species fed alone. Contrary to expectations, the subordinate monkey species moved less per fruit ingested in two species of trees and was not affected in two others when they co-fed with a dominant monkey species (Table 3). In contrast, dominant species were never affected in their feeding height, food ingestion rates, or distance moved per fruit eaten by the presence of subordinate species (28 tests out of 28; Table 3). Overall, subordinate species were more likely to be affected in their foraging (lower feeding height, variation in ingestion rates, and distance moved per fruit eaten) by the presence of dominant species in the same patch (same fruit tree), while dominants were never affected by the presence of subordinates (G test for independent samples, $G_{adj}=17.03$, $p<0.001$, William's correction). This was also the case when we used a Bonferroni-adjusted alpha ($G_{adj}=6.08$, $p<0.025$).

Aggressive interactions

We found that the loser of an interspecific aggressive interaction either fled the aggressor but stayed in the tree (40.9% of 1,646 conflicts related to food) or left the tree completely (59.1%; Table 2). When the subordinate stayed in the tree, it retreated from a mean standardized feeding height of 0.83 to resume feeding lower in the same tree at a mean height of 0.48 (paired t test, $t_{84}=12.69$, $p<0.001$). This was true for the two species of tree considered (*F. exasperata*, mean tree height=25 m, crown height=10 m, DBH=126 cm, crown volume=1,750 m³, 31 trees: $t_{70}=11.61$, $p<0.001$; *S. mitis*, mean tree height=15 m, crown height=8 m, DBH=41 cm, crown volume=348 m³, five trees: $t_9=4.18$, $p=0.002$). Tree data here are based on different individual trees and thus differ from those in the preceding paragraphs.

We observed that, after dominant species left the tree, the subordinate species did not return to feed at the height that was associated with aggression. For instance, red-tailed monkeys were aggressed in *F. exasperata* trees by blue monkeys and mangabeys at respective mean heights of 0.84 and 0.79 (Table 2). When the blue monkeys and the mangabeys left those trees, red-tailed monkeys resumed feeding at 0.66 and 0.65, respectively. The same pattern occurred in two more tree species between the red-tailed and the blue monkeys (*S. mitis* and *Uvariopsis congensis*; Table 2). We also noted that dominant species aggressed

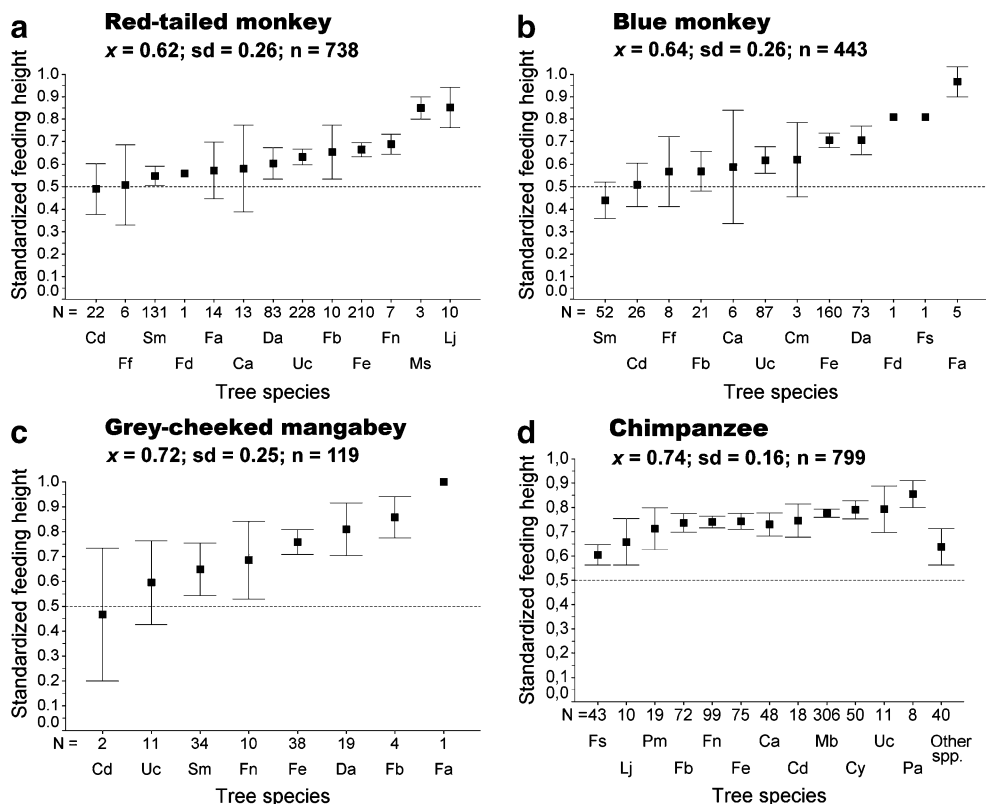


Fig. 2 Standardized feeding height of social groups of primate frugivores when feeding alone. **a–c** Monkeys (1999–2000), **d** chimpanzees (2004–2005). The Y-axis represents the standardized feeding height (animal feeding height above the base of the crown divided by crown height). We recorded the height at the end of 1-min focal follows during which observers measured feeding rates (n fruit ingested/min). Tree species codes are as follows: Ca *Celtis africana*, Cd *Celtis durandii*, Cm *Cordia millenii*, Cy *Cordia abyssinica*, Da *Diospyros abyssinica*, Fa *Fagaropsis angolensis*, Fb *Ficus sansibarica* (formerly *brachylepis*), Fd *Ficus saussureana* (formerly *dawei*), Fe *F. exasperata*, Ff *Funtumia africana*, Fn *F. natalensis*, Fs *F. sur* (formerly *capensis*), Lj *Linociera johnsonii*, Mb *Mimusops bagshawei*, Ms *Macaranga* spp., Pa *Pouteria altissima* (formerly *Aningeria*), Pm *Pseudospondias microcarpa*, Sm *Strychnos mitis*, and Uc

subordinates, on average, when the subordinate fed at a relative height of 0.83, but tolerated co-feeding subordinates when the latter fed at a relative height of 0.55.

Conflicts were not always associated with vertical stratification of interspecific foraging to occur, however. Subordinate species significantly retreated to lower feeding sites on the arrival of a dominant species, without direct conflict between the co-feeders but climbed up again in the upper crown after the dominant had left the tree (Table 4). Dominant species did not significantly move from their feeding sites on the arrival or departure of a subordinate species (Table 4).

Co-feeding sessions between frugivores and folivores

Red-tailed or blue monkeys did not significantly change their feeding height at the arrival of a primate folivore

Uvariopsis congensis. To increase clarity in Fig. 2d (chimpanzee), we included as “Other spp.” the tree species for which we had the smallest sample size ($n \leq 6$): *Ehretia cymosa* ($n=1$), *Fern* spp. (1), *Ficus thoningii* (1), *Morus lactea* (1), *Pterygota mildbraedi* (1), *C. millenii* (1), *Clausena anisata* (2), *Aphania senegalensis* (2), *C. abyssinica* (2), *Phytolacca dodecandra* (3), *Ficus ottoniifolia* (3), *Monodora myristica* (4), *Ficus cyathistipula* (6), *F. saussureana* (6), and *Ficus vallis-choudae* (6). Sample size (N) represents the number of feeding sessions (first to last individual primates feeding in the tree) when the focal species was feeding alone, i.e., during which no other primate species was present in the same individual tree; these 2,099 feeding sessions are derived from 15,696 1-min focal follows from 32 tree species. Dashed lines separate the upper (≥ 0.5) and lower (< 0.5) tree-crown layers; squares and bars mean ± 2 SEM

(black and white colobus, *Colobus guereza*, average body weight, 11.4 kg, or red colobus, *Procolobus rufomitratus*, 8.3 kg; Table 4). The pattern held even though each folivorous monkey dominated both frugivorous monkeys. Folivores won 73 conflicts against frugivores but, frugivores, only 16 against folivores. In the latter 16 cases, adult male and adult female frugivores won conflicts against respectively adult female and juvenile folivores.

Discussion

The red-tailed monkey, blue monkey, gray-cheeked mangabey, and chimpanzee in Kibale National Park forage in tree crowns that produce feeding sites of unequal quality (Fig. 1; Houle et al. 2007). While it is true that different

forests in the world produce different amounts of food of different qualities (compare for instance Chapman et al. 2003 in Africa, Medway 1972 in Asia, and Schaefer et al. 2002 in Central America), we predict that the vertical stratification of the fruit within tree crowns will apply to various fruit-producing forests. We suspect that variation of light within tree crowns will be manifested in most areas of the world because light availability itself limits in-crown photosynthate production (Brady 1987; Lynch and Gonzalez 1993; Mehrotra et al. 1998; Taiz and Zeiger 1998; Proietti et al. 2000; Sellin and Kupper 2005). It will be interesting to test the effect of this vertical stratification on foraging interactions, both intra- and interspecifically. Our study demonstrates that primate frugivores respond to this vertical stratification. When alone, all four species studied preferred to feed in the upper tree crown where the largest dry pulp density (and possible highest quality; Houle et al. 2007) was available (Fig. 2). The gray-cheeked mangabey and the chimpanzee each fed higher on average when alone than the red-tailed monkey and the blue monkey (Fig. 2), perhaps because the latter two species foraged in larger social groups producing more intraspecific competition and thus forcing some individuals to forage lower in the crown.

Generally, subordinate species ate lower in the crown when dominants were present (Tables 2, 3, and 4) than when they were alone. Dominant species were unaffected by the presence of subordinates. Surprisingly, subordinate red-tailed monkeys occasionally increased their feeding rates and moved less between the ingestion of two successive fruits in the presence of dominant blue monkeys. This was unexpected considering that red-tailed monkeys fed lower in tree crowns in the presence of blue monkeys, thus in feeding sites of lower fruit density (data on fruit density available in Houle et al. 2007). It is possible that the subordinate species moved less per fruit ingested to minimize disturbance to avoid aggression from the dominant species. A complementary explanation is that subordinate red-tailed monkeys ate faster on lower quality food (semi-ripe fruit or green unripe fruit for instance). If true, it means that the intra- and interspecific cost for a subordinate to co-feed with a dominant is to ingest more food of lower quality. We hypothesize that dominant animals feeding higher in tree crowns also benefit from foraging on fruit of higher nutritional quality. Preliminary data on the nutritional quality of the fruit support this view in that the upper crown produces higher concentrations of carbohydrates and lower concentrations of condensed tannins and saponin (potential toxins) than the lower crown (Houle et al. 2007, unpublished data, in progress).

Subordinate species did not return to feed at the height that was associated with aggression after the dominant species had left the tree. Why not go back up to higher strata where the best food presumably was? One possibility

is that the dominant species had depleted the upper canopy before departure to a level not worthwhile for the subordinate species to feed in. It was interesting also to note that dominant species aggressed the subordinates, on average, when the subordinate fed high in the tree crown but tolerated co-feeding subordinates when the latter fed at a relative height close to the middle of the crown. This suggests that initial aggressions could have been triggered because subordinates were feeding too high for the taste of dominants, and the latter forced the former to feed lower in the tree crown or to leave the tree. Co-feeding in a fruit tree with a dominant may be a compromise between the subordinate feeding as high as possible to access the best feeding sites and not too high as to provoke an aggression.

The retreat of the subordinate from the best feeding sites suggests that subordinates experienced contest competition even though no overt aggression was observed. Interestingly, red-tailed and blue monkeys did not change their preferred feeding height in tree crowns at the arrival or departure of primate folivores (Table 4). The most parsimonious explanation is the lack of direct (contest) competition over the ripe and semi-ripe fruit. Folivorous monkeys did eat the green unripe fruit however (AH, personal observation; no quantitative data). This suggests a form of scramble competition over the fruit between folivores and frugivores (green unripe fruit removed by the folivore are not available some days later for the frugivore). A pilot study revealed that tree crowns also produced feeding sites vertically stratified of young leaves and seeds (Houle—variation in density and biomass and Rothman and Chapman; unpublished data). It would be interesting to observe interactions when both the folivore and frugivore were feeding over the same young leaf resource.

Quantitative interspecific literature is rare among the primates. We found one study in which within-plant variability in fruit availability may have affected the behavior of two coexisting frugivorous primates. In Brazil, the wild mustached tamarin (*Saguinus mystax*) was dominant to and systematically fed higher in trees than the saddle-back tamarin (*Saguinus fuscicollis*; Peres 1996). Small and clumped patches were monopolized by the dominant mustached tamarins (average body weight, 520 g) to the physical exclusion of the smaller bodied saddle-back tamarins (390 g). The saddle-backs were kept “waiting outside” until most, if not all, food items had been depleted. Peres (1996) also discovered that only larger patches of food allowed co-feeding sessions.

Many primate studies have shown the importance of food distribution and how it affects contest competition intraspecifically. Whitten (1983) showed that intraspecific rank-related differences in the diet of semi-terrestrial omnivorous vervet monkeys (*Cercopithecus aethiops*)

occurred when food was clumped in distribution but not when it was randomly distributed. Other studies have found similar results in various species of monkeys from different continents (Africa, *Papio anubis*, Barton and Whiten 1993; Central America, *Cebus apella*, Janson 1985; Asia, *Macaca sinica*, Dittus 1977; *Macaca fuscata*, Mori 1979). The vertical stratification of the fruit could affect other species of primates. For instance, in social groups of indris (*Indri indri*), dominant females consistently fed higher in the fruit-bearing sites than subordinate males and used aggressive displacements to force males to feed in the lower crown (Pollock 1977).

The vertical stratification of the food in tree crowns is predictable and can be estimated from the ground. One can use it to clarify contest competition among species where conflicts are rare and subtle. This might happen in species such as South American miquis (Strier et al. 2002), African colobines (Koenig 2000; Snaith and Chapman 2007; Saj and Sicotte 2007a, b; Snaith et al. 2008), female orangutans (Knott et al. 2008), bonobos (Ihobe 1992; Furuichi and Ihobe 1994; Stevens et al. 2005), and female chimpanzees (Kahlenberg 2006; AH, unpublished data).

We hypothesize that species benefit from co-feeding with others, by lowering their own predation risks (*polyspecific or mixed-species associations*, Cords 1987, 1990; Chapman and Chapman 1996; Gautier-Hion et al. 1997; Brown 1999; Buchanan-Smith 1999; Rehg 2006). In Kibale, birds of prey (the augur buzzard, *Buteo rufofuscus*; the harrier hawk, *Polyboroides radiatus*; and the African hawk eagle, *Hieraetus africanus*; Houle 2004; Houle et al. 2006) directed all of their attacks toward the red-tailed monkeys (five unsuccessful attempts by harrier hawks and one successful kill by African hawk eagle). Blue monkeys made 14 alarm calls that potentially protected red-tailed monkeys during the 1-year monkey field study, but the opposite was not true (Houle 2004).

In summary, we have found that (1) feeding sites in the upper layers of tree crowns produced more dry pulp per unit of volume than sites in the lower layers, (2) all four species of primate frugivores preferred to feed in the upper crown feeding sites when feeding alone, (3) species established a linear and transitive social dominance hierarchy among themselves, and dominant species both spatially monopolized and aggressively usurped the best feeding sites in tree crowns during co-feeding sessions, and (4) subordinate species were more likely to face multiple foraging costs (the height at which the animal feeds, ingestion of food of possible lower nutritional value) when co-feeding with dominant species. By contrast, sharing a fruit tree with subordinate species had no foraging effect for dominant species. Interestingly, frugivores did not move down the tree crown at the arrival of dominant folivores,

but because folivores did feed on green unripe fruits, some form of scramble competition occurred between the two groups of primates. Our findings suggest that the vertical stratification of the fruit supply in tree crowns contributes to structuring contest competition among frugivores.

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