

# Testing mechanisms of coexistence among two species of frugivorous primates

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## Summary

1. We examined mechanisms of coexistence between two congeneric species of frugivorous primates, the blue monkey (*Cercopithecus mitis*) and the red-tailed monkey (*C. ascanius*).
2. We used giving-up densities (the amount of food which animals leave in a patch) in fruit trees to measure foraging efficiency and to evaluate possible mechanisms of coexistence. Animals with higher giving-up densities are less likely to persist in the company of those with lower giving-up densities because the former are not able to exploit food patches used previously by the latter. We climbed trees to estimate giving-up densities by counting the fruit which primates left behind.
3. We tested five possible mechanisms of coexistence. Three mechanisms proposed that each frugivorous species has a lower giving-up density than the other in at least one of the following: (1) different tree species, (2) within-tree foraging zones or (3) seasons. The fourth mechanism predicted that the socially dominant species exploits resources first and that the subordinate species has lower giving-up densities. The final mechanism predicted that one species would find resources more quickly than the other, which would in turn have a lower giving-up density.
4. Four of the five mechanisms received no support from our data. Only a trade-off between interspecific dominance and giving-up densities was supported.
5. We discuss the generality of our results and possible interactions with other factors.

*Key-words:* coexistence mechanism, contest competition, foraging efficiency, frugivory, giving-up density (GUD), Kibale National Park, patch depletion, Uganda.

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## Introduction

Species coexistence depends in part on partitioning resources in such a way that each species has sufficient access to ensure its survival and reproduction. Coexistence, surviving together in a given place, is possible among species which use the same resources (Basset 1995), provided that each species is limited by a different resource (Tilman 1977). Based on optimal foraging theory, Brown (1988, 1989) developed an approach for

testing whether two species are limited by different resources, thus producing a ‘mechanism of coexistence’. He used giving-up density (GUD), a measure of food which animals leave behind because they are no longer able to extract a net gain in a food patch. The GUD is related inversely to foraging efficiency, in that a species which has a low GUD forages efficiently at lower food densities than a species with a higher GUD. From this measure, Kotler & Brown (1988) suggested that a potential mechanism of coexistence exists if the environment is heterogeneous and one species is able to exploit resources at a lower density (has a lower GUD) than another in one part of the environment, while the other species has a lower GUD elsewhere in the environment (perhaps a different habitat or microhabitat). This approach has been used to study coexistence among desert rodents (Brown, Kotler & Mitchell 1994; Jones, Mandelik & Dayan 2001), squirrels (Guerra & Vickery

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1998) and mice (Yunger, Meserve & Gutierrez 2002), and even among granivorous desert birds and rodents (Kotler & Brown 1999). Among primates, divergent resource use has generally been used to explain how species coexist (Cords 1986; Peres 1996; Stanford & Nkurunungi 2003). In this paper we attempt to identify coexistence mechanisms among primates. This approach has not, to our knowledge, been used before in primate studies.

Congeneric species often coexist despite extensive overlap in diet and habitat use (Pianka 1994). This happens with many congeneric frugivorous primates. In Kenya, annual dietary overlap between blue (*Cercopithecus mitis*) and red-tailed (*C. ascanius*) monkeys reaches 70% (Cords 1986). In Madagascar, crowned lemur (*Eulemur coronatus*) and Sanford's lemurs (*E. sanfordi*) share 61–100% of their diet (Freed 1996). In Brazil, saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins show about 85% diet overlap (Peres 1996). Extensive overlap applies to folivorous primates as well (Bocian 1997; Chapman, Chapman & Gillespie 2002). The two *Cercopithecus* monkeys in this study also have extensive diet overlap (Houle 2004).

In this paper, we test five possible mechanisms of coexistence (three derived from Brown 1989) in two species of closely related African frugivorous primates; blue (*C. mitis* Wolf) and red-tailed monkeys (*C. ascanius* Audebert). The first mechanism predicts that a trade-off in the ability to use different habitats promotes coexistence (Brown 1989); for our study 'habitats' refer to different species of fruit trees. This mechanism predicts that each primate species will have at least one tree species (and thus food type) in which it has a lower GUD than the other primate species. The second mechanism suggests that a similar trade-off among microhabitats promotes coexistence (Brown 1989). For our study 'microhabitats' refer to different foraging zones within trees (upper and lower crowns). This mechanism is of particular interest as we have shown that the upper part of a tree crown contains more and bigger fruit, possibly of higher nutritional quality than the lower crown, and that monkeys prefer to forage in the upper crown (Houle 2004). The third mechanism proposes a seasonal trade-off due to climate, predation risk or food availability (Brown 1989), with each species having a season when its GUD is lower than the other species. Our fourth mechanism combines aspects of the first three with aggressive interference (contest competition). It predicts that a trade-off between social dominance and foraging efficiency explains species coexistence (Ziv *et al.* 1993). In this case, the dominant species of a pair has priority access to food, but is not as efficient as other species at exploiting this food when it becomes rare. Thus, the subordinate species will have a lower GUD. The fifth mechanism contrasts foraging efficiency and travel efficiency. It proposes that one species of a pair is more efficient at foraging, while the other discovers new food patches at a higher rate and therefore is the first to exploit them.

Primates are diurnal and eat foods which are count-

able (unlike most rodents); one can observe when animals leave a natural food patch and then estimate the number of food items left behind (the GUD, see Olsson *et al.* 1999). The use of such 'natural' GUDs can avoid distortions which can occur when artificial food patches are used (Brown 1988). Here we extend the use of GUDs to detect mechanisms of coexistence among social foragers, such as the blue and red-tailed monkeys; unlike the rodents studied elsewhere, these primates search for and exploit food as a group, leaving a food patch at approximately the same time. As mechanisms of coexistence apply to the population (or group) level it is also appropriate to evaluate them for foraging groups.

## Methods

### FIELD SITE AND ANIMALS STUDIED

We observed the feeding behaviour of red-tailed monkeys (*C. ascanius*, mean body weight: females, 2.9 kg, males, 3.7 kg) and blue monkeys (*C. mitis*, females, 4.3 kg, males, 7.9 kg) in Kibale National Park from December 1999 to November 2000 (body weight from Fleagle 1999). Both species are primarily frugivores (Rudran 1978; Houle 2004; Lambert *et al.* 2004). Most of the dietary overlap between blue and red-tailed monkeys involves fruit in both Kenya (Cords 1986) and Uganda (Houle 2004).

During our study, primates were the major fruit consumers in our study area. We saw little evidence of competition with birds or insects. However, there may have been competition with other primates, as grey-cheeked mangabeys (*Lophocebus albigena* Gray) and chimpanzees (*Pan troglodytes* Blumenbach) foraged in the same trees as our study species (see Houle 2004 for details of interactions with these species). We saw no evidence that these larger primates influenced the mechanism of coexistence between blue and red-tailed monkeys.

Kibale (795 km<sup>2</sup>) is located in western Uganda near the foothills of the Ruwenzori Mountains (0°13'–0°41' N and 30°19'–30°32' E) and contains moist, evergreen forest (57%), colonizing forest (20%), grassland (15%), swamp (4%) and woodland (4%) (Chapman & Lambert 2000). The forest receives a mean annual rainfall of 1749 mm (1990–2001, or 1547 mm from 1903 to 2001), and has two distinct wet and dry seasons. Mean daily minimum temperature is 14.9 °C; mean daily maximum, 20.2 °C (1990–2001). Our study took place in a forested area known as K-30, a 282-ha area that has not been harvested commercially (Struhsaker 1997). Altitude was approximately 1500 m asl. Details of the ecology of Kibale forest can be found elsewhere (Chapman *et al.* 1997, 2000; Struhsaker 1997). There was extensive overlap in the home range of these two species at this site (Houle 2004).

### PRIMATE OBSERVATIONS

We used two different observation methods. We watched specific trees in which large crops of fruit were about to

ripen ('tree sampling method') from dawn to dusk and collected data on animals that entered them. This provided 174 h of observation data (average visit 18.5 m, SD = 16.7, range = 1–128,  $n = 562$ ) over 1381 h of tree-watching. We also followed groups of primates from dawn to dusk (2479 h). GUDs were estimated and foraging behaviour observed using both methods.

We observed feeding behaviour (number and ripeness of fruit eaten) for both species in 1-min focal sampling periods. We collected data for both sexes and for all age groups. We noted whether other species were present in the same tree or nearby (< 50 m) while the focal animal was feeding.

We inferred interspecific dominance based on the outcome of agonistic interactions. For every interspecific agonistic interaction detected we noted which species, sexes and age classes were involved and whether or not food was involved. We noted which individual was the aggressor and which, if any, adopted a submissive behaviour. Of 460 interspecific agonistic interactions observed between the blue and the red-tailed monkeys, 72% involved a conflict over food.

We sampled blue monkeys (1219 h, 22 090 individual follows, three social groups) and red-tailed monkeys (1260 h, 27 781 individual follows, four social groups) alternately every 4 days. We saw no evidence of observer effects on monkey behaviour or movement.

#### TREE CLIMBING AND EVALUATION OF GIVING-UP-DENSITIES

We climbed trees using a modified version of the single rope technique (Perry 1978; Houle, Chapman & Vickery 2004) and the climbing spur method (Mitchell 1982; Houle *et al.* 2004) to estimate GUDs once animals had left a tree (normally within 30 min).

We used GUDs in fruit trees to evaluate which species could forage profitably at lower food densities. We estimated GUDs for the upper half of the tree crown (hereafter upper crown), the lower half (lower crown) and the entire tree crown. GUDs (g of fruit pulp per m<sup>3</sup> of tree) were calculated as the product of (1) the number of fruit of a given ripeness stage in a predetermined volume of the upper or lower crown; (2) the number of predetermined volumes of this size needed to fill the upper or lower crown, as determined visually while in the tree and based on the mean of four different counts; and (3) the mean biomass of fresh pulp per fruit for the upper or lower crown. We then divided this product by the volume of the upper or lower crown (one-half of tree crown volume). Repeated counts yielded a margin of error ranging from 3.5% to 5.8% [mean coefficient of variation (CV): 4.8%,  $n = 10$  trees]. We counted ripe food and ripening food separately (unripe fruit was rarely eaten).

GUDs are appropriate to the question of coexistence if animals experience diminishing returns while foraging in a patch (Brown 1988). We have tested and confirmed this assumption in a previous study (Houle 2004).

We estimated GUDs in four of the most commonly used fruit-bearing trees: *Diospyros abyssinica*, *Ficus exasperata*, *Strychnos mitis* and *Uvariopsis congensis*. As *Uvariopsis congensis* grows in groves and groups forage throughout the grove, we estimated GUDs over the whole grove rather than for single trees as we did with the other species. We climbed 36 trees to estimate GUDs; an additional 104 trees (74 *S. mitis* and 30 *U. congensis*) were small enough that we could count GUDs without climbing. From 12 December 1999 to 5 October 2000 we counted 20, 16, 202, 37, 120, 218, 270, 441, 483, 67 and 20 GUDs, respectively, per month. Sometimes we estimated initial fruit densities by climbing promising fruit-bearing trees before primates used them to estimate the quality of the upper and lower crowns. Both species were able to access all fruit in the tree even at the tips of fine branches. When necessary monkeys folded branches toward themselves or even broke the branches to obtain fruit.

#### RAINFALL, FRUIT AVAILABILITY AND PREDATION PRESSURE

We measured rainfall (mm) daily using a rain gauge. We (always the same observer) scored fruit availability once a month on a scale from 0 (no fruit) to 4 (full of fruit) (Freed 1996; Peres 1996) in 156 trees [diameter at breast height (d.b.h.) > 10 cm] for 20 fruit species eaten by the primates (Chapman *et al.* 2004). A monthly score for fruit availability was obtained from the mean score per tree combining all tree species.

We estimated predation risk from monkeys' reactions to potential predators: (1) an alarm call when a bird of prey was seen over head; (2) an alarm call accompanied by monkeys descending within the canopy when no aerial predator was observed; (3) monkeys ascending within the canopy, vocalizing (alarm call or low-intensity grunt) or hiding among vines when chimpanzees were observed nearby; and, of course, (4) any successful or attempted attack on a monkey by a predator. During this study we saw the augur buzzard (*Buteo rufofuscus*), the harrier hawk (*Polyboroides radiatus*) and the African hawk eagle (*Hieraetus africanus*) attack primates or provoke alarm calls. The number of predation risk events seen per month was used as a monthly index of predation risk. We observed no attacks on monkeys by non-avian species. Monkeys did not react to any species other than birds of prey and chimpanzees as though they were dangerous. Two risk events were considered independent when they were separated by at least 12 min, the median time (11.5 min,  $n = 56$ ) taken by monkeys to resume their normal activities (traveling, foraging, etc.) after a risk event. We found no difference in time to resume normal activities between blue (median 22 min for birds of prey and 10 min for chimpanzees) and red-tailed (median 6.5 min for birds of prey and 15 min for chimpanzees) monkeys following predator threats (Kruskal–Wallis,  $\chi^2 = 6.684$ , d.f. = 3,  $P = 0.083$ ), and all risk events were consequently pooled.

## STATISTICAL ANALYSIS

We tested interspecific differences in GUDs using Mann–Whitney tests because GUD data were rarely normally distributed and variances were typically heterogeneous, even after transformations (Sokal & Rohlf 1995; Zar 1999). Because GUD distributions were very asymmetrical, we present median values rather than means throughout the text (Sokal & Rohlf 1995). In figures (box-plots) median GUDs of zero mean that more than half the GUDs for that tree were zeros. A median with no variation above or below (no boxes) means that more than 75% of the GUDs were zeros.

We tested whether one species located new fruiting trees more often than another, using an exact binomial test (Crawley 2002: 180), with expected frequencies proportional of time spent observing each monkey species. We compared the proportion of time that subordinate vs. dominant species were the last to leave a food patch, depending on whether or not there was a conflict during coexploitation, with a test of independence using the *G*-statistic, with a Williams correction (Sokal & Rohlf 1995). Statistics which accompany a figure are shown in the figure legend. Although figures show GUDs of ripe fruit only, statistics for ripening fruit are also presented in the figure legend for comparative purposes. All tests were two-tailed, with alpha set at 0.05, and were computed with SPSS 8.0 (SPSS Inc. 1998).

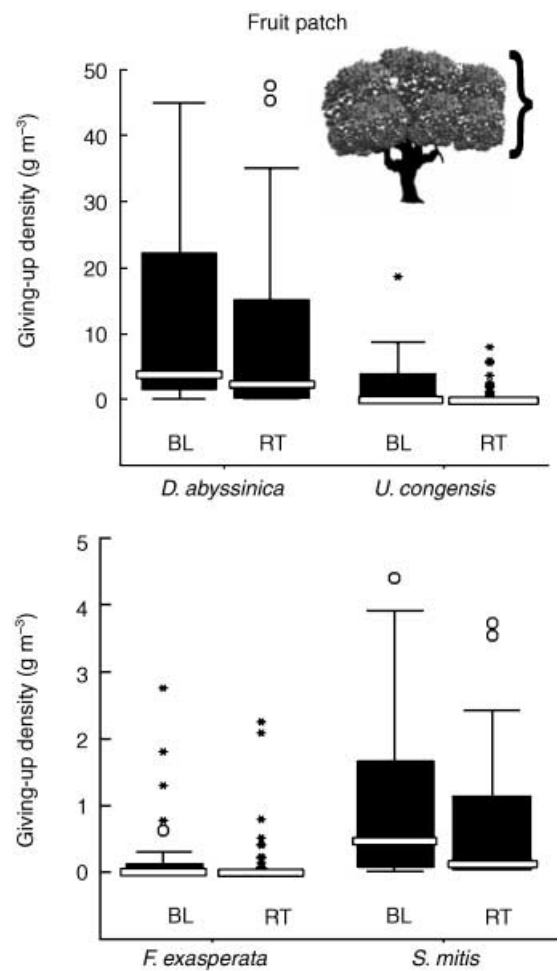
## Results

DO HABITAT TRADE-OFFS PROMOTE  
COEXISTENCE?

In every habitat (species of fruit tree) studied, we found that the red-tailed monkey had a GUD smaller than or indistinguishable from the blue monkey (Fig. 1). In *D. abyssinica* trees, GUDs did not differ significantly between red-tailed and blue monkeys for either of the two ripeness categories (Fig. 1). Blue monkeys left GUDs about 3.5 times higher than red-tailed monkeys in *F. exasperata* and 3.4 times in *S. mitis* (Fig. 1). In *U. congensis*, blue monkeys left GUDs of ripening fruit 3.6 times higher, and GUDs of ripe fruit 5.3 times higher than red-tails (Fig. 1). As we found no tree species for which the blue monkey had a lower GUD than the red-tailed monkey our data show no support for the ‘habitat (or fruit species) promotes coexistence’ mechanism.

DOES MICROHABITAT PROMOTE  
COEXISTENCE?

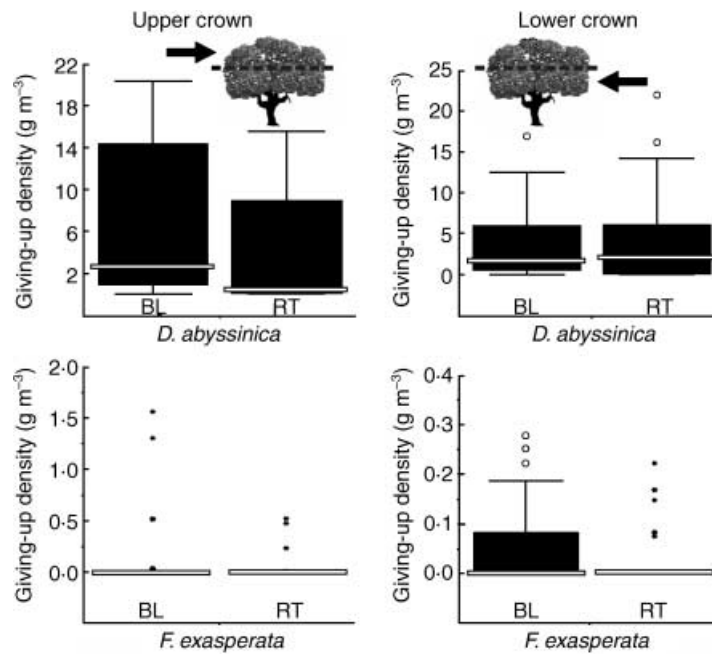
The blue monkey never had a lower GUD than the red-tailed monkey in either ‘microhabitat’ (upper or lower crowns) within any tree species (Fig. 2). In *D. abyssinica*, GUDs did not differ significantly, even though the blue monkey showed a threefold higher median GUD than the red-tailed monkey in the upper crown (Fig. 2). In *F. exasperata*, blue monkeys left a median of 3.4 times



**Fig. 1.** Giving-up densities (GUDs) of ripe fruit as a function of fruit species (whole crown). In this and following figures, only ripe fruit are shown in the graphs (ripening fruit omitted). However, statistics of both ripe and ripening fruit are gathered in the figure legend for comparative purposes. Open circles represent outliers (1.5 to three times box lengths from the upper or lower edge of the box) and stars represent extreme values (more than three times box lengths). Median GUDs of zero in the figures mean that more than half of our observations for that tree were zeros. A middle line with no variation above or below that line (no boxes) means that more than 75% of observations had GUDs of zero. In this and subsequent figures, all tests are Mann–Whitney. *D. abyssinica*:  $U_{\text{ripening}} = 324$ ,  $P = 0.402$ ;  $U_{\text{ripe}} = 296$ ,  $P = 0.190$ ;  $n_{\text{blue}} = 22$ ,  $n_{\text{red-tailed}} = 34$ . *F. exasperata*:  $U_{\text{ripening}} = 1079$ ,  $P = 0.002$ ;  $U_{\text{ripe}} = 1348.5$ ,  $P = 0.008$ ,  $n_{\text{blue}} = 44$ ,  $n_{\text{red-tailed}} = 79$ . *S. mitis*:  $U_{\text{ripe}} = 1713$ ,  $P = 0.045$ ,  $n_{\text{blue}} = 38$ ,  $n_{\text{red-tailed}} = 115$ . Ripening fruit of *S. mitis* were not exploited by monkeys. *U. congensis*:  $U_{\text{ripening}} = 243.5$ ,  $P = 0.002$ ;  $U_{\text{ripe}} = 594$ ,  $P = 0.027$ ;  $n_{\text{blue}} = 20$ ,  $n_{\text{red-tailed}} = 80$ .

more food than red-tails. In *U. congensis*, blue monkeys left GUDs for ripening fruit 4.2 times higher in the upper crown and 1.9 times higher in the lower crown than red-tails, but both monkeys had similar GUDs for ripe fruit in both crown layers (Fig. 2). Thus we found no support for the microhabitat hypothesis because there was no within-tree foraging zone (upper or lower crown) in which the blue monkey was more efficient than the red-tailed monkey.





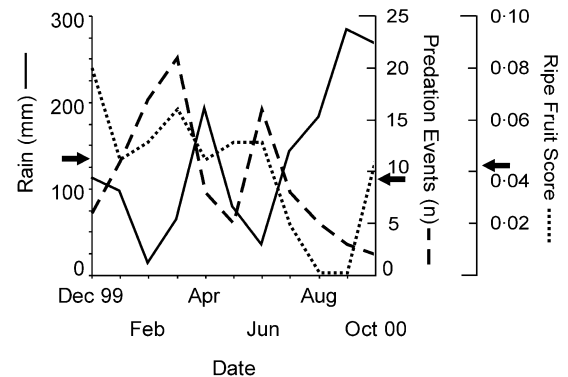
**Fig. 2.** GUDs of ripe fruit as a function of microhabitat (upper and lower crowns). Data for *S. mitis* not available. Data for *U. congensis* not shown because most GUD values are close to zero in all cases. Sample size for each microhabitat the same as in Fig. 2. *D. abyssinica*:  $U_{\text{ripening UPPER}} = 306.5$ ,  $P = 0.257$ ;  $U_{\text{ripening LOWER}} = 373.5$ ,  $P = 0.993$ ;  $U_{\text{ripe UPPER}} = 267$ ,  $P = 0.071$ ;  $U_{\text{ripe LOWER}} = 346.5$ ,  $P = 0.643$ . *F. exasperata*:  $U_{\text{ripening UPPER}} = 1176.5$ ,  $P = 0.005$ ;  $U_{\text{ripening LOWER}} = 1140.5$ ,  $P = 0.004$ ;  $U_{\text{ripe UPPER}} = 1555$ ,  $P = 0.108$ ;  $U_{\text{ripe LOWER}} = 1290$ ,  $P = 0.001$ . *U. congensis*:  $U_{\text{ripening UPPER}} = 259.5$ ,  $P = 0.003$ ;  $U_{\text{ripening LOWER}} = 304.5$ ,  $P = 0.024$ ;  $U_{\text{ripe UPPER}} = 394.5$ ,  $P = 0.313$ ;  $U_{\text{ripe LOWER}} = 405.5$ ,  $P = 0.313$ .

**DOES TEMPORAL VARIATION PROMOTE COEXISTENCE?**

We looked for seasonal trade-offs in GUDs among primate species using three different measures (rainfall, fruit availability and predation risk) of seasonal variation. Our data are based on those tree species whose fruit was exploited in both seasons. In no case did we find the blue monkey with a significantly lower GUD than the red-tailed monkey.

Rainfall (monthly mean: 135 mm, SD: 90) varied seasonally with two peaks during the year (Fig. 3). GUDs from blue and red-tailed monkeys did not differ in either season in *D. abyssinica* (Fig. 4), even though blues had estimated median GUDs 11 times and 17 times higher than red-tails for ripe and ripening fruit, respectively, during the rainy season. With *F. exasperata*, blue monkeys' GUDs were about 5.5 times higher than those of red-tails in the rainy season, but there was no difference in the dry season (Fig. 4). In *U. congensis*, the blue monkey had GUDs 5.1 times higher than the red-tailed monkey for ripening fruit in the rainy season, but showed no difference for ripe fruit during the rainy season or for any fruit during the dry season (Fig. 4).

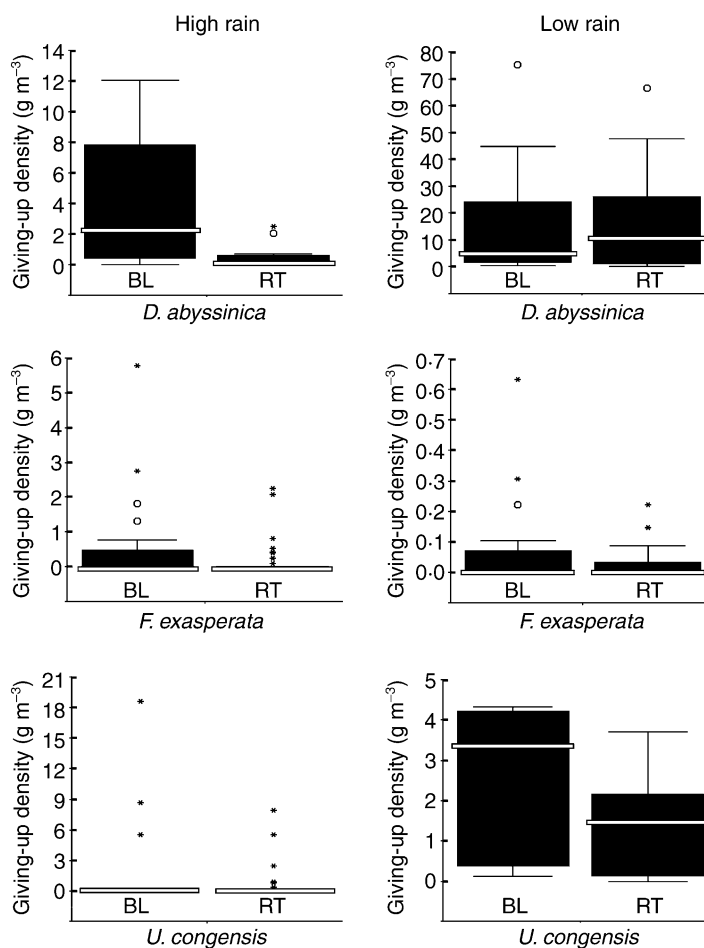
Predation risk showed a bimodal distribution over the year, distributed a little ahead of rainfall, and overlapping the seasonal availability of ripe fruit (Fig. 3). For *D. abyssinica*, we found no differences between blue and red-tailed monkeys during either the high or low predation season (Fig. 5). Monkeys showed similar *F. exasperata* GUDs for both ripening and ripe fruit



**Fig. 3.** Seasonality of rain, predation pressure and ripe fruit availability in Kibale National Park (Kanyawara station), between December 1999 to October 2000. Arrows indicate monthly means for each factor.

during high predation risk, but blues left 4.6 times more fruit than red-tailed monkeys under low predation risk. With *U. congensis*, we found no difference between the red-tailed and blue monkeys during the high predation season for both ripening and ripe fruits, but blues left GUDs 6.6 times higher in ripening fruit than red-tails during the low predation season (Fig. 5).

Ripe fruit availability varied seasonally, with a high-fruit season ranging from December to June followed by 3 months of low-fruit availability, and a high-fruit season again in October (Fig. 3). During periods of low fruit availability blue monkeys left five to seven times more *F. exasperata* than red-tailed monkeys, but the



**Fig. 4.** GUDs of ripe fruit in wet and dry seasons. *D. abyssinica*:  $U_{\text{ripening RAINY}} = 11$ ,  $P = 0.396$ ;  $U_{\text{ripe RAINY}} = 12$ ,  $P = 0.133$ ,  $n_{\text{blue}} = 4$ ,  $n_{\text{red-tailed}} = 12$ ;  $U_{\text{ripening DRY}} = 166$ ,  $P = 0.170$ ,  $U_{\text{ripe DRY}} = 189$ ,  $P = 0.819$ ,  $n_{\text{blue}} = 18$ ,  $n_{\text{red-tailed}} = 22$ . *F. exasperata*:  $U_{\text{ripening RAINY}} = 293.5$ ,  $P < 0.001$ ,  $U_{\text{ripe RAINY}} = 436$ ,  $P = 0.16$ ,  $n_{\text{blue}} = 20$ ,  $n_{\text{red-tailed}} = 59$ ;  $U_{\text{ripening DRY}} = 179.5$ ,  $P = 0.745$ ,  $U_{\text{ripe DRY}} = 203.5$ ,  $P = 0.308$ ,  $n_{\text{blue}} = 24$ ,  $n_{\text{red-tailed}} = 20$ . *U. congensis*,  $U_{\text{ripening RAINY}} = 187.5$ ,  $P = 0.002$ ,  $U_{\text{ripe RAINY}} = 452$ ,  $P = 0.495$ ,  $n_{\text{blue}} = 14$ ,  $n_{\text{red-tailed}} = 70$ ;  $U_{\text{ripening DRY}} = 1$ ,  $P = 0.190$ ,  $U_{\text{ripe DRY}} = 18.5$ ,  $P = 0.220$ ,  $n_{\text{blue}} = 6$ ,  $n_{\text{red-tailed}} = 10$ . (Fruit of *S. mitis* were available during high rain seasons only, and thus could not provide data for this analysis.)

species did not differ when fruit was abundant (Fig. 6). We also found no difference for *U. congensis*, except that blue monkeys' GUDs were 4.9 times higher than red-tailed monkeys during the low fruit season (Fig. 6).

While GUDs evaluate resource levels at which a species can forage efficiently, one can actually measure foraging efficiency at both high and low resource density by estimating the ratio of foraging benefits to costs. A comparison of the ratio harvest rate/basal metabolic rate revealed that the smaller frugivorous red-tailed monkey was systematically more efficient than the larger blue monkey (see Houle 2004 for details). This was true at both high and low seasons of fruit availability for each species of trees (Mann–Whitney, in all tests  $P < 0.001$ ).

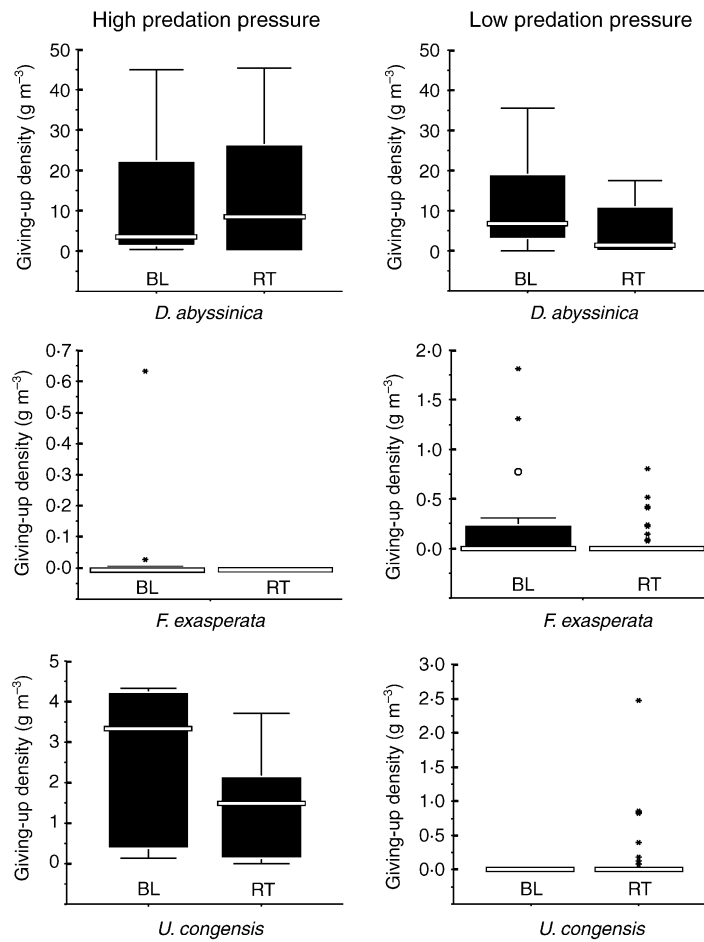
Overall, the blue monkey often had higher GUDs than the red-tailed monkey when food was scarce, when predation risk was low and during the rainy season, but not when food was abundant or predation risk was high or during the dry season. At no time did the blue monkey have a significantly lower GUD or a smaller benefits/costs ratio, than the red-tailed species. Thus, three tests of this seasonality hypothesis show no support for it.

#### DOES A TRADE-OFF BETWEEN SOCIAL DOMINANCE AND FORAGING EFFICIENCY PROMOTE COEXISTENCE?

Blue monkeys dominated red-tailed monkeys in agonistic interactions (Houle 2004). Furthermore, blue monkeys displaced red-tailed monkeys in over 95% of all interactions, effectively excluding them from fruit trees or forcing them to forage lower in the tree where fruit is smaller, less abundant and possibly of lower nutritional value (Houle 2004).

Tests of preceding hypotheses (Figs 2–6) showed that the red-tailed monkey regularly had lower GUDs than the dominant blue monkey. In fact, in every test that showed significant differences in GUDs (18 tests in all) red-tails had a lower GUD than blues. Combined, these two observations provide strong support for the dominance–foraging efficiency hypothesis.

Another test of this hypothesis asks which species left the patch last (i.e. which species was able to forage at the lowest food density). We found that this depended on whether or not there was at least one conflict during



**Fig. 5.** GUDs of ripe fruit as a function of seasonal predation pressure (aerial predators and chimpanzees preying on monkeys). *D. abyssinica*:  $U_{\text{ripening HIGH}} = 80$ ,  $P = 0.593$ ,  $U_{\text{ripe HIGH}} = 85$ ,  $P = 0.771$ ,  $n_{\text{blue}} = 13$ ,  $n_{\text{red-tailed}} = 14$ ;  $U_{\text{ripening LOW}} = 60$ ,  $P = 0.167$ ,  $U_{\text{ripe LOW}} = 60$ ,  $P = 1.67$ ,  $n_{\text{blue}} = 9$ ,  $n_{\text{red-tailed}} = 20$ . *F. exasperata*:  $U_{\text{ripening HIGH}} = 24.5$ ,  $P = 0.574$ ,  $U_{\text{ripe HIGH}} = 22.5$ ,  $P = 0.442$ ,  $n_{\text{blue}} = 12$ ,  $n_{\text{red-tailed}} = 5$ ;  $U_{\text{ripening LOW}} = 64.5$ ,  $P = 0.001$ ,  $U_{\text{ripe LOW}} = 856.5$ ,  $P = 0.004$ ,  $n_{\text{blue}} = 28$ ,  $n_{\text{red-tailed}} = 73$ . *U. congensis*:  $U_{\text{ripening HIGH}} = 30$ ,  $P = 1.00$ ,  $U_{\text{ripe HIGH}} = 18.5$ ,  $P = 0.220$ ,  $n_{\text{blue}} = 6$ ,  $n_{\text{red-tailed}} = 10$ ;  $U_{\text{ripening LOW}} = 275.5$ ,  $P = 0.003$ ,  $U_{\text{ripe LOW}} = 452$ ,  $P = 0.495$ ,  $n_{\text{blue}} = 14$ ,  $n_{\text{red-tailed}} = 70$ . (Fruit of *S. mitis* were available during seasons of low predation pressure only.)

**Table 1.** Last species to leave a food patch (fruit tree) as a function to presence or absence of interspecific conflicts during patch coexploitation

Coexploitation with/ without conflict	Last species to leave the fruit tree	
	Blue monkey (dominant)	Red-tailed monkey (subordinate)
With conflict	132	3
Without conflict	78	128

coexploitation ( $G_{\text{adj}} = 151.4$ ,  $P < 0.001$ , Table 1). When agonistic interactions occurred, the subordinate red-tailed monkey left the tree first 132 times out of 135. However, when there was no agonistic interaction, red-tails left last more often (128 occasions of 206, exact binomial test,  $P < 0.001$ ). In such cases, blue monkeys fed systematically in the higher-quality, upper crown while red-tailed monkeys fed lower in the tree. When the blue monkeys left, most of the red-tailed monkeys, particularly the alpha male and high-ranking females,

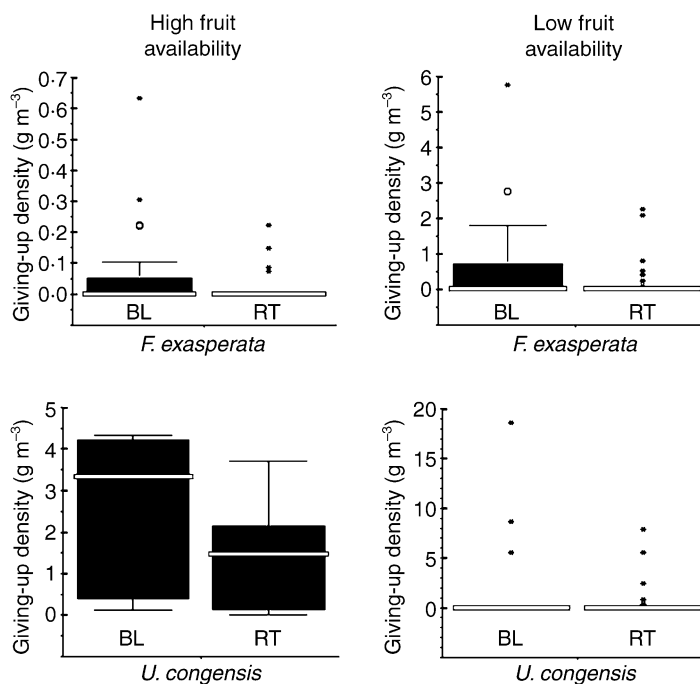
climbed higher in the canopy and exploited the food left behind by the blue monkeys. Our data suggest that blue and red-tailed monkeys may coexist because blue monkeys aggressively defend food resources from red-tails, but red-tails are able to survive by feeding at the low fruit density which blues leave behind.

#### DOES A TRADE-OFF BETWEEN DISCOVERY OF NEW FOOD PATCHES AND FORAGING EFFICIENCY PROMOTE COEXISTENCE?

Of 293 fruit trees observed (15 species), 106 trees were first exploited by blue monkeys and 187 by red-tailed monkeys (exact binomial test,  $P < 0.001$ ). Thus red-tailed monkeys discover new food sources more frequently and exploit them to lower densities eliminating this hypothetical mechanism of coexistence.

#### Discussion

Our data support only one of the five tested mechanisms of coexistence between the red-tailed and the blue



**Fig. 6.** GUDs of ripe fruit as a function of seasonal fruit availability. *F. exasperata*:  $U_{\text{ripening HIGH}} = 312$ ,  $P = 0.659$ ,  $n_{\text{blue}} = 23$ ,  $n_{\text{red-tailed}} = 29$ ;  $U_{\text{ripe HIGH}} = 326$ ,  $P = 0.103$ ,  $n_{\text{blue}} = 27$ ,  $n_{\text{red-tailed}} = 30$ ;  $U_{\text{ripening LOW}} = 185.5$ ,  $P < 0.001$ ,  $n_{\text{blue}} = 17$ ,  $n_{\text{red-tailed}} = 49$ ;  $U_{\text{ripe LOW}} = 289$ ,  $P = 0.015$ ,  $n_{\text{blue}} = 17$ ,  $n_{\text{red-tailed}} = 49$ . *U. congensis*:  $U_{\text{ripening HIGH}} = 30$ ,  $P = 1.00$ ,  $U_{\text{ripe HIGH}} = 18.5$ ,  $P = 0.220$ ,  $n_{\text{blue}} = 6$ ,  $n_{\text{red-tailed}} = 10$ ;  $U_{\text{ripening LOW}} = 275.5$ ,  $P = 0.003$ ,  $U_{\text{ripe LOW}} = 452$ ,  $P = 0.495$ ,  $n_{\text{blue}} = 14$ ,  $n_{\text{red-tailed}} = 70$ .

monkey. We suggest that blue monkeys are able to coexist with red-tailed monkeys through aggressive interference. In fact, we frequently saw blues drive red-tails from trees which the latter had started to exploit, forcing them to feed lower in the canopy or to leave the tree. On the other hand, red-tails can coexist with blues because they can feed efficiently at fruit densities below those at which blues give up.

This mechanism operates over a short time span, the few hours or days it takes for a tree's fruit to ripen and be exploited. It can promote coexistence because the time interval for fruit renewal (ripening on the same tree or other trees, Houle 2004) is shorter than the time it would take for one of the species to go locally extinct through starvation. While the mechanism operates locally and over a short time scale it can facilitate coexistence throughout the range in which the species overlap and over longer time periods because the dominance and foraging efficiency differences are repeated over time and space.

This dominance-foraging efficiency mechanism has been observed on a similar time scale in rodents (Kotler, Brown & Subach 1993; Ziv *et al.* 1993; Jones *et al.* 2001) and possibly among three congeneric Scandinavian tit birds (Kullberg & Ekman 2000). Our results add tropical frugivorous primates to this list.

The dominance-foraging efficiency mechanism does not assume that competing species are associated positively with each other in space and time; for example, gerbils coexist in the Negev desert because the efficient subordinate species avoids contact with the dominant species (Kotler *et al.* 1993; Ziv *et al.* 1993). We have not tested for positive association between blue and red-

tailed monkeys. Such an association may exist. Blue monkeys may use new sources of food discovered by red-tailed monkeys or each species may benefit from the other in detecting or escaping from predators (Cords 1984, 1987, 1990; Heymann 1990; Peres 1992, 1993; Chapman & Chapman 2000; Shultz 2004).

Predation may interact with the dominance-foraging efficiency mechanism to promote coexistence. We found that red-tailed monkeys were generally more efficient than blue monkeys during periods of low predation pressure, but these differences disappeared under high predation pressure perhaps because red-tailed monkeys were more often the target of birds of prey. This higher predation risk for red-tails may impose a higher cost of foraging on red-tails than on blues during the high-predation season. This may be a critical time for red-tail survival as they face not only increased predation risk, but also a consequent loss of foraging advantage due to the cost imposed by this risk.

Combining all fruit species, the red-tailed monkey generally had lower GUDs ( $0.03 \text{ g m}^{-3}$ ) during periods of food shortage than the blue monkey ( $0.08 \text{ g m}^{-3}$ ). One possible explanation for this is that periods of both low predation pressure and low food availability often coincide in Kibale (Fig. 3). This pattern may promote the coexistence of red-tailed and blue monkeys. On one hand, the subordinate species is able to forage profitably and with little predation risk, at low food density during the critical period of low food abundance. On the other hand, when food is more abundant, the dominant species has priority access to food trees and forages as efficiently as the subordinate.



A trade-off between foraging efficiency and predation risk can theoretically lead to species coexistence (Holt, Grover & Tilman 1994; Kneitel & Chase 2004). Our results do not, however, suggest that this mechanism promotes coexistence on its own because high predation risk only allows blue monkeys equal access to resources when resources are abundant (resource abundance and high predation risk coincide) and not in the critical seasons when they are rare. Rather, the dominance of blue monkeys appears the primary factor promoting coexistence; the foraging efficiency–predation risk trade-off can then further facilitate this coexistence.

Another observed behaviour that may also promote coexistence as a supplement to the dominance–foraging efficiency mechanism is that red-tailed monkeys found new resources more frequently than did blue monkeys. The dominance of blue monkeys may then trade off with the efficiency with which red-tailed monkeys find food. We often saw blue monkeys exclude red-tailed monkeys from food sources which the latter had exploited first.

A preliminary analysis of two additional Kibale primate species, grey-cheeked mangabeys (*L. albigena*) and chimpanzees (*P. troglodytes*), suggests that the dominance–foraging efficiency mechanism of coexistence could operate in the whole guild of primate frugivores. The diminishing returns hypothesis was confirmed and the smaller subordinate species showed lower GUDs than the larger dominant species for at least some fruit tree species (*F. natalensis* between mangabeys and chimpanzees, *S. mitis* between blues and mangabeys and *S. mitis* and *F. exasperata* between mangabeys and red-tails; Houle 2004).

While subordinate species had GUDs lower than or equal to dominant species for ripe fruit, this difference was more striking for ripening fruit implying that subordinates started eating fruit earlier (when it is less ripe) than dominants. This priority access to resources might be particularly important because GUDs for ripe fruit were often zero, even for the dominant species. This may force subordinates to feed on ripening fruit to survive. This dominance–food choice trade-off, a form of resource partitioning, is another mechanism which may contribute to species coexistence. An analysis of diet suggests that the whole frugivorous guild of Kibale primates may be structured this way (observed number of green-unripe fruit species exploited by red-tails: 27, blues: 16, mangabeys: four, chimpanzees: none). We do not know whether this resource partitioning is the result of competition (present or past) or other processes which have led to differences in species' digestive abilities. Whatever the cause, the difference may promote species coexistence.

The dominance–foraging efficiency mechanism of coexistence may operate among other primate species, although no GUD data are available. In Kenya, the annual dietary overlap of species-specific items between blue and red-tailed monkeys is very high, and evidence showed that blue monkeys dominated red-tailed

monkeys (Cords 1984; Cords 1986). At least half of conflicts occurred for food, and the loser usually left feeding trees, but fed on them after the dominant species was gone (Cords 1990). This suggests that these red-tailed monkeys have lower GUDs than blue monkeys and thus that coexistence in Kenyan forests is also based on a trade-off between contest competition and foraging efficiency. Similar patterns have been described elsewhere. In Madagascar, crowned lemurs (*E. coronatus*) and Sanford's lemurs (*E. sanfordi*) showed a very high diet overlap (Freed 1996). Sanford's lemurs won 86% of conflicts forcing crowned lemurs to leave trees and wait for the Sanford's lemur to leave before returning to forage. In Brazil, the saddle-back (*S. fuscicollis*) and the moustached (*S. mystax*) tamarins showed a diet overlap close to 85% (Peres 1996). Several studies (Heymann 1990; Peres 1996) suggest that the moustached tamarin is dominant over the saddle-back tamarin, as the former feeds higher in trees, is the first visitor at a food patch in 90% of cases (Peres 1996) and leaves monopolizable trees sooner than the latter (Peres 1996). However, the moustached tamarin left monopolizable trees before the saddle-back tamarin (Peres 1996).

The effects of social dominance on diet and competition for food within and among species have long been discussed in primate ecology (Dittus 1977; Whitten 1983; Cords 1987; Altmann 1998). We hypothesize that interspecific social dominance among coexisting taxa is critical when food is distributed patchily, and thus is defensible. Whitten (1983) showed that intraspecific rank-related differences in the diet of vervet monkeys, *C. aethiops*, occurred when food items were clumped in distribution, but not when they were distributed randomly, a discovery that supports our hypothesis. If so, three conditions would be necessary for the dominance–foraging efficiency mechanism to be effective among coexisting animals: (1) food availability is sometimes limited (producing competition); (2) food is distributed patchily (and is thus defensible); and (3) coexisting species meet in food patches. It is interesting to note that a higher foraging efficiency pattern for the subordinate species holds for species of trees of low density in the forest (*F. exasperata* and *F. natalensis*, 3.8 and 0.4 trees ha<sup>-1</sup>, respectively), and trees that grow in grove-like patches (*S. mitis* and *U. congensis*, 7.5 and 60.4 trees ha<sup>-1</sup>, respectively), but not for the one abundant tree species which is distributed in a more random manner (*D. abyssinica*, 40.0 trees ha<sup>-1</sup>, tree density after Chapman *et al.* 1997).

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