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Challenge of Neotropical Frugivory: Travel Patterns of Spider Monkeys and Bearded Sakis

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We compared travel patterns of two neotropical frugivores, *Ateles paniscus* (black spider monkeys) and *Chiropotes satanas* (bearded sakis), during a 6-month study at Raleighvallen-Voltzberg Nature Reserve in Surinam. *Ateles* were typically found in small foraging parties that changed in size and composition throughout the day. *Chiropotes* troops moved from one feeding area to the next, fragmenting "locally" when they entered an area with more than one feeding tree. *Chiropotes* moved through fewer half-hectare quadrats before encountering a feeding tree, and were more likely to locate multiple trees per quadrat than were *Ateles*. Several investigators have suggested that fission-fusion travel patterns (sensu *Ateles* and *Pan*) have the potential to reduce feeding competition among troop members. We suggest that even slight modifications in the size and composition of foraging parties, such as "local" temporary troop fragmentation, have the same effect, and may be common among frugivorous primates.

Key words: *Ateles paniscus, Chiropotes satanas,* diet, seed predation, foraging party, travel index, troop fragmentation, competition

INTRODUCTION

Neotropical primates are forest-dwelling, arboreal, and predominantly frugivorous. Fruit, particularly ripe fruit, is seasonally limited [Leigh & Windsor 1982; Terborgh 1983] and primate frugivores are faced with two alternatives during periods of fruit scarcity: a) shift to alternative resources, such as leaves, insects, exudates, or nectar; or b) develop behavioral strategies or morphological specializations that enhance the ability to search for or ingest fruit despite its reduced availability. Our study bears more directly on the latter alternative. Both *Ateles paniscus* and *Chiropotes satanas* are able to locate and use fruit resources during seasons of fruit shortage.

Phenological studies have established a wide range of variability in tropical fruiting cycles. Duration of fruiting cycles varied from 10 days to 7 months in Surinam [van Roosmalen, 1985] and, since most arboreal frugivores choose ripe

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over unripe fruit, the temporal window of fruit availability can be quite narrow. Leighton and Leighton [1982] estimated that ripe fruit of *Trichilia* remained in the canopy only one or two days. Milton [1988], using a sample of 12 species, found that individual trees bore ripe fruit an average of 0.8 months per year, but trees bore both ripe *and* unripe fruit an average of 2.1 months. Despite higher relative abundance of unripe fruit, many consumers wait until fruit reaches maturity. Sweet mesocarp is developed only in ripe fruit and seeds of unripe fruit may be protected from predation either mechanically (embedded in a hard pericarp) [Janzen, 1985] or chemically (usually in the form of toxic or indigestible seed coats) [Baker et al., 1983].

The nature of fruit being both clumped and at times rare may lead to competition among consumers and some platyrrhine characteristics could be the result of long-term competition. Specializations in the anterior dentition of the pitheciins provide significant phylogenetic cues that characterize this subfamily [Kinzey, 1992] and functionally permit early access to young fruit [Kinzey & Norconk, 1990]. Thick molar enamel [Kay, 1984], coupled with a robust mandible [Kinzey, 1974], allow *Cebus apella* to prepare and ingest nuts at faster rates than sympatric *C. albifrons* [Terborgh, 1983]. Several explanations have been proposed to account for the evolution of prehensile tails in two platyrrhine families (Atelidae and Cebidae) [classification after Ford & Davis, 1992]: increase stability while bearing weight on fragile or discontinuous supports [Emmons & Gentry, 1983], reduce distance and time traveling between feeding patches [Milton, 1984; Cant, 1986], and enhance the ability to feed in terminal branches [Grand, 1972, 1984; Janson & Boinski, 1992]. The latter explanation could also reduce interindividual or interspecific competition, if hanging below branch increased the number of fruit available within an arm's reach of each individual.

Competition for limited resources among conspecifics can result in fitness differences among competitors in the classic Darwinian sense and competition among individuals of closely related sepecies can result in character displacement and morphological specialization [Brown & Wilson, 1956]. Documentation of "scramble" or "contest" (direct) competition [sensu Milinski & Parker, 1991] among individuals of different primate species is typically anecdotal. Even when it does occur, it is difficult to determine whether losers suffer with respect to survival and/or fitness. Individuals may also compete indirectly and "exploit" or reduce food abundance in the absence of a competitor. By its very nature, exploitation is both subtle and notoriously difficult to document [e.g., Connell, 1980; Conner & Simberloff, 1986].

Early in the 1980s, ecologists attempted to sort out the significance of competition as the primary force in "constructing" community relations and the nature of the evidence needed to support competition models [e.g., Connell, 1983; Lewin, 1983a,b; Roughgarden, 1983; Strong, 1983]. Despite their historical precedence and explanatory elegance, a sufficient number of alternative hypotheses exist to account for the biodiversity of tropical communities [e.g., stochastic effects of climate, catastrophes and predation: Kinzey, 1982; Connell, 1983; den Boer, 1986]. Competition arguments are clearly not without alternative explanations. In fact, Chivers [1991] undermined the role of competition for primates by suggesting that primate feeding strategies are characterized by flexible behavior and generalized morphology compared with other mammals. Examples of this flexibility are abundant. Some Neotropical primates manipulate the length of day range or size of core area, particularly during seasonal shortages of fruit [*Saimiri sciureus:* Terborgh, 1983; Podolsky, 1990; *Ateles paniscus:* van Roosmalen, 1985; *Cebus apella:* Terborgh, 1983]. Other primates respond to fruit shortages by adjusting foraging group size [Garber, 1987]. Flexibility in group size or home range use is more likely to be a response to competitive interactions among conspecifics that are sharing the same resources than among individuals of different species. Atelins are remarkable for frequent changes in sub-troop size and membership [Fedigan & Baxter, 1984; van Roosmalen, 1985; Chapman, 1988, 1989; Symington, 1988a,b; Strier, 1992]. What role might competition have played in the evolution of behavioral flexibility?

"Fission-fusion" travel patterns may have originated as a temporary adjustment to (regular or predictable) seasonal fruit shortages or as a response to feeding interference among troop members. These two explanations are not mutually exclusive. Individuals in smaller feeding groups can be expected to expend less energy on food search complicated by scramble or contest competitive interactions. If fission-fusion social organization enhances the probability of finding small, ephemeral fruit sources and reduces competition among group members once these sources are located, then it is surprising that it has not been reported more frequently among frugivores. We compared travel patterns of two Neotropical frugivores, *Ateles paniscus paniscus* (black spider monkey) and *Chiropotes satanas chiropotes* (northern bearded saki), in order to examine the relationship between frugivory and temporary troop fission.

METHODS

Study Area

We conducted our research in undisturbed, predominantly lowland forest of the Raleighvallen-Voltzberg Nature Reserve in Surinam (4°41′N, 56°10′W) from September 1986 through February 1987 (last half of the long dry season, through the short wet season, and the onset of the short dry season) [Kinzey and Norconk, 1990]. The study area consists of 250 ha of predominantly high forest with a grid trail system [van Roosmalen, 1985]. Mittermeier and van Roosmalen [1981] and van Roosmalen [1985] provide descriptions of the primates and the field site.

A single troop of spider monkeys (12 individuals) inhabited the study area which appeared to overlap narrowly the ranges of two or three other *Ateles* troops. Two troops of bearded sakis (one of 13 and one of 9 individuals) had home ranges that included the study area and probably considerable area outside the study area. The home range of a *Chiropotes* troop has never been accurately measured. Ayres [1981] found three troops of *C. albinasus* to occupy an area of 500 ha, and this would not be an unreasonable estimate for the two study troops of *C. satanas* in Surinam. *Ateles* were followed on 30 days (including 14 complete days) for a total of 242 h and 3,539 feeding min. *Chiropotes* were more difficult to locate (although both *Ateles* and *Chiropotes* were well habituated to the presence of observers). Bearded sakis were followed on 19 days (including 9 complete days) for a total of 134 h during which we recorded 2,086 feeding min. Only complete days in which we followed monkeys from sleeping tree to sleeping tree were used in the statistical analyses.

Terms Used in the Study

"Day range" or distance traveled per day was calculated from dawn to dusk observations and traced on study area maps overlaid with a grid of 0.5 ha quadrats (see below). Because we measured point-to-point distances between feeding trees, day ranges are underestimates of individual daily travel distance. A "feeding unit" is a group of animals feeding in the same tree or in trees with overlapping crowns; for spider monkeys, this is a subset of the entire troop, referred to as a "foraging party." We calculated "feeding time" as total time a feeding unit spent in a feeding tree, beginning from the moment the first individual entered a feeding tree and ending when the last individual left. The term "reuse of feeding tree" refers to feeding trees revisited on the same day by the same feeding unit. "Pericarp hardness" and "seed hardness" are quantitative terms that have allowed us to discriminate among kinds of fruit ingested by primates [Kinzey & Norconk, 1990, 1993].

Measuring Overlap of Fruit Species

We cannot make definitive statements about the intensity of competition between bearded sakis and spider monkeys, since we did not directly measure fruit availability, nor did we consider the effects of other consumers feeding on the same resources. However, we can estimate interspecific overlap in fruit species eaten by using a simple index of similarity: $C = 2W/(A + B)$, where W = shared fruit species; A = number of fruit species used by species A; B = number of fruit species used by species B [Fleming, 1979]. An index of ≥ 0.50 was considered by Fleming [1979] to be "relatively high" in his comparison of dietary similarity among several avian and mammalian tropical frugivores. We next calculated a similarity index using the *total feeding minutes* for each of the top 20 fruit species ingested by both *Ateles* and *Chiropotes*. This may be a more sensitive measure of overlap, since this measure reflects use of both shared and high ranking resources.

Measuring Dispersion of Feeding Trees

Van Roosmalen [1985; and unpublished] systematically identified, sequentially numbered, and marked (with metal tags) more than 10,000 feeding trees and lianas within the home range of the *Ateles* study troop. He divided the approximately 250 ha study area into 0.5 ha (50 m × 100 m) quadrats. Due to long day ranges and extensive areas covered by both species, we could often locate a feeding tree with greater accuracy within a given quadrat than by measuring distance between feeding trees.

We used two quantitative methods to examine interspecific differences in distribution of feeding trees used by *Ateles* and *Chiropotes*. The "travel index" addresses the question, "How many quadrats must a feeding unit enter, on average, before it locates a feeding tree?" The index requires that quadrats be identified as either travel quadrats (Q_T) or feeding quadrats (Q_F). If the monkeys fed in a quadrat, it was designated a "feeding" quadrat. If they traveled through or rested in a quadrat and did not feed, it was designated a "travel" quadrat. An index of 0 indicates the group fed in all quadrats entered that day; an index of 100 would indicate that no quadrats were fed in; an index of 50 indicates that a feeding unit found feeding trees in half the total quadrats entered. The second measure addresses the question, "What is the probability of encountering more than one feeding tree once a troop (*Chiropotes*) or foraging unit (*Ateles*) enters a quadrat?" This measure (A_F) is the average number of trees fed in per day within a given quadrat. The maximum number of daily feeding trees within a single quadrat was four.

For all interspecific comparisons, we used two-tailed Mann Whitney (U) tests; for intraspecific comparisons we used Wilcoxon matched pairs signed-ranks test (T), and Kendall's Tau ($\hat{\tau}$) to compare feeding troop size and feeding duration for *Ateles* [Daniel, 1990]. α values were set at ≤ 0.05.

RESULTS

Fruit comprised over 90% of the feeding samples for both *Ateles* and *Chiropotes*, but the species differed in the portion of fruit ingested and masticated [Kinzey and Norconk, 1990]. *Ateles* swallowed seeds with adherent mesocarp (69.6% of total feeding minutes), whereas *Chiropotes* masticated seeds of fruit without mesocarp during the majority of feeding samples (86.4%).

Fruit eaten by bearded sakis had more resistant pericarp and softer seeds than fruit eaten by spider monkeys [Kinzey & Norconk, 1990]. The diet of *Chiropotes* is not limited to fruit with hard pericarp, however. We found that 50% (17 of 34 species) of the fruit opened by *Chiropotes* fell within the range of hardness values for fruit ingested by *Ateles* (0.03 to 1.4 kg/mm^2) [Kinzey & Norconk, 1990], and "ripe" fruit accounted for 30% of the samples collected during an earlier study [van Roosmalen et al., 1988]. Do *Chiropotes* and *Ateles* compete for access to soft fruit?

Dietary Similarity: Fruit Species

We estimated overlap in fruit species shared between spider monkeys and bearded sakis using a similarity index (*C*) (see Methods). The two species shared 43% of the total fruit species during the study. This figure is below the value (0.50) considered to be "relatively high" by Fleming [1979], but a higher level of overlap was noted when the data set was limited to the top twenty fruit species (*Ateles* overlap with *Chiropotes:* 0.85; *Chiropotes* overlap with *Ateles:* 0.69). Still, direct competition appeared to be low for three reasons: 1) High ranking fruit of one primate ranked low for the other (e.g., *Virola melinonii* [Myristicaceae], the highest ranking fruit species for *Ateles,* ranked No. 44 for *Chiropotes:* Table I). 2) Fruit was eaten at a different stage of maturity (e.g., *Prieurella* [Sapotaceae]). Both *Chiropotes* and *Ateles* fed on the mesocarp of *Prieurella,* but the first feeding date of *Ateles* postdated the first feeding date by *Chiropotes* by almost one month [Kinzey & Norconk, 1990]. 3) *Chiropotes* and *Ateles* fed on different parts of the same fruit (e.g., *Licania majuscula* [Chrysobalanaceae]), the former only eating the seed, whereas *Ateles* ate only the mesocarp. The second and third observations cannot exclude the possibility that *Ateles* and *Chiropotes* were competing indirectly for the same resources.

Interspecific Travel Patterns

We found no significant difference in number of fruit species eaten, duration of feeding time, or number of feeding quadrats entered (Table II). Day ranges were significantly longer for larger *Chiropotes* troops than for *Ateles* foraging parties ($U_{14,9} = 86, P < 0.05$).

Travel Index and Distribution of Feeding Trees

Daily activities for both sakis and spider monkeys appear to entail significant travel costs. Foraging parties of both species entered more travel quadrats than feeding quadrats during each sample day ($T = 1, n = 14, P < .0002$ [*Ateles*] and $T = 4, n = 9, P < 0.04$ [*Chiropotes*], Table II). The travel index (I_T) was significantly higher for *Ateles* than for *Chiropotes* ($U_{14,9} = 110, P < 0.001$); *Ateles* traveled through more quadrats than did *Chiropotes* before locating a feeding tree. The travel index for *Chiropotes* approached 50 and, on average, they traveled through one quadrat and encountered a feeding tree in the next quadrat. In contrast, *Ateles* traveled through approximately three quadrats before locating a feeding tree ($I_T = 70$) (Table II).

Once a feeding tree was located, sakis were also more likely to find other suitable feeding trees in the same area (quadrat) than spider monkeys (A_F: $U_{14,10} = 111, P < 0.01$ (Table II). Forty percent of the feeding quadrats entered by the sakis had multiple feeding trees ($\bar{x} = 2.39$, range 2–4), while only 24% of the

TABLE I. Top Twenty Fruit Species Eaten by *Ateles* and *Chiropotes*, Feeding Minutes, and Percent of Total Feeding Minutes[a]

Rank	*Ateles paniscus*			*Chiropotes satanas*		
	Fruit species	Minutes	%	Fruit species	Minutes	%
1	*Virola melinonii*[a]	774	22.1	*Ecclinusa guianensis*[a]	947	44.2
2	*Ficus* sp.	288	8.2	*Licania majuscula*[a]	133	6.2
3	*Bagassa guianensis*[a]	285	8.1	*Laetia procera*[a]	131	6.1
4	*Ecclinusa guianensis*[a]	283	8.1	*Couratari stellata*[a]	128	6.0
5	*Brosimum lactescens*[a]	214	6.1	*Lecythis corrugata*[a]	96	4.5
6	*Hyeronima laxiflora*	160	4.6	*Achrouteria pomifera*	58	2.7
7	*Cecropia sciadophylla*	133	3.8	*Eremoluma sagotiana*[a]	39	1.8
8	*Alchorneopsis floribunda*	130	3.7	*Swartzia schomburgkii*[a]	38	1.8
9	*Swartzia schomburgkii*[a]	127	3.6	*Xylopia nitida*	38	1.8
10	*Inga alba*[a]	121	3.5	*Brosimum lactescens*[a]	34	1.6
11	*Prieurella* sp.[a]	95	2.7	*Moutabea guianensis*[a]	32	1.5
12	*Buchenavia capitata*	49	1.4	*Prieurella* sp.[a]	28	1.3
13	*Parinari excelsum*	41	1.2	*Potamoganos microcalyx*	26	1.2
14	*Virola surinamensis*[a]	40	1.1	*Inga cinnamonea*	21	1.0
15	*Cordia sericicalyx*	37	1.1	*Qualea dinizii*	21	1.0
16	*Laetia procera*[a]	32	0.9	*Clarisia racemosa*[a]	21	1.0
17	*Clusia grandiflora*[a]	26	0.7	*Carapa procera*[a]	20	0.9
18	*Swartzia benthamiana*[a]	25	0.7	*Inga marginata*[a]	17	0.8
19	*Pourouma guianensis*	23	0.7	*Clusia grandiflora*[a]	16	0.7
20	*Guettarda acreana*	23	0.7	*Inga alba*[a]	15	0.6
	Subtotal feeding minutes	2,906	82.9	Subtotal feeding minutes	1,862	86.9

[a] Fruit species shared by the two primates.

feeding quadrats entered by a spider monkey foraging unit contained more than one feeding tree ($\bar{x} = 1.92$, range 2–3).

Foraging Patterns and Size of Foraging Units

Ateles foraging units were small, averaging 3 individuals per unit. Expansion and contraction of unit size occurred throughout the day and did not appear to depend on the activity of feeding. For example, we did not find a significant correlation in matched samples, comparing foraging group size and feeding duration ($\hat{\tau} = .16$, n = 226, ns).

Chiropotes troops traveled from one group of feeding trees to the next in a relatively cohesive manner, fissioning "locally" after they arrived in a new feeding area (Fig. 1), so that individuals were within a radius of approximately 50 to 75 meters. Even *Ateles* foraging units subdivided to feed in separate trees if the units contained more than four individuals, i.e., when they were larger than average.

Day Range

Day ranges were positively correlated with measures of daily feeding rates (i.e., number of feeding trees entered: *Chiropotes* $r_s = .85$, $P < 0.01$; *Ateles* .77, $P < 0.01$; and number of feeding quadrats entered: *Chiropotes* .86, $P < 0.01$; *Ateles* .70, $P < 0.01$) and feeding tree species diversity (*Chiropotes* .75, $P < 0.05$; *Ateles* .65, $P < 0.05$). Both frugivores increased the variety of plant species in the daily diet and the number of trees visited by extending travel distance. Travel distance and total feeding duration (feeding minutes) for the day were strongly correlated for *Chiropotes* (.79, $P < 0.01$), but not for *Ateles* (.30, ns). This suggested to us either

TABLE II. Feeding and Ranging Parameters Compared for *Ateles* and *Chiropotes* Feeding Units

	Ateles x̄ ± sd	*Chiropotes* x̄ ± sd[a]
Feeding parameters		
Feeding trees entered (no.)	15.1 ± 6.7	22.8 ± 10.0*[b]
Fruit species eaten (no.)	6.9 ± 3.5	10.1 ± 5.4
Feeding time (min)	180.5 ± 53.4	178.9 ± 50.2
Reuse of feeding trees (%)	25.2 ± 27.2	6.4 ± 9.0*
Ranging parameters		
Day range (km)	2.3 ± 0.8	3.2 ± 1.1*
Feeding unit size[c]	3.1 ± 1.7	9.0 ± 0*
		13.0 ± 0*
Feeding quadrats (Q_F)[d]	10.1 ± 4.5	14.1 ± 5.1
Travel quadrats (Q_T)[d]	23.4 ± 8.8	17.7 ± 6.2*
Travel index (I_T)[e]	70.0 ± 12.4	55.7 ± 6.1*
Feeding trees/Quadrat (A_F)[f]	1.15 ± 0.1	1.31 ± 0.2*
Quadrats with >1 fruit tree(%)[g]	24.0 ± 14.0	40.0 ± 10.0*

[a] Values represent average and standard deviation of daily samples.

[b] The asterisk (*) indicates a significant difference in a two-tailed Mann-Whitney (U) test between *Ateles* and *Chiropotes* in this value ($P < 0.05$).

[c] *Ateles* feeding unit size was an average of 226 ad lib observations. The *Chiropotes* troop was the feeding unit whose size was stable for all daily samples; data on feeding unit size were analyzed separately for each of the two troops of *Chiropotes* (see Methods).

[d] Absolute number of quadrats entered.

[e] Travel index = $QT(QT + QF)^{-1} \times 100$ (see Methods).

[f] A_F is the average number of feeding trees of the same species in the same feeding quadrat.

[g] Percent of total feeding quadrats with more than one feeding tree.

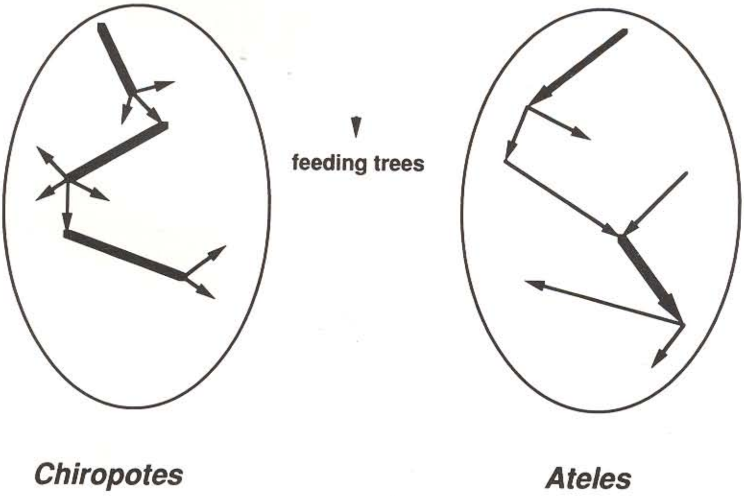

Fig. 1. Schematic diagram of travel patterns demonstrating differences between *Chiropotes* and *Ateles*. Heavy lines indicate coalescence of troop members, and narrow lines indicate smaller feeding/foraging parties. Arrows symbolize feeding tree locations, and length of lines simulate relative dispersion of feeding trees.

that activities other than feeding have a significant effect on day range of *Ateles* (e.g., moving to join another foraging unit) or that a foraging unit might take advantage of an abundant resource by reducing travel. We found some support for the latter alternative. *Ateles* travel distance was occasionally reduced due to a repetitive activity pattern of feed, rest, and reenter a productive feeding tree. Twenty-five percent of *Ateles* feeding trees were reused on the same day, compared with <10% of *Chiropotes* feeding trees (Table II).

DISCUSSION

One critical difference between *Ateles* and *Chiropotes,* two upper-canopy primate frugivores, may simply be related to the timing of fruit consumption, i.e., the ability of *Chiropotes* (by virtue of dental specializations) to take advantage of a fruit crop early in its maturity, particularly fruit covered by a hard pericarp which *Ateles* cannot penetrate [Kinzey & Norconk, 1990]. While this strategy may remove individuals of these two species from direct competition for any given set of resources, it does not exclude the possibility that individuals compete indirectly with one another. For example, if population density were high or if they remained in one area to feed for long periods of time, *Chiropotes* might reduce the fruit crop available to ripe fruit consumers. Dental adaptations, travel patterns, and demography help to explain why *Ateles* and *Chiropotes* are unlikely competitors.

Interspecific Competition Between *Ateles* and *Chiropotes*

While we found similarities in the top-ranked fruit species used by bearded sakis and black spider monkeys, two more specific measures of their ecology (timing of fruit ingestion and travel patterns) appear to remove individuals from "direct" interspecific competition. The critical interspecific difference in the feeding strategies of these two species is the "timing" of fruit consumption. If *Chiropotes* waited to open fruit at a late stage of maturity (as does *Ateles*), seeds would have been too hard to be masticated. *Seed* hardness appears to be insignificant to *Ateles* as long as fruit is soft enough to open and seeds are swallowed intact. While specialized anterior dentition allow *Chiropotes* to open very hard fruit, they are seed predators and masticate relatively soft (usually young) seeds [Kinzey & Norconk, 1990]. We suspect that variable toxicity in seed coats [Janzen, 1978; Waterman, 1984] also provides limits on food selection. Bearded sakis remove some seeds from their endocarp or seed coats and preliminary biochemical data show seed coats discarded from seeds eaten by *Chiropotes* to be high in fiber, lignin, cellulose, and condensed tannins (Kinzey, Norconk, & Conklin, unpublished).

We also found significant interspecific differences in travel patterns (day range length and home range size). Rapid movement between feeding sources allowed *Chiropotes* to exploit a wide variety of potential resources, but in a more cursory manner than *Ateles* (Fig. 1). Trap-lining from one feeding tree to the next may be the most effective way to locate fruiting trees in areas that are not visited regularly, although it is becoming increasingly clear that *Chiropotes* can implement previous knowledge about feeding tree location and make use of phenological cues when home range size is restricted [Norconk & Kinzey, 1993]. In contrast, *Ateles* appear to treat feeding trees as renewable resources by tracking the phenological status of fruit and confining their search to smaller areas of the home range, particularly when fruit resources are scarce [van Roosmalen, 1985].

The Ghost of Competition Past?

Despite overall similarity in general ecology, we failed to demonstrate strong competitive interactions between *Ateles* and *Chiropotes*. But, do our observations of contemporary *Ateles* and *Chiropotes* populations exclude the possibility that these relatively large bodied frugivores were competitiors in the past? The continuity of some defining behavioral characteristics across geographical and species boundaries suggests that these adaptations are not necessarily a response to interspecific competition.

Unstable subtroop size and composition is characteristic of all *Ateles* populations, whether or not they are sympatric with *Chiropotes* [e.g., in allopatry: Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1990; in sympatry: van Roosmalen, 1985; Norconk & Bruni, unpublished report]. *Chiropotes* has not been studied throughout its geographic distribution, but we have observed them in sympatry with *Ateles paniscus paniscus* (this study), sympatric with *A. belzebuth belzebuth* (Norconk & Bruni, unpublished report) in Venezuela, and allopatric to *Ateles* in Venezuela [Kinzey & Norconk, 1993]. Ayres [1981] observed *Chiropotes satanas chiropotes* and *C. albinasus* in Brazil. *Ateles paniscus chamek* was observed at the same study site as *C. s. chiropotes,* but outside the distribution of *C. albinasus* [Ayres & Milton, unpublished, cited in Ayres, 1981]. General travel patterns of *Chiropotes* do not appear to be different from what we have described above. MacArthur [1969] described the nature of a tropical community using the metaphor of a "balloon which resists further invasion proportionally to its present contents but which can always hold a little bit more if necessary." Although available data are limited, there is no evidence for competitive release in the members of these two genera. If at all, we suspect that they are better examples of the diffuse nature of trophic level competition within complex communities than specific examples of character displacement.

Intraspecific Competition: *Ateles* and *Chiropotes*

Intraspecific competition has not been easy to document during studies of *Ateles* or *Chiropotes*. Ranked relationships are subtle and agonistic behavior is relatively rare. Our use of the term "fragmentation" implies that some individuals of a social group are, at least temporarily, isolated from one another. If group size increases the potential for competition within feeding or foraging units, then temporary fragmentation should reduce the number of occasions that conspecifics compete with one another. Indeed, both Symington [1988b] and Chapman [1990] found that *Ateles* day range length increased with foraging party size. Symington [1988b] also reported that low-ranking *Ateles paniscus chamek* females who suffered from competitive interactions in feeding trees had longer interbirth intervals than high-ranking females.

While troop fragmentation would have the effect of reducing the rate or intensity of competitive interactions (Fig. 2), it is probably not cost-free. We identified three potential costs of troop fragmentation to *Ateles* and *Chiropotes*. 1) *Ateles* troops use large home ranges, although adult females stake out overlapping smaller areas within the home range, called "core areas" [e.g., van Roosmalen, 1985; Symington, 1988a]. Core areas are not defended by resident females and individuals may have difficulty assessing short-term resource use in their absence and regulating return time. 2) Age to independence is relatively long for both male and female *Ateles,* since "independence" implies the ability to undertake solitary food search forays. This translates into extended periods of juvenile dependency on *Ateles* mothers and long interbirth intervals. Mother's rank may contribute to variance in the length of interbirth intervals and indirectly to female reproductive success as suggested by Symington [1988b], but interbirth intervals of three or more years appears to be characteristic for all *Ateles* females [Robinson & Janson, 1987]. 3) *Chiropotes* troops move so rapidly between clusters of feeding trees that individuals are sometimes left behind as the troop moves on. It was not unusual to find a single bearded saki (usually a subadult) lost for days or weeks and tempo-

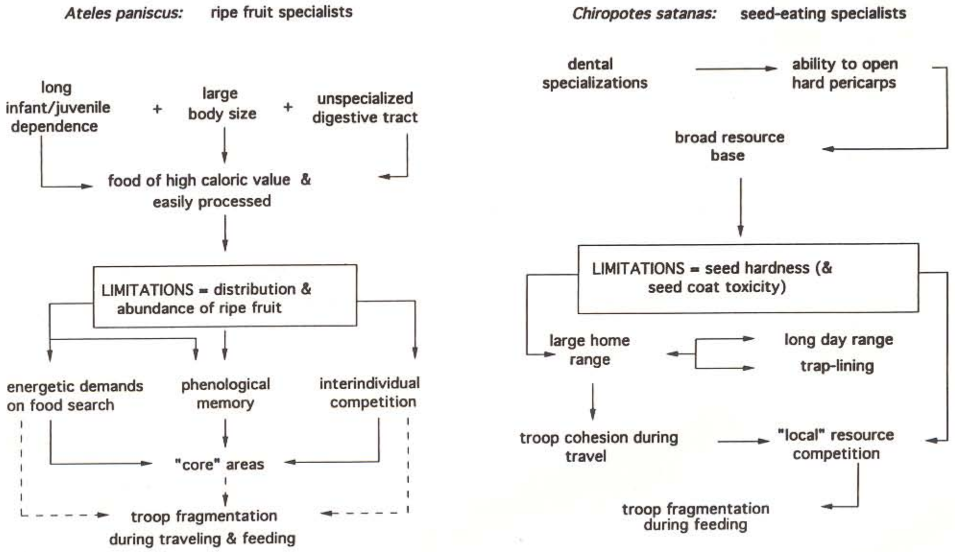

Fig. 2. Flow charts comparing ecological, developmental, morphological, and social constraints on troop size and fragmentation. Solid lines indicate direct relationships (not necessarily causation) between morphological or ecological "traits." Dashed lines suggest a more indirect relationship between terms (see text).

rarily attached to *Ateles* troops or *Cebus apella/Saimiri sciureus* mixed-species troops in Surinam (personal observation).

Primate Variations on Fission-Fusion Travel Patterns

The term "fission-fusion" (as defined by Symington [1990]) may strictly apply only to the social organizations exemplified by atelids and *Pan* spp., but other primates exhibit temporary fission [*Papio papio:* Dunbar & Nathan, 1972; *Cercocebus albigena:* Waser, 1977; *Cebus apella* and *Cacajao calvus:* Ayres, 1986; *Varecia variegata:* Pereira et al., 1988; *Alouatta palliata:* Chapman, 1990]. Given this range of species with different dietary preferences and phylogenetic histories, temporary troop fission may be a general response to a variety of stimuli. It does emphasize the flexible nature of primate societies [Chivers, 1991; Kinzey & Cunningham, 1994].

We support the view that travel patterns are not simply the result of the distribution of feeding trees. Frugivores face similar problems in the temporal and spatial distribution of fruit, and there is often wide overlap in the annual fruit sources used by different species. Foraging patterns are, instead, the result of a combination of developmental, social, and morphological species-specific traits, some of which add to ecological constraints (dispersion of feeding trees, seasonal fruiting, and fruit abundance) to influence foraging abilities (Fig. 2).

CONCLUSIONS

1. *Ateles* and *Chiropotes* are sympatric fruit specialists that demonstrate a low degree of similarity in the stage of maturity and portion of fruit ingested; they are unlikely competitors for the same food items.

2. Relative rarity and wide disperson of ripe fruit sources (high travel index) contribute to fragmentation of *Ateles* troops and probably serve to reduce potential competition among troop members.

3. A *Chiropotes* troop fragments when it is in the vicinity of multiple feeding trees (saki feeding trees were more clumped than spider monkey feeding trees), but the troop remains relatively cohesive while moving between feeding areas; whereas, an *Ateles* troop fragments into smaller foraging parties to search for food.

4. Temporary troop fission need not be as dramatic as the "fissioning" of *Ateles* and *Pan;* individuals may benefit from uninterrupted feeding while maintaining visual or vocal contact with other troop members.

5. Travel patterns are best understood within the context of multiple factors, including diet, food distribution, morphological specializations, and physiological constraints.

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