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Monospecific vs Polyspecific Life: A Comparative Study of Foraging and Antipredatory Tactics in a Community of *Cercopithecus* Monkeys

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Summary. The analysis of ranging patterns of both mono and polyspecific troops of *Cercopithecus cephus, C. pogonias,* and *C. nictitans* has shown that association results in a change of habitat use, including a less intensive exploitation and a better selection of the areas with the richest supply of fruit species. Consequently, associated species of *Cercopithecus* showed a more efficient search for fruit and a more diversified diet. In contrast, no such evidence was found for insect foraging.

A clear interspecific division of roles in the patterns of warning about aerial and terrestrial predators has been demonstrated. The *nictitans* and *pogonias* species, living in the higher strata, were informed of terrestrial predators by *C. cephus* monkeys, which live lower. In turn, the latter benefitted from the *C. pogonias* male's loud calls given in the presence of aerial danger. Some evidence suggests that predation by the monkey-eagle upon *C. cephus* was decreased by the association.

Although both foraging efficiency and predator avoidance appeared to be improved by polyspecific association, several facts suggest that predation pressure, notably by the crowned hawk eagle, was the prime factor for the evolution of this life style.

Introduction

Many hypotheses have been proposed to explain the function of polyspecific associations among forest primates. Recently, a review of the data was published by Struhsaker (1981), who states that (1) although such associations are observed in all continents, they are most common among African species; (2) the most plausible explanations rely partly on diet (there could simply be aggregation at a common food source) and partly on predation. Based on our own observations (Gautier and Gautier-Hion 1969; Gautier-Hion and Gautier 1974), we agree with Struhsaker that most types of association do not occur by chance (Waser 1982) and that their role in defence against parasites, proposed by Freeland (1977), has not been demonstrated.

It is in West Africa that associations among species of *Cercopithecus* monkeys seem to last longest. For example, in 1972 observations of a community including *C. nictitans, C. pogonias* and *C. cephus* showed that *C. nictitans* and *C. pogonias* troops spent 97% of observation time in association, while a neighbouring troop of *C. cephus* associated with the above bispecific troop for 15% of its time (Gautier-Hion and Gautier 1974). Observations in 1976 of the same community gave similar results (unpublished data).

If selection has favoured associations among these species, one or more of the associated species can be expected to benefit, either by optimising foraging patterns or by improving defence against predators, even if the same advantage is not gained by every species. The complexity of tropical rain forests makes costs and benefits difficult to quantify: it is difficult to estimate the availability of food because of the great diversity of both plant and animal species and because of the complexity of their phenological cycles; it is also difficult to measure consumption accurately and to quantify the impact of predation. One way to avoid these difficulties is to show changes in the patterns of use of space and resources and in anti-predatory behaviour, which result from polyspecific associations.

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To this end, we resumed our study of the community mentioned above in 1977 and focussed our attention on comparing two troops of *C. cephus*, one shown to live an essentially monospecific life, the other a polyspecific life. Two important questions were asked: (1) Are the ranging and feeding patterns of the two troops similar? If not, in what ways do they differ and why? (2) how is protection against predators organized and how is danger signaled in the two types of troops?

Results concerning the monospecific troop of *C. cephus* have been analysed in detail (Gautier-Hion et al. 1981) and will only be considered in comparative analyses. Ranging patterns of this troop were shown to be directly dependent on the physical structure of the forest while the availability of fruit influenced the movements of the animals only during a limited period of the day; the animals seemed to compromise, forsaking areas with too open undergrowth even if they were rich in fruit. These results were interpreted in terms of predation: to cope with terrestrial, nocturnal predators, the monkeys choose high and open forest; for defence against the monkey-eagle, they confined themselves to low, dense areas.

If association leads to benefit with respect to predation, one may expect the dependence of *C. cephus* on the physical structure of the environment to be less important when this species is in association, whereas if association optimises the search of food, there should be significant modifications to its foraging patterns.

Materials and Methods

The Animals. *Cercopithecus cephus* and *C. pogonias* are the lighter species (mean body weight, ♂♂ = 4.1 kg, ♀♀ = 2.9 kg and ♂♂ = 4.5 kg, ♀♀ = 3.0 kg, respectively) and *C nictitans* the heaviest (♂♂ = 6.6 kg, ♀♀ = 4.2 kg, Gautier-Hion and Gautier 1976).

The diet of *C. pogonias, C. cephus* and *C. nictitans* consisted of fruit, insects and leaves in the following proportions: 82.5%, 16.5% 1%; 81%, 13%, 6%; and 73%, 10%, 17%, respectively (Gautier-Hion 1980). Of the 93 species of fruit identified in their diets 63 (68%) were shared by all three species. *C. nictitans* preyed primarily on caterpillars and ants, *C. pogonias* on various orthopterans; the insectivorous diet of *C. cephus* was intermediate and overlapped considerably with that of *C. pogonias* and even more with that of *C. nictitans*.

The Observations. Methods of observation have been described in detail (Gautier-Hion et al. 1981) and will be reviewed only briefly. The study took place in tropical rain forest, in the protected area near the research centre at Makokou, Gabon, from July 1977 to the end of October 1977, which included 2 months in the dry season and two in the wet season. Intersecting paths were cut every 100 m, marking out plots of 1 ha.

Analysis of the Vegetation. The area occupied by the study community was mapped, recording canopy height, height of emergent trees and density of undergrowth. Three categories of forest were then classified: F1 forest was the tallest (canopy at 20–30 m, energents at 40–50 m) and clearest (visibility at breast height more than 30 m). F3 forest was the lowest, with no clearly defined structure, and its canopy shrouded with lianas, often reaching the ground; visibility was less than 10 m and there were many fallen trees. F2 forest was intermediate, with a canopy between 15 and 25 m and visibility of 10–30 m.

The availability of fruit was estimated by sampling 6 ha per week in the area used by the monkeys and recording all trees or lianas carrying ripe fruit for the 17 plant species preferred by the monkeys during the study period.

Habitat Use. One *C. nictitans* male, one *C. cephus* male and two *C. cephus* females (in both mono and polyspecific troops) were captured and then released with transmitters. Their positions were marked by triangulation every 30 min during half-day periods and some all-day periods. 1872 position-checks (more than 900 h) by radio-tracking were carried out on the whole community, with minimal disturbance to the animals, which were normally out of sight of the observer. At closer range, observations consisted of recording every 5 min the activity of the first visible animal, its height above the ground, and the forest type being used. Rates of occupation of the three types of forest were calculated after mapping the position of the troops every 30 min onto the vegetation map.

Results

Composition and Structure of the Community

The community studied comprised two troops of *C. cephus,* one of 15 individuals (troop C1), the other of at least 15 (troop C2); one troop of *C. pogonias* of about 18 individuals (troop P); and one of *C. nictitans* of 20 individuals (troop N). These troops interact fairly frequently, while their contact with the surrounding population was limited to vocal exchanges between adult males. Occasional contact with two neighbouring troops of *C. cephus* (C3) and *C. pogonias* (P2) was seen, and twice the area of this community was crossed by a group of about 100 *Mandrillus sphinx*.

We define an association as one troop that includes two or more troops of different species between which there is no spatial discontinuity. Thus, while either moving or resting, a polyspecific troop can comprise two or more adjacent troops, without any spatial discontinuity among individuals of different species, or a mixture of individuals from different species (named hereafter, e.g. NP = *C. nictitans* plus *pogonias,* NPC2 = *nictitans* plus *pogonias* plus *cephus* C2).

Troop C1 lived essentially a monospecific life (Table 1): it associated with troops NP or NPC2 no more than 6.5% of time. In contrast, troop C2 associated with NP for 42% of its time, and occasionally with NPC1. Troops N and P were

Table 1. Percentage occurrence of different types of troops

Different types of troops	Monospecfic troops				Polyspecific troops				
	C1	C2	N	P	NP	NPC1	NPC2	NPC1C2	NPP2C3
Occurrence (%)	93.5	55.4	0	0	50.1	4.1	42.1	2.4	1.3

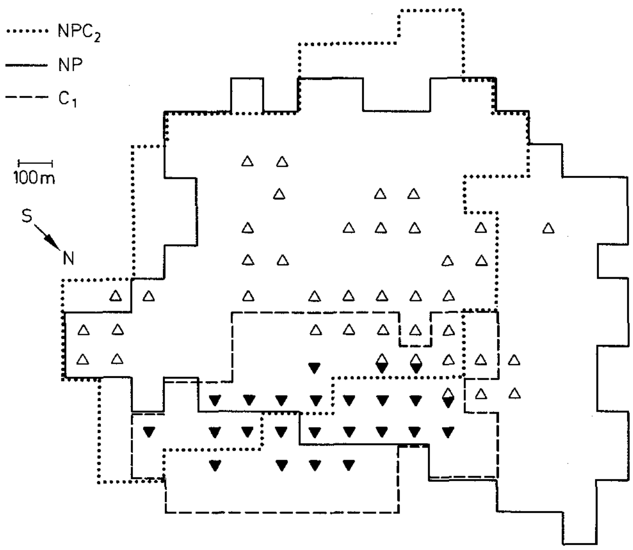

Fig. 1. Home ranges of different troops in the community. *White triangles:* NPC2 sleeping sites; *black triangles:* C1 sleeping sites

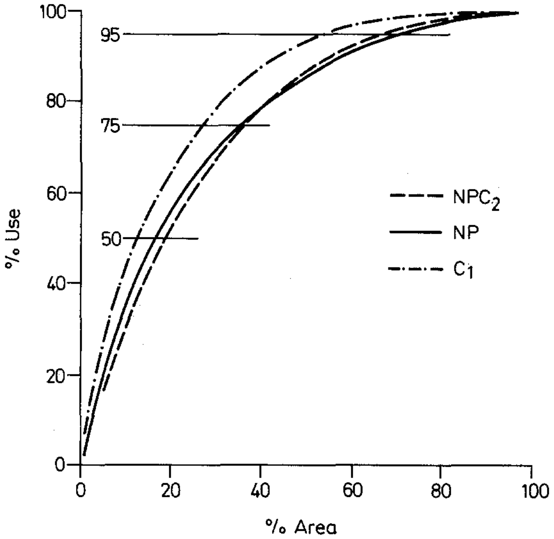

Fig. 2. Overall pattern of home range use by NP, NPC2 and C1 troops; *along the ordinate:* percentage of use; *along the abscissa:* surface area as percentage. Number of position-checks: NP, $n=273$; NPC2, $n=343$; C1, $n=1238$. Number of hectares: NP, $n=148$; NPC2, $n=119$; C1, $n=52$. (Different patterns have been compared by Kolmogorof-Smirnof two-tailed test)

never observed as monospecific troops: they were found either together (NP = 50%), with C2 (NPC2 = 42%) and more rarely with C1 (NPC1), with C1 and C2 (NPC1C2), or with C3 and P2 (NPC3P2, Table 1). The two troops of *C. cephus* were only seen together in the presence of *C. nictitans* and *C. pogonias*.

The degree of association between NP and C2 did not especially fluctuate during the day and the animals were seen continuously together for several consecutive days and nights before separating. The occasional association of troop C1 with NP or NPC2, however, lasted on average only 3–4 h and was rarely seen at dawn, dusk and night.

Overall Use of Space

In this analysis, both monospecific and polyspecific troops are considered as single entities. Consequently, we will speak about home ranges of each type of troop, even if a species might be included in more than one type.

Size and Use of Home Ranges. NP troop had a larger home range than NPC2 (148 ha and 119 ha respectively, Fig. 1); 93 ha were used by both NP and NPC2. When monospecific, C2 troop exploited a smaller area of about 60 ha which was completely overlapped by the ranges of NP or NPC2. The range of C1 troop covered 52 ha of which 71% was overlapped by NP or NPC2. Thus, when associated with *C. pogonias* and *C. nictitans*, the movements of *C. cephus* were significantly altered: this is especially true for C2 troop, which used an area more than twice the size of C1s range. In return, NP was partially constrained by *C. cephus*. Consequently, home range size was not directly correlated with troop size: with 38 individuals, NP troop exploited 148 ha; while with 53 members, NPC2 ranges over 119 ha. Finally, the infrequent NPC1C2, with 68 animals, did not cover more than 21 ha.

There were no significant differences between NP and NPC2 in the use of their home ranges (Fig. 2): in both cases, 95% of time was spent in

70% of the range. Although the difference is not significant (at $P>0.05$), C1 showed a more concentrated usage, spending 95% of its time in half the surface area used.

Influence of Forest Structure. The habitat occupied by this community was a mosaic of different types of forest. Table 2 shows that: (1) different structural types were not equally represented in each home range. C1s range had less high forest F1 and more dense forest F3; in NPs range, the reverse was true, while NPC2 had a higher proportion of intermediate forest F2. These differences in vegetational composition seemed to reflect specific choices (C1 and NP) or a compromise between them (NPC2). (2) The daily use of these different types of forest varied between troops. Only NP used these different habitats in proportion to their availability: high forest, the most widely available, was thus most commonly occupied. In contrast, C1 avoided such forest and selected dense forest while NPC2 showed a slight preference for intermediate forest.

Once again, a compromise was shown: *C. cephus* tended primarily to exploit low dense forest, while *C. pogonias* and *C. nictitans* chose high and open habitat. In association, *C. cephus* was drawn into areas less dense than it usually inhabited, while *C. pogonias* and *C. nictitans* incorporated more intermediate forest into their ranges. Thus the association of these three species led to an enlargement of their habitat niche, giving access to types of vegetation that were more rarely used when each species was alone.

Vertical Use of Space. C. nictitans and *C. pogonias* occupied the same higher strata when in either NP or NPC2 troops, while, when monospecific, *C. cephus* occupied lower levels than when associated with the two other species. Association thus led to a potential increase in the vertical niche of *C. cephus*. However, in NPC2, *C. cephus* used lower strata than the other species (Table 3).

Daily Patterns of Use. The mean daily distance travelled by marked individuals was 1,295 m for C1, 1,825 m for NP and 1,980 m for NPC2. In association, *C. cephus* were thus led by *C. nictitans* and *C. pogonias* and their presence neither accelerated nor significantly slowed the movement of these latter species.

On average, C1 covered 11 ha daily, NP 20 ha and NPC2 26 ha (Table 4). To account for the rate at which each troop explored its home range, a 'renewal' index was established per 30 min. For every position-check, the number of new plots used by monkeys, with regard to those used the previous

Table 2. Percentage area and use of each forest type for the three types of troops. $n=30$ min scan records. χ^2 was used to test overall differences between the percentage use of different forest types and the percentage expected from their respective surface area

Forest types	% of area			% of daily use		
	C1	NPC2	NP	C1	NPC2	NP
F1	28.8	34.8	44.1	14.8	34.2	48.8
F2	32.1	45.3	38.0	35.5	51.1	37.8
F3	39.1	19.9	17.9	49.7	14.7	13.4
n				1238	343	273
χ^2				^{a}	^{b}	NS

[a] $p<0.001$; [b] $p<0.05$; NS $p>0.05$

Table 3. Mean height class (m) used by each species according to troop composition. Z standard normal deviation; n number of individual scan records

Species troop	*C. cephus*			*C. pogonias*		*C. nictitans*	
	C1	NPC1	NPC2	NPC2	NP	NPC2	NP
Mean height	15.0	20.3	21.6	24.3	26.3	27.6	26.6
SD	7.1	7.5	10.9	9.8	8.2	9.0	8.0
n	1380	34	27	36	109	96	371
Z		4.07^a	0.52 NS		1.13 NS		0.94 NS
Mean height	15.0	20.9		25.8		26.8	
SD	7.1	9.1		8.6		8.2	
n	1380	61		145		467	
Z		4.98^a		3.65^a		1.14 Ns	

[a] $p<0.001$; NS $p>0.05$

Table 4. Daily patterns of habitat use (n refers to all-day observations). Wilcoxon matched pairs signed-ranks compares mean renewal index for paired 30 min scans, throughout the whole day cycle

Troops	Distance per day (m)	Area (ha) visited daily (06.00 to 18.30 h)	Renewal index	Wilcoxon test
C1	1295	10.9 ± 2.3 ($n=12$)	0.42	^{a}
NPC1/ NPC1C2	–	–	0.69	^{a}
NPC2	1980	25.9 ± 5.4 ($n=8$)	0.87	^{a}
NP	1825	20.3 ± 5.2 ($n=6$)	0.83	

[a] $p<0.01$

30 min, was noted. A mean was then calculated for the total values. Results show that the index is lowest for C1 and highest for NPC2 with all intertroop differences being significant (Table 4). Thus NPC2 used their range less intensively: for only a slight increase in locomotor cost each day, compared with NP, it visited a greater area (on average an extra 6 ha). The difference was even more marked for C1, which visited nearly 2.5 times fewer different plots each day for a daily distance only 1.5 times lower.

The rare associations of NP or NPC2 with C1 resulted for this latter troop in a significant increase in mobility, but its presence seemed to act as a brake on other species. This philopatric tendency of C1 is easily explained by the proximity of C2 with which C1 occasionally conflicted when the association led it into the other's range.

Fruit Feeding

To clarify differences between troops in their search for fruit and insects, in resting or in dealing with predators, the monkeys' use of space was analysed while controlling for the rhythms found in these activites (Gautier-Hion et al. 1981; Quris et al. 1981 and unpublished data). Time spent in the search, collection and ingestion of fruits was maximal between 06.30 and 08.00, and between 16.30 and 18.00 hours: these two periods were used in the analysis of patterns of fruit feeding. To improve comparisons between NP and NPC2 troops and avoid the bias due to differential representation of the various forest types in their respective home ranges, only the communal part of these ranges will be considered, totalling 93 ha.

Analysis of the Frugivorous Diet. Twenty-eight species of fruit were seen to be eaten by the three species (see Appendix): 21 by *C. cephus* (C1); 22 by *C. pogonias* and 24 by *C. nictitans*. Unfortunately, observations on C2 were too sparse. The overlap between frugivorous diets (calculated according to Pianka 1973, the overlap can vary between 0 and 1 according to whether overlap is nil or total) was great, being 0.97 between *C. pogonias* and *C. nictitans*, 0.79 between *C. cephus* and *C. nictitans* and 0.74 between *C. cephus* and *C. pogonias*. Nevertheless, the diversity of the fruit diet of monospecific *C. cephus* (calculated according to Simpson's formula, Levins 1968) was lower than that of *C. pogonias* and *C. nictitans* ($D = 6.87$, $D = 13.35$ and $D = 14.35$ respectively, the dietary diversity index D varies from 1 to N; 1 when only one fruit species is present; N when the N species are of equal importance).

Table 5. Percentage area and use of each forest type by troops during the fruit feeding period. For NP/NPC2, only the area common to both home ranges is considered. χ^2 is used as in Table 2. $n = 30$ min scan records

Forest types	% of area		% use, fruit feeding		
	C1	NP/NPC2	C1	NPC2	NP
F1	28.8	39.9	16.3	46.8	43.9
F2	32.1	47.2	43.6	48.3	42.5
F3	39.1	12.9	40.1	4.9	13.6
n			380	117	58
χ^2			[a]	NS	NS

[a] $p < 0.001$

Table 6. Fruit availability in terms of mean number of fruiting species and fruiting plants according to forest types; comparative ratios of use (C1 vs NPC2) were calculated to account for differences in utilization of each forest type

Forest types	Surface area analysed (ha)	Mean no. fruiting plants/ha	Mean no. fruiting species/ha	Ratios of use	
				C1	NPC2
F1	48.5	3.58	2.40	0.55	1.33
F2	66.0	3.23	1.96	1.36	1.01
F3	24.5	2.58	1.25	1.02	0.30

Patterns of Fruit Feeding, Forest Types and Fruit Availability. During the main period of fruit feeding, NP and NPC2 troops used the different types of forest according to the available proportion of their home ranges (Table 5). In contrast, C1 exploited more intermediate forest at the expense of high forest.

Individuals from C1 fed on average at lower levels than all members of NPC2 (19.6 m for *cephus* vs 24.8 m, 27.2 m, 25.8 m for *cephus*, *pogonias* and *nictitans* in NPC2, $P < 0.001$). In contrast, there were no significant differences between these latter species in association, which confirms the direct observations of the succession or simultaneous presence of all members of a trispecific troop in the same fruiting trees.

The richness in terms of the number of trees and lianas and number of fruiting species (for a total of 17 main species eaten by monkeys during the study period) was analysed for each type of forest in a total of 100 ha. The results show (Table 6) that high open forest F1 was richest in quantity and variety of fruiting species and low dense forest F3 was the poorest. Comparison of the relative use made of these different habitats during the period of fruit feeding showed that NPC2 used forest that was relatively rich while C1 left the richest forest for the other habitats.

To clarify this phenomenon, we looked for correlation between rates of use of different hectares in the home range, during a limited period (8–10 days) and their richness in fruit during the same period. This analysis was done once in the dry season, and once in the wet season. The dry season was characterized by a small number of species providing fruit eaten by the monkeys, species that often occurred at high density, while in the wet season, there were twice as many species, but often species that were less abundant: hence the number of plants bearing fruit did not differ significantly between the two seasons (Gautier-Hion et al. 1981). For C1 and NPC2 troops, use of space in the dry season was significantly correlated with its richness in number of trees bearing ripe fruit (Spearman coefficient, $rs = 0.704$, $P < 0.01$ and $rs = 0.742$, $P < 0.01$ respectively), but not with the number of different fruiting species ($rs = 0.362$, $P > 0.05$ and $rs = 0.371$, $P > 0.05$ respectively).

In the wet season, there was a positive correlation for NPC2 between rates of use and richness in quantity and variety of fruit ($rs = 0.506$, $P < 0.05$ and $rs = 0.527$, $P < 0.01$ respectively), while no such correlation was found for Cl ($rs = 0.306$, $P > 0.05$ and $rs = 0.294$, $P > 0.05$ respectively). Thus, whatever the season, the movements of NPC2 were directly influenced by the characteristics of fruit availability, the animals choosing to seek either the areas richest in fruiting trees (true for the dry season, during which few species were fruiting) or the areas richest in quantity and variety (true for the wet season, when many species were fruiting). For C1, the correlations were less clear, notably those concerning the influence of species richness: the results conformed to observations showing a lower species diversity in the diet of these animals.

Patterns of Fruit Feeding and Troop Movements. When comparing NPC2 and C1 troops, we saw that the increase in area visited daily by NPC2 was greater than expected from the increase in distance travelled (Table 4). We tried to evaluate these differences by estimating the 'predictability' in the direction of movements for both troops. To do this, we noted the orientation of each troop every 30 min; three possibilities were envisaged, based on the hypothesis of random movements: if a troop is in a given place at time t, at time $t+1$, it could be either straight ahead (50% of cases), in the forward quadrant (25% of cases) or have retraced its steps (50% of cases). It can be seen (Fig. 3) that during the main period of fruit collecting, the movements of NPC2 were much more direct than those of C1, whose members retraced their steps in 36% of cases against only 16.5% for NPC2, whose movements were straight ahead in 53% of cases.

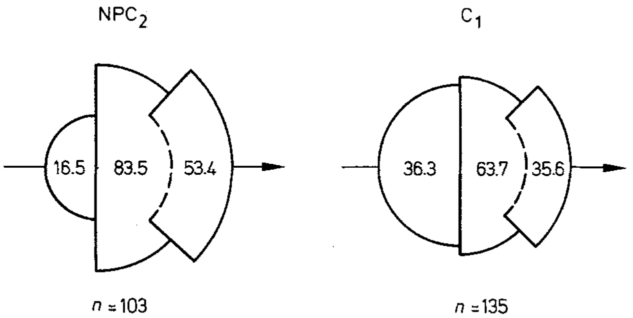

Fig. 3. Analysis of the 'predictability' of movement for NPC2 and C1 troops

Table 7. Percentage area and use of each forest type by individuals of the three species during insect foraging. χ^2 is used as in Table 2. n = individual scan records. *NS* not significant

Forest type	% of area		% use during insect foraging		
	C1	NPC2/NP	*C. cephus*, C1	*C. pogonias*	*C. nictitans*
F1	28.8	39.9	3.85	46.7	63.5
F2	32.1	47.2	49.05	53.3	31.75
F3	39.1	12.9	47.10	0	4.75
n			104	30	63
χ^2			[a]	NS	[b]

[a] $p < 0.001$; [b] $p < 0.05$

These differences in the pattern of movements displayed by the two troops account for those found in the number of new hectares visited daily.

Patterns of Search and Collection Prey

The search for animal prey was fairly constant when there was enough light, i.e. from 08.00 to 17.30 hours. Since it was infrequent at dawn and dusk, it was not observed in F1 forest for troop C1, which made significant use of this forest only during these two periods (Gautier-Hion et al. 1981), but occurred normally in F2 and F3. *C. nictitans* preferred to capture prey in F1 forest while *C. pogonias* foraged for prey in both F1 and F2 forests (Table 7). For these activities, the two latter species occupied the same mean height class (27.2 m and 25.9 m respectively), while *C. cephus*, either alone or in association, captured prey at lower levels than *C. pogonias* and *C. nictitans* (11.5 m and 17.5 m respectively, vs 27.2 m and 25.9 m, $P < 0.01$). Thus, although *C. cephus* used

Table 8. Percentage area and use of each forest type by the three species for night and daily resting periods. For night resting, n represents the number of sleeping sites observed. For day-resting, $n = 30$ min scan records. χ^2 as in Table 2. *NS* not significant

Forest types	% of area		% use night resting			% use day resting		
	C1	NP/NPC2	C1	NPC2	NP	C1	NPC2	NP
F1	28.8	39.9	27.4	52.6	54.2	12.4	25.9	43.0
F2	32.1	47.2	53.4	39.5	35.5	26.4	55.6	50.0
F3	39.1	12.9	19.2	7.9	10.3	61.2	18.5	7.0
n			69	20	19	462	113	66
χ^2			[a]	NS	NS	[a]	[b]	NS

[a] $p<0.001$; [b] $p<0.05$

highest strata when they associated with other species, it was when they were searching for prey that the amplitude of vertical levels used by the trispecific troop was greatest. This suggests greater interspecific competition for this activity than for fruit feeding.

Patterns of Rest and Anti-Predatory Behaviour

Troop activity stopped just before nightfall and started again at daybreak. During the night, the monkeys slept and only an unusual disturbance elicited any activity; various studies have shown that predation determines choice of sleeping sites (e.g. Gautier-Hion 1971; Crook 1970). During the day, vulnerability varies according to the type of activity, high risk situations being notably the gathering of fruit in certain emergent trees and the periods of daily rest and social exchanges, during which vigilance is reduced.

Pythons (*Python sebae*), golden cats (*Felis aurata*) and leopards (*Panthera pardus*) are potential nocturnal predators of *Cercopithecus* monkeys. The leopard is essentially a terrestrial animal, however, and in the study area its main prey are pangolins (*Manis tricuspis*) and duikers (*Cephalophus* sp., Charles-Dominique, personal communication). Nevertheless, it is capable of climbing and cannot be excluded as a predator of monkeys (see Gandini and Baldwin 1978). Pythons and golden cats are seen in the trees; the latter were observed on several occasions prowling around talapoin sleeping sites, and once the remains of a talapoin were found in the intestines of a python (personal observation). Young *Cercopithecus* monkeys are similar in size to adult talapoins, and adults do not weigh more than the duiker *Cephalophus monticola*, which is eaten by pythons (personal observation).

Apart from humans, the main diurnal predator of monkeys is the crowned hawk eagle (*Stephanoaetus coronatus*): *Cercopithecus* fur left by eagles was seen fairly frequently. During our observation of the study community, we saw three attacks by eagles of which one succeeded, and we once found fresh pieces of fur on the ground. The three attacks involved the monospecific C1 troop; the fresh fur was also from a *C. cephus*, from either C1 or C2. These incidents involved without doubt the same predators as only a single pair of eagles lived in the study area (Brosset, personal communication). Based on these observations, the annual pressure of predation by eagles on *Cercopithecus* monkeys is estimated as at least eight individuals from the entire community: the monkey-eagle is thus a primary element in population regulation.

Patterns of Night-Resting. At night, danger comes from the ground. To climb, predators need supports that are neither too large nor too thin: in 80–90% of cases, the three monkey species investigated chose sleeping sites in forests F1 and F2 (Table 8). This is the case even for C1 troop, which significantly left the dense F3 forest for the night. Direct observations showed that the animals chose to sleep in the crowns of large trees and in forest without any substantial lower canopy.

Patterns of Day-Resting. During the day-resting period, danger comes from above. C1 troop sought F3 forest more than at any other time, whereas NP used all three types of forest randomly. NPC2 differed significantly ($P<0.02$) in showing greater use of denser forest (Table 8), seeming thus to come under the influence of *C. cephus*.

Anti-Predator Behaviour. Improved detection and communication of danger, the arguments often put forward as one of the advantages of life in large groups (see review in Struhsaker 1981), are difficult parameters to measure. Such an advantage can result simply from the multiplication of the number of vigilant eyes and of the area under surveillance.

However, an advantage might also result from the sharing of roles between associated species. Such a possibility was tested for all situations of potential predation where the type of predator was known without ambiguity, by analysing which individuals from NPC2 gave the first alarm calls and which adult male was the first to give 'loud calls' (see Gautier and Gautier-Hion, 1977, 1983). The results showed that: (1) When the danger came from the ground ($n=36$), *C. cephus* adult females and sub-adults of both sexes gave the alarm in 75% of cases, *C. pogonias* in 22% of cases and *C. nictitans* in less than 3% of cases; the loud calls of males followed immediately afterwards or more rarely preceeded. The *C. cephus* male was the first caller in 47% of cases, followed by the *C. pogonias* male (44%); the *C. nictitans* male was rarely the first to react. (2) When the danger came from above ($n=9$), the alarm call was most often given directly by male loud calls: in 8 out of 9 identified cases, the *C. pogonias* male was the first caller; it was never the *C. cephus* male. (3) In other situations involving loud calls and potential danger such as sudden violent noises, the *C. nictitans* male was first to react in 8 out 11 cases.

Thus depending on the source and nature of the danger, the probability of detection and warning was not the same for each species. *C. cephus* situated in the lowest vegetational strata, had the major role in signalling danger coming from the ground. The adult male *C. pogonias* seemed to be the most vigilant individual with regard to birds of prey. Curiously the *C. nictitans* male, situated as is the latter in the highest levels of the forest, reacted later except to vocal stimuli.

Discussion

In the light of these results, we can determine some of the changes that come about when a troop of *C. cephus* associates with a mixed troop of *C. nictitans* and *C. pogonias:* these changes can then be analysed in terms of cost and benefit to provide explanations for the evolution of such polyspecific societies.

This study had several limitations which resulted partly from breakdown of the *C. cephus* 2 transmitter and partly from the characteristics of the species studied. Originally, we planned to quantify the time budgets of the animals in each type of troop, C1, C2, NP and NPC2. This analysis, achieved for C1 (Quris et al. 1981), failed for C2, a troop that was unfamiliar and could not be followed effectively without disturbance. Also, observations of NPC2 were subject to an important bias: for every ten observations of *C. nictitans,* about three were carried out on *C. pogonias* and only one on *C. cephus*. In addition, these differences in observation varied according to the type of activity: they were less serious when animals were feeding in fruit trees, but became extreme during periods of least activity (ratio becoming 10:1.4:0.5 respectively). Consequently, comparison of the temporal distribution of activities, either between species or within the same species, was impossible. We have discarded all results susceptible to these observational biases. Nevertheless the data explain much.

The timid and cryptic *C. cephus* may well 'use' other species and benefit immediately by safety in numbers. By associating with species that are more 'perceptive' like *C. nictitans* and more 'vocal' like *C. pogonias*, the discreet *C. cephus* reduces the probability of any individual being singled out and captured, as predators have a limited prey capacity. Such an advantage has already been reported in the case of small troops of *C. cephus* dispersed amongst large troops of *Miopithecus talapoin* (Gautier-Hion 1971) and appears also to be the strategy displayed by *Colobus verus* in polyspecific troops found on the Ivory Coast (Galat-Luong and Galat 1978).

Does Association Modify Foraging Efficiency?

Association clearly results in a change of habitat use. In the trispecific troop, *C. cephus* had a larger home range, increased the distance travelled daily and visited more hectares each day. Simply by visiting at random 26 ha daily instead of 11, and giving the distribution of fruiting species, the animals had a 95% chance of encountering 5 plant species instead of 3–4 in the dry season, and 11 species instead of 7–8 in the wet season (Fig. 4). But troop movements were not performed at random.

In NPC2 polyspecific troop, probably by reason of a better 'predictability' and directionality of movements, we have shown a less intensive exploitation of the habitat, a significant choice, during the fruit-feeding period, of high forest zones richer in fruit and a better selection inside these zones of areas richer in fruiting trees, fruiting species or both. Associated with C2, *C. nictitans* and *C. pogonias* also cover a larger area each day without any extra locomotor cost and thus seem to benefit from the same advantages. Consequently

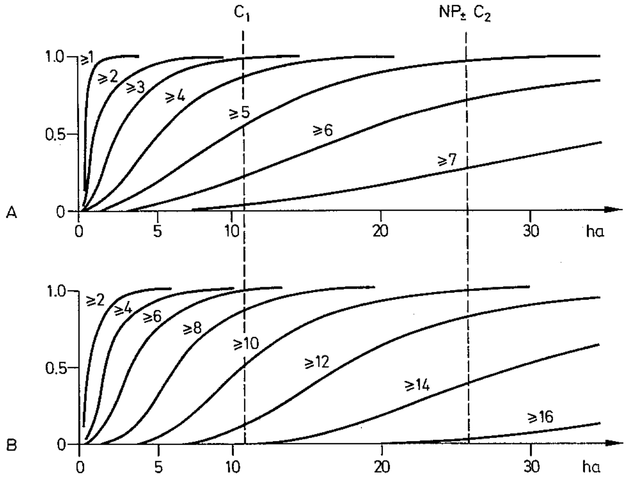

Fig. 4 A, B. Theoretical calculation of the number of plant species fruiting that the animals have a 95% of chance of discovering, given the species density and according to the surface area visited. **A** Dry season; **B** wet season. *Vertical lines* indicate the mean number of hectares visited daily by troops C1 and NPC2

with equal fruit availability, species that associate have a more diversified diet. Another mutual benefit in NPC2 troop, given that the home range of C2 is completely overlapped by the range of NP, is that monkeys did not run the risk of visiting areas already explored by the neighbor, thus reducing the duplication of effort.

It can be argued however that if the search for fruit by the three species together is maximised, it only serves to compensate for the increase in number of consumers and to reduce competition between individuals. Nevertheless, from a quantitative point of view, nothing is altered by association in the short-term since the total biomass of the community living on the study area is unchanged. In fact, the only disadvantage seems to be a slight increase of locomotor cost for *C. cephus*.

The problem appears to be different for catching insect prey; we have no evidence that one or other species benefitted from insect flushed out by a third, as we hypothesised (Gautier-Hion and Gautier 1974; see also Rudran 1978 and Waser 1980). The fact that individuals of the three species are spread out more vertically when collecting insects than for any other activity suggests a potential increase in competition. Given the large overlap in insect diet between *C. cephus* and *C. nictitans* on the one hand, and *C. pogonias* on the other, it is difficult to see what advantage the three species could draw from association during this type of activity.

Why Is Foraging Efficiency Improved in the Trispecific Troop?

The evidence suggests that an association is not simply an aggregation of individuals and its movements are not simply induced by the increase in numbers. Besides, we did not find any correlation between the troops' size and the surface area covered nor the distance travelled daily. Mutual interspecific influences and permanent adjustments between species have been demonstrated: e.g. reduction, except when insect foraging, in the amplitude of the vertical strata used; reciprocal attraction to one or other type of forest according to the type of activity; sharing roles for defence against predators. In addition, we have described elsewhere (Gautier-Hion and Gautier 1974; Gautier and Gautier-Hion 1983) how the organization of the polyspecific troop is controlled by loud adult male calls, with *C. pogonias* taking the leader role and *C. cephus* appearing as a follower species.

One can hypothesise that decisions guiding movement in polyspecific troops are more efficient because sources of information are better and more numerous, owing to the increased number of individuals and their intimate knowledge of their ranges. Thus, *C. cephus* might have a better knowledge of their smaller home range, from which *C. nictitans* and *C. pogonias* would benefit by ranging with them. However, it remains difficult to prove since most movements of the trispecific troop are initiated by *C. pogonias,* while *C. cephus* always seem to follow.

Does Association Diminish Vulnerability to Predators?

Associated with NP, the *C. cephus* are less dependent on the physical structure of the forest than when alone, seeking the low dense forest less. If, as we have hypothesised (Gautier-Hion et al. 1981), this dependence on closed forest is a response to diurnal eagle predation, we can say that *C. cephus* in association is less vulnerable to this type of danger. This could result from the clear division of roles shown in patterns of signalling danger that would increase the probability of detection of predators. The species living in the higher strata would be better informed of terrestrial predators by the species living lower, which in turn is warned of aerial predators by those above. Also, we have seen that cryptic *C. cephus* would make use of the other individuals so as to pass unnoticed, reducing the risk of being captured.

Despite the small number of direct observations of predation by eagles, it seems significant that all involved the smallest *C. cephus*, of which three or four were *C. cephus* living in a monospecific troop. This could explain why this species, as well as its ecological equivalents, has one of the highest rates of association (Gautier and Gautier-Hion 1969, for *C. cephus* in Gabon; Gartlan and Struhsaker 1972, for *C. erythrotis* in Cameroun; Struhsaker 1978, for *C. ascanius* in Uganda; Galat-Luong and Galat 1978, for *C. petaurista* on the Ivory Coast).

Alternatively, association may be disadvantageous for *C. cephus* as regards terrestrial predation, as we experienced at the beginning of the study. While following NPC2 in order to capture and mark a *C. cephus* monkey, we noticed that excessive pursuit of the troop led to the break-up of the association, at the initiative of *C. cephus* who made use of a dense forest zone to stop and hide in silence, sometimes for several hours, while the other monkeys continued on their way. This strategy of hiding in silence is similar to that described in the small groups of *C. neglectus* (Gautier-Hion and Gautier 1978): it is frequently adopted by monospecific *C. cephus* troops, replacing the tactic of alarm calls and flight.

Foraging Efficiency vs Predator Avoidance

We found no relationship between the formation of a mixed troop and the activity of one species around an abundant source of food, nor between variation in the relative abundance of fruit and the seasonal rates of association, nor did daily variations in association correspond with periods of maximum fruit searching. The last point relates in particular first to troop NPC1, which occurred above all during periods of daily resting, second to troop NPC2 in which the three species often share the same sleeping sites during the night. This suggests that the feeding advantage should not be the essential element determining the formation and maintenance of associations.

This led us to propose that predator avoidance constitutes the prime factor in the evolution of polyspecific life. In the case of *C. cephus* in particular, the life in association would have evolved as an efficient strategy to cope with the predation by the monkey-eagle. For this species, two alternative strategies are possible. To live alone, in a small home range, avoiding day-time stops in too open forests and choosing the safest places in dense forest; the disadvantages being the lack of easy access to the richest zones. The second strategy is to live in a polyspecific troop, the most widespread tactic: in this case, the protective cover offered by *C. nictitans* and *C. pogonias* would reduce the impact of predation by the eagle while allowing exploitation of the richest zones. Clearly, as Struhsaker (1981) pointed out, predator avoidance and foraging benefit are not mutually exclusive.

Moving from one way of life to the other would mean an imbalance in one or the other of these factors. Thus an abnormal increase in pressure from terrestrial predators, and notably the pressure of hunting, would remove the benefit of aerial protection and lead to dissociation. In addition, certain differences between troops would simply result from the composition of the populations, a consequence of the physical forest structure. Thus troop C1 had no other opportunity for association, except that offered by NP, since its range was in a forest zone bordering a river, occupied uniquely by *C. neglectus* whose strategy of hiding from predators is incompatible to life in association (Gautier-Hion and Gautier 1978). But NP troop was primarily partner to C2, living closer to it, and the coexistence of C1 and C2 was found to be unstable because of intraspecific competition.

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Appendix

List of fruit species eaten (consumers are indicated by N = ***Cercopithecus nictitans***, P = ***C. pogonias***, C = ***C. cephus***).

Annonaceae: *Polyalthia suaveolens* (N, P, C); *Xylopia hypolampra* (N, P, C); *X. quintasii* (N, C). Apocynaceae: *Landolphia* sp. (N, P, C); indet. (N, P, C). Burseraceae: *Dacryodes buttneri* (N, P); *Santiria trimera* (N, P). Combretaceae: *Combretum* sp. (N, C). Connaraceae: *Byrsocarpus dinklagei* (C); *Castanola paradoxa* (N, P, C). Dichapetalaceae: *Dichapetalum* sp. (P, C). Euphorbiaceae: *Macaranga* sp. (N, P); *Uapaca* sp. (N, P, C). Flacourtiaceae: *Caloncoba* sp. (C). Hippocrateaceae: *Salacia* sp. (N, P, C). Irvingiaceae: *Klainedoxa gabonensis* (N, P, C). Meliaceae: *Trichillia prieureana* (N, P, C). Mimosaceae: *Entada gigas* (N). Moraceae: *Musanga cecropioides* (C). Myristicaceae: *Coelocaryon preussii* (N, P, C); *Pycnanthus angolensis* (N, P, C); *Staudtia stipitata* (N, P). Rubiaceae: *Cuviera* sp. (C); *Nauclea diderrichii* (C). Sapindaceae: *Pancovia pedicellaris* (N, P, C). Sapotaceae: *Gambeya africana* (N, P). Vitaceae: *Cissus dinklagei* (N, P, C)

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