

Cooperation and competition in two forest monkeys

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Putty-nosed monkeys, *Cercopithecus nictitans stampflii*, occur at various sites in West Africa, particularly in the transition zone between rainforest and savannah. The species is sometimes seen in primary rainforest, although at a curiously low density compared with that of other monkey species. We conducted a 24-month field study in the tropical rainforest of Taï National Park, Ivory Coast, and found that putty-nosed monkeys require an ecological niche almost identical to that of the Diana monkeys, *Cercopithecus diana diana*. Moreover, the niche breadth of putty-nosed monkeys was significantly decreased in the presence of Diana monkeys, suggesting that feeding competition with Diana monkeys kept putty-nosed monkeys from successfully colonizing a rainforest habitat. However, contrary to the interspecies competition hypothesis, groups of both species almost completely overlapped in home ranges and formed near-permanent mixed-species associations, rather than avoiding each other. We hypothesized that Diana monkeys tolerated immigrating putty-nosed monkeys and formed mixed-species groups with them, despite high levels of competition, because of their merit in predation defense. Direct observations and a series of field experiments confirmed that male putty-nosed monkeys play a vital role in defense against crowned eagles, suggesting that putty-nosed monkeys obtain access to feeding trees by offering antipredation benefits to Diana monkeys. We discuss these findings in light of biological market theory. *Key words*: alarm calls, biological markets, feeding ecology, mutualism, niche overlap, predation, semantic.

Primates living in tropical forests regularly form large mixed-species associations, often containing several different species. The Taï forest of Ivory Coast is a particularly striking example with six arboreal simian species (*Cercopithecus diana*, *C. campbelli*, *C. petaurista*, *Colobus badius*, *C. polykomos*, *C. verus*), as well as two terrestrial ones (*Cercocebus atys*, *Pan troglodytes*) coexisting at high densities of up to more than two groups per square kilometer (Zuberbühler and Jenny, 2002). The tacit assumption is that these high densities in primate biomass are made possible by species-specific ecological adaptations, in which species exploit a subsegment of the available resources only. Niche separation is thought to decrease interspecies competition and make coexistence of closely related species possible (Gautier-Hion, 1978; Korstjens, 2001; McGraw, 1998, 2000; Wachter et al., 1997; Wolters and Zuberbühler, 2003; Mitani, 1991). Although niche separation explains the coexistence of the seven different monkey species in the Taï forest at high densities, it has left occasional reports of an eighth species, the putty-nosed monkey, largely unexplained.

Putty-nosed monkeys are relatively widespread in both Cameroon and Nigeria, where they can be found in patches of high and gallery forests along rivers (Oates, 1988). The Western subspecies *Cercopithecus nictitans stampflii*, however, is exceedingly rare and only occurs in some very restricted regions of Western Ivory Coast bordering on Liberia (Oates, 1988). Groups are typically found in regions where the rainforest belt borders on the savannah woodland. Occasionally, however, the monkeys can be observed in the rainforest of Taï National Park, but group densities are very low compared

with that of other primate species (Galat and Galat-Luong, 1985; Zuberbühler and Jenny, 2002). In addition, their distribution in the Taï forest follows a north-south gradient, and the species has never been seen in the southern parts of the park, despite regular and long-term survey work (Radl G, personal communication). There are no obvious ecological gradients that would explain the skewed north-south distribution, and no other Taï primate species shows a similar geographical distribution. Diana monkeys (*Cercopithecus diana diana*), for example, are found throughout the Taï forest, originally having occupied the entire range covered by rainforest belt between Ivory Coast and Sierra Leone. Figure 1 illustrates the current distribution pattern of the two species.

These and other observations have led to the hypothesis that the skewed distribution of putty-nosed monkeys is the result of interspecies competition with Diana monkeys (Gautier-Hion, 1978; Gautier-Hion et al., 1983; Oates, 1988, Oates and Whitesides, 1990). Here, we report the results of a 24-month field study launched to investigate this hypothesis. We reasoned that putty-nosed monkeys could not establish themselves successfully in the rainforest habitat owing to competition with the more dominant Diana monkeys. In the first part of the present study, we tested this idea by comparing the ecological niches occupied by the two monkey species. We predicted that if both species competed for the same ecological niche, then their niche overlap must be substantially larger than what is normally reported from closely related sympatric species, and the outcome of this competition must be in favor of the Diana monkeys. Second, we expected that the niche breadth of the competitively weaker species should be compromised by the presence of the more dominant species.

Various studies have found that in tropical forests the different primate species often not only tolerate each other but also form mixed-species groups, presumably to cooperate

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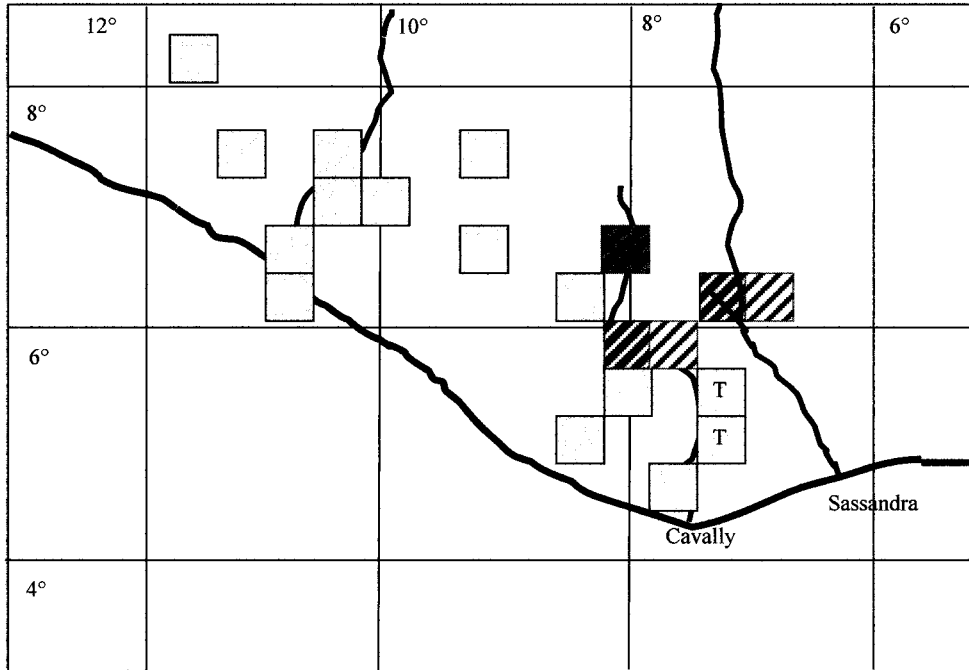


Figure 1
Geographic distribution of *C. nictitans stampflii* (hatched light areas) and *C. diana diana* (gray areas; data from Oates, 1988; Oates J, records 1950–1988). T indicates Tai National Park. Diana monkeys are common, but putty-nosed monkeys are very rare in the northern part of the park and absent in the southern part. In 2002, several groups of putty-nosed monkeys have been found in the savannah Mont Sangbé National Park, along the forests of the Bafing river (Rainey H, personal communication).

in antipredation defense against leopards (*Panthera pardus*, Zuberbühler and Jenny, 2002; Zuberbühler et al., 1999a), crowned eagles (*Stephanoaetus coronatus*, Shultz, 2001), and chimpanzees (*Pan troglodytes*, Boesch and Boesch, 1989). A series of observational and experimental studies has shown that these mixed-species associations have evolved as anti-predator strategies (see Noë and Bshary, 1997; Wachter et al., 1997). Mixed-species associations are common throughout Africa both East and West (see Marler, 1973; Struhsaker, 1975) and only very few species, such as *C. neglectus*, are known to avoid them (Gautier-Hion and Gautier, 1974). In light of the presumed high competition between Diana monkeys and putty-nosed monkeys, their mixed-species associations are of particular interest. Given their potentially high niche overlap, we expected that putty-nosed monkeys actively avoided the Diana monkeys, similar to the behavior observed in *C. neglectus* toward potential partner species. In addition, we expected groups of putty-nosed monkeys to establish the core area of their home range in the periphery of the local Diana monkey groups' home ranges to avoid competition over food.

An alternative hypothesis suggested that Diana monkeys might tolerate putty-nosed monkeys despite high levels of feeding competition, if putty-nosed monkeys were valuable partners in predation defense. In that case, we expected members of the putty-nosed monkey group to engage in antipredator behavior, particularly also when associated with or nearby a group of Diana monkeys. We tested this idea by playing back various predator-related stimuli to imitate the presence of a crowned eagle or a leopard, two of the main predators of the Tai monkeys (Zuberbühler, 2002). We analyzed the locomotor and vocal behavior of putty-nosed monkeys in response to these stimuli and assessed their potential benefit for the Diana monkeys.

METHODS

Study site and species

Data were collected in the Tai National Park, Côte d'Ivoire, about 25 km southeast of the township Tai close to the field

research station of the Centre de Recherche en Ecologie (5°50' N, 7°21' W). The observational study began in January 2000 with a 12-month habituation phase, during which we habituated two mixed-species groups of putty-nosed monkeys and Diana monkeys to observers on foot. Both species form one-male groups with several adult females and their offspring. However, in July 2001 data collection on the first mixed-species group had to be discontinued because of high levels of poaching in the area, which impeded the progress of habituation and systematic data collection. Habituation of the second mixed-species group was continued normally, and data collection took place between January and December 2001. The Diana monkey group of the second mixed-species association consisted of one adult male, 12 adult females, five subadults, seven juveniles, and two infants born in October, resulting in a group size of about 25–27 individuals. The putty-nosed monkey group consisted of one adult male, four adult females, five subadults, two juveniles, and no infants, resulting in a group size of 12 individuals.

Observational data collection and analyses

The monkey groups were followed during full (0800–1700 h GMT) or half days (0800–1230 h or 1230–1700 h GMT). The Diana monkey group was observed for 1163.5 h ($N = 149$ days), the putty-nosed monkey group for 1179.0 h ($N = 157$ days). Data were collected by using scan sampling (Altmann, 1974). To make the data comparable with previous studies (see McGraw, 1996; Shultz et al., 2003; Wolters and Zuberbühler, 2003), we conducted scans at every 30 min throughout the day. Scans were usually completed within the first 5–10 min of each 30-min interval but never lasted longer than 15 min, suggesting that data points were largely and equally independent of each other. For each scan, the association state of the focal group with the other monkey species was determined as either associated (the distance between the individuals of two groups was less than 50 m) or not associated (the distance between the individuals of two groups was more than 50 m).

During each scan the observer tried to sample as many

individuals as possible by walking underneath the group to determine the vertical position of every sighted individual. Following the method of Bshary (1995), we distinguished six vertical strata, which we then collapsed into three groups: ground (0 m), lower canopy (1–15 m), and higher canopy (more than 15 m). Larger trees are likely to have bigger crowns, offering more plant parts and, thus, bigger food patches. If monkeys were eating during a scan, we also determined the diameter of the tree at breast height (DBH), measured in centimeters, as an indicator of food patch size. DBH has been shown to positively correlate with food availability (Chapman et al., 1992). DBH is an unreliable indicator of food patch size in liana and ficus species, and we therefore excluded them from analysis.

If a monkey was foraging during a scan, we noted the species and part of the plant that the monkey was eating, distinguishing the following categories: fruit (unripe versus ripe), leaf (young versus mature), flower (bud versus blossom), invertebrate animal, or other items (stem, mushroom, bark, termite soil). We used these data to calculate diet overlap by using the percentage overlap method by Renkonen (Krebs, 1989) based on the various plant categories. For example, if individuals of both species fed on the same tree, but on different parts (e.g., young versus mature leaves), then we did not consider this as a case of diet overlap:

$$P_{jk} = \left[\sum_{i=1}^n (\min p_{ij}, p_{ik}) \right] 100 \quad (1)$$

where P_{jk} is the percentage overlap between species j and species k ; p_{ij} is the proportion resource i is of the total resources used by species j ; p_{ik} is the proportion resource i is of the total resources used by species k ; and n is the total number of resource states.

Previous work on three species of Colobines in the Taï National Park has shown an average monthly percentage overlap of 12.4% between *Procolobus verus* and *C. badius* and of 1.9% between *P. verus* and *C. polykomos* (Bergmann, 1998), indicating clear niche separation between the three Colobine species. Hence, if Diana monkeys and putty-nosed monkeys competed for the same ecological niche, their average diet overlap should be substantially larger than the one observed for the Colobines. We also calculated Morisita's index (Krebs, 1989) because it has been suggested that this is a better estimate of niche overlap compared with percentage based overlap measures, including the Renkonen index (Smith and Zaret, 1980):

$$C = \frac{2 \sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij} [(n_{ij} - 1)/(N_j - 1)] + \sum_i^n p_{ik} [(n_{ik} - 1)/(N_k - 1)]} \quad (2)$$

where C is Morisita's index of niche overlap between species j and species k ; p_{ij} is the proportion of resource i is of the total resources used by species j ; p_{ik} is the proportion of resource i is of the total resources used by species k ; n_{ij} is the number of individuals of species j that used resource category i ; n_{ik} is the number of individuals of species k that use resource category i ; and N_j and N_k are the total number of individuals of each species in sample

$$\sum_{i=1}^n n_{ij} = N_j, \quad \sum_{i=1}^n n_{ik} = N_k$$

Finally, we calculated niche breadth by using the standardized Levins index (Krebs, 1989) to determine how each species' feeding behavior was affected by the presence of the association partner:

$$B = \frac{1}{\sum p_j^2} \quad B_A = \frac{B-1}{n-1} \quad (3)/(4)$$

where B is Levin's niche breadth; p_j is the proportion of resource category of the total diet; B_A is Levin's standardized niche breadth; and n is the number of resources.

We predicted a decrease of niche breadth in the competitively weaker species, but a smaller or no change in the competitively stronger species. In addition, we noted all instances of interspecific aggression between both monkey species on an ad libitum basis throughout the day. We also noted all observations of interactions with predators both during playback experiments and during observed and suspected predator encounters.

Home range size, finally, was determined with a global positioning system (GPS) receiver (Garmin 12 XL). Readings were taken every 30 min during scans from end of August–December 2001 by using the group's center of mass. These data were transcribed onto a coordinate system with a 0.25-ha grid cells (i.e., 50 × 50 m). Grid cells containing at least one GPS reading were considered part of the home range. There is some concern that the sampling period was not long enough to get an accurate measure of home range size, because some rarely used grid cells might not be included in the data set. However, in the present study we were interested in core area overlap between the two species, rather than absolute home range size.

Experimental data collection and analyses

Experiment 1: putty-nosed monkey responses to predator stimuli

Playback experiments were conducted to establish whether putty-nosed monkeys produced acoustically distinct predator alarm calls. We focused on the vocal behavior of the adult male because other studies have shown that adult male guenons produce predator-specific alarm calls in response to eagles and leopards (see Seyfarth et al., 1980; Zuberbühler, 2000, 2001). Real encounters with crowned eagles have shown that adult male putty-nosed monkeys regularly attack this predator, while producing very loud and conspicuous alarm calls, which are acoustically different from the calls of other group members. To determine whether there is a relationship between the acoustic structure of the alarm calls and the eliciting stimuli, we conducted a series of playback experiments by using predator vocalizations (eagle shrieks and leopard growls). During a playback trial, the equipment was positioned close to the ground (0–2 m). Both crowned eagles and leopards have been observed to vocalize from the ground, indicating that the experiment simulated a natural situation. All sounds were recorded in the study area (crowned eagle shrieks) or purchased from the National Sound Archive, London (leopard growls). Playbacks of predator vocalizations consisted of a 15-s continuous recording. Each playback tape was edited such that a 5-min period of empty tape preceded the actual playback stimulus. During this time the experimenter (W.E.) positioned herself about 50 m away from the playback equipment and started recording the monkeys' vocal behavior and noted all direct observations on the monkeys' locomotor behavior. Playback stimuli were broadcast with a Sony WMD6C Professional Walkman connected to a Nagra DSM speaker-amplifier. Vocalizations were tape-recorded with a Sony Portable Minidisc (MZ-R91) recorder and a Sennheiser directional microphone.

Experiment 2: Diana monkey responses to putty-nosed monkey eagle alarm calls

Pilot observations suggested that male putty-nosed monkeys play an important role in defense against crowned eagles by

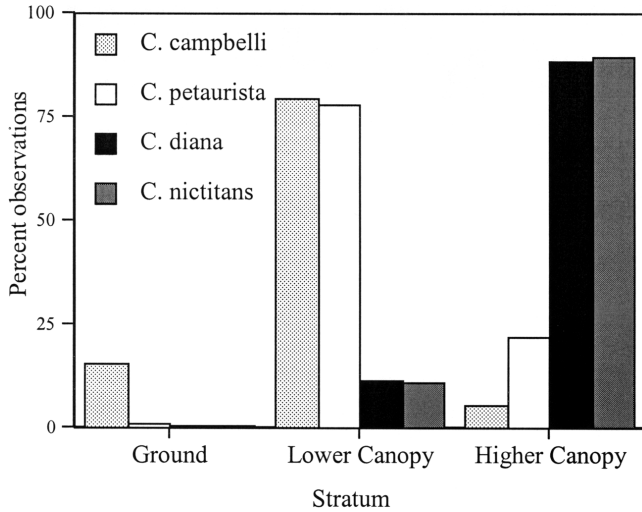


Figure 2
Use of vertical forest strata by the two study groups of putty-nosed monkeys ($N = 8425$) and Diana monkeys ($N = 10,888$) compared to the other guenon species in the Taï forest (data from McGraw, 2000).

attacking the predator and giving alarm calls. To determine whether the male putty-nosed alarm calls inform Diana monkeys about the presence of crowned eagles, we played back recordings of putty-nosed alarm calls given to a crowned eagle to five different groups of Diana monkeys located throughout a 100-km² study area. The putty-nosed monkey eagle alarm calls used as playback stimuli were recorded in the study area by using a Sony WMD6C Professional Walkman connected to a Sennheiser directional microphone. Two different master recordings were used to make the playback tapes. In both cases, a male putty-nosed monkey responded to a playback of eagle shrieks by giving loud and conspicuous alarm calls. The vocal response of putty-nosed monkeys to leopards is much less striking compared with their response to crowned eagles, and systematic investigations will be presented elsewhere. None of the five Diana monkey groups examined in this experiment were habituated to human presence, but all of them lived in areas of the forest where putty-nosed monkeys had been located before, suggesting that they were familiar with putty-nosed alarm calls. We predicted that if the Diana monkeys were able to use the putty-nosed monkey alarm calls as semantic signals to indicate eagle presence, then they should respond to them as if the corresponding predator were present (see Zuberbühler, 2000). The five groups were located at least 1 km apart from each other, which ensured that each group was only tested once. These playback experiments were conducted between August and October 1996 by K.Z., using the same standard playback methods described earlier (Zuberbühler et al., 1997). Because these groups were not habituated to human presence, groups were kept unaware of the experimenter's presence.

RESULTS

Interspecies competition and niche overlap

As predicted by the interspecies competition hypothesis, both Diana and putty-nosed monkeys occupied a very similar ecological niche. Both species used the vertical strata in the same way, with a clear preference for the upper forest canopy. This contrasted strongly with the strata use of other frugivorous primates of Taï forest, particularly the other

guenon species, which occupied niches in the lower forest canopy (Galat and Galat-Luong, 1985; McGraw, 2000) (Figure 2). Strata use of Diana and putty-nosed monkeys did not differ significantly from each other ($z = 0.632$; $p > .5$; $N = 5$ strata; Kolmogorov Smirnov-test; two-tailed).

Similarly, the use of food patches by the two study groups as measured by DBH was virtually identical and statistically indistinguishable for the 12 months considered (monthly average *C. diana* = 167.6 ± 23.6 cm; $N = 12$ months; $N = 709$ trees; monthly average *C. nictitans* = 160.4 ± 28.8 cm; $N = 12$; $N = 574$ trees; $z = 1.112$; $p > .2$; Wilcoxon test; two-tailed).

The food preferences of the two monkey species were also very similar (*C. diana*, $N = 1,828$; *C. nictitans*, $N = 1,442$). Both species relied heavily on fruits (*C. diana*, 70.9%; *C. nictitans*, 58.9%) and invertebrates (*C. diana*, 26.5%; *C. nictitans*, 31.2%), together accounting for more than 90% of all consumed food items in both monkey species. The remaining food items consisted of leaves, flowers, and other items. The vegetal diet of *C. nictitans* over the entire year consisted of items from 71 plant species (29 families), which was somewhat more diverse than the vegetal diet of *C. diana*, which contained items from 49 plant species (21 families). Items from 25 plant species (35.2%) consumed by *C. nictitans* were not consumed by *C. diana*, however, this accounted for only 7.8% of the total vegetal diet. Similarly, *C. diana* consumed items from 9 (18.4%) plant species exclusively, which accounted for 3.6% of their vegetal diet. *C. nictitans* was more likely to consume items from liana species than were *C. diana*. The fruit diet was extremely diverse in both monkey species (*C. diana*, more than 44 tree species; *C. nictitans*, more than 56 tree species); 97.8% of all fruits consumed by *C. diana* came from trees with fruits that were also consumed by *C. nictitans*. Conversely, 90.8% of all fruits consumed by *C. nictitans* were from trees with fruits that were also consumed by *C. diana*. Table 1 lists the most popular fruit species (i.e., more than 2% in one or both monkey species).

Average monthly niche overlap between the two monkey species was 69.7% ± 9.7 (Renkonen's formula) or 93.7 ± 9.7 (Morisita's index), revealing extremely high niche overlap, a crucial prerequisite for high feeding competition between the two species. Visual inspection of the two measures indicated that both curves had the same shape, suggesting that the percentage-based method by Renkonen generated an accurate estimate of niche overlap. There was no significant relationship between rainfall and niche overlap over the 12 study months (Renkonen $r_s = -.018$; $z = 0.058$; $p > .9$, Spearman rank correlation; Morisita's index: $r_s = -.018$; $z = 0.058$; $p > .9$, Spearman rank correlation).

Interspecies competition and niche breadth

Next, we determined niche breadth for both species as a function of association, using Levins' standardized measure (Krebs, 1989). The niche breadth of putty-nosed monkeys significantly decreased when associated with Diana monkeys compared with other times (Wilcoxon test, two tailed, $z = 2.201$; $N = 6$ months; $p < .03$). In comparison, the niche breadth of Diana monkeys was not significantly affected by the presence of the putty-nosed monkey group (Wilcoxon test, two-tailed; $z = 0.845$; $N = 7$ months; $p > .3$), indicating that the Diana monkeys are less affected by interspecies competition than were the putty-nosed monkeys.

Interspecies competition and feeding behavior

The following analyses were conducted to provide further evidence for competition between the two species. First, we analyzed whether the competitively weaker putty-nosed

Table 1

The most preferred fruit species for Diana monkeys and putty-nosed monkeys (more than 2% in diet in at least one of the two species)

Species	Family	DBH (cm)	DIA (N = 1,297)	NIC (N = 840)
<i>Dialium aubrevillei</i>	Caesalpiniaceae	171.5 ± 34.0 (N = 929)	45.7	42.0
<i>Sacoglottis gabonensis</i>	Humiriaceae	370.9 ± 85.1 (N = 290)	15.1	12.1
<i>Oldfieldia africana</i>	Euphorbiaceae	255.7 ± 61.5 (N = 77)	5.9	0.2
<i>Scytopetalum tieghemii</i>	Scytopetalaceae	124.9 ± 27.2 (N = 61)	4.3	0.6
<i>Castanola paradoxa</i>	Connaraceae	*	4.2	3.5
<i>Diospyros sanza-minika</i>	Ebenaceae	101.4 ± 27.0 (N = 68)	3.4	3.5
<i>Uapaca guinensis</i>	Euphorbiaceae	349.5 ± 57.9 (N = 51)	2.5	2.4
<i>Pycnanthus angolensis</i>	Myristicaceae	249.1 ± 53.5 (N = 55)	2.2	3.1
<i>Hippocratea myriantha</i>	Hippocrataceae	^a	0.8	3.7
<i>Xylopia quintasii</i>	Annonaceae	79.6 ± 19.2 (N = 20)	0.1	2.5
<i>Connarus africanus</i>	Connaraceae	^a	—	3.1
Total			84.2	76.7

^a Liana species: DBH unreliable as an indicator of food patch size.

monkeys suffered from a reduction of food intake owing to the presence of the Diana monkeys. Food intake was assessed by comparing feeding rates, that is, the percentage of individuals occupied with feeding behavior per scan. On average, Diana monkeys were occupied with feeding behavior in 17.0%, putty-nosed monkeys in 17.2% of the time, not a significant difference ($z = -0.800$; $N = 12$; $p > .42$; Wilcoxon test; two-tailed). It was also not the case that the two species fed less while in associations with each other than at other times (*C. nictitans*: $z = 0.085$; $n = 7$; $p > .9$; *C. diana*: $z = 0.338$; $N = 7$; $p > .7$; Wilcoxon tests; two-tailed).

Second, interspecies competition had significant effects on the quality, rather than the quantity of consumed food items. Diana monkeys consumed significantly more fruit than did putty-nosed monkeys ($z = -2.353$; $N = 12$; $p < .02$; Wilcoxon test; two-tailed). Both groups showed a clear preference for feeding on the fruits of *Dialium aubrevillei* from March–August. The feeding rates of the two species on *Dialium* fruits were highly and significantly correlated ($r_s = .895$; $z = 2.960$; $p < .004$; Spearman rank correlation). The Diana monkeys' intake of this desired fruit was significantly higher than that of the putty-nosed monkeys' ($z = 2.073$; $p < .04$; $N = 12$; Wilcoxon test; two-tailed) (Figure 3), further suggesting that putty-nosed monkeys were the competitively weaker species.

Third, in both species, there was a significant negative relationship between fruit and invertebrate consumption throughout the 12 months, suggesting that both species of monkey compensated for the lack of fruit by increasing invertebrate consumption (ANOVA: *C. diana*: $F_{1,10} = 171.1$;

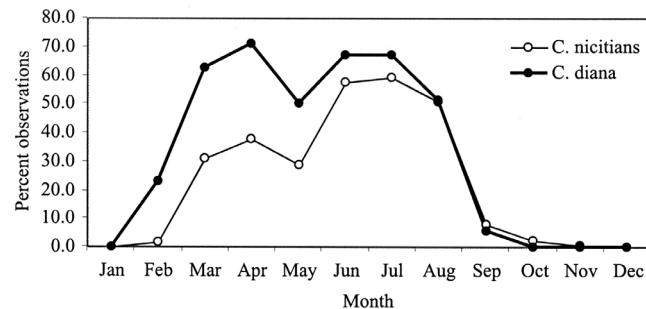


Figure 3
Annual pattern of consumption of *Dialium aubrevillei* fruits in putty-nosed and Diana monkeys. *Dialium* fruits are available.

$p < .001$; *C. nictitans*: $F_{1,10} = 31.923$; $p < .001$) (Figures 4 and 5). However, *C. nictitans* was affected more strongly by this shift in diet than was *C. diana*. During three out of 12 months, consumption of invertebrate items was higher than was

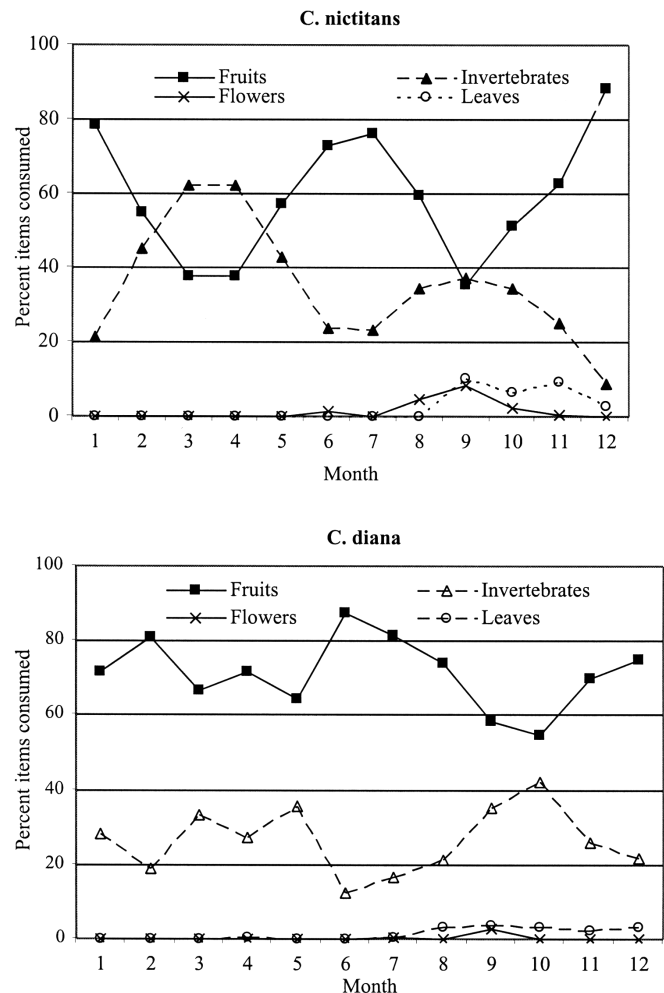


Figure 4
Relative proportion of four different food items in both species throughout the year.

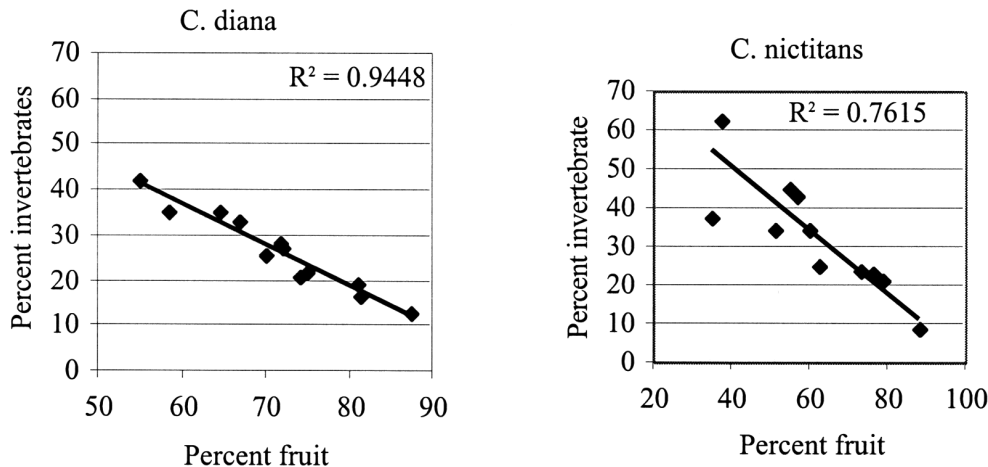


Figure 5
Relationship between consumption of fruit and invertebrates.

consumption of fruit items. In addition, both monkey species compensated the decrease in fruit availability from July–September by increasing their consumption of flowers and leaves, but again the putty-nosed monkeys were affected much more strongly than were the Diana monkeys (Figure 4).

Interspecies competition and interspecies aggression

Although both monkey species frequently fed on the same trees, interspecific aggression was rarely observed. At the end of the *Dialium* season in late July, however, aggressive interactions between the two species increased dramatically and occurred regularly (Table 2).

There was a significant negative relationship between *Dialium* availability (as measured by *C. nictitans* consumption) and aggression by Diana monkeys, suggesting that putty-nosed monkeys were increasingly harassed as fruit availability decreased from June–November (ANOVA: $F_{1,4} = 25.574$; $p < .008$). As a consequence, putty-nosed monkeys were rarely seen in the same tree with Diana monkeys during August and September. Instead they rapidly fled from feeding trees upon arrival of the Diana monkey group. Sometimes, they progressed before the Diana monkey group, presumably to reach a feeding tree first. Upon arrival, the Diana monkeys typically chased all putty-nosed monkeys out of the tree before starting to feed themselves. Sometimes, the putty-nosed monkeys appeared to wait until all Diana monkeys had left the feeding tree before entering it for whatever fruits the Diana monkeys had left behind. This period of interspecies aggression initiated by the Diana monkeys was not restricted to the

feeding context but occurred often and without any apparent reason. As a consequence, association rates of the Diana monkey group with the putty-nosed monkeys were lowest in these 2 months, dropping from more than 90% ($N = 249$) in July to about 60% in August ($N = 170$), to less than 50% in September ($N = 264$). The same drop from 90% ($N = 249$) to 60% ($N = 183$) was also found in the putty-nosed group, although they were able to compensate somewhat in September (about 70%; $N = 290$) by forming short and temporary associations with two neighboring Diana monkey groups, which did not normally associate with them. In conclusion, these observations suggested that Diana monkeys tolerated the putty-nosed monkeys in their vicinity as long as food resources were not a limiting factor.

An alternative hypothesis suggested that the increased levels of aggression were not owing to food shortage but a mere byproduct of the two monkey species being forced to feeding in smaller trees, after the end of the *Dialium* season. A comparison of the median size of feeding trees throughout the year showed that tree size was not a relevant factor in causing interspecies aggression and competition (Figure 6).

The two monkey species did not differ in their selection of tree size throughout the year ($z = -1.112$; $p > .2$; $N = 12$; Wilcoxon test, two-tailed). Moreover, contrary to the tree size hypothesis, the median size of trees visited during August and September was slightly larger than the annual average for both species (Figure 6).

Interspecies competition and mixed-species associations

Given that both monkey species occupied the same ecological niche and feeding competition was extremely high, one might reasonably predict that the two species should actively avoid each other and establish their home ranges so that interspecies interactions are minimized. In particular, (1) the two species should avoid forming mixed-species associations with each other, and (2) the competitively weaker species, *C. nictitans*, should establish its home range in the periphery of the neighboring Diana monkey groups. Figures 7 and 8 show that this was not the case. Despite intense feeding competition, both groups formed semipermanent associations at almost all times. Similarly, the home ranges of the two study groups overlapped to a very large degree. The putty-nosed group used 89.4% (Figure 8) of the Diana monkey home range. The latter occasionally associated with one of the neighboring Diana monkey groups as well, which explained the slightly bigger home range and lesser degree of overlap.

Table 2

Diana monkey aggression towards putty-nosed monkeys

Period	Focal observation of mixed group (h)	Aggression rate (observations/h)	<i>Dialium</i> availability (% <i>C. nictitans</i> diet)
June	73.8	0.000	57.2
July	115.9	0.043	58.9
August	48.4	>0.000a	50.7
September	103.7	0.125	7.8
October	116.2	0.232	2.5
November	74.8	0.187	0.5

^a Underestimated value owing to interim data collection by a field assistant.

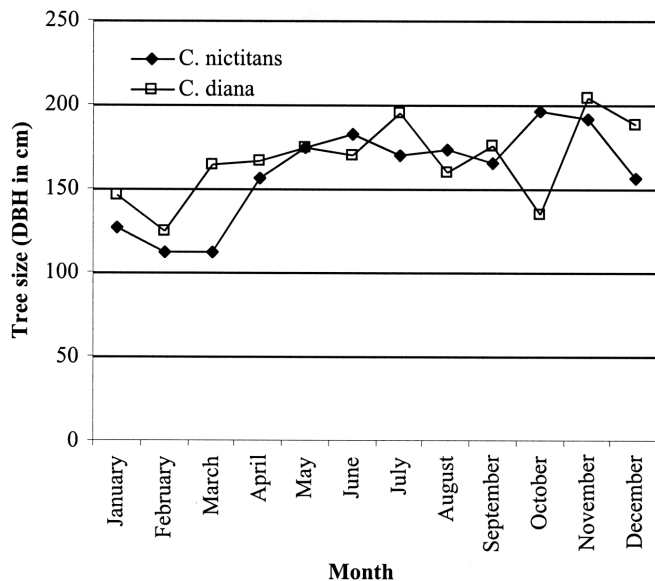


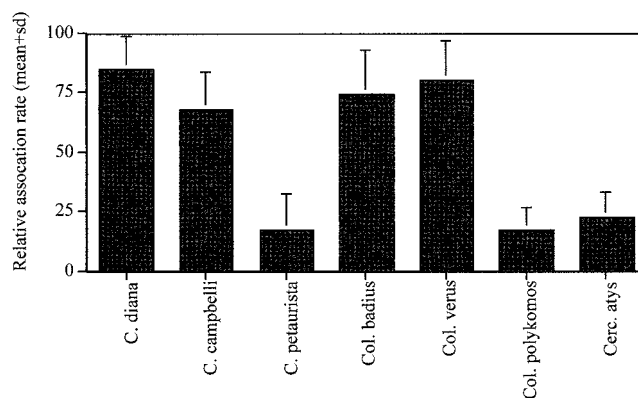
Figure 6
Average food patch size of both species throughout the year.

Interspecies cooperation: putty-nosed monkey responses to predators

Association patterns and home range use suggested that Diana monkeys benefited from the presence of putty-nosed monkeys in some important way, outweighing the costs of feeding competition. A number of observations suggested that putty-nosed monkeys are extremely valuable as a partner species because of their vigorous antipredator behavior in the presence of crowned eagles, which exert strong predator pressure on the study groups. Although real predator encounters occur very frequently, they are exceedingly difficult to observe, let alone to study systematically in the extremely dense Tai forest. Nevertheless, it was often possible to infer the occurrence of antipredator behavior by putty-nosed monkeys indirectly. Almost daily, and sometimes even several times per day, we heard alarm calls of the adult male putty-nosed monkey, most likely in response to eagle presence or attacks. We never saw a leopard or chimpanzee attack, although both are abundant in the study area (Herbinger et al., 2001; Jenny, 1996). In the presence of an eagle, the adult males of both groups engaged in vigorous antipredator behavior. The following observed case illustrates the general pattern: both groups were foraging close to a clearing. Suddenly, the putty-nosed monkey male ran into one direction while giving loud alarm calls. From the opposite side, the Diana male also started calling and ran toward the same location. Together, both males then attacked a large raptor, presumably a crowned eagle, which subsequently flew away, as both males chased it for another 20 m.

To investigate the predation-defense hypothesis more systematically, we conducted a series of field playback experiments to determine whether putty-nosed monkeys engaged in predator-specific alarm calling and whether Diana monkeys were able to use these calls as indicators of predator presence. Recordings of predator-related stimuli played back to the study groups caused strong vocal responses in both species. Diana monkeys responded with their predator-specific alarm calls as described in previous studies (see Zuberbühler et al., 1997). Putty-nosed males and females also responded by giving alarm calls. The calls of the adult male were particularly

(a) Putty-nosed monkeys



(b) Diana monkeys

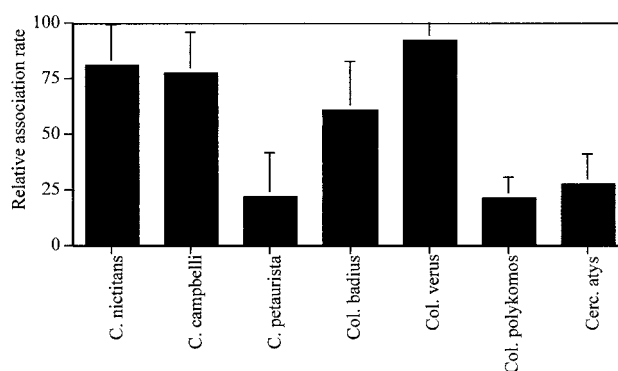


Figure 7
Monthly mean association rates (including standard deviation) of the putty-nosed monkey (a) and the Diana monkey (b) study group with the other Tai monkeys.

striking. Two different call types could be distinguished by ear, the “tock” and the “zeck” calls (Figure 9). Call structure appeared to be determined by the predator type present (Table 3).

During the first playback experiment with eagle shrieks, the adult male and two adult females of the putty-nosed monkey group were seen resting in the higher canopy strata in two different trees grouped around a clearing. The male immediately responded by giving loud alarm calls to the sound of eagle shrieks. At the same time, he climbed higher and circled around the group, continuously scanning the environment and particularly the sky. The adult females stayed together and did not change their position in the canopy. Visibly agitated, they continuously vocalized and scanned the environment, too. After the first three alarm calls of the putty-nosed male, the adult male of the nearby Diana monkey group also began calling and suddenly appeared next to the putty-nosed male to scan the sky as well.

Interspecies cooperation: Diana monkey responses to putty-nosed monkey alarm calls

Five different Diana monkey groups, which were located in the vicinity of a putty-nosed monkey group throughout the forest, responded to playback of putty-nosed eagle alarm calls as if a crowned eagle were present (Figure 10). All groups responded by increasing their contact, general alert, and eagle alarm call rates. Comparisons with the Diana monkeys' typical responses to two of their predators, as well as their own males' alarm calls, suggested that the five Diana monkey

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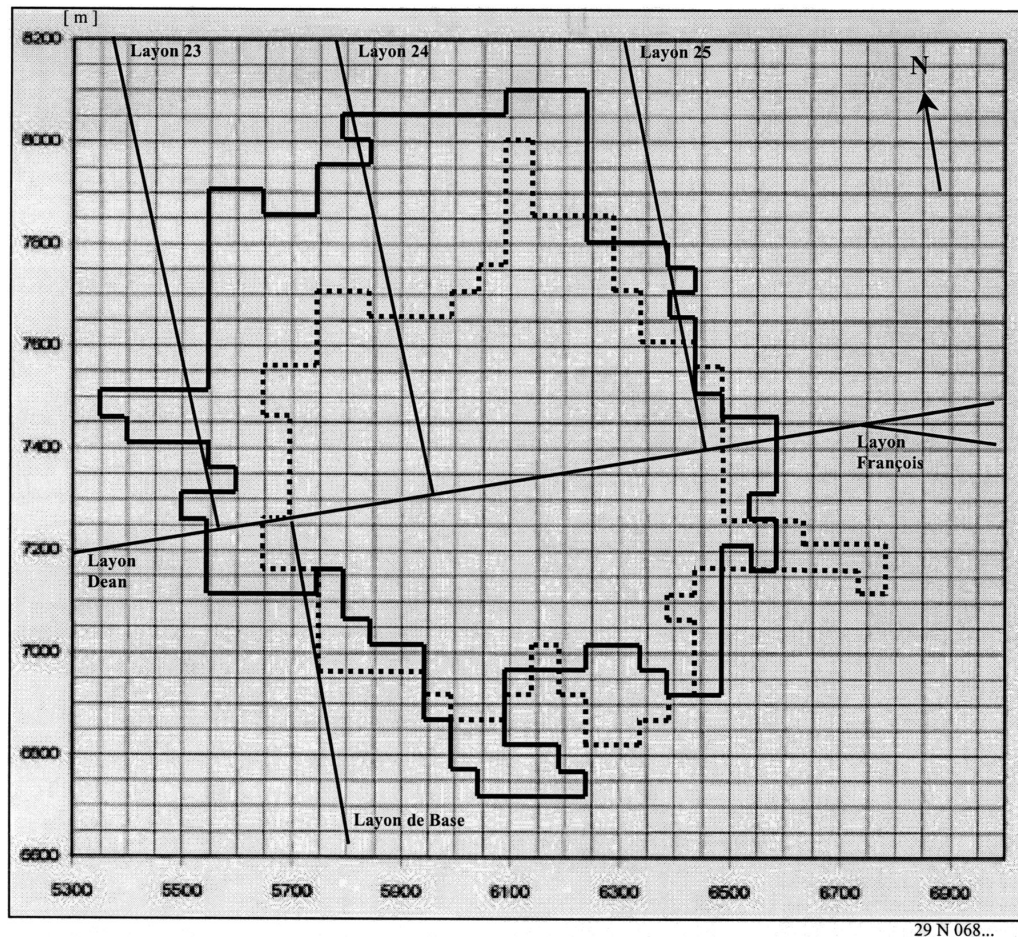


Figure 8

Home range of the two study groups (solid line indicates putty-nosed monkeys; $N = 987$ GPS locations; hatched line indicates Diana monkeys; $N = 595$ GPS locations; each square represents an area of 50×50 m).

groups tested interpreted the putty-nosed eagle alarm calls as a clear sign of eagle presence (Figure 10).

Fisher Exact probability tests were used to compare the vocal responses of the adult females. In these tests, we asked whether the utterance of one or more calls of a specific type was independent of the playback stimulus. None of the experimental groups were habituated to human presence, and so it was impossible to ascertain which and how many individuals were responsible for the recorded calls. However, previous work has shown that in Diana monkeys usually two to three adult females produce predator-specific eagle or leopard alarm calls (Zuberbühler et al., 1999b). Thus, we determined whether or not at least one eagle or leopard alarm call was given in response to a particular playback stimulus. This analysis was conservative because it treated each trial as an independent event and made no assumption about the extent to which individuals in any given trial responded independently of one another. Female Diana monkeys were significantly more likely to give one or more of their eagle alarm calls when hearing a playback with putty-nosed eagle alarm calls ($N = 5$) than when hearing a playback with leopard growls ($N = 12$; $p < .001$; Fisher test) or a playback with their own males' leopard alarm calls ($N = 11$; $p < .001$; Fisher test). Females were significantly less likely to give one or more of their leopard alarms when hearing a playback with putty-nosed eagle alarm calls than when hearing a playback

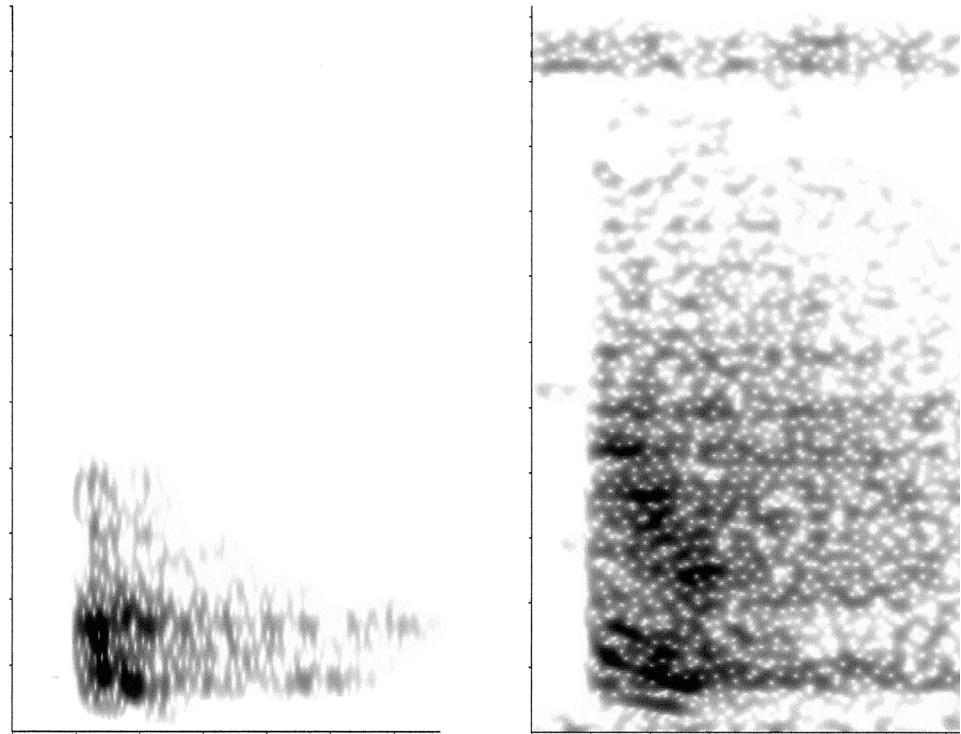
with leopard vocalizations ($N = 12$; $p < .001$; Fisher test) or a playback with their own males' leopard alarm calls ($N = 11$; $p < .02$; Fisher test). There was no significant difference, however, in the occurrence of one or more of their own female eagle alarms after hearing playbacks of putty-nosed eagle vocalizations or eagle shrieks ($N = 13$; $p > .3$; Fisher test) or a playback with their own males' eagle alarm calls ($N = 9$; $p > .6$; Fisher test).

DISCUSSION

The purpose of the present study was to determine why putty-nosed monkeys were so rare in the Taï forest, despite high food availability and relative protection from human activity (Anderson, 2002; Bshary, 2001). Our analyses showed that niche overlap between putty-nosed monkeys and Diana monkeys was very strong, suggesting a high degree of feeding competition. Further, both species used the forest strata in the very same way, which was substantially different from the other guenon species, *C. campbelli* and *C. petaurista*. Both species occupied similarly sized food patches, mainly consuming fruits and invertebrates, but only small amounts of leaves, flowers, and other items. There was a large overlap in the tree species from which the two species consumed food items, and only a small proportion of the vegetal diet was consumed by one species only. Although feeding competition was high,

Eagle

Leopard

**Figure 9**

Male putty-nosed monkey alarm calls given in response to crowned eagle or leopard. Calls were digitized with ESS Audio Drive Record 220 software at a sampling rate of 44.1 kHz with 16 bits accuracy. A 5.5-kHz segment of the entire 22-kHz frequency range is depicted. The spectrograms were made with the software package CANARY 1.2.4 (Charif et al., 1995). The following settings were used: 1024-point Fourier transformation; Hanning window function; 171-Hz analysis resolution; 10.77-Hz spectral resolution; 4096 points window length; and 0.36-ms temporal resolution.

interspecific aggression was rarely observed. Individuals frequently sat in the same trees, both during feeding and other activities. However, from the end of July when fruits of *D. aubrevillei* became more rare while ripe fruits of *Sacoglottis gabonensis* were still unavailable (Anderson, 2002), aggressive interactions between the two species increased dramatically. During these months, putty-nosed monkeys were rarely seen in the same tree with Diana monkeys, but seemed to avoid them, using various tactics. During this period, interspecies aggression occurred frequently at any time of the day and in any context. For example, during one resting period two Diana monkeys attacked four putty-nosed monkeys, apparently for no reason, and chased them over a considerable distance. Shortly thereafter, the two groups separated. Aggression by female Diana monkeys can be very dangerous, sometimes resulting in fatal injuries (McGraw et al., 2002). In contrast, none of the six other monkey species ever showed any overt aggressive behavior toward members of the putty-nosed monkey group.

Both species compensated for low fruit availability with increased consumption of invertebrates, although putty-nosed monkeys were affected more strongly. Aggressive behavior of

Diana monkeys toward putty-nosed monkeys was inversely related to the availability of two of the key fruits, *Dialium* and *Sacoglottis*, suggesting that putty-nosed monkeys' expansion into the rainforest habitat could be constrained by the availability of food. Availability of invertebrates during the poorer fruit months also seemed to play a role, particularly for putty-nosed monkeys. The individuals' ability to capture invertebrates, therefore, might be another constraining factor in the expansion of this species into the forest habitat.

We showed that despite high levels of interspecies feeding competition, both species regularly formed mixed-species associations at rates exceeding most previous reports in the Taï forest (see Galat and Galat-Luong, 1985). Moreover, the home range of the putty-nosed monkey group overlapped almost completely with one Diana monkey group (Figure 8). These findings seem counterintuitive and are clearly at odds with the interspecies competition hypothesis, thus requiring further explanation. A number of studies have suggested that Diana monkeys are very popular association partners for other monkey species (Bshary, 1995), probably because of their high rates of vigilance and predator alarm calling behavior.

Table 3
The predator alarm call behavior in putty-nosed monkeys

Stimulus	Date	Response (<i>N</i> calls)		Male call structure ^a	
		Females	Male	“Tock”	“Zeck”
Eagle shrieks	30 June 2001	21	23 (1)	100%	0%
	16 September 2001	11	34 (2)	100%	0%
Leopard growls	12 July 2001	9	2 (1)	0%	100%
	9 October 2001	1	1 (2)	0%	100%

^a First 10 calls considered only; numbers in parentheses refer to male 1 and 2.

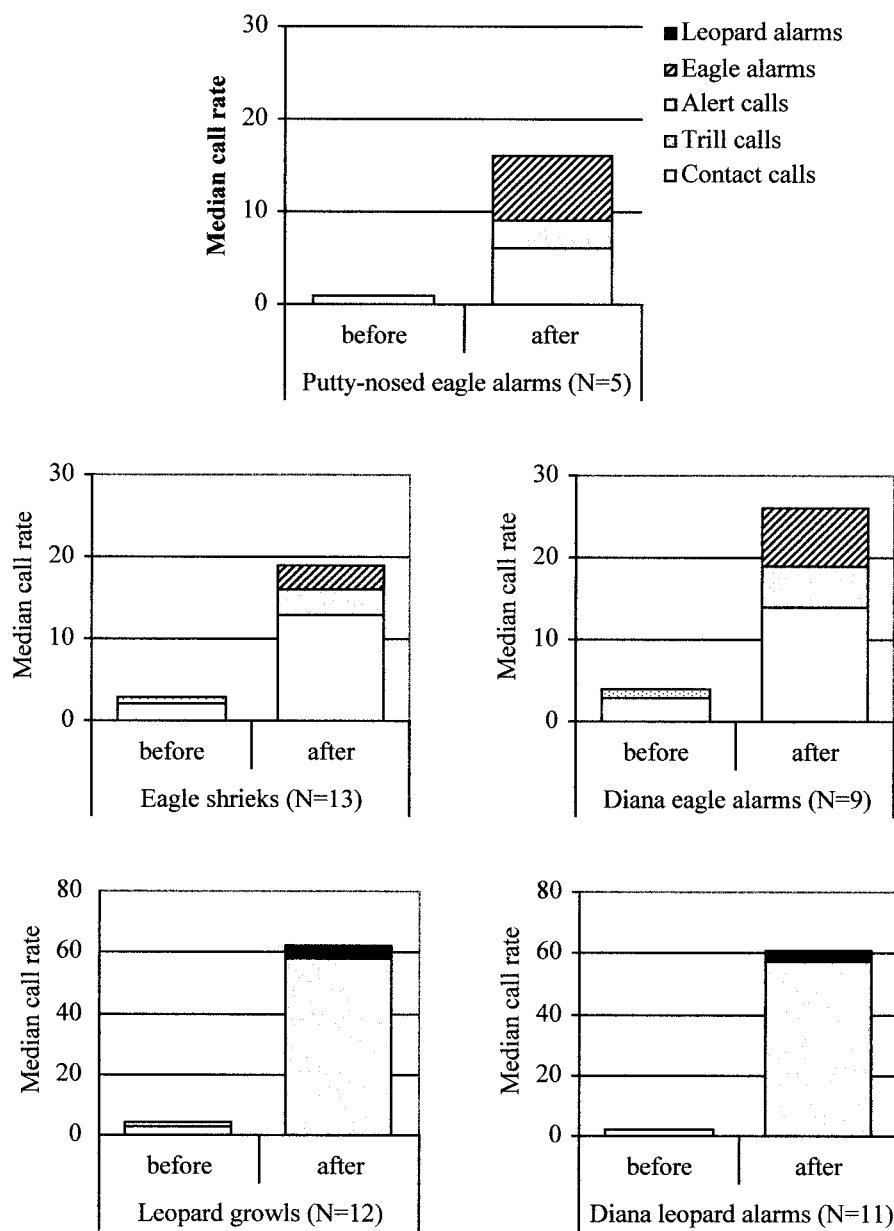


Figure 10
Responses of Diana monkey groups to predator-related playback stimuli. Each graph depicts the median vocal response of the entire group 1 min before and after the onset of the playback stimulus (see Zuberbühler et al., 1997).

Although this explains why putty-nosed monkeys are attracted to Diana monkeys, it does not explain why Diana monkeys are willing to tolerate the proximity of putty-nosed monkeys, especially considering their impact as competitors.

Our data suggested that Diana monkeys tolerated putty-nosed monkeys because they provided important protection against predation. Our playback experiments have shown that the male putty-nosed alarm calls are beneficial for nearby Diana monkeys because they reliably indicate the presence of a crowned eagle, suggesting that these alarm calls function as semantic labels for eagle presence. Adult males of both species regularly attack and drive away eagles and produce highly conspicuous low-pitched loud calls that carry over considerable distances even in dense rainforest habitat. Unlike other Taï primate species, putty-nosed monkeys are exceptional in that the adult males also attack crowned eagles, even if associated with Diana monkeys, whose males are notoriously aggressive toward eagles (Zuberbühler et al., 1997).

Mixed-species associations and biological market theory

Primate mixed-species associations have probably evolved in response to predation pressure (Noë and Bshary, 1997). Rather than tolerating more conspecific group members, many forest primates keep their groups small and instead associate with members of other species. This way feeding competition is kept low, whereas the antipredation benefits increase with each additional member. However, the Diana-putty-nosed monkey association is not well explained by this model. Both species compete for the same resources, suggesting that they should prefer to increase their own group size rather than forming mixed-species groups with each other. Mixed-species associations with high levels of feeding competition have also been found in some neotropical callitrichine primates (see Heymann and Buchanan-Smith, 2000). Here, individuals are forced to form mixed-species groups because their own rigid social structure prevents them from increasing conspecific group size.

A number of observations are consistent with the idea that putty-nosed monkeys trade their services in eagle defense for their increased tolerance by Diana monkeys at the feeding site, suggesting that the two species could be involved in a biological market game (Noë and Hammerstein, 1994; Noë et al., 2001). An important feature of a biological market is that there is an element of choice involved and that the partners are able to adjust the benefits they offer each other. Our observations showed that Diana monkeys were astonishingly tolerant toward putty-nosed monkeys throughout most of the year, despite the presumably high costs of competition. In August and September, however, when the fruit availability deteriorated, the Diana monkeys became overtly aggressive toward putty-nosed monkeys, and the association rates were very low. More systematic data will be necessary to establish a relationship between interspecies tolerance and food availability. Similarly, it would be necessary to investigate to what degree Diana monkey tolerance is dependent on predation pressure by crowned eagles. As biannual seasonal breeders, predation pressure by eagles is likely to vary in an orderly way, suggesting that the Diana monkeys' tolerance toward putty-nosed monkeys varies accordingly. Finally, Diana monkey groups whose home range is close to an eagle nest could be expected to be more tolerant toward putty-nosed monkeys than are groups whose home range is more distant. Diana monkeys respond to and therefore benefit of putty-nosed alarm calls, a clearly highly valuable service.

Biological market theory also makes a number of predictions concerning the behavior of putty-nosed monkeys. For example, putty-nosed monkeys should provide relatively more predator-defense behaviors when in association with Diana monkeys than when alone or when with association partners that are less strong competitors. Another prediction might be that male putty-nosed monkeys adjust their antipredation activity as a function of food availability, showing lower activity in periods of food abundance. Third, putty-nosed monkey groups might choose to associate with the most tolerant group from a set of neighboring Diana monkey groups. Our focal group occasionally visited neighboring Diana groups, and the prediction would be that those groups are less tolerant than is the focal group. Finally, putty-nosed monkey groups with a male that is less active in eagle defense might be able to form less stable associations with Diana monkeys than are groups with a more active male. One observation is particularly intriguing. In early August, the resident adult male of the putty-nosed group disappeared for unknown reasons, and a new male did not take over the group until the end of the month. Consequently no male alarm calls were given during this time period. Upon his arrival the new male exhibited remarkable alarm call behavior. Soon after his takeover, he was observed on two separate occasions to produce extraordinary calling bouts of 100 to 200 calls, a behavior never seen before. In both cases, the group was not associated with Diana monkeys but probably within their acoustic range, suggesting that the male advertised his commitment to antipredator protection to his new group and the local Diana monkey group. Clearly, although a number of crucial conditions are met, more systematic studies will be necessary before it can be determined whether a biological market is operating or whether the current patterns can be explained by simple by-product mutualism (see Dugatkin and Mesterton-Gibbons, 1996).

The tribulations of an immigrant

The putty-nosed monkey groups found in the Taï forest are probably the descendants of individuals that emigrated from the northern savannah woodland habitats in the primary

rainforest belt, perhaps because of increasing pressure owing to human activity. Upon arrival, these individuals had to compete with the resident Diana monkey groups, which already occupied their preferred ecological niche. High predation pressure combined with a strong commitment of male putty-nosed monkeys to engage in antipredator behavior could explain why the Diana monkeys are mostly tolerant toward this competitor, particularly when food availability is high. The presence of Diana monkeys, as well as the one-male social structure, could prevent the putty-nosed monkeys from forming large groups, forcing them to accept mixed-species associations with Diana monkeys to access their preferred ecological niche. Interspecies aggression, particularly in periods of low food availability, might effectively limit the reproductive success of female putty-nosed monkeys, keeping group sizes below fission threshold.

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