

**MIXED-SPECIES ASSOCIATIONS OF DIANA  
AND CAMPBELL'S MONKEYS:  
THE COSTS AND BENEFITS OF A FOREST PHENOMENON**

by

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**Summary**

One of the most striking behavioural patterns of many forest primates concerns their tendency to live in semi-permanent mixed-species groups. Functional investigations have ascertained that individuals obtain some antipredator benefits without paying the costs of intra-species resource competition. Despite these advances, very little is known about the subtle mechanisms that keep mixed species groups together on a daily basis. Our results showed that in the Diana–Campbell's monkey association both species benefited from each other in diverse and idiosyncratic ways. In the presence of Campbell's monkeys the conspicuous Diana monkeys were more likely to descend into the lower forest strata, increased their foraging behaviour, and individuals became less vigilant. The cryptic Campbell's monkeys, in turn, were able to use the higher forest strata and exposed areas more often, spread out over larger areas, were more likely to travel, and engaged in more conspicuous vocal behaviour when associated with Diana monkeys. These data suggested that both species benefited from each other in ways that went beyond passive group-size related antipredator benefits, such as a dilution effect and increased chances of predator detection. Instead, the increased safety of

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the mixed species group allowed individuals to exploit their ecological niche more broadly, to forage more efficiently, and to engage in more social behaviour, suggesting that the benefits of mixed species groups are much more varied and diverse than currently thought.

*Keywords:* association, *Cercopithecus diana*, *Cercopithecus campbelli*, polyspecific, predation, mixed species, competition, calls, vigilance.

## Introduction

Several studies have shown that primate mixed-species associations do not simply occur by chance but can be the result of groups actively seeking each other to maintain close contact throughout the day (Waser, 1982; Holenweg *et al.*, 1996). It is usually assumed that the same principles that determine the evolution of mono-specific group size also apply to polyspecific associations, and that group size is positively related to predation risk (Dunbar, 1988). In long-tailed macaques (*Macaca fascicularis*), for example, increased predation risk by felid predators was related to larger group size (van Schaik & van Noordwijk, 1985). However, if living in large groups is advantageous for individuals, then it needs to be clarified why forest primates prefer to associate with another species rather than increasing the size of their conspecific groups.

### *Adaptive advantages of polyspecific groups*

The usual assumption is that by associating with another species individuals get group size related benefits at lower costs if the partner species relies on different food resources. Moreover, as many primates live in rather rigid one-male social systems increasing group size might only be feasible by forming polyspecific associations. This allows individuals to respond to changes in predation pressure and food availability more quickly and to adjust the optimal group size on a moment-to-moment basis. This is especially useful as only few species of primates, such as chimpanzees (*Pan troglodytes*), can temporarily break up social groups of conspecifics if conditions warrant. Finally, recently published data on leopard hunting behaviour suggests that forming large mono-specific groups can have dangerous and maladaptive consequences in forest habitats because leopards appear to bias their prey preferences towards species living in larger groups (Zuberbühler & Jenny,

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2002). Individuals of the various monkey species might thus effectively compete with each other in their attempts to avoid leopard predation, such that forming large mixed species groups might be a more adaptive response to predation pressure than increasing conspecific group size.

*Anti-predation benefits of polyspecific groups*

A series of studies conducted in the Tai forest, Ivory Coast, has emphasized the importance of predation as an ultimate factor for the evolution of mixed species associations (Holenweg *et al.*, 1996; Höner *et al.*, 1997; Bshary & Noë, 1997, 1998; Noë & Bshary, 1997). More recent work has confirmed that predation pressure and food availability are probably the most crucial determinants of primates' mixed species associations (Chapman & Chapman, 2000). But how exactly does life in a polyspecific association result in lower predation pressure per individual? Apart from simple passive safety-in-number and confusion effects at least two behavioural mechanisms have been identified.

First, Gautier-Hion *et al.* (1983) have conceptualised mixed species associations as mutualistic events with individuals combining their species-specific predator sensibilities: Whereas one species might be specialized in detecting avian predators, the other species is specialized in terrestrial predators, so that in association the two shield each other mutually against predators (McGraw & Bshary, 2002). A similar suggestion has been made for the Diana monkey-red colobus association in Tai National Park (Bshary & Noë, 1997): Diana monkeys shield Colobus monkeys against terrestrial predators, while colobus monkeys protect Diana monkeys against avian predators.

Second, improved predator detection seems to be another group-size related benefit: the more individuals scan the environment the more likely the group will detect a hiding or approaching predator (Hardie & Buchanan-Smith, 1997). This is especially useful in species that have evolved predator-specific warning calls, a behaviour that will ensure rapid spread of information across all group members. Both Campbell's and Diana monkeys produce predator-specific alarm calls to leopards and eagles (Zuberbühler *et al.*, 1997; Zuberbühler, 2001) and experimental work has shown that members of both species understand each other's alarm calls (Zuberbühler, 2000). It is likely, thus, that a main incentive for keeping contact with members of another species is rooted in the fact that individuals can monitor a much larger

area of forest for predators due to the increased numbers of potentially alarm calling sentinels. In sum, most authors agree that mixed species associations offer significant anti-predator benefits, particularly due to the fact that individuals can continuously monitor a much larger area of dense forest habitat for predators, without having to endure costly increases in conspecific group size.

*The Diana–Campbell’s monkey association*

We studied two neighbouring semi-permanent mixed groups of Diana monkeys (*Cercopithecus diana*) and Campbell’s monkeys (*C. campbelli*). This association is of particular interest for various reasons. First, as mentioned before previous work has shown that both species reliably produce predator-specific alarm calls to two of their predators, the crowned eagle (*Stephanoaetus coronatus*) and the leopard (*Panthera pardus*; Zuberbühler *et al.*, 1997; Zuberbühler, 2001) and that both understand each other’s alarm calls (Zuberbühler, 2000, 2001), suggesting that individuals of these two species are especially attractive partners for forming a mixed species group. Second, the two species are phylogenetically closely related to each other (Purvis, 1995) and rely on similar food resources, suggesting that the costs of feeding competition are much higher than, for example, in the well-studied red colobus (*Colobus badius*)–Diana monkey association (Wachter *et al.*, 1997). At the same time, the two species have undergone various behavioural and morphological adaptations that make them especially adapted to particular forest habitats: Diana monkeys behave very conspicuously, both visually and acoustically, and they usually occupy the highest forest strata (Uster & Zuberbühler, 2001; McGraw, 1996). Campbell’s monkeys, on the other hand, are very cryptic monkeys, both in coloration and vocal behaviour and they consistently occupy the lowest forest strata and often come to the ground (McGraw, 1996). A predator shielding mutualism as described for the Diana–red colobus association, therefore, does not seem to apply here because it would require the Diana monkeys to undergo a role reversal: as the higher living species their role should be to shield against aerial predators. In sum, although both species are likely to gain antipredator benefits from associating with the partner species, there are also substantial costs involved due to feeding competition and incompatible overall lifestyles, suggesting that individuals should be particularly careful in their decisions as to whether or not to form a mixed species group.

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In this study, we were concerned with whether improved predator detection was the only incentive that monkeys have to form a mixed species association. If that were the case, then associations should have little effect on the behaviour of the study animals in their daily attempts to find food and interact with social partners. In particular, one would not predict any behavioural differences in individuals when they alone or with the partner species, as the mere presence of having additional sentinels within acoustic range is the necessary and sufficient condition. Alternatively, we predicted that the formation of a mixed species association might generate additional subtle, but perhaps equally important, social and foraging benefits for individual group members (Cords, 1990a, b), such as decreased amounts of vigilance behaviour and increased amounts of foraging and social behaviour.

## Methods

### *Study site and subjects*

The study was conducted in the Taï forest, Ivory Coast, about one kilometre from the C.R.E. research station (5°50'N, 7°21'W). The Taï Forest has been classified as a tropical moist forest, with a protected area of roughly 4000 km<sup>2</sup> of largely undisturbed forest, the largest remaining block of primary forest in West Africa (Martin, 1991). The following monkey species can be observed: the red colobus, the black-and-white colobus, *Colobus polykomos*, the olive colobus, *Procolobus verus*, the Diana monkey, the Campbell's monkey, the lesser spot-nosed monkey, *Cercopithecus petaurista*, the putty-nosed monkey, *C. nictitans*, and the sooty mangabey, *Cercocebus torquatus*. All monkeys are hunted by leopards (Zuberbühler & Jenny, 2002), crowned eagles (Shultz, 2001), chimpanzees (Boesch & Boesch, 1989), and human poachers (Martin, 1991). Data were collected on four different Diana and Campbell's monkey groups, which occupied stable home ranges and formed two semi-permanent mixed-species associations with one another. Observers had followed these groups for several years and individuals were fully habituated to human presence. Association A consisted of a Diana monkey and a Campbell's monkey group that had been followed on a regular basis since November 1992. Association B consisted of a Diana and Campbell's monkey group that had been followed on a regular basis since July 1997. The two associations had adjacent territories. Table 1 summarises the study groups' demographical composition.

### *Individual-level parameters*

The first author collected data between May and November 2000, usually between 06:30 and 17:30 GMT ( $N = 110$  observation days). 10-min scan samples were taken every 30 min. In each scan, the observer walked underneath the group to locate as many individuals as possible in order to collect data on behaviour, vertical location, and exposure. The following behavioural elements were scored: *foraging*: looking at, pursuing, or consuming food items;

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TABLE 1. *Demographical composition of the four study groups*

	Association A		Association B	
	Diana monkeys	Campbell's monkeys	Diana monkeys	Campbell's monkeys
Adult males	1	1	1	1*
Adult females	10	5	4	3
Subadults <sup>†</sup>	6	3	≤4	2
Juveniles <sup>†</sup>	8	5	6	3
Infants <sup>†</sup>	≥2	3	2	1
Total	≥27	17	≤17	10

<sup>†</sup> Sexing not reliably possible; \* male takeover on 15 August, 2000.

*locomotion*: moving along a substrate; *social*: grooming or playing with another group member, sucking or suckling behaviour of mother or infant; *other*: Any other type of behaviour, such as aggressive behaviour, copulations, or sleeping. The focal individual was then assessed for its vertical location in the canopy. The following three distinctions were made, following McGraw (1998): <2.5 m: on or close to ground or on tree trunks; 2.5-12 m: on tree, but below closed canopy; >12 m: on tree, but within the closed canopy. Finally, the individual was assessed for its exposure to a potential predator. The following distinctions were made: *exposed*: on ground or outer exposed branches; *intermediate*: in vegetation of average density, *covered*: in dense foliage.

Between June and November 2000, the observer also collected data on the *vigilance* behaviour of the individuals. These data were not collected as part of the regular 30-min scans because it was difficult to reliably locate an individual with an unobstructed view of the face during the 10 minutes sampling period. Therefore, we conducted a second data collection procedure, which took place in-between two scans. Individuals of all age-sex classes (except for infants) were sampled if the following conditions were met. First, the observer was able to observe the individual for ten continuous seconds, which was often difficult in the dense vegetation of the Taï forest. Second, the individual was not moving during this time. Third, the face of the individual was clearly visible and not obstructed by foliage. The observer then decided whether or not the individual was vigilant, that is, whether it had conducted at least one head movement of >30 degrees upwards, downwards, or sideways.

#### *Group-level parameters*

In addition to the data taken from individual monkeys, the observer also recorded the following group-level parameters: *association*, *group spread*, *progression*, and *call rate*. The criterion for *association* was taken from Struhsaker (1981), that is, whether or not a member of the partner species was located within 50 metres of the focal group. *Group spread* was determined to be large for Campbell's monkeys if individuals occupied an area of more than 25 m in diameter. The Diana monkeys usually occupy larger areas than the Campbell's monkeys, both due to their larger group size and their different way of using the habitat. Hence, group spread was scored to be large for Diana monkeys if individuals occupied an area of more than

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50 m in diameter. Members of both species tend to constantly move about when foraging. However, when the entire group changed position during a scan, this was scored as a *progression*. Finally, during the entire 10-min scan the observer counted the number of contact (or clear) calls emitted by all group members with a manual counter (*call rate*). Both Diana monkeys and Campbell's monkeys produce clear calls in relaxed non-predatory contexts. In Diana monkeys, these calls change in acoustic structure and emission rate depending on the external context, providing individuals with important information about ongoing events in the environment (Uster & Zuberbühler, 2001). Call rates of 10 calls or fewer per 10 min. were considered as cryptic vocal behaviour, whereas all higher call rates were considered as conspicuous.

*Data analyses*

To obtain a high and uniform level of independence between successive scans we only analysed the results of the very first individual observed in each scan, not including infants. As the data sets were not normally distributed we used non-parametric statistics throughout (Siegel, 1956). If a set of data were used for several tests we adjusted the *p*-values using the sequential Holm's procedure (Holm, 1979), which successively corrects the significance level rather than adjusting individual probabilities. For this data set the Holm's procedure is a more powerful method for multiple testing than the better-known Bonferroni correction (Wright, 1992).

**Results***Association rates*

Overall, Diana and Campbell's monkeys were found in association in 75.4% of all scans ( $N = 1054$ ). The two mixed species groups (see Table 1 for demographic data) differed somewhat in their association rates. Association A was found together in 87.0% of all scans ( $N = 633$ ); association B in 55.9% of all scans ( $N = 392$ ).

*Habitat usage*

In both species, the use of strata was significantly different when in association with the partner species than when not (Campbell's monkeys:  $N = 614$ ;  $\chi^2 = 7.678$ ,  $p < 0.03$ ; Diana monkeys:  $N = 437$ ,  $\chi^2 = 35.878$ ,  $p < 0.001$ ;  $\text{Chi}^2$  tests, two-tailed; Fig. 1). Both Diana and Campbell's monkeys were more likely to use the middle strata when in association than when alone, at the expense of the lower strata (Campbell's monkeys) and the higher strata (Diana monkeys).

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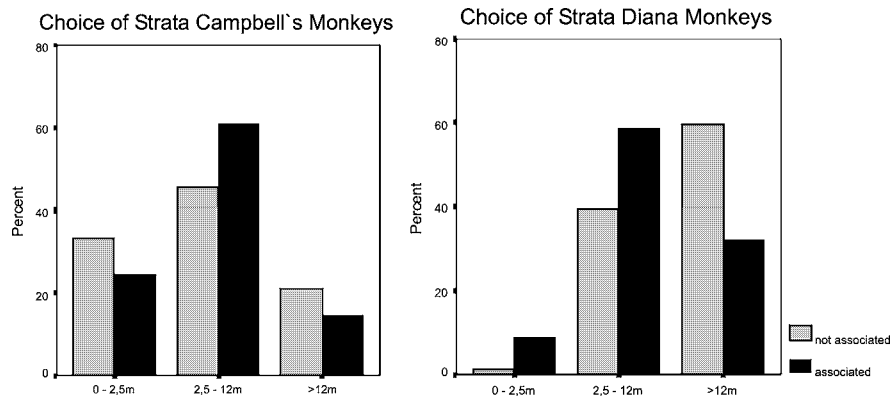


Fig. 1. Choice of strata as a function of association: Both species converged to the middle strata when in association at the expense of the lower strata (Campbell's monkeys) or the higher strata (Diana monkeys).

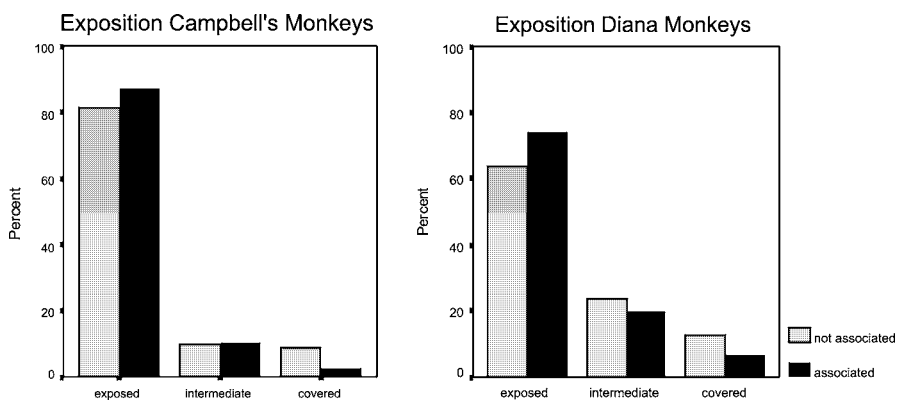


Fig. 2. Exposition to predators as a function of association: Both species used the more exposed parts of the vegetation more often in association.

Campbell's monkeys used the more exposed parts of the vegetation more often when in association with Diana monkeys than when not ( $N = 614$ ;  $\chi^2 = 9.551$ ;  $p < 0.01$ ; Chi<sup>2</sup>; two-tailed). The same trend was found for the Diana monkeys ( $N = 437$ ;  $\chi^2 = 6.925$ ;  $p < 0.03$ ; Chi<sup>2</sup>-tests, two-tailed; Fig. 2), however the effect was not statistically significant because the Holm's correction procedure raised the significance level to  $p < 0.0125$ .

Campbell's monkeys were significantly more dispersed when in association with Diana monkeys than when not ( $N = 510$ ;  $p < 0.009$ ; Fisher

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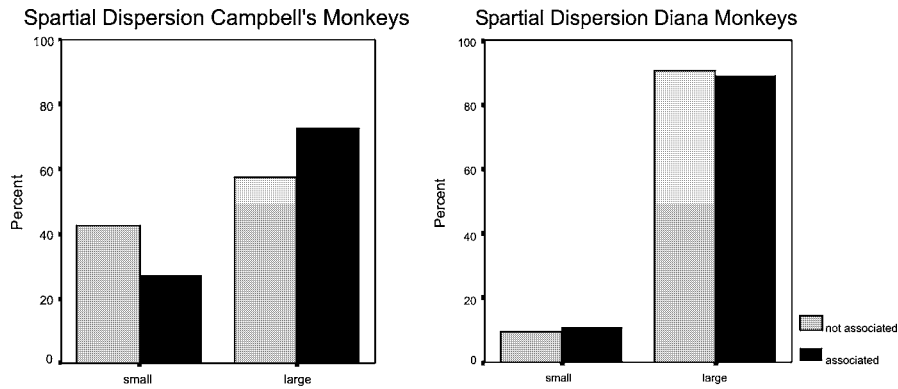


Fig. 3. Group spread as function of association: Campbell's monkeys were more dispersed in association.

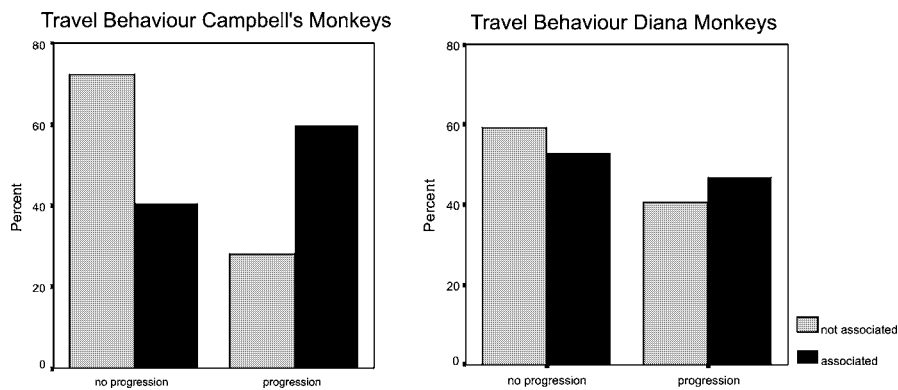


Fig. 4. Travel as function of association: Both species travelled more in association.

exact probability test). No significant effect was found for the Diana monkeys ( $N = 392$ ,  $p > 0.7$ , Fisher exact probability test, Fig. 3).

Campbell's monkeys travelled significantly more when in association with Diana monkeys than when not ( $N = 566$ ,  $p < 0.001$ ; Fisher exact probability test). The same trend was found for Diana monkeys, but the difference was not significant ( $N = 415$ ,  $p < 0.3$ ; Fisher exact probability test, Fig. 4).

#### *Behavioural effects*

Diana monkeys were significantly less vigilant when in association with Campbell's monkeys than when not ( $N = 106$ ;  $p < 0.004$ ; Fisher exact probability test). The same trend was found for Campbell's monkeys, but the

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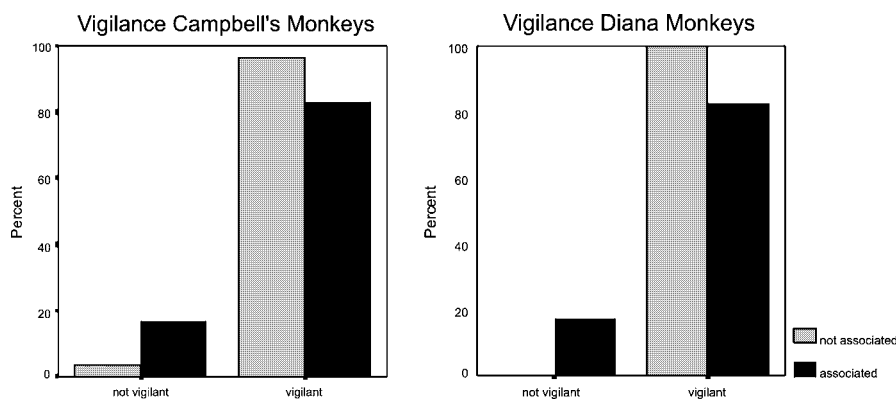


Fig. 5. Vigilance behaviour as a function of association: Both species were less vigilant in association.

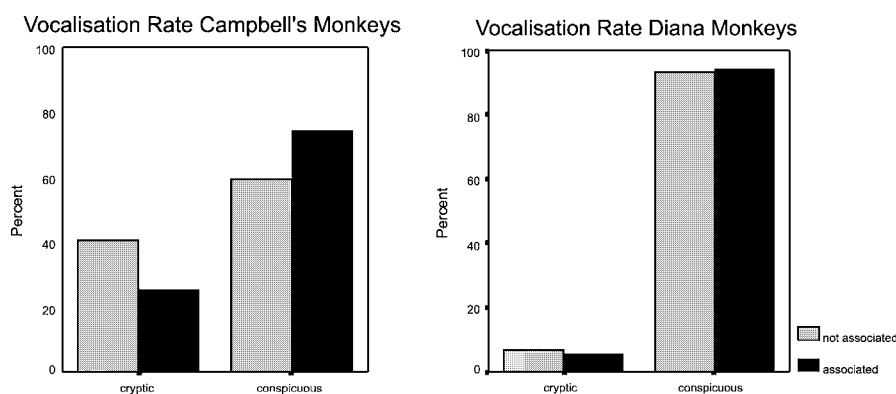


Fig. 6. Vocalisation rate as a function of association: Both species vocalised more often in association.

difference was not significant ( $N = 110$ ,  $p < 0.2$ ; Fisher exact probability test; Fig. 5).

Campbell's monkeys vocalised significantly more often when in association with Diana monkeys than when not ( $N = 289$ ,  $p < 0.02$ ; Fisher exact probability test). The same trend was found for Diana monkeys, but the difference was not significant ( $N = 278$ ,  $p > 0.8$ ; Fisher exact probability test, Fig. 6).

Diana monkeys foraged significantly more often in presence of Campbell's monkeys ( $N = 433$ ,  $p > 0.01$ ; Fisher exact probability test, Fig. 7).

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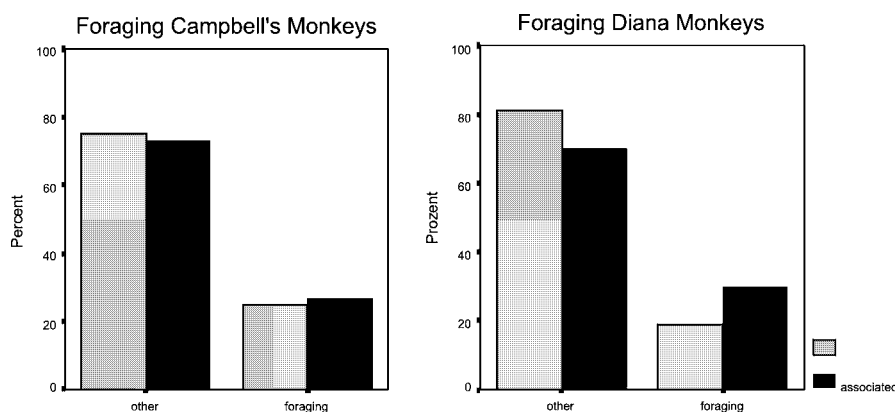


Fig. 7. Foraging behaviour as a function of association: Diana monkeys foraged more often in association.

No effect was found for Campbell's monkey ( $N = 609$ ,  $p < 0.7$ ; Fisher exact probability test).

Finally, we did not find any association-related changes in the other social activities (grooming, playing, or nursing behaviour) although this might have been due to the fact that these behaviours occurred very rarely.

## Discussion

The monkeys of Taï forest frequently form semi-permanent mixed-species groups. In the case of the Diana and Campbell's monkeys mixed species groups occur in more than 75% of the time, despite the fact that the two species are closely related to one another and probably compete for very similar food resources. This strongly suggests that these associations are not the result of chance encounters, but an adaptive response to high predation pressure (Noë & Bshary, 1997). However, simple passive group-size related anti-predator benefits (dilution effect, predator detection) were not sufficient to explain the behavioural patterns observed in these monkeys. We were able to show that both species benefited from each other in ways that went beyond improved predator detection and included advantages such as the exploitation of a broader ecological niche and the ability to engage in a more diverse behavioural spectrum, including higher proportions of social behaviour. The latter finding was particularly striking in the Campbell's monkeys,

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a normally highly cryptic species. In association with Diana monkeys, individual Campbell's monkeys became significantly more conspicuous in their vocal behaviour and habitat use: Individuals foraged in more exposed areas and in higher strata, while they kept a larger distance to each other. We also found that Campbell's monkeys were more likely to progress in association with Diana monkeys, which are considered notoriously dangerous events (Boinski & Garber, 1999).

Many of the effects found in the Campbell's monkeys were also present in Diana monkeys, although often to a smaller degree. However, Diana monkeys clearly benefited from the presence of Campbell's monkeys in the following two ways. The normally highly vigilant Diana monkeys decreased their scanning rates significantly in the presence of Campbell's monkeys, suggesting that the monkeys had more of their time and energy available for other activities, such as finding food or social interactions. Indeed, we found that Diana monkeys foraged more often in presence of Campbell's monkeys, suggesting that the mixed species association had important positive effects on the Diana monkeys' overall time and energy budget.

It appears that the mixed species association allowed the monkeys to use their ecological niche more broadly, presumably due to the decreased predation pressure and increased perception of safety by individual monkeys. Our data stem from two different mixed species groups (Table 1), both of which showed similar patterns although sometimes to different degrees, allowing us to pool the data for both groups (Wolters, 2001). Niche broadening was particularly apparent in the observed changes in habitat use of the two species: When alone, both species showed high degrees of vertical niche separation, with the Campbell's monkeys preferring the lower strata and the Diana monkeys favouring the higher strata. When associated with each other, however, both species converged to the middle stratum. Monkeys might perceive the middle strata as particularly dangerous, a suggestion that seems somewhat counterintuitive. However, observations on primate-hunting crowned eagles suggested that this predator sometimes engaged in sit-and-wait hunting (Shultz, 2001). The middle forest strata might thus be particularly dangerous with monkeys being exposed to lurking eagles perched in the crowns. Thus, mixed species associations might enable the monkeys to exploit the middle strata more efficiently due to safety-in-number effects (see also Buchanan-Smith *et al.*, 2000). Similarly, the main effect for

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the Campbell's monkeys was that in the presence of Diana monkeys, individuals behaved much more conspicuously: When alone, Campbell's monkeys rarely vocalized and moved in a tightly cohesive way. When with Diana monkeys, the monkeys spread out and vocalized much more often (Figs 4 & 6), suggesting that associations with Diana monkeys allowed them to engage in social communication more freely. Both species were more likely to engage in group progressions when associated with each other (Fig. 4), suggesting that the larger groups provide animals with higher levels of perceived safety allowing them to explore their habitat more efficiently.

In sum, our study shows that the formation of a mixed species groups caused a number of benefits at multiple levels. These changes seemed to be the result of individuals benefiting from decreased predation pressure due to safety-in-number effects and better changes of predator detection. The low-living Campbell's monkeys were able to afford a less cryptic life style while in association with Diana monkeys, which in turn allowed them to engage in higher rates of social communication, and to exploit their habitat more broadly. The Diana monkeys, in turn, needed to devote less time to vigilance behaviour and instead could spend more time with foraging behaviour and exploit the strata more efficiently. The increased safety of the mixed species group, in other words, provided monkeys with a basis for a more secure existence less constrained by the constant threat of predation.

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