Behav Ecol Sociobiol (2003) 53:238–245
DOI 10.1007/s00265-002-0575-y

ORIGINAL ARTICLE

Susanne Shultz · Charlotte Faurie · Ronald Noë

Behavioural responses of Diana monkeys to male long-distance calls: changes in ranging, association patterns and activity

Received: 20 June 2002 / Revised: 13 December 2002 / Accepted: 15 December 2002 /

Abstract Although much is known about the relationship between vigilance, group size and predation risk, behavioural responses to predation risk and their resultant costs are less clear. We investigated the response of Diana monkeys to increased predation risk by looking at behavioural changes associated with male long-distance calls, which are reliably given to certain predators. After male long-distance calls, group spread and nearest-neighbour distance decreased whilst travel and association rates for the group increased. The average height and exposure level of individuals in the group did not change after calls. Individual Diana monkeys changed their behaviour and were more likely to be vigilant or travel and less likely to engage in social or resting behaviours after long-distance calls. In addition, movement rates increased with the number of species the Diana monkeys were associated with. Diana monkey long-distance calls facilitate the joining of groups of other species. Black and white colobus and lesser spot-nosed monkeys were more likely to be in an association following a long-distance call than before. Behavioural responses, such as increased travel or association rates, that reduce foraging efficiency are interpreted as evidence of a non-lethal impact of increased predation risk.

Keywords Mixed-species associations · Alarm calls · Taï National Park · Predation risk · *Cercopithecus diana*

Communicated by S. Boinski

S. Shultz (✉)
School of Biology, Biosciences Building,
University of Liverpool, L69 7ZB Liverpool, UK
e-mail: smshultz@liverpool.ac.uk
Fax: +44-151-7954408

C. Faurie
Institut des Sciences de l'Evolution (UMR 5554), CC 065,
Université Montpellier II, 34095 Montpellier cedex 05, France

R. Noë
Ethologie et Ecologie comportementale des Primates,
CEPE (CNRS UPR 9010), Université Louis Pasteur,
7 rue de l'Université, 67000 Strasbourg, France

Introduction

One of the complications for understanding the impact of predation on a prey population is determining the relevant behavioural or ecological variables to measure. Although predation rate is the most obvious direct cost, it does not necessarily reflect the selective importance of the indirect costs of predation. To begin with, it is nearly impossible to measure predation rate in most populations accurately. In populations that suffer low actual predation rates, missing even a small number of predation events can drastically bias estimates. Additionally, species with very effective yet costly anti-predator strategies may experience high levels of predation pressure but a low realised predation rate (Hill and Dunbar 1998). However, it is precisely the risk of predation, or the likelihood of encountering potential predators, that maintains these behaviours in a population. Thus predation risk rather than predation rate may be a more relevant indication of the selective role of predation.

Species' typical behavioural responses to predation risk have been documented across many taxa. Individuals alter habitat use, activity patterns, foraging habits and grouping patterns when confronted by increases in predation risk (Lima 1998). Aggregations enable individuals to mitigate their predation risk through increased vigilance levels, dilution effects, confusion and communal defence. Despite the numerous theories about the role that predation risk has on aspects of sociality, such as group size, composition and behaviour, the empirical and observational data supporting theoretical predictions are limited to a few consistent results (Janson 1998). For example, individual vigilance levels have been shown to decrease with increasing group size and to increase under heightened predation risk amongst some taxa (e.g. Magurran et al. 1985; Lima 1987; Elgar 1989). Prey have been shown to prefer larger groups when exposed to predators (e.g. Hagar and Helfman 1991; Tegeder and Krause 1995), and predator encounters can induce flocking behaviour both in the short and long term (e.g. Seghers 1974; Myers 1980, 1984; Whitfeld 1988). However, as resource competition increases with group size, there is an inevitable trade-off between predation avoidance and acquisition of resources (Isbell 1991; Janson and Goldsmith 1994).

Prey aggregations are not limited to mono-specific groups. Multi-species associations are a commonly documented phenomenon amongst a variety of vertebrate species, including passerines, ungulates, primates and fish. In mixed-species groups, group sizes can be effectively increased with lower intragroup resource than in single-species groups of the same size (Buskirk 1976). Individuals are still expected to incur costs by forming these mixed-species flocks, either through increased resource competition or through adjusting their foraging behaviour or habitat use in order to maintain the association. Some species appear to promote mixed-species associations, functioning as "nuclear" species to which other "satellite" species are attracted (Dolby and Grubb 1999). Increased predation risk has been shown to cause the formation of mixed-species associations (e.g. passerines, Greig-Smith 1981; primates, Bshary and Noë 1997; Noë and Bshary 1997). Nearest-neighbour distance and group density within such associations have been shown to decrease after predator exposure in several bird studies (Forsman et al. 1998).

In primate studies, there appears to be a prevalent inconsistency between theoretical predictions of the anti-predator benefits of sociality and observed behaviour. Group size has been shown to be positively (Anderson 1986), negatively (Isbell 1994), and not correlated (Cheney and Wrangham 1987) to predation rate. Group size effects on vigilance levels have been found in some studies (e.g. de Ruiter 1986), but not in others (reviewed in Treves 2000). Although such studies of vigilance may not have found consistent results because primate group sizes are generally larger than models predict an effect for, results are still ambiguous even in smaller groups (Treves 2001). Nearest-neighbour distance has been shown to be more important than group size in determining vigilance levels of some arboreal primates (Treves 1998). Such results do not negate the importance of predation in the evolution of sociality, as group-size effects on vigilance are only one of the theorised benefits of sociality. For example, dilution and mobbing may be more important benefits than vigilance in reducing an individual's susceptibility to predation.

Mixed-species associations are commonly documented in primates. In several primate communities, the time spent in association has been related to diet overlap and community structure (Whitesides 1989; Cords 1990). However, measures of indirect costs and the impact of predation risk on associations have been demonstrated in few contexts (Noë and Bshary 1997; Chapman and Chapman 2000). In the Taï National Park, monkeys regularly form mixed-species groups, with some of the species in nearly continuous association (Höner et al. 1997). Diana monkeys (*Cercopithecus diana*) are the "sentinel" species in Taï, as they are the first to detect predators (Bshary and Noë 1997) and give alarm calls more often than other species (Shultz and Noë 2002). Diana monkey communication has been well studied in Taï. When they encounter predators, male Diana monkeys give long-distance calls that function as alarm calls, which travel farther than the diameter of a group's home range (Zuberbühler et al. 1997). The behavioural changes following these long-distance calls can therefore be considered as a response to increased predation risk. Other typical intragroup vocalisations such as "alert" and "clear" calls (also called contact calls) are given at elevated levels by Diana monkeys after disturbances and in situations of high predation risk (Zuberbühler et al. 1997; Uster and Zuberbühler 2001). The other common intragroup vocalisation, the "trill" call, does not appear to be associated with disturbance, predator encounters or group movement.

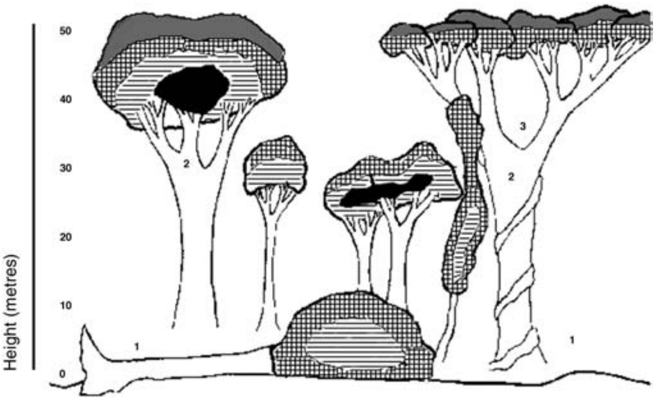

Fig. 1 Diagram of the habitat use categories. Height estimated by 15-m categories. Exposure levels estimated by relative thickness of vegetation and accessibility either from above or below the canopy. Coding for exposure levels (level 1 most exposed and level 4 least exposed): *shaded* level 1, *cross-hatched* level 2, *horizontal lines* level 3, *solid black* level 4

Here we investigated the impact of long-distance calls given by male Diana monkeys on behaviour and mixed-species association patterns. If Diana male long-distance calls are an indication of increased predation risk, several predictions can be made about behavioural responses to such calls. (1) Vocalisation rates of calls that have been clearly related to predator encounters, group disturbance or group-level changes in behaviour, namely "alert" and "clear" calls (see Zuberbühler et al. 1997; Uster and Zuberbühler 2001), should increase as individuals become aware of a potential danger. (2) Group spread and nearest-neighbour distances should decrease according to the predictions of the selfish herd (Hamilton 1971). (3) Individuals within groups should move to areas within the canopy where they are less exposed (Fig. 1). (4) Individuals should engage in less risky behaviour (i.e. those behaviours that necessitate lowering vigilance levels or remaining in exposed areas in the canopy, such as social or foraging activities). (5) Association rates with other species should increase with elevated loud-call call rates to maximise the group size and the benefits of dilution. (6) If there is any increase in feeding competition in mixed-species associations, we expect to see an increase in travel rate with increased association rates.

Methods

Study site and subjects

The data were collected in the Taï National Park, in Southwestern Côte d'Ivoire, from 13 April to 18 June 2000. Eight species of diurnal monkeys are found in Taï: Diana monkeys, Campbell's guenon (*C. campbelli*), lesser spot-nosed monkey (*C. petaurista*) putty-nosed monkey (*C. nictitans*), sooty mangabey (*Cercocebus atys*), western red colobus (*Procolobus badius*), olive colobus (*P. verus*) and western black and white colobus (*Colobus polykomos*). The subjects were members of a group of habituated Diana monkeys (known as DIA 3) consisting of 20–25 individuals within the main study grid of the Taï Monkey Project. For more information on the study site, Diana monkey communication, and sympatric monkey species, see Bshary and Noë (1997), McGraw (1998) and Zuberbühler et al. (1997).

Data collection

The following sampling methods were used: group and focal scans, vocalisation samples, and continuous recording of rare occurrences. Group scans were completed each half-hour, recording information on location, behaviour and association patterns. The location of the group within the study grid was recorded to a resolution of 50 m. The species of each monkey group associated with the focal group was recorded. Association was defined by whether any individuals from another species were found within a perimeter defined by the peripheral group members of the Diana 3 group at the time of a group scan. We estimated the approximate group spread as an ordinal category of the longest chord across the group (1=0–25 m, 2=25–60 m, 3=60–100 m, 4>100 m). The height, exposure level and behaviour were recorded for each individual seen in the focal group. Height and exposure levels were recorded as interval data using the criteria shown in Fig. 1. The following behavioural categories were used: scanning (directed-looking past arms' length), foraging (manipulating vegetation or feeding – including ingestion and chewing), travel, rest and social. At 20-min intervals between group scans and immediately following each long-distance call, observers recorded all audible vocalisations given by group members during a 5-min interval. The following vocalisations were recorded: clear calls, male long-distance call, alert calls and trills. In the remaining time between group scans and vocalisation samples, we located focal individuals. For each focal individual the following information was recorded: location (as a grid reference), height and exposure (as described in Fig. 1) and behaviour (as above). We also estimated approximate vertical and horizontal distance to the nearest non-infant neighbour to within 5 m. These estimates were used to calculate the straight-line distance to nearest-neighbouring individuals. Although we were unable to identify all adults, we attempted to avoid duplication of the same individuals within a given day by observing neighbouring individuals in consecutive samples and then moving to different parts of the group after group scans. The intention of the study was to document differences in behaviour before and after long-distance calls are given, and not to document differences in behaviour between individuals. Similar methodology used in other studies has not shown a bias when comparing recognisable individuals (Treves 1998). Movement rates and calling rates were determined over each observation period. Continuous sampling records were collected for rare behaviours including group encounters, long-distance calls and predator encounters. Although male Diana monkeys have been shown to have acoustically distinct calls for different predators, these calls are difficult for human observers to distinguish (Zuberbühler et al. 1997). For this reason, it was not possible to categorise the stimulus for the long-distance calls without recording and acoustically analysing all calls. The vocalisation pattern of the group is different following playbacks of different predator vocalisations, and thus these vocal responses following long-distance calls are a potential way of typing alarm stimuli (Zuberbühler et al. 1997).

Statistical analysis

We used paired sample *t* -tests to compare nearest-neighbour distance, group spread, canopy height, exposure level, group movement, number of associated species and vocalisation rates before and after a long-distance call was given. The non-independent categories of nearest-neighbour and group spread were Bonferroni corrected. We used a Goodness-of-Fit test to look at behaviour changes for group scans where a long-distance call had been given in the previous 5, 5–15, 15–30 or more than 30 min before a group scan was taken. Group scans were labelled as to whether a long-distance call had been given during each of these preceding time intervals. These data are independent because group scans were taken at each half-hour interval. Thus each group scan could fall into only one of these categories and only one group scan occurred in the half-hour period following an alarm call. For each species, we used a Wilcoxon signed rank to test whether they were more likely to be in association either before a call was given (indicating they leave an association with the Diana group following calls) or after a call was given (indicating a tendency to join an association following calls).

We used linear regression to test whether there was a significant relationship between associated species, call rate and group travel rate. Presence/absence of each species when each long call was given as a binary variable. We tested whether the presence of each species affected the likelihood of a long-distance call being given by the Diana male, as some species are louder and easier for human observers to locate (Whitesides et al. 1988) and may also have higher encounter rates with predators. We made the assumption that noisier groups would be easier for predators to locate, would have more predator encounters and thus there would be a greater probability of a long-distance call being given per unit time. In order to look at the effect of overall group size and of the presence of each species on the probability of a long-distance call being given, we used a logistic regression. The dependent variable for the logistic regression analysis was the likelihood of a long-distance being given as a function of the presence or absence of each species.

Results

Total contact time with the group was 309 h over 48 days. We recorded 134 long-distance calls during this period. There was a range of between 0 and 6 long-distance calls recorded per observation period, with an average of 2.65 (±1.33 SD). The average call rate was 0.17 (±0.08 SD) calls/hour. We recorded the stimuli causing the long-distance call where possible; 66 (49.3%) following or simultaneously with a long-distance call of another Diana group or other species, 41 (30.6%) of calls were given in response to unknown stimuli, 19 (14.2%) were given following tree falls, and 8 (6.0%) in response to eagle calls or sightings The long-distance calls were associated with elevated "clear" and "alert" calling rates, which is the same vocalisation pattern shown experimentally in response to predator vocalisations by Zuberbühler et al. (1997). As observers do not have a canopy-level view, it is likely that there were predator encounters when stimuli were not recorded, or when multiple groups gave long-distance calls.

To determine whether larger groups attracted more predators or were more likely to detect a predator, we

Table 1 Behavioural changes after long-distance calls (mean±SD). Alpha level for group spread and nearest Diana neighbour tests Bonferroni corrected

Variable	Long-distance call previous 30 min	No long-distance call previous 30 min	Statistics
Group movement (m) (df=41)	93.17±9.45	51.95±5.69	t =3.84, P=0.0004
Group spread (n=100)	75.88±2.95	84.65±2.85	t =2.77, P=0.007, α=0.025
Height (m) (df=200)	20.35±0.56	20.85±0.50	t =0.90, P=0.0928
Nearest Diana neighbour (m) (df=106.8[a])	9.46±0.46	10.54±0.24	t =2.07, P=0.041, α=0.05
N.N. other species (m) (df=402[b])	12.44±.98	12.21±0.36	t =0.22, P=0.826
Associated species (df=111)	4.41±0.49	3.00±0.12	t =2.85, P=0.005
Exposure (n=69)	2.79	2.78	z =0.07, P=0.941

Significance level as follows: [a] unequal variances, [b] equal variances.

Table 2 Vocalisation rates during schedules scans and 5 min following long-distance calls

Vocalisation	Average (898 five-min samples)	Following long-distance (115 five-min samples)	Statistics
Alert (df=1013[a])	0.89±0.13	5.86±1.28	t =4.48, P<0.001
Clear (df=116.37[b])	38.82±1.23	54.37±3.16	t =3.86, P<0.001
Trill (df=135.47[b])	6.9±0.22	8.2±0.73	t =1.58, P=0.117

Significance level as follows: [a] unequal variances, [b] equal variances.

looked to see whether group size or association patterns affected the probability of a long-distance call being given. Both black and white colobus and the lesser spot-nosed monkey were more likely to be in association with the Diana 3 group following a long-distance call than before the call was given, but there was no change in the probability of association after calls for the other species (Table 1). Table 2 provides vocalisation rates during schedules scans and 5 min following long-distance calls. The probability of Diana monkeys having given a long-distance call was not affected by which species were in association, and overall group size was not significantly associated with whether a long-distance call was or was not given in the past half-hour (Table 3).

Behavioural changes following long-distance calls

Long-distance calls were consistently associated with several short-term behavioural changes: the group travelled farther in the 30 min following a long-distance call than before, group spread decreased, as did nearest-neighbour distance, while the number of associated species was higher after a call was given (Table 1). However, long-distance calls had no apparent effect on exposure level, height in the canopy, or nearest neighbour of other species (Table 1). The frequency distribution of individuals recorded in different behaviour categories was significantly different during group scans when a long-distance call had been given in less that the previous 5 min or in the previous 5–15 min than when a long-distance call had been given in either the previous 15–30 min or more than 30 min prior to the group scan (>30 min vs <5 min, G=10.19, P=0.037; vs 5–15 min, G=9.72, P<0.049; vs 15–30 min, G=1.33, P=0.86). More individuals were recorded scanning and travelling in the 5 min following a long-distance call, while fewer were recorded engaging in resting or social behaviours (Fig. 2).

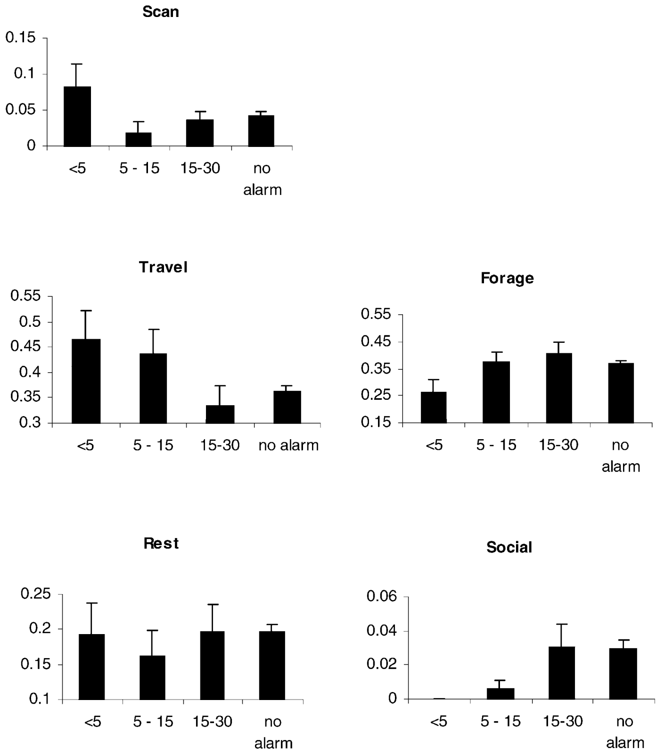

Fig. 2 Proportion of individuals recorded in different behavioural categories when no long-distance call has been given in the previous half-hour and when a long-distance call has been given in the previous 5, 5–15 or 15–30 min. Error bars represent standard error of the mean

Behaviour during observation periods with elevated calling rates

Over observation periods, elevated long-distance calling rates were also associated with several longer-term behavioural changes. There was a positive correlation be-

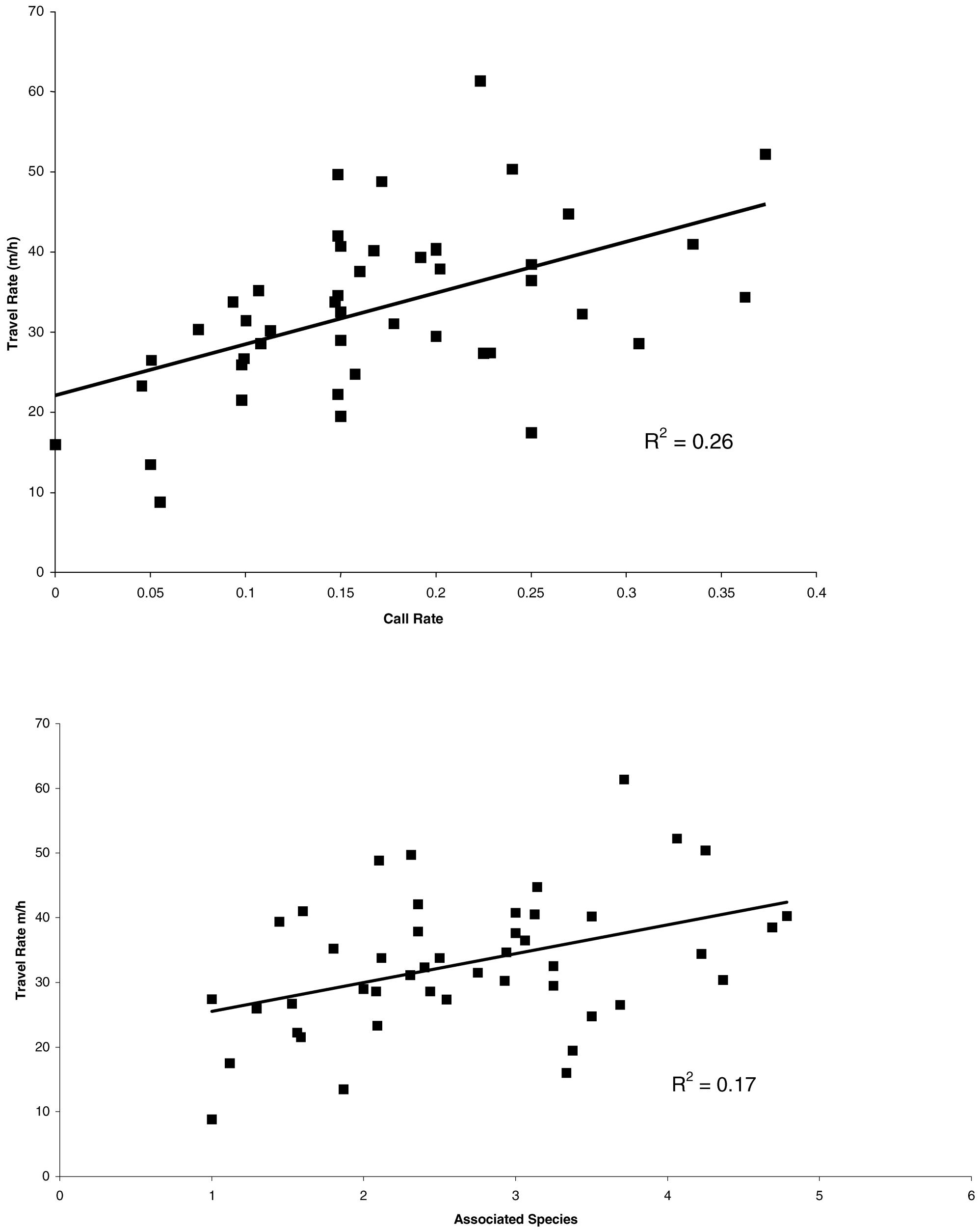

Fig. 3 The effects of long-distance call rate and number of associated species on travel rate of a Diana-monkey group over each observation period. Number of associated species is the average of associated species at each group scan over an observation period

Table 3 Species comparisons in likelihood of joining an association following a long-distance call. Negative *Z*values indicate species were more often in association following than preceding a long-distance call. Logistic regression results for likelihood of long-distance calls based on group size and species association patterns

Species	Joining likelihood		Logistic regression	−2 log likelihood	r^2	Wald	χ^2	*df*	*P*
	Z-test	*P*							
			Group size	493.99	0.005	2.96	2.90	1	0.09
			Species	490.262	0.011		6.63	6	0.36
Procolobus badius	0.00	1.00				0.171		1	0.90
Cercopithecus campbelli	0.00	1.00				0.035		1	0.85
Cercocebus atys	−1.73	0.08				1.89		1	0.17
Cercopithecus petaurista	−3.30	0.001				0.099		1	0.75
Colobus polykomos	−2.50	0.012				0.750		1	0.38
Colobus verus	−1.00	0.32				2.036		1	0.15

tween both call rate (calls/hour) and group travel rate (metres/hour) and the average number of associated species during a given observation period and the group travel rate (Fig. 3). To separate out the effects of these two independent variables (call rate and number of associated species) on travel rate, we used a stepwise multiple regression. There was a significant positive relationship for both long-distance call rate and number of associated species on the group travel rate (r^2=0.32, $F_{2,45}$=11.69, P<0.001). The regression coefficient for call rate was 54.35 (t=3.43, n=88, P<0.001) and for average number of associated species was 3.31 (t=2.47, n=88, P=0.02). The increase in travel rate is probably an effect of overall group size as there was a significant relationship between estimated total group size (calculated by summing the estimated average group size in Taï for each species present at each group scan interval) and metres moved during each half-hour period (r^2=0.17, $F_{1,513}$=9.97, P=0.002). The relationship between overall call rates and number of species in association was not significant (r^2=0.06, $F_{1,44}$=2.75, P=0.104), although more species were in association following a long-distance call than before (as shown in Table 1).

Discussion

Diana monkeys altered their behaviour following male long-distance calls; distance travelled, group cohesion and association rates increased, while nearest-neighbour distances decreased. Vocalisation rates for "alert" and "clear" calls increased in periods following long-distance calls. Similar results have been reported by Zuberbühler et al. (1997) and Uster and Zuberbühler (2001), who found that Diana monkeys' clear calling rates were significantly elevated after male long-distance calls. As these calls are given in contexts of increased predation risk and clear calls serve to co-ordinate group movement, they can be the proximate mechanism causing the observed increase in travel rates following long-distance calls. As expected, because they have not been associated with increased levels of predation risk or group disturbance, "trill" vocalisation rates did not increase. After long-distance calls, individuals were also more likely to engage in the costly activities of travel and vigilance, and were less often engaged in feeding, resting and social activities. Group movement rates increased during periods with more species in association and during periods with elevated calling rates.

Increased travel rates, group cohesion and association rates with other species cause individuals to suffer from reduced foraging efficiency. As these behaviours are maintained despite their costs, it can be assumed they have an adaptive benefit. Previous studies of behavioural responses to predation risk across many taxa have generally reported that individuals respond to increased predation risk by decreasing movement and increasing time spent in or near refuges (reviewed in Lima 1998). In view of that, a particularly interesting result of the present study is the clear increase in movement and travel rates under increased risk. A possible explanation for this apparent discrepancy is the different types of prey studied. Arboreal primates may be able to reduce exposure levels, but may also move faster and farther through the forest as a way to evade a predator. Similar increases in movement rates have been documented in other primate studies (Sigg 1980). Additionally, social species typically rely on a "safety-in-numbers" strategy, making crypsis unattainable for all members of a large group.

Other studies of the behavioural responses of primates to increased predation risk have not always found consistent patterns. For example, in Treves's study (1999) on redtails (*Cercopithecus ascanius*) and red colobus (*P. badius*), neither group cohesion nor vigilance levels consistently responded to either predator encounters or playbacks; time spent scanning increased after all encounters for both species, but frequency of scanning bouts did not. The number of nearest neighbours, within 2 m, decreased consistently for red-tailed monkeys, but not for red colobus. In contrast, we may have found increased group cohesion because we recorded total group spread and the distance to the nearest neighbour and did not constrain our definition of cohesion as tightly. Even so, we did not find that distance to nearest allo-specific neighbour was different following long-distance calls.

Zuberbühler et al. (1997) argued that male long-distance calls function not only to warn conspecifics of potential danger, but also to advertise to predators that they have been detected. As both leopard and eagles are "ambush" predators, once their presence is detected, an attack will be less successful than if the prey are taken by surprise. Male long-distance calls have been shown to cause leopards to move away from a Diana group sooner than if they were not detected (Zuberbühler et al. 1999). If long-distance calls indicate the immediate presence of a predator, the actual risk of attack may momentarily increase if an attack is imminent but soon decrease if predators are warned off. In this case, we would expect behaviour variables to respond to increases in risk over very short intervals. In our study, we found that behavioural changes were only significant over very short intervals (less than 15 min following a long-distance call). Anecdotal evidence from Taï suggests that eagles may appear during chimpanzee hunts and vice versa. Predators can conceivably use long-distance calls to locate prey species. If multi-predator attacks are common, then interpreting the appropriate behavioural responses may not be particularly straightforward. In such circumstances, group movement away from the site of an encounter, polyspecific association rates and overall group spread may be more reliable long-term responses than changes in height or exposure.

Grouping benefits for individuals in mixed-species groups are essentially the same as for individuals in a mono-specific group, with potentially lower costs. Mixed-species groups have been shown in several other studies to have group-size benefits in terms of individual vigilance levels (Sullivan 1984; Cords 1990). Males from mixed-species groups have also been shown to attack eagles simultaneously, providing a more effective defence against an attack than a single-species group (Gautier-Hion and Tutin 1988). An additional benefit of mixed-species associations may be that group size is more plastic when made up of several easily divisible sub-groups that can join or split with varying predation risk. In general, groups are more stable amongst primates than in many other social species (Wrangham 1987), with membership changing only through dispersal, births and deaths, rather than the daily response to changes in resource availability and predation risk we see in some non-primates (but see fission-fusion examples of spider monkeys and chimpanzees; Chapman et al. 1995). In this study, association rates with other species were correlated with long-distance call rates, indicating that mixed-species associations increase in response to predation risk. Similar results have been shown in passerines (Greig-Smith 1981) and primates (Bshary and Noë 1997; Noë and Bshary 1997). As group movement increased when the Diana monkeys were in association with other species, these results support the occurrence of inter-specific competition between Diana monkeys and other species in Taï. Because they are common in Taï, the benefits of these associations must then outweigh the costs, at least for the species that initiate and maintain the associations.

In some cases, the costs to the nuclear species may be greater than the benefits, but lower than the costs of excluding the "joiners", effectively creating a producer-scrounger situation. Downy woodpeckers alarm call less often and are less vigilant when in mixed-species associations, effectively parasitising the vigilance of the individuals in the flocks they join (Sullivan 1984). Diana monkeys have larger groups and forage higher in the canopy than the other guenons (McGraw 1998) and they have been shown to be better at detecting eagle predators (Bshary and Noë 1997). Diana monkeys and black and white colobus are also the species most likely to approach or attack eagles during an encounter (Bshary and Noë 1997). Together, these behavioural and ecological traits indicate that Diana monkeys are good association partners for other species, probably conferring detection, deterrence and dilution benefits. Red colobus decrease their vigilance levels when in association with Diana, while the reverse is not true (Bshary and Noë 1997). It is likely that the "nuclear species", in this case Diana monkeys, benefit less from the associations than the initiating species. As in Taï, primate species in other communities have been shown to vary in their ability to detect different types of predators (Gautier-Hion et al. 1983), making these species effective sentinels for less vigilant or observant species.

To look at individual cost-benefit pay-offs in mixed-species associations, we need to look at the proximate mechanisms causing association patterns. For example, by determining which species are joiners, or satellite species, we can assess which species gain larger pay-offs. In this study, it appears that black and white colobus and the lesser spot-nosed monkey were the species most likely to join an association following long-distance calls. However, Noë and Bshary (1997) found that, under simulated predation risk by chimpanzees, red colobus were the species more likely to join red colobus-Diana associations, while Diana monkeys were more likely to leave these associations. From these results, we can predict that the pay-off structure is asymmetrical, perhaps benefiting other species more than Diana monkeys, and these pay-off structures may vary depending on the specific predator. It is also important to compare the behavioural changes and foraging efficiency for different species. We would expect measures of competition, such as the Relative Ranging Costs from Janson and Goldsmith (1994), to be less sensitive to group size in a mixed-species group than in a mono-specific group. We would also expect that species with smaller dietary overlap suffer lower costs than those with higher overlap, while species with different ranging behaviour have to compromise more to stay in association. Thus it may be possible to look at both ranging changes and dietary shifts to gain a measure of costs of association.

Very little attention has been paid to the resultant effects of costly anti-predator behaviour at the population level. Comparisons between and within species and populations under different levels of predation risk may provide insights into how predation risk and rate interact with resource competition to determine observed patterns of group size, population density, community composition and inter-specific interactions. The more predator encounters individuals experience, the more energy they must devote to anti-predator behaviour. In non-social insects, behavioural responses to increased predation risk have been shown to reduce foraging efficiency and, therefore, growth and reproductive rates (e.g. Peckarsky et al. 1993; Scrimgouer and Culp 1994). Among vertebrates, the relationship between predation risk and the fitness consequences of anti-predator behaviour probably leads to a decline in general body condition (Hik 1995), but there are limited comparative data to assess the prevalence of these findings. Amongst primates, Boinski et al. (1999) have shown that captive brown-capuchin alarm call rates correlate with stress levels, through measuring faecal cortisol levels. Shultz and Noë (2002) have shown that monkey alarm calls are inversely correlated to the distance from the nests of crowned eagles, indicating that groups near the centre of an eagle pair's territory experience higher levels of predation risk. Because increased predation risk causes costly behavioural responses, as shown here, we should be able to detect ecological manifestations of predation risk among monkey groups under different levels of predation risk.

Acknowledgements Financial support for this project was provided by a Wildlife Conservation Research Fellowship, the Leakey Foundation, the Raptor Research Foundation Leslie Brown Memorial Fund, the Peregrine Fund, the Max Planck Institut Seewiesen and the Ecole Normale Supérieure de Paris. We thank the Ministère de la Recherche Scientifique, and Department pour la Protection de la Nature for permission to conduct this work in Taï. We thank the C.S.R.S. in Abidjan and the C.R.E. for logistic support. We also thank Robin Dunbar, Steve Sait, Adrian Treves and two anonymous reviewers for insightful comments on previous versions of the manuscript.

References

Anderson CM (1986) Predation and primate evolution. Primates 27:15–39

Boinski S, Gross TS, Davis JK (1999) Terrestrial predator alarm vocalizations are a valid monitor of stress in captive brown capuchins (Cebus apella). Zool Biol 18:295–312

Bshary R, Noë R (1997) Red colobus and Diana monkeys provide mutual protection against predators. Anim Behav 54:1461–1474

Buskirk WH (1976) Social systems in tropical avifauna. Am Nat 110:293–310

Chapman CA, Chapman LJ (2000) Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. Behav Ecol Sociobiol 47:129–139

Chapman CA, Wrangham RW, Chapman LJ (1995) Ecological constraints on group-size. An analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70

Cheney DL, Wrangham RW (1987) Predation. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 227–239

Cords M (1990) Vigilance and mixed-species association of some East African forest monkeys. Behav Ecol Sociobiol 26:297–300

Dolby AS, Grubb TC (1999) Functional roles of mixed-species foraging flocks: a field manipulation. Auk 116:557–559

Elgar MA(1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol Rev Cambridge Philos Soc 64:13–33

Forsman JT, Mönkkönen M, Inkeröinen J, Reunanen P (1998) Aggregate dispersion of birds after encountering a predator: experimental evidence. J Avian Biol 29:44–48

Gautier-Hion A, Tutin CEG (1988) Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. Folia Primatol 51:149–151

Gautier-Hion A, Quris R, Gautier JP (1983) Monospecific vs polyspecific life: a comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. Behav Ecol Sociobiol 12:325–335

Greig-Smith PW (1981) The role of alarm responses in the formation of mixed-species flocks of heathland birds. Behav Ecol Sociobiol 8:7–10

Hagar MC, Helfman GS (1991) Safety in numbers: shoal choice by minnows under predatory threat. Behav Ecol Sociobiol 29:271–276

Hamilton WD (1971) Geometry of the selfish herd. J Theor Biol 31:295–311

Hik DS (1995) Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshow hares. Wildl Res 22:115–129

Hill RA, Dunbar RIM (1998) An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411–430

Höner OP, Leumann, L, Noë R (1997) Dyadic associations of red colobus and Diana monkey groups in the Taï National Park, Côte d'Ivoire. Primates 38:281–291

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behav Ecol 2:142–155

Isbell LA (1994) Predation on primates: ecological and evolutionary consequences. Evol Anthropol 3:61–71

Janson CH (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135:389–410

Janson CH, Goldsmith ML (1994) Predicting group size in primates: foraging costs and predation risks. Behav Ecol 6:326–336

Lima SL (1987) Vigilance while feeding and its relation to the risk of predation. J Theor Biol 124:303–316

Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Stud Behav 27:215–290

Magurran AE, Oulton WJ, Pitcher TJ (1985) Vigilant behaviour and shoal size in minnows. Z Tierpsychol 67:167–178

McGraw WS (1998) Comparative locomotion and habitat use of six monkeys in the Taï Forest, Ivory Coast. Am J Phys Anthropol 105:493–510

Myers JP (1980) Territoriality and flocking by buff-breasted sandpipers: variations in non-breeding dispersion. Condor 82:241–250

Myers JP (1984) Spacing behavior of non-breeding shorebirds. In: Burger J, Olla BL (eds) Behavior of marine animals, vol 6. Shorebirds: migration and migratory behavior. Plenum, New York, pp 271–321

Noë R, Bshary R (1997) The formation of red colobus-Diana monkey associations under predation pressure from chimpanzees. Proc R Soc Lond B 264:254–259

Peckarsky BL, Cowan CA, Penton MA, Anderson C (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836–1846

Ruiter JR de (1986) The influence of group size on predator scanning and foraging behaviour of wedge-capped capuchin monkeys (Cebus olivaceous). Behaviour 98:240–258

Scrimgouer GJ, Culp JM (1994) Feeding while evading predators: the effect of predator species on a behavioural trade-off by a lotic mayfly. Oikos 69:71–79

Seghers BH (1974) Schooling behavior in the guppy (Poecilia reticulata): an evolutionary response to predation. Evolution 28:486–489

Shultz S, Noë R (2002) Primate perceptions of predation risk varies with the distance from nests of crowned eagles. Proc R Soc Lond B 269:1797–1802

Sigg H (1980) Differentiation of female positions in hamadryas one-mail units. Z Tierpsychol 53:265–302

Sullivan K (1984) Information exploitation by downy woodpeckers in mixed-species flocks. Behaviour 91:294–311

Tegeder RW, Krause J (1995) Density dependence and numerosity in fright stimulated aggregation behaviour of shoaling fish. Philos Trans R Soc Lond Ser B 350:381–390

Treves A (1998) The influence of group size and neighbors on vigilance in two species of arboreal monkeys. Behaviour 135:435–481

Treves A (1999) Has predation shaped the social systems of arboreal primates? Int J Primatol 20:35–67

Treves A (2000) Theory and method in studies of vigilance and aggregation. Anim Behav 60:711–722

Treves A (2001) Vigilance and aggregation in black howler monkeys (Alouatta pigra). Behav Ecol Sociobiol 50:90–95

Uster D, Zuberbühler K (2001) The functional significance of Diana monkey 'clear' calls. Behaviour 138:741–756

Whitesides GH (1989) Interspecific associations of Diana monkeys, Cercopithecus Diana, in Sierra Leone, West Africa, biological significance or chance? Anim Behav 37:760–776

Whitesides GH, Oates JF, Green SM, Kluberdanz RP (1988) Estimating primate densities from transects in a west African rain forest: a comparison of techniques. J Anim Ecol 57:345–367

Whitfeld DP (1988) Raptor predation on wintering waders in southeast Scotland. Ibis 130:284–287

Wrangham RW (1987) Evolution of social structure. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 282–298

Zuberbühler K, Noë, R, Seyfarth RM (1997) Diana monkey long-distance calls: messages for conspecifics and predators. Anim Behav 53:589–604

Zuberbühler K, Jenny D, Bshary R (1999) The predator deterence function of alarm calls. Ethology 105:190–477