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THE FUNCTIONAL SIGNIFICANCE OF DIANA MONKEY 'CLEAR' CALLS

by

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Summary

In their natural West African rainforest habitat, Diana monkeys continuously produce high rates of a close-range clear-sounding call, but the function of this behaviour is unknown. In other primate species, close-range calls are typically given in socially relevant situations, for example, to gain access to grooming partners or food. Quite contrarily, we tested a number of hypotheses and found that Diana monkey 'clear' calls primarily function to avoid predation. Call rates were significantly elevated when predation threat was high, for instance when the visibility was poor, when the group spread was large, when the group was not associated with other monkey species, or after alarm calls. Call rates were not significantly elevated, however, in circumstances of high social competition, for instance when the group spread was small, during resting phases, while feeding on clumped food sources, or when foraging in the periphery where inter-group encounters were more likely to occur. Calling was contagious in that calls typically elicited vocal responses from out-of-sight group members within a few seconds. Because of this, callers can effectively monitor a much larger area than is visually accessible to single individuals, suggesting that Diana monkey clear calls act as an essential element in a mutualistic system of co-ordinated vigilance.

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Introduction

In many primate species, individuals produce close-range vocalisations in relaxed, friendly and non-predatory social contexts. These tonal calls are given by most group members and have often been termed 'contact calls' (*e.g.* Gautier & Gautier, 1977; Zuberbühler *et al.*, 1997). For most species, there is no empirical information about the functional significance of these calls, but it is often assumed that they regulate some aspect of group life. Since gregarious individuals are in constant competition over the same resources, calling may play a role in regulating competitive social interactions. Indeed, some studies have found specific functional roles of primate close-range calls in the regulation of intra-specific competition (the 'social competition hypothesis'). Competitive interactions arise in a number of circumstances, for example, when individuals disagree about the direction of an upcoming progression (*e.g.* Boinski & Garber, 1999) or while trying to access food sites or social partners (*e.g.* Boinski & Campbell, 1996). Adult female squirrel monkeys (*Saimiri oerstedi*), for instance, give 'twitters' to initiate and lead troop movements (Boinski, 1991), toque macaques (*Macaca sinica*) produce 'whees' when detecting food (Dittus, 1984), and baboons (*Papio cynocephalus)* emit 'grunts' to facilitate social interactions with group members and to reconcile with former opponents (Cheney *et al.*, 1995).

However, not all social interactions are competitive: primates not only suffer but also benefit from the presence of conspecifics. For instance, when threatened by a predator, individuals benefit from each other due to safety-in-number effects (Hamilton, 1971; Rendall *et al.*, 2000) or improved vigilance (Cords, 1990). An alternative hypothesis states, therefore, that contact calls play an important role in modulating and co-ordinating these anti-predation benefits (the 'anti-predation hypothesis'). Although predation has long been thought to explain the evolution of alarm calls (*e.g.* Maynard-Smith, 1965) the effect of the predation on the evolution of other call types has not been well investigated.

West African Diana monkeys (*Cercopithecus diana*) live in groups of about 20-30 individuals with one adult male and several adult females with their offspring. In their natural rainforest habitat of the Taï forest Diana monkeys are hunted by leopards (*Panthera pardus*, Zuberbühler *et al.*, 1999a), crowned-hawk eagles (*Stephanoaetus coronatus*: Shultz, in press), chimpanzees (*Pan troglodytes*: Boesch & Boesch, 1989), and in some areas by human poachers (Martin, 1991). In response to this, Diana monkeys frequently associate with other sympatric primate species to better protect themselves against predation (Noë & Bshary, 1997). With the exception of the adult male, most group members regularly produce close-range 'clear' calls at high rates throughout the day. These calls are audible over about 50 metres and have also been referred to as 'contact calls' in earlier studies (*e.g.* Zuberbühler *et al.*, 1997).

Here, we investigated the functional significance of Diana monkey 'clear' calls. We analysed several putative functions, which could serve both in alleviating the costs and increasing the benefits of living in a social group, as outlined before. We investigated whether Diana monkeys used clear calls in socially competitive situations, such as during social interactions, before progressions, during feeding bouts, or when inter-group encounters were more likely. Alternatively, we investigated whether Diana monkeys used these calls to protect themselves against predation by maintaining close cohesion with other group members and by benefiting from each other's vigilance.

Methods

Study site and subjects

Data were collected by the first author between 16 October, 1999 and 27 April, 2000 on a group of Diana monkeys (DIA2), located about one kilometre east of the CRE research station ('Centre de Recherche en Ecologie,' 5°50′N, 7°21′W) in the Taï National Park, Côte d'Ivoire. DIA2 has been under constant observation since September, 1992 and is well habituated to human presence. During the data collection DIA2 consisted of one adult male, 10 adult females, 4-6 sub-adults, 8 juveniles and 0-4 infants. In an earlier study the average home range size of DIA2 was estimated to be about 0.6 km^2 (Höner *et al.*, 1997), which coincides approximately with our results (0.69 km^2).

The vocal repertoire of the Diana monkey

Diana monkeys show an age/sex dimorphism in their vocal repertoire (Zuberbühler *et al.*, 1997). Adult females, sub-adults, and juveniles account for most of the vocal activity and produce clear calls and a variety of other call types (trills, barks, screams, alert calls, and alarm calls to crowned-hawk eagles and leopards). The single adult male of a Diana monkey group does not utter any of these vocalisations. Instead, the male restricts his vocal communication to acoustically different loud alarm calls given in response to crowned-hawk eagles, leopards, and other disturbances, such as fleeing animals, falling trees or other sudden loud noises (Zuberbühler, 2000d). In the spectrogram, clear calls appear as a symmetrically arched tonal signal (see Zuberbühler *et al.*, 1997).

Data collection

Data were collected either at the group level ('*group scans*', comparing the call rates of all animals) or at the individual level ('*focal scans*', comparing the call rates of specific individuals). '*Group scans*' consisted of 10-min observation periods conducted at the beginning of every full hour between 6:30 and 17:30 GMT ($N = 111$ days, $N = 879$ group scans). 50 of them (5.7%) were excluded from subsequent analyses, mostly because individuals were involved in inter-group aggression, which made determination of call rates unreliable due to neighbouring individuals' calling. During all group scans the observer determined the behaviour of the group and estimated their vertical position in the stratum. To get a reliable estimate of the general behaviour of the group we sampled at least six different individuals of all age-sex classes (except for infants born during the study period) per group scan. At the same time, the observer recorded various independent variables as defined below (Table 1) and the total number of clear calls produced over the 10-min sampling period (determined with a manual counter). Each data point, therefore, represented the cumulative number of all clear calls produced by the entire group. Data collection on some variables started 3-7 weeks after the beginning of the study.

Between two group scans the observer conducted 15 min-long '*focal scans*' on individual monkeys ($N = 83$ days, adult females: $N = 500$, adult male: $N = 20$, sub-adults: $N = 20$, juveniles: $N = 20$). For each scan, the observer selected one individual, either one of the ten individually known adult females, the adult male, or one of the sub-adults or juveniles and determined the number of calls over the 15 min interval. The adult male was easily recognised by his large body size and testicles. Their nipples, characteristic scars, and other features individually identified the 10 adult females. Sub-adults were defined as individuals with an adult body size, but without visible nipples. Two male sub-adults left the group during the study. Juveniles were smaller and born before the beginning of the study. All four infants were born within the study period between November and January. Sexing and individual recognition of sub-adults, juveniles, or infants was not reliably possible. For the adult females the observer determined the behaviour, stratum use and various other independent variables as defined below (Table 1). Females were not sampled more than twice per day. Individual focal scans were separated from one another by at least one hour.

Hypotheses and predictions

Social competition

If monkeys use clear calls to alleviate the costs of everyday competition, then they should call more in situations when social competition is high. First, this might be the case during resting (*versus* foraging) periods when monkeys are more likely to try to get access to others for grooming, play, or other forms of social interactions. Second, calling might be more frequent before (*versus* during or after) group progressions when monkeys are likely to have

TABLE 1. *Independent variables used in the study*

	Variable	Definition
1	Group spread	Group is (not) dispersed over an area of more than 25 × 25 m
2	Proximity*	Distance to the next group member is (not) more than 5 m
3	Vegetation	Local vegetation is (not) exceptionally dense. See (1) for details
4	Illumination	Illumination of the habitat is (not) exceptionally dark. See (1) for details
5	Stratum	Focal animal is 0-5 m, 5-12 m, 12-25 m, or 25 m off the ground. See (2) for details
6	Alarm call	Adult male has (not) given alarm calls during scan. See (3) for details
7	Associations	Group is (not) intermingled with another monkey species. See (4) for details
8	Behaviour	Individual does (not) locomote during observation time
9	Progression	The group is (not) beginning to move $\geqslant$ 25 m in one direction during the first 5 minutes following the scan
10	Food distribution	Individuals are (not) feeding on a clumped food source
11	Location	The group is (not) located in a peripheral grid cell, bordering on never visited grid cells. See (5) for details

* 'Proximity' was sampled during *focal scans* only. (1) Zuberbühler, 2000c, (2) McGraw, 1998, (3) Zuberbühler *et al.*, 1997, (4) Bshary & Noë, 1997, (5) Höner *et al.*, 1997.

divergent interests about the timing and direction of movements. Third, calling might be more frequent when monkeys are feeding on a clumped (*versus* distributed) food source and hence more likely to compete over food. Finally, calling might be more frequent when monkeys are foraging in a peripheral (rather than central) grid cell where interactions with a neighbouring group are more likely.

Anti-predation

If monkeys use clear calls to stay close to other group members to benefit from safety-in-number effects, then they should call more when they are more likely to lose contact with each other. This is the case when the group spread is large or the visibility is low, due to dense vegetation or dark habitat. If monkeys use clear calls to benefit from each other's vigilance, then monkeys should adjust their clear calling as a function of their vigilance behaviour. For example, monkeys should call more when predator presence is more likely or more difficult to assess. This is the case when the group spread is large or the visibility is low, but also when the monkeys sit in the higher strata where it is more difficult to monitor events on the ground, after a male alarm call when predator presence is more likely, or when the group is not associated with another monkey species so that the number of sentinels is smaller. Table 2 summarises key predictions of the 'social competition' and 'anti-predation' hypotheses.

Callers would benefit most from the vigilance behaviour of others if their calls elicit calling responses in out-of-sight group members, allowing the caller to obtain spatial

TABLE 2. *Predicted increases in Diana monkey clear call rates under the two functional hypotheses*

	Variable	Anti-predation	Social competition
1	Group spread	large	small
2	Proximity*	far	close
3	Vegetation	dense	open
4	Illumination	dark	light
5	Stratum	high	*no effect*
6	Alarm call	yes	no
7	Associations	no	*no effect*
8	Behaviour	travelling	resting
9	Progression	during	before
10	Food distribution	distributed	clumped
11	Location	*no effect*	peripheral

* Individual scans only.

information about the dimensions of the area surveyed and whether or not relevant changes have occurred. In such a case, the overall emission pattern should manifest in bouts of calls rather than consistent equally spaced calls. To quantify this, we determined the distribution of inter-call intervals from a large sample ($N = 3018$; $N = 40$ observation days) with a stopwatch. Samples in which an individual's call followed its own call were not further considered. The observed inter-call intervals were compared to expected rates calculated from the distribution of call rates in the group scans.

Results

Group scans

In the first analysis, we determined the overall calling behaviour of Diana monkeys at the group level ($N = 829$). Each data point, in other words, represented the cumulative number of calls produced by the entire group. We reasoned that external contexts were the main determinants of calling behaviour, and that they similarly affected all callers. Hence, although some group members might have contributed more calls than others to a particular group scan, all callers were exposed to the same context. Figure 1 illustrates the median call rates the group produced as a function of the different variables. We conducted a multiple regression analysis using SPSS 9 (variables were included in one step, missing cases were excluded pair-wise) to investigate which variables explained significant

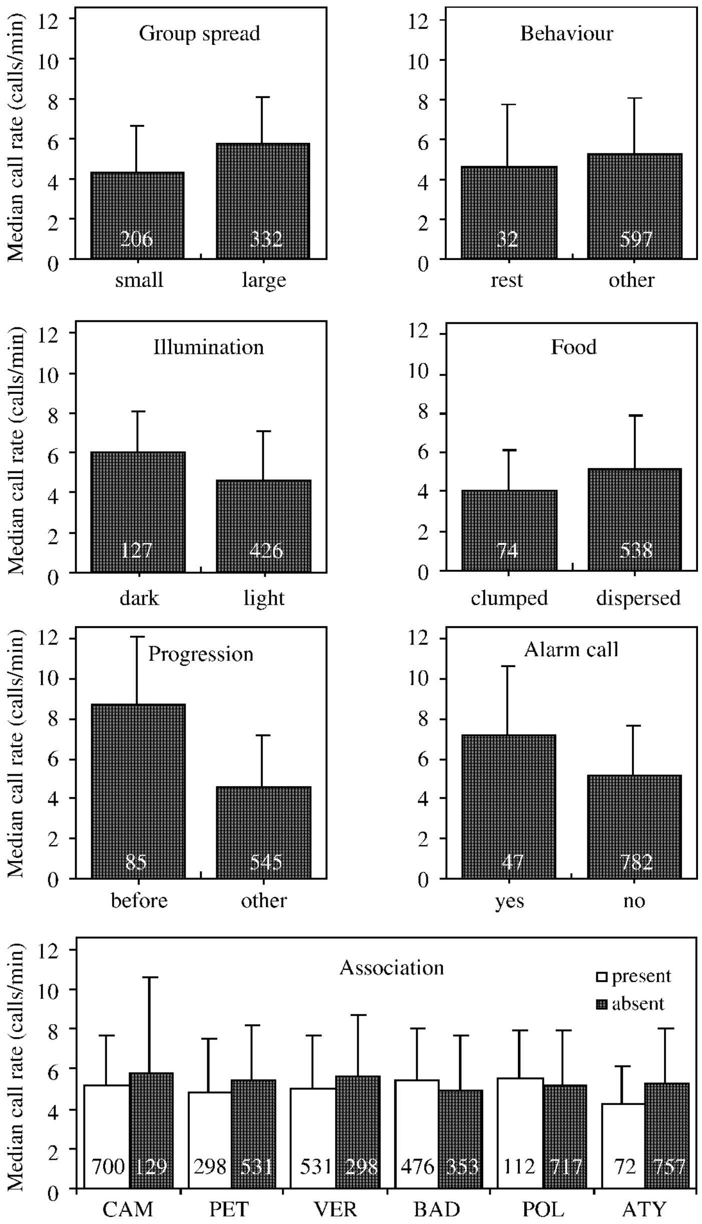

Fig. 1. Significant relationships between call rates and context. Solid bars refer to the median call rates; error bars indicate the third quartile. CAM *Cercopithecus campbelli*; PET *C. petaurista*; VER *Procolobus verus*; BAD *Colobus badius*; POL *C. polykomos*; ATY *Cercocebus atys.*

amounts of variance in the clear call rates. To meet the requirements for regression analysis, we log-transformed ($x' = \log(x + 1.5)$) the data to obtain a distribution that was not significantly different from a normal one (Kolmogorov-Smirnov-test, $z = 0.585$, $p > 0.8$, two-tailed). No auto-correlation was found between adjacent residuals (Durbin-Watson-test, Dw = 1.712). In some cases, fewer than half of the sampled individuals showed the same behaviour (24.1% of all scans) or were located in the same stratum (13.0% of all scans). When this occurred, we did not enter a data point for that variable.

Several of the variables explained significant amounts of the overall variance in the call rates (Table 3). The social competition hypothesis was supported by that fact that the group called more before progressions than during or after. However, call rates were significantly *lower* during resting periods or when feeding at *clumped* food sources, in contrast to the predictions of the social competition hypothesis. Also, if the group was located in the periphery of their home range the calling rate did not increase significantly.

TABLE 3. *Regression analysis of Diana monkey clear call rates*

	Variable	DF	F-ratio	p-value	Hypothesis supported
1	Group spread	1	3.919	<0.001	A
2	Vegetation	1	−0.176	NS	–
3	Illumination	1	2.053	0.041	A
4	Stratum	3	−1.212	NS	–
5	Alarm call	1	2.635	0.009	A
6	Associations				
	Cercopithecus campbelli	1	−1.792	0.074	(A)
	Cercopithecus petaurista	1	−1.444	NS	–
	Cercebus atys	1	−1.684	0.093	(A)
	Procolobus verus	1	−0.092	NS	–
	Colobus badius	1	1.380	NS	–
	Colobus polykomos	1	0.452	NS	–
7	Behaviour	1	−1.996	0.047	A
8	Progression	1	5.871	<0.001	S
9	Food distribution	1	−3.289	<0.001	A
10	Location	1	1.051	NS	–

A: Anti-predation hypothesis; S: Social competition hypothesis. Multiple $R = 0.442$; Multiple $R^2 = 0.195$; adjusted $R^2 = 0{,}165$; SE = 0,2001; $N = 829$; actual sample size for certain variables could be smaller due pair-wise exclusion of cases with missing values because of incomplete scans.

The anti-predator hypothesis was supported by the fact that call rates were significantly higher when the group was spread out and when the habitat was dark. Vegetation density had no significant effect. Also, call rates were significantly higher in scans where the male gave alarm calls (*i.e.* where predator presence was more likely). Stratum use had no overall effect, but call rates tended to be higher in the intermediate strata (*i.e.* where the visual range was lowest). Associations with other monkey species also affected the clear call rates. Call rates were lower when Diana monkeys were associated with monkey species that foraged in lower strata (*i.e.* when the number of sentinels was higher). There was an almost significant effect of the presence of Campbell's monkeys (*Cercopithecus campbelli*: 84% of the time associated) and sooty mangabeys (*Cercocebus atys*: 9% of the time associated), both of which forage lower than Diana monkeys (McGraw, 1998). Similarly, during, the presence of lower-foraging spot-nosed monkeys (*Cercopithecus petaurista*: 36% of the time associated), and olive colobus (*Procolobus verus*: 64% of the time associated) call rates were lower, but that effect was much weaker. During the presence of black-and-white colobus (*Colobus polykomos*: 14% of the time associated) and red colobus (*Colobus badius*: 57% of the time associated) call rates were not lower. Both species tend to forage in the upper forest canopy and are less likely to detect ground predators.

Individual scans

One particular concern when analysing behaviour at the group level is that the different individuals or age/sex classes might be affected differently by a particular context. For example if a particular behavioural pattern is not shown by one large age/sex class, even though it is present in all others, this could lead to false negative results, when data are analysed at the group level. In the following, therefore, we repeated the previous analyses with the focal scan data set. Each age/sex class was sampled 20 times and the following results emerged (Fig. 2). First, we found significant differences in the call rates between the different age/sex classes (Kruskal-Wallis H-test, $\chi^2 = 26.8$, $p < 0.001$, two-tailed). The adult females produced the highest calling rates with an average of 0.33 calls/min, followed by juveniles (0.17 calls/min) and sub-adults (0.13 calls/min). The adult male of the group did not produce clear calls. The 10 adult females were responsible for 63.7%

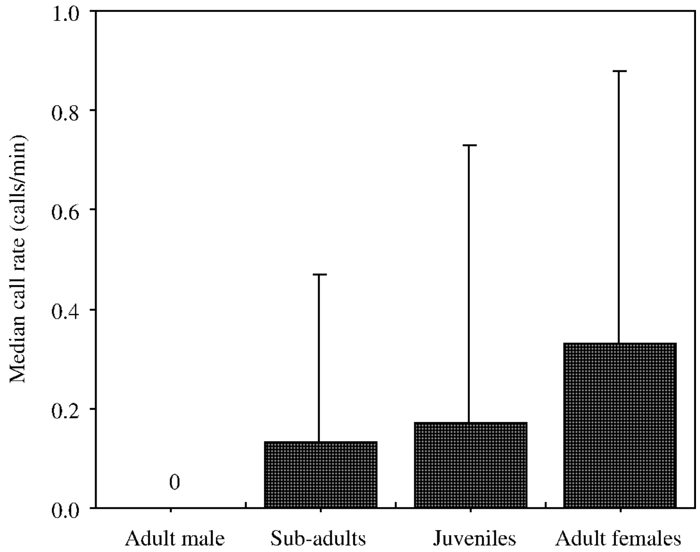

Fig. 2. Median call rates of four different age-sex classes in Diana monkeys ($N = 20$ each). Solid bars refer to the median call rates; error bars indicate the third quartile.

of all clear calls (expected 43.5%), the 8 juveniles accounted for 26.3% (expected 34.8%), and the 4 sub-adults for 10.0% (expected 17.4%), while the adult male never called (expected 4.3%).

Clear calling in Diana monkeys was highly contagious and found to be given in bouts (Fig. 3). 42.5% of all inter-call intervals ($N = 3018$) lasted for only one second or less (expected <0.1%). The majority of all clear calls (63.5%) were given in inter-call intervals that lasted three seconds or less (expected 1.1%). The expected values were calculated from the observed overall call rates and were based on the assumption that inter-call intervals were randomly distributed.

In the following, we analysed the individual calling behaviour of the ten individually recognizable adult females. Each female's call rate and the corresponding independent variables (Table 1) were measured during 50 focal scans. The sample size was too small to conduct a regression analysis without violating the normality assumption. The resulting non-parametric analysis was consistent with the previous results found at the group level (Table 4).

Again, the social competition hypothesis was only supported by the fact that females called significantly more often before group progressions than

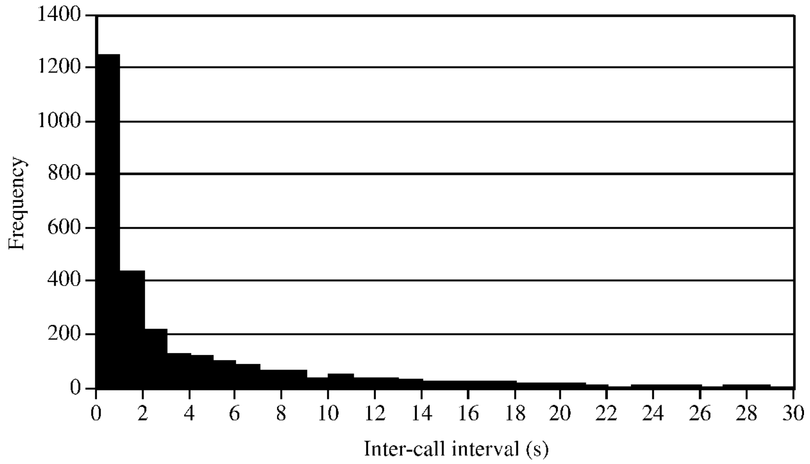

Fig. 3. Call emission pattern of Diana monkey clear calls.

TABLE 4. *Matched-pairs comparisons of the changes in median call rates in the adult females*

	Variable	*N* females	Mean call rate change (Δ calls per min)	*z*-value	*p*-value
1	Group spread (small — large)	10	+0.2167	2.668	0.008
2	Next neighbour (close — far)	10	+0.2300	2.136	0.033
3	Associations (present — absent)				
	Cercopithecus campbelli	10	−0.0900	1.436	NS
	Cercopithecus petaurista	9	−0.0467	0.459	NS
	Procolobus verus		−0.0700	1.130	NS
	Colobus badius		+0.0050	0.297	NS
	Colobus polykomos		−0.0482	0.476	NS
4	Behaviour (rest — other)	9	−0.1926	1.825	NS
5	Progression (yes — no)	8	−0.3458	2.384	0.017
6	Food (clumped — dispersed)	8	+0.2166	2.388	0.017
7	Location (periphery — central)	7	−0.1047	1.781	NS

Wilcoxon-test, two-tailed. The variables ‘vegetation’, ‘illumination’, ‘stratum’, ‘alarm call’, and ‘association with *C. atys*’ were excluded from statistical analysis due to insufficient sample size.

during or after. They also called more often in peripheral than in central grid cells, but this effect did not reach significance. In accordance with the anti-predator hypothesis female call rates were significantly lower while feeding on clumped compared to dispersed food sources, when the group spread was large, and when there was no neighbour within five metres.

Discussion

Close-range 'contact' calls have been reported from a number of different primate species, and these calls have typically been found to function in social contexts. For the Diana monkey clear call, we tested two main hypotheses to determine whether calls have evolved either to compete with conspecifics or to avoid predation. Our evidence points to the latter function. Calls could be useful for individuals to maintain proximity to other group members. At the group level analysis, call rates were significantly elevated when the group spread was large and when the visibility was poor due to a dark habitat. At the focal level analysis, adult females called significantly more often when the group was spread out or when no other conspecific was within five metres. Similar effects had been found in long-tailed macaques (*Macaca fascicularis*: Palombit, 1992) and chacma baboons (*Papio cynocephalus ursinus*: Rendall *et al.*, 2000). The anti-predation hypothesis was further supported by the fact that call rates were significantly higher after male alarm calls, when the probability of predator presence was high. Call rates were lower when the group was associated with lower foraging Campbell's monkeys or sooty mangabeys. Call rates also tended to be lower in the presence of lower-foraging spot-nosed monkeys and olive colobus monkey, suggesting that Diana monkeys adjust their call rates depending on the number of sentinels present.

The social competition hypothesis was only supported in the context of progression. In this context, call rates were significantly higher *before* progressions than during or after, which is when individuals are most likely to have divergent interests about the timing and direction of the forthcoming travel (*e.g.* Sigg & Stolba, 1981). Similar findings come from squirrel monkeys (*Saimiri oerstedii*: Boinski, 1991), white-faced capuchins (*Cebus capucinus*: Boinski, 1993), and gorillas (*Gorilla gorilla*: Stewart & Harcourt, 1994), which also signal their readiness to depart with increased calling rates. In some sense, however, this data set might also be taken in support of the anti-predator hypothesis. Increased calling prior to progression could be the result of individuals anticipating decreased group cohesion caused by individual differences in the timing and direction of the upcoming progression. Some support for the social competition hypothesis came from the inter-group context because adult females called more often in the periphery of their home range where inter-group encounters are more likely to occur. Similarly, in vervet monkeys (*Cercopithecus aethiops*) adult females are responsible for vocal behaviour in inter-group interactions (Cheney & Seyfarth, 1981). However, increased calling rates in the periphery could also be a consequence of individuals seeking information from each other about whether or not a neighbouring group has been detected. Diana monkeys did not use clear calls to facilitate access to social partners, as it has been found in Japanese macaques (*Macaca fuscata*: Masataka, 1989) and baboons (Cheney *et al.*, 1995). Similarly, clear calls did not play a role in feeding competition, since clumped food distribution was linked with significantly *decreased* clear call rates. In fact, under these circumstances clear call rates were among the lowest ever observed. This contrasts with observations on toque macaques (Dittus, 1984) or spider monkeys (*Ateles geoffroyi*: Chapman & Lefebvre, 1990) where call rates were higher after the discovery of a food source, which informed others about the presence, quantity, and location of food.

Diana monkeys respond to each other's clear calls. Individual calls have an extremely high probability of being answered by an out-of-sight group member within the next few seconds (Fig. 3). Call exchanges have been reported from a number of primate species, but typically in social contexts. Gorillas, for example, typically respond to each other's calls within half a second (Harcourt *et al.*, 1993). In squirrel monkeys (*Saimiri sciureus*), preferred partners exchange contact calls more often and with a shorter latency of response than animals with few affiliate contacts (Biben *et al.*, 1986; Biben, 1993). Although no formal acoustic analysis is presented here, the acoustic structure of Diana monkey clear calls consistently changes in response to some events, such as the appearance of a predator or a neighbouring group. Moreover, observers can with some certainty identify individuals by their clear calls. Previous studies have shown that Diana monkeys are extremely skilled in interpreting the semantic information in their own and other species' alarm calls (*e.g.* Zuberbühler *et al.*, 1999b, Zuberbühler, 2000a, b, c). Hence, Diana monkey clear calls have the potential to convey information not only about the location and identity of the caller but also about relevant changes occurring in areas outside the callers' visible range.

In Diana monkeys, the adult females are most active in calling, accounting for more than half of the entire clear call production in a group (Fig. 2). A striking aspect is the complete absence of this call in the adult male and possibly also in the sub-adult males. Perhaps, males produce clear calls as juveniles, decrease their calling rates as sub-adults, and finally stop upon becoming adult (see also Gautier, 1974). This pattern seems to represent a species-specific feature. Despite long-term observations starting in 1991 (*e.g.* Zuberbühler, 1993) adult males have never been seen to produce any of the vocalisations that the females and sub-adults produce. At the same time, the call usage described here is likely to be representative for individuals living under similarly natural and undisturbed conditions. Large parts of the Taï National Park, including our study area, show few traces of human influence and the density of primates and their predators is still very high (Boesch & Boesch, 1989; Jenny, 1996; Shultz, in press). Moreover, predation attempts of all three predators have been observed on the study groups. This suggests that Diana monkeys are likely to show behaviour as naturally evolved.

Diana monkeys spend a large proportion of their time with scanning for predators (Bshary & Noë, 1997), but individuals are typically out of each other's visual contact. Individuals benefit from the presence of others by sharing vigilance, even across species (Metcalfe, 1984). In some species of babblers (*Timaliidae*), one member of the group remains perched above the ground with the rest of the group feed below. After some time, the individual is replaced by another group member who will take over the role as the sentinel. Coordination of vigilance is regulated acoustically: about every five seconds the sentinel produces a low-pitched, short-ranged, and difficult to locate call, the watchman's song, which informs others that the individual is watchful and that nothing has happened (Wickler, 1985). Our results suggest that Diana monkey clear calls function in a similar way. Since callers can reliably elicit responses in conspecifics, they possess an effective tool to obtain important information about the watchfulness and location of other out-of-sight group members. Moreover, by assessing structural changes in the calls, monkeys can obtain important information as to whether others have witnessed crucial changes in the environment, such as the appearance of a predator or a neighbouring group.

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