



Snake alarm calls as a public good in sooty mangabeys

Alexander Mielke^{a, b, c, d, *}, Catherine Crockford^{b, c, 1}, Roman M. Wittig^{b, c, *, 1}

^a Department of Psychology, University of Portsmouth, Portsmouth, U.K.

^b Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

^c Tai Chimpanzee Project, Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Abidjan, Cote d'Ivoire

^d Primate Models for Behavioural Evolution Lab, Institute for Cognitive and Evolutionary Anthropology, Oxford, U.K.

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Transmitting information about the location of a predator in social animal species can be seen as an investment in a public good, where information is the resource and group members benefit from reduced fatalities of kin and cooperation partners in their community. As few empirical tests of this idea exist in natural settings, we conducted a field experiment using snake models in wild sooty mangabeys, *Cercocebus atys atys*. We tested sooty mangabey alarm-calling patterns when exposed to viper models, investigating whether individuals called to signal fitness, to warn specific group members, or when information about the threat is not public, as would be predicted by public goods games. Strong inter-individual differences in the likelihood of alarm calling existed. We found that overlap between callers was rare. Individuals were more likely to call if fewer individuals were present at the encounter site and if they had not heard other alarm calls before arriving at the site, indicating that alarm calls extended the information about the threat to following group members. This group size effect is in line with predictions of the volunteer's dilemma, a public goods game. We found no indications that individuals called specifically to warn ignorant individuals, kin or cooperation partners. Calling when information about the threat was not public allowed individuals to warn following group members while avoiding redundancy. Public goods games have not been employed widely in studies of the evolution of primate cooperation and animal communication in general but may provide useful models for understanding group level cooperation.

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Reducing predation risk is considered one of the main reasons for animals to form social groups (Janson & Goldsmith, 1995). Alarm signals facilitate predator avoidance and allow for communal defence (Isbell, 1994), and are often seen as a form of cooperation (Caro, 2005), as they increase receiver fitness (Ostreiher, 2003). Hypotheses explaining the evolution of alarm calls focus on inclusive fitness benefits by protecting kin (Griessler, 2009; Hamilton, 1964), reducing the risk for the caller through selfish herd effects (Curio, 1978; Wheeler, 2008), and recruiting others to mob the predator (Crofoot, 2013; Curio, 1978) and deter further pursuit (Hasson, 1991; Zuberbühler, Jenny, & Bshary, 1999). Tied to these

ultimate functions are proximate mechanisms that allow callers to optimize call outcomes, by adapting to the predator type (Griessler, 2009; Manser, Seyfarth, & Cheney, 2002; Seyfarth, Cheney, & Marler, 1980; Zuberbühler, 2001), threat level (Manser et al., 2002; Murphy, Lea, & Zuberbühler, 2013; Papworth, Böse, Barker, Schel, & Zuberbühler, 2008), receiver behaviour (Wich & Sterck, 2003; Zuberbühler, 2008) and inferred receiver knowledge (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, & Zuberbühler, 2017; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013). Experiments with predator models provide a reliable external experimental stimulus to compare species' differences in communication and cognition (Wittig & Crockford, 2018; Zuberbühler, 2014). Calling behaviour can differ in flexibility, ranging from a stereotypical and instinctive response to a predator to intentional communication specifically tailored to the behaviour and attentional state of the audience (Crockford et al., 2017; Schel et al., 2013). The species-specific predator response will be determined partially by the way information is transmitted in communities, as different social structures

* Correspondence: A. Mielke, Department of Psychology, King Henry Building, Portsmouth PO1 2DY, U.K. and R. M. Wittig, Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany.

E-mail addresses: mielke.alexand@gmail.com (A. Mielke), wittig@eva.mpg.de (R. M. Wittig).

¹ Joint senior author.

require different strategies to optimize the distribution of information. The variable social structures of different primate species allow us to study the flexibility of information processing underlying alarm-calling behaviour. Here, we conducted snake model experiments to understand the evolution of cooperative alarm calling in sooty mangabeys, *Cercocebus atys atys*.

Many hypotheses explaining the evolution of alarm calling focus on direct benefits to the caller (Caro, 2005). While this can explain the reaction of many animal species to ambush or pursuit predators, stationary snakes with a sit-and-wait hunting strategy, such as Gaboon vipers, *Bitis gabonica*, and rhinoceros vipers, *Bitis nasicornis*, mainly pose danger to primates if approached too closely (McGrew, 2015; Penner, Fruteau, Range, & Rödel, 2008). They are therefore rather a threat than a predator. Once primates detect these snakes, the risk for the monkey is removed as the snake does not pursue them. These vipers can also remain in the same location for several weeks. Thus, once their location is uncovered, this information can remain viable for future visits. It is unlikely that calling acts as a deterrent for these snakes as they do not actively follow primates. Mobbing, which can result in the viper relocating to an unknown location, is thus rarely in the interest of the prey. Even though the costs of calling have not been measured in sooty mangabeys, it has been argued that alarm callers potentially incur a small cost (Caro, 2005) by exposing themselves to other predatory species, ceasing to forage, and drawing other individuals into closer proximity, which could subsequently increase contest competition. This is a useful context to study the evolution of cooperation in alarm calling as individuals decide to transmit information about the threat to other group members (Seyfarth et al., 2010) despite the limited costs and lack of direct benefits.

Here, we tested different hypotheses as to why sooty mangabeys call to inform others about the threat. Calling could constitute an honest signal of fitness, increasing the likelihood that the caller is chosen as a mate (Bergstrom & Lachmann, 2001; Walker, York, & Young, 2016), with males predicted to call more than females (Wheeler, 2008). Individuals could also signal their cooperative intent, increasing the likelihood that they are chosen as cooperation partners (Kern & Radford, 2018), in which case individuals would be predicted to call more in larger groups. Alarm calls could be produced by individuals that gain from protecting specific group members, delivering benefits to the rest of the group as a by-product (Gavrillets, 2015). Transmitting information leads to potential fitness benefits by alarming kin, potential mates or cooperation partners, and individuals should increase calling when these individuals are potentially able to hear them (Caro, 2005; Cheney & Seyfarth, 1985).

Another mechanism that could solve the social dilemma of cooperative alarm calling is the broadcasting of information about a threat following the rules of a public goods game (Archetti, 2011; Kollock, 1998). A public good is a resource whose benefits are shared among group members, and individuals cooperate because their benefit outweighs the benefits of free riding (Willem, Arseneau, Schleuning, & van Schaik, 2015). In the volunteer's dilemma (Archetti, 2009; Arseneau-Robar et al., 2016; Diekmann, 1985; Willem et al., 2015), the public good can be successfully produced by a small number of group members, so most individuals should opt for a strategy of defection (Schneider, Melis, & Tomasello, 2012). However, if no individual decides to cooperate, the public good might be lost for everyone, and cooperating serves the individual's interest (Archetti, 2009; Arseneau-Robar et al., 2016). This could be directly applied to the case of vipers here: the public good could be information about the presence and location of the threat. Sharing this information reduces risk of injury for group members, including kin and cooperation partners of the caller. As alarm calls are often loud and conspicuous, multiple

individuals calling at the same time would create redundancy while not increasing the public good (Archetti, 2011). Thus, individuals should opt to pay the cost of calling only if no other source of information about the threat is available for other group members. This should most directly be expressed in a group size effect: the more individuals are present around the threat, the less likely it should be for each individual to vocalize.

The level of spatial cohesion of a community influences how information about predators is distributed: In highly cohesive systems, knowledge about a predator is evenly distributed after the first alarm call, as all group members will hear it. In species with low spatial cohesion and strong fission–fusion dynamics (Aureli et al., 2008), distinct subgroups form units with unevenly distributed information: initial calling will only reach some individuals and form the public good of that subgroup, while others remain ignorant (Crockford et al., 2012). If knowledgeable individuals have an interest in transmitting information about the threat, the burden is on them to adapt their behaviour, potentially leading to the evolution of skills that allow tracking the knowledge state of others (Crockford et al., 2017).

Many primate species live in large communities with relatively low fission–fusion dynamics (Aureli et al., 2008). Groups are generally cohesive, but due to the territory structure or the size of the group, not all group members will share the same knowledge and hear all calls. To transmit information to specific recipients, individuals could monitor the threat and inform ignorant arrivals and valuable partners directly (Crockford et al., 2017, 2012; Schel et al., 2013). This individualistic strategy ensures high transmission fidelity but is time consuming for the sender. Alternatively, individuals could ensure that the presence of the threat remains public knowledge. This strategy does not involve constant processing of the knowledge states of other group members, decreasing transmission fidelity. The costs for each group member, however, are low and if defection rates are low, this strategy could be equally efficient.

Here, we tested whether sooty mangabeys, a species with low fission–fusion dynamics and large multimale, multifemale groups (Mielke et al., 2017; Range & Noë, 2002), use alarm calls to maintain information about the threat as a public good, or specifically inform ignorant or valuable group members. Sooty mangabeys encounter highly camouflaged and venomous Gaboon and rhinoceros vipers two to three times a week (Range & Fischer, 2004). Not detecting a snake could lead to a lethal outcome for monkeys (Penner et al., 2008). Mangabeys produce snake-specific alarm calls that draw other group members towards the threat (Penner et al., 2008; Range & Fischer, 2004). Mangabeys approaching several group members showing extended attention to a specific spot on the ground without feeding and with alert body posture will probably be able to infer the location of a threat. However, calls are necessary to inform individuals outside the visual range, which can be below 10 m in parts of the mangabey territory (A. Mielke, personal observation).

We describe sooty mangabey signaller behaviour during experimental snake encounters, and tested what determines whether an individual calls upon detecting the snake, what determines the number of calls produced and whether they restart calling upon the arrival of ignorant group members (Crockford et al., 2012). We focused on the signaller behaviour, as decision making of recipients (Micheletta et al., 2012) could not be observed due to the group size and visibility. We tested whether mangabey snake alarms fulfil the predictions of costly signalling, the protection of valuable partners, informing ignorant group members, or the volunteer's dilemma. All predictions were based on the assumption that mangabey communities do not form clear subgroups and individuals mainly know the position of visible group members at a given time, possibly mitigated by short-range contact

calls (Mielke, Crockford, & Wittig, 2019). As sooty mangabey females are highly promiscuous, alarm calling could be a way for males to signal fitness by showing their willingness to take risks and cooperate, so males should be more likely to call than females and calling should be more likely with a large audience (Wheeler, 2008). If individuals call to warn specific others, calling likelihood should increase if kin or grooming partners (as indication for frequent reciprocal exchanges) are close by. They should restart calling after having stopped if valuable partners arrive at the encounter site (Crockford et al., 2012). Like chimpanzees, *Pan troglodytes*, mangabeys could specifically warn ignorant group members, in which case their calling likelihood would be higher if they arrive together with other individuals that have not seen the snake before (Crockford et al., 2012), and lower if they arrive on their own. Alternatively, mangabeys could follow the predictions of alarm calling as a volunteer's dilemma (Archetti, 2009): individuals should call more with fewer individuals around the snake or when no other alarm call was heard recently.

METHODS

Study Group

The study was conducted from November 2014 to June 2015 with the Audrenissrou sooty mangabey community of the Tai Chimpanzee Project in the Tai National Park, Côte d'Ivoire (Wittig, 2018). Sooty mangabeys live in large multimale, multifemale communities that move through the forest terrestrially and cohesively, but often spread out over a relatively large area (up to 150 m, Mielke et al., 2018). It is unlikely that all group members can hear snake alarm calls, which are generally subdued compared to leopard or eagle alarm calls. The community does not form distinct subgroups. While individuals seem to associate assortatively due to sex, kinship, reproductive state and age, predicting the composition of group members around each individual is near impossible, making it unlikely that individuals know the location of all group members at all times (Mielke, Crockford, et al., 2019). The community has been fully habituated and subject to near-daily behavioural data collection since June 2013 (Mielke et al., 2017). During the study period, the community consisted of 62–67 individuals, including 17–19 adult (>5 years), four subadult (4–5 years) and eight juvenile (1–4 years) females and seven adult (>7 years), five subadult (4–7 years) and 12 juvenile (1–4 years) males. Mother–daughter kin relationships between individuals were established from noninvasively sampled faecal samples using microsatellite analysis and pedigree data (Mielke, Preis, Samuni, et al., 2019). Information about sibling dyads was only available for subadult individuals, and paternal kinship was not known.

Snake Experiments

We created three models of Gaboon or rhinoceros vipers using wire mesh, plaster, acrylic paint, and varnish (Crockford et al., 2012), which we selected randomly and repainted after each use to avoid stimulus habituation. Sooty mangabeys in Tai National Park find Gaboon vipers and rhinoceros vipers on average two to three times per week (Range & Fischer, 2004). To avoid habituation and minimize stress, we conducted two to four trials per calendar month. While we did place the snake in the travel path of the community, mangabeys spread out when travelling, so it was unlikely that the first individual to encounter the model would always be the same, even if individuals should have a specific travel order. In total, we conducted 17 trials over 7 months. One trial was removed as the large number of individuals present at the same time and the foliage made it impossible to accurately determine all

callers and present individuals. The maximum number of snakes any individual encountered was 12 of 16, with a median of six of 16 trials per individual. We also filmed 14 natural snake encounters, but rarely observed their beginning and only one camera angle was usually available. Where possible, we extracted the same descriptive information for natural encounters as for experimental trials to ensure the response to the model was comparable. The set-up of the snake model experiment is described in the Appendix.

Ethical Note

Experiments included the presentation of snake models in a naturalistic setting at rates that were comparable to natural encounters. Individuals were free to decide their own distance to the model and whether to leave or not. Permissions to conduct the research were granted by the Ministry of Higher Education and Scientific Research of Ivory Coast (379/MESRS/GGRSIT/tm) and Office Ivorien des Parcs et Reserves. Methods were approved by the Ethikrat der Max-Planck-Gesellschaft (4.08.2014).

Video Analysis

Videos were analysed in Mangold Interact 14 (Mangold International GmbH, Arnstorf, Germany). Videos from each camera for each model presentation were cut to share the same starting point using the first vocalization recorded on all cameras. For each individual that entered the visible range of any camera, we noted their identity, time of arrival, time of detection of snake (defined by the first direct look towards the snake), whether they startled (jumped away from the snake) and the time they left the encounter (turned their back to the snake, moved away). The visibility range differed between trials due to the vegetation; however, as we generally conducted trials in relatively open areas where possible, we could usually identify individuals within a 10–15 m radius of the snake. Mangabeys have snake-specific alarm calls (Penner et al., 2008; Range & Fischer, 2004), and we coded each alarm call each individual gave. We could visually verify all caller identities. For the observed natural encounters, we counted alarm calls given over the course of available video material and identified callers where possible (157/226 calls). As no second observer was familiar with the identity of the mangabeys, an additional observer (Cédric Girard-Buttoz) blind-coded the timing and number of mangabey alarm calls in five of 16 trials, resulting in an interrater reliability of Cohen's kappa = 0.89 for calls.

Statistical Analysis

We answered two main questions using statistical analyses: who called upon arrival and how many calls per caller the snake elicited. Restarted or delayed calling occurred at such a low rate that statistical analysis was impossible (see below). All statistical analyses were implemented with R 3.5.1 statistical software (R Core Team, 2017). We included all individuals above 1 year of age in the analysis, as they move independently from their mother.

The following variables were included in the models, based on the predictions outlined above. We created a variable depicting the order of detecting the snake, with the first individual to see the snake getting assigned the value 1, and so on. We calculated the number of individuals present at the encounter site (i.e. visible on any of the cameras) the moment an individual detected the snake. As individuals might still have seen individuals that recently left and short-distance contact calls could transmit location information, we chose to also include individuals that left within 15 s before the individual arrived. To test whether the knowledge state of the audience influenced calling behaviour, we coded whether any

individuals arrived at the same time as the individual, thereby being in immediate danger but also potentially ignorant of the threat. We included individuals that arrived between 5 s before and 30 s after the individual, as this time window should capture the group members that arrived simultaneously. The variable was coded as binary (0=arrived alone, no ignorant group members; 1=arrived simultaneously with others, ignorant group members). We also included a binary variable quantifying whether another group member had vocalized in the 30 s before the individual detected the model. We assumed that individuals arriving 30 s after the last call were less likely to be able to pinpoint the snake's location. We tested whether maternal kin were present at the site when an individual first detected the snake. We included individual dominance rank, calculated using feeding supplants and modified Elo-ratings (Mielke et al., 2017). To test whether mangabeys warn close grooming partners of the threat, we calculated a dyadic grooming score using the dynamic dyadic sociality index (DDSI (Kulik, 2015; Mielke et al., 2017);). The DDSI provides a daily measure of the amount of grooming two individuals have shared with each other compared to all their other partners (Samuni, Preis, Mielke, et al., 2018), with high values (above 0.5) depicting regular grooming partners, while low values (below 0.5) indicate dyads that rarely groomed. We used the maximum DDSI value each individual had with those present upon the detection of the snake. The individuals' sex was included to test whether males use calling behaviour to signal their fitness. We included the age of individuals as a control variable.

To test calling likelihood, we fitted a generalized linear mixed model (GLMM) with binomial error structure (McCullagh & Nelder, 1989), using calling yes or no as the response variable. We included all the above-mentioned variables in the model. To test what determined the number of calls elicited (range 1–18), we fitted a GLMM with Poisson error structure (McCullagh & Nelder, 1989), with the number of distinct calls per individual per trial as the response variable. We included all variables except the presence of kin, as there were no cases in which callers had kin present. All continuous variables were z-transformed.

To test whether the test predictors collectively had a significant effect, we conducted full null model comparisons for both models, using a likelihood ratio test (Dobson, 2002), with the null model including only age and sex as control predictors and using the same random effect structure as the full model. As random effects, we included the individual identity (including the random slopes for order of arrival and number of individuals present) and the trial ID (including the random slopes for order of arrival and number of individuals present; Baayen, Davidson, & Bates, 2008; Schielzeth & Forstmeier, 2009). For the model testing the number of calls, most trials and individuals had only a single case available, so only random intercepts were included. To quantify how much variation in the response the fixed effects explained, we calculated the R^2 (Nakagawa & Schielzeth, 2013) as an effect size for the explained variance of the fixed effects portion of the full model using the function 'r.squaredGLMM' from the R package 'MuMIn' (Barton, 2018). We tested the significance of fixed effects by systematically dropping them from the full model (Barr, Levy, Scheepers, & Tily, 2013; Dobson, 2002) using the 'drop1' function in R (R Core Team, 2017).

We addressed possible multicollinearity issues by examining the variance inflation factors (VIF; Field, Miles, & Field, 2012) using the R-package 'car' (Fox et al., 2014). Collinearity was not a problem for any model (maximum VIF = 2.9). We tested for the presence of influential cases by systematically removing levels of the random effects (Field et al., 2012), which revealed that the inclusion of one individual created strong instability for the model parameters when testing the number of calls. As the individual showed overall

idiosyncratic behaviour (only caller below 2 years of age, calling at every model he observed, calling at much higher rates than any other caller; see Description of snake response in the Results), we removed him from this model, which increased the stability of the results. For the Poisson model, we tested for overdispersion, which was not an issue (dispersion parameter: 0.78).

To test when individuals restarted calling after they had stopped, or whether they gave their first call only after a delay, we identified cases where a call followed on from a previous one by the same individual by more than 60 s ($N=4$ cases) and cases where individuals called for more than 60 s after they had detected the snake model ($N=4$ cases). This low number did not allow for statistical testing as to whether restarting was driven by new arrivals or their relationship to the caller, and the cases are described below.

RESULTS

Description of Snake Response

Signaller behaviour

Over the 16 snake model encounters, the first individual to detect the snake was the first caller in 11 trials (69%), and the second individual to detect the snake was the first caller in three trials. In one trial each, the fourth and sixth individual to detect the snake were the first to call. Encounters lasted between 1.1 and 14.4 min. In total, of 316 snake detections by a mangabey (range 2–40 individuals per trial), 45 detections led to alarm calls (range 1–5 callers per trial). Alarm calls were only given by individuals that had seen the snake and could see it when calling. There was a median of 9 calls per trial, comparable to a median of 10.5 calls per natural encounter.

Some individuals were considerably more likely to call, with one juvenile male calling each time he detected a snake model, while 31 of 53 individuals that saw the snake at least once never called. Just four individuals gave half of all calls across trials, independent of whether they were among the first individuals to detect the snake or not. The 22 individuals that called included seven of 18 adult females, five of eight adult males, three of four subadult females, five of seven subadult males, none of six juvenile and infant females and two of 10 juvenile and infant males. Including identifiable callers from the 14 natural snake encounters (18 individuals) only added four individuals that did not call in the experiments despite seeing the model, indicating that the individual bias is not the result of the low number of trials. In the experimental trials, around half of calls occurred within 5 s of individuals detecting the snake (26/45 cases), and 40 of 45 cases were calls within the first 30 s, with a maximum of close to 5 min after they first detected it. On average, callers gave 3.7 calls (range 1–18), but in 16 of 45 cases (36%), individuals only gave a single call, and in an additional 11 of 45 cases (24%), individuals gave two calls. When individuals called more than once, the median latency between calls was 4.1 s (range 0.4–137.7 s). We only observed two cases where individuals overlapped in their calling (i.e. one individual called while another individual was already calling), and in both cases the second individual only called once. In the natural encounters, we observed more overlap between callers (in 5/14 encounters), but also here overlap was usually a single intermission by a newly arriving individual rather than coordinated chorusing. Over the 16 trials, we only observed two individuals startling and jumping away when detecting the model, after approaching the snake within 0.5 m without detection. In the natural encounters, we observed three cases of startling co-occurring with alarm calls, also when detecting the snake at very close range.

Receiver response

Snake alarm calls seemed to facilitate snake detection and increase the distance at which individuals were able to detect the snake. The original detector usually saw the model from a close distance (below 5 m), which would increase the risk of being bitten in natural encounters. Subsequently, individuals that could see other group members gather around the stimulus could locate the snake from more than 10 m away, making it highly unlikely that they would step on it. Thus, the snake alarm effectively reduced the risk for informed group members. The number of group members that joined the encounter after the snake was detected and the number of alarm calls given differed markedly between trials, probably owing to the movement patterns of the community. Other individuals usually accompanied the initial detector or followed closely after. On average, 20 individuals (30% of the community) saw the snake per trial, and an average of 10.8 individuals (maximum 27 individuals) were present at the encounter site at the same time. Between the first individual detecting the snake model and the last individual leaving, we observed no cases in which no individual was present at the encounter site. For any individual arriving, a conglomeration of several mangabeys around the same spot and passively monitoring the ground, especially after an alarm call was heard, would be an accurate cue that a threat was present. When individuals arrived at the encounter site and detected the snake, infants usually climbed low branches, while larger group members approached the snake model on the ground and observed it from close range (usually <5 m), standing quadrupedally and sitting on roots and dead trees. This was also the case in natural snake encounters. We did not observe any cases of snake-directed behaviour (threat gestures, stick throwing, aggressive signals), either in natural snake encounters or in the experimental set-up, making it unlikely that sooty mangabeys mob vipers. Individuals would sometimes sniff the ground around the snake model and branches of trees close by, as if gathering information through secondary cues. The median time individuals remained at the encounter site was 56 s, with a maximum of 11.5 min.

Restarted calling

Individuals restarted calling after they had ceased to call for more than 60 s in only four cases, and they only started calling with a delay of at least 60 s in four further cases, making it likely that this behaviour does not fulfil an important function in transmitting information depending on the knowledge state of the audience. All individuals that renewed calling were juvenile or subadult males, and half of the cases were made up by the juvenile male that called in all his encounters. In none of these cases did kin or individuals with a strong grooming relationship to the caller arrive in the 30 s time window around the call. Only in half of the cases of delayed or renewed calling ($N = 4$) did new individuals arrive that might have triggered renewed calling. The number of individuals present around the snake varied between one and 26 individuals at the time of the renewed or delayed call.

Call or Not Call

The full null model comparison for the binomial GLMM testing call likelihood showed a significant impact of the test predictors (likelihood ratio test: $\chi^2_8 = 26.87$, $P < 0.001$). The effect size for the fixed effects was $R^2 = 0.40$ and for the whole model including random effects $R^2 = 0.91$. Thus, as described, interindividual differences accounted for a large part of the variation. Individuals were less likely to call if another group member had given a call in the previous 30 s ($\chi^2_1 = 4.01$, $P = 0.045$; Fig. 1, Table 1). Individuals were more likely to call if fewer group members were present at the encounter site when they detected the snake ($\chi^2_1 = 6.74$, $P = 0.009$;

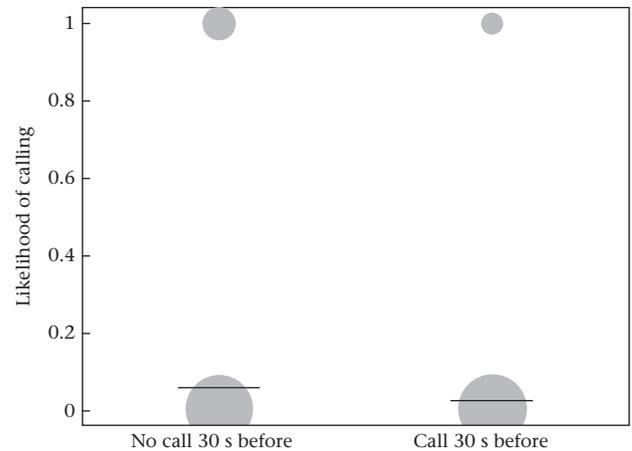


Figure 1. The probability of an individual alarm calling upon detecting the snake depending on whether another individual alarm called in the 30 s before (1; $N=206$) or not (0; $N=107$). Points represent the observed probabilities of giving an alarm call (larger point areas denote a larger number of observations, range 13–137) and lines represent the model results.

Fig. 2). Age, sex or dominance rank of potential callers, the order of arrival and the presence of maternal kin, grooming partners or ignorant group members had no significant impact on the calling likelihood.

Number of Calls

The number of alarm calls was affected significantly by the test predictors (full null model comparison: likelihood ratio test: $\chi^2_7 = 21.02$, $P = 0.004$). The effect size for the fixed effects was $R^2 = 0.48$ and for the whole model including random effects $R^2 = 0.60$. Individuals gave more calls when fewer individuals were present at the encounter site ($\chi^2_1 = 4.42$, $P = 0.035$; Fig. 3, Table 1). The number of calls given was not influenced by the order of arrival, the presence of grooming partners, sex or age. It was also not affected by whether individuals arrived together with potentially ignorant others or whether other individuals had recently called.

DISCUSSION

The goal of this study was to understand how cooperative alarm calls allow for the transmission of predator-related information. The social organization of sooty mangabey communities leads to

Table 1

The effect of present individuals and recent calls on alarm call likelihood and number of calls given

Variable	Call yes/no		Number of calls	
	Estimate	P	Estimate	P
Intercept	-2.80	–	0.42	–
Age	-0.20	0.567	-0.08	0.679
Sex	0.57	0.430	0.59	0.099
Kin present	1.01	0.296	–	–
Maximum grooming relationship present	-0.41	0.232	0.23	0.501
Simultaneous arrival with others	-0.47	0.131	0.17	0.557
Order of arrival	-0.16	0.282	0.07	0.602
Number of individuals present	-1.26	0.009	-0.48	0.042
Call heard	-0.93	0.028	-0.87	0.048

Results of generalized linear mixed models testing which individuals called or not and the number of calls given. Estimates are from the full model, and P values are the result of a likelihood ratio test of the reduced model lacking this term with the full model. Significant predictors are in bold.

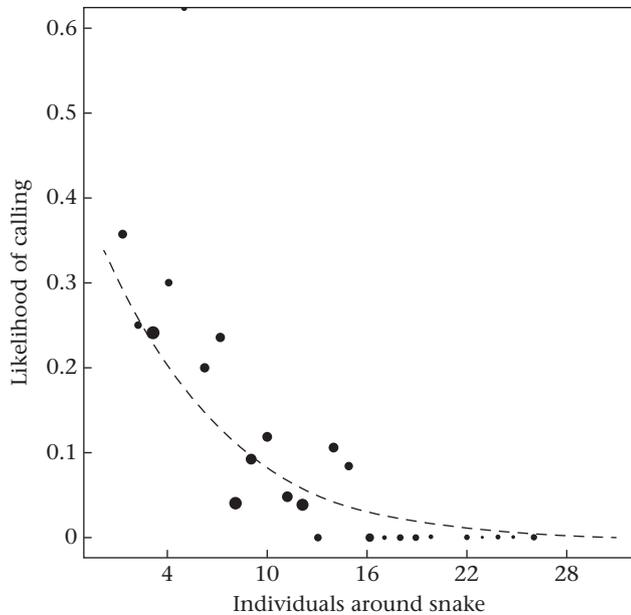


Figure 2. The probability of an individual alarm calling upon detecting the snake in relation to the number of individuals around the snake. Points represent the observed probabilities of giving an alarm call (larger point areas denote a larger number of observations, range 1–5) and the dashed line represents the model results.

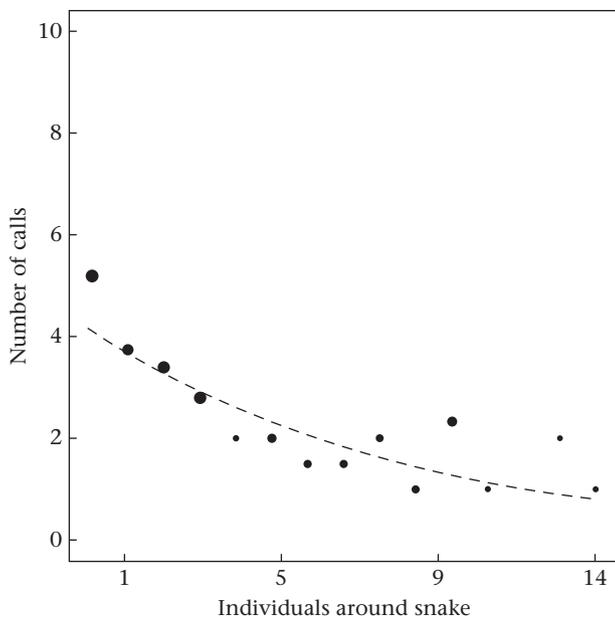


Figure 3. The number of alarm calls given by a caller upon detecting the snake in relation to the number of individuals around the snake. Points represent the observed probabilities of giving an alarm call (larger point areas denote a larger number of observations, range 1–5) and the dashed line represents the model results.

unevenly distributed information, but also creates a continuous chain of possible informants that could relieve each individual of the need to inform ignorant group members directly. We observed two effects. On the one hand, some individuals had a considerably higher likelihood of calling independent of their rank, sex and age, indicating interindividual differences in their reaction to threats. On the other hand, mangabeys followed a strategy consistent with the evolution of alarm calling for vipers as a public goods game, with information about the threat being the public good.

Individuals mainly called when few other group members were present around the snake and no call had occurred recently, making this an efficient system to transmit information about the threat while limiting redundancy.

One important aspect of the mangabey snake response was its relatively low intensity, both in natural encounters and in experiments. If call intensity is related to the perceived threat posed by a predator (Leavesley & Magrath, 2005; Manser et al., 2002; Ridley, Raihani, & Bell, 2010; Wheeler, 2010), then sedentary vipers are seen as a mild threat by sooty mangabeys. Two of three callers only gave one or two calls, and a large proportion of group members did not call in our experiments or natural encounters. Startle responses as a reaction to the snake models or during natural encounters were rare, and we did not observe mobbing (Crofoot, 2013). Calling behaviour effectively transmits information about the presence of a threat, as group members that arrived after the first calls were made detected the threat from a safe distance, did not approach closely and did not startle. Future studies should focus on what motivates group members to participate in the snake encounter (Kern & Radford, 2016; Micheletta et al., 2012).

Around half of all alarm calls were given by the same four individuals, and more than half of the community never called. These four individuals differed markedly in their demographic or social category (one male juvenile with a high-ranking mother in the community, one juvenile male orphan, one recently immigrated subadult male, one subadult female orphan), and only one of them was repeatedly the first to detect the snake. Three of them had no mother present in the community (migrants or orphans), but this was also true for 15 of 25 juvenile or subadult individuals that did not call regularly. As we rarely observed overlap between callers, the presence of individuals with high calling likelihood would ensure the transmission of information without any investment by other group members. Adult females were not more likely than other group members to give alarm calls, making it unlikely that alarm calling functioned to facilitate learning about threats by offspring (Seyfarth & Cheney, 2010). Future research should investigate whether regular callers were somehow rewarded for contributing more to the public good (Arseneau-Robar et al., 2016; Kern & Radford, 2018), or whether there is simply large interindividual variation in boldness (Massen, Antonides, Arnold, Bionda, & Koski, 2013). In all the demographic or social categories (age, sex, orphaned, rank, etc.) of the regular callers, we had a large number of other group members that did not call at high rates, making it unlikely that a greater need for tolerance or support drove high calling rates.

We found no evidence for individuals directly warning valuable group members and, in contrast to the costly signalling hypothesis, males did not call more than females. One caveat is that we do not know all sibling dyads in adults and do not know paternal kinship, potentially underestimating the number of kin dyads. Individuals did not call more when larger audiences were present, thereby advertising their willingness to cooperate. Animals often engage in behaviour that requires the cooperation of more than two individuals when interacting with predators, other communities or prey (Clutton-Brock, 2009; Langergraber, Watts, Vigilant, & Mitani, 2017; Schneider et al., 2012; Willems, Hellriegel, & van Schaik, 2013). Public goods games can be one way to explain the evolution of group level cooperation (Kollock, 1998): Individuals contribute to the public good as long as they receive a larger return than investment in the long run. Communal group defence in different primate species (Arseneau-Robar et al., 2016; Willems et al., 2015) indicates that primate group level cooperation follows patterns predicted by public goods games. Here, we have shown that one scenario that could explain alarm calls for stationary snakes in sooty mangabeys is a

special case of the public goods game, the volunteer's dilemma (Archetti, 2009). Players should choose to defect (i.e. not call) as long as the public good (information about the threat) is widely available, but change their strategy when group sizes are small and fewer group members know about the threat (Schneider et al., 2012). Owing to the travelling pattern of the mangabeys, between the first and the last individual to detect the snake, other mangabeys were continuously present around the snake and could have called. Mangabeys were more likely to call if fewer individuals were present at the encounter site, and if no other individual had called recently. Calling was also almost exclusively restricted to one individual at a time. At the same time, the information about the threat was kept updated efficiently until all community members had passed, reducing the risk for each individual, their kin and dyadic cooperation partners. Especially in social structures where individuals might not always know who has already seen the snake or heard a call, as is likely to be the case in sooty mangabeys, this strategy could maximize the number of protected group members.

In contrast to chimpanzees in a similar set-up (Crockford et al., 2012, 2017; Crockford, Wittig, & Zuberbühler, 2015; Schel et al., 2013), sooty mangabeys did not call more when maternal kin or grooming partners were present. They also did not call more when they arrived with others that were potentially ignorant of the snake, and they did not restart calling for ignorant group members. We suggest that the distributed nature of the information in the mangabey community made it unnecessary to monitor the knowledge state of specific others. Rather, individuals called more when a larger number of individuals in the overall community were likely to be ignorant. The heuristic approach in sooty mangabeys highlights the challenges species face in social systems with strong fission–fusion dynamics. In chimpanzees and other species with low spatial cohesion, information can only be transmitted widely and efficiently if group members invest time and effort into monitoring the threat and informing others specifically. Previous studies have highlighted the need for greater behavioural flexibility in species with high fission–fusion dynamics (Amici, Aureli, & Call, 2008; Aureli et al., 2008). Here, the difference between sooty mangabeys and chimpanzees in monitoring group members' knowledge about external stimuli is indicative of different challenges solved by the two species and the potential need for higher information-processing skills in the chimpanzees (Crockford et al., 2012).

We have provided evidence that alarm calling for some threats in nonhuman primates could have evolved as a public good that optimizes the amount of information each group member has and minimizes the risk each of them faces. While public goods games have not been employed widely in studies of the evolution of primate cooperation (Arseneau-Robar et al., 2016; Willems et al., 2015), they may provide useful models for understanding group level cooperative behaviours such as group defence, hunting (Samuni, Preis, Deschner et al., 2018) or predator responses. Sooty mangabeys called upon detection of the snake model if no one else had called recently or few individuals were close by. The presence of some individuals that called at very high rates allowed most group members to gather information without the need to call. Significantly, our results show how the distribution of information as a resource in animal societies with different structures can influence the evolution of different cognitive skills to transmit information within a group (Freeberg, Dunbar, & Ord, 2012).

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Appendix

For each experiment, we placed a snake model on the forest floor prior to the mangabeys' arrival, and strategically placed three or four cameras around the snake to provide maximum video coverage of the mangabeys' behaviour and vocalizations elicited by the snake (Fig. A1). This procedure was conducted as follows. As it is difficult to predict the travel path of individual mangabeys, the experimenter (A.M.) would move ahead of the mangabey community, while a field assistant and A.M. both held a Garmin Rino 610 Handheld GPS. The field assistant would follow the leading individuals of the community. Rino GPS devices communicate their position and enable direct vocal exchange between them. Thus, the experimenter could track the movement of the group while being away from the group. When the mangabeys moved in a predictable direction, the experimenter placed the snake model about 100 m ahead in a hollow, behind a log or partially hidden by undergrowth, as the snake species would naturally be found. A.M. was careful to choose a clear patch of forest floor for the snake placement with

visibility > 10 m on each side. A.M. arranged the four cameras as follows. One stationary GoPro Hero3 was attached to a tree 1 m from the ground, behind the snake opposite the experimenter, to gain wide-angle footage of mangabey movements while arriving, observing the snake and leaving the area. A Panasonic DMC-FZ200 camera was attached to the experimenter's chest at around 10 m from the snake and A.M. would additionally film with a Panasonic HC-V770 handheld camera with attached external Sennheiser 300 Video microphone to obtain high-resolution visual and auditory footage of callers. The field assistant who arrived with the man-

gabey would position themselves perpendicular to the experimenter and the snake model and film from there with a Canon Powershot D30. With this set-up, even when mangabeys surrounded the snake model or moved around it, footage of their faces was available for most individuals, allowing us to determine at which point they first detected the snake and when they called. The experiment ended and the snake model was removed after the whole community had left the area and was out of sight of the snake.

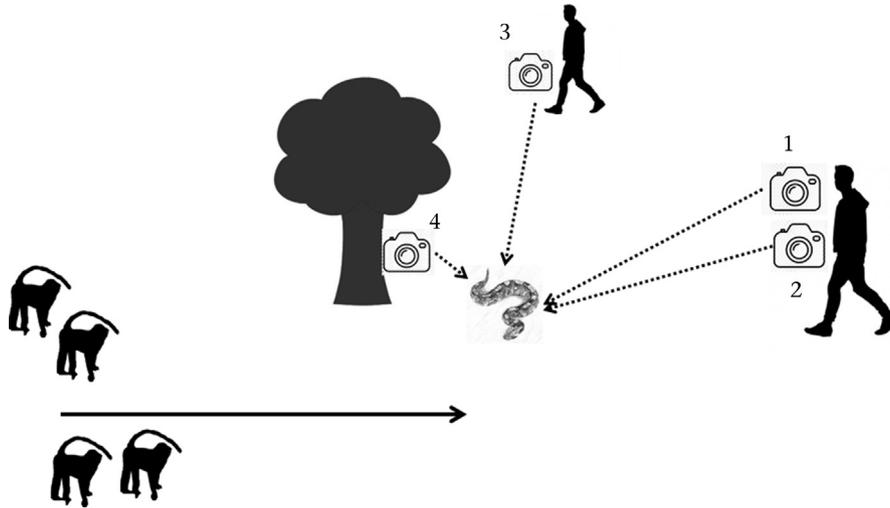


Fig. A1. Set-up for the snake model presentation. The snake model was positioned in the travel path of the mangabey community, usually behind a log or bush, with up to four cameras filming from different angles: experimenter handheld (1) and chest camera (2) facing the approaching mangabey group, assistant camera (3) perpendicular to the travel direction and a GoPro action camera attached to a tree close to the snake (4) to film individuals surrounding the snake.