

## Manipulating foraging group size: spider monkey food calls at fruiting trees

COLIN A. CHAPMAN\* & LOUIS LEFEBVRE

Department of Biology, McGill University, 1205, av Dr. Penfield, Montréal, Québec, H3A 1B1, Canada

**Abstract.** The food calling behaviour of the Costa Rican spider monkey, *Ateles geoffroyi*, was studied to determine if food calls function as conditional signals designed to attract conspecifics and thereby manipulate the size of the feeding subgroups. First, individuals were shown to manipulate the number of conspecifics joining them by altering the frequency of calling. Then, based on the expected levels of feeding competition and male–female strategies, four predictions were made concerning the frequency with which individuals should call. As predicted, calls were given more often by subgroups containing dominant individuals than by subgroups with only subordinate individuals, in large trees more often than in small ones, and more frequently when food resources were abundant than when they were scarce. However, contrary to what was predicted, subgroups containing males did not call more than subgroups with only females. In general, the observations suggest that spider monkeys can conditionally broadcast information to manipulate their subgroup size and do so in ways that may decrease feeding competition.

Several authors have argued that animal communication should not be viewed as the sharing of information, but as the attempt of the sender to manipulate the actions of the recipient (Maynard Smith 1974; Dawkins & Krebs 1978). Using such a perspective, we can see that the sender can provide information to the mutual benefit of both the sender and recipient, or it may manipulate and/or deceive the recipient to the benefit of only the sender. The calling that sometimes accompanies the discovery of a food source is a situation where animals may manipulate information. For instance, house sparrows, *Passer domesticus* (Elgar 1986), and toque macaques, *Macaca sinica* (Dittus 1984), are known to give calls when entering food patches; the calls appear to be conditional to food abundance. Similarly, observations in nature (Wrangham 1977) and experimental evidence (Hauser & Wrangham 1987) both suggest that chimpanzees, *Pan troglodytes*, withhold information from other group members to avoid food sharing.

In this paper, we examine food calling at fruit trees by Costa Rican spider monkeys, *Ateles geoffroyi*. Spider monkeys have a flexible pattern of social organization in which subgroup size is extremely variable; the size and composition of a subgroup can change a number of times a day (Klein 1972; Symington 1987; Chapman 1988a). When a spider monkey enters a fruit tree, it often

utters a 'whinny' (Klein 1972). Eisenberg (1976) describes the whinny as a position indicator that accompanies feeding and suggests that the call may serve to indicate food availability. During a feeding bout, other monkeys may join the caller at the fruit tree and feed with it. We examine whether whinnies function as conditional signals to attract conspecifics to the feeding site. In addition, we look at the frequency of food calling to determine whether variation in calling frequency is associated with variation in the number of monkeys attracted, a pattern that suggests that calling spider monkeys manipulate the size of their foraging subgroup.

The ecological literature contains a number of field and experimental studies that have addressed the question of why animals feed in groups (van Schaik 1983; Pulliam & Caraco 1984). These studies have examined the relationships between some assumed measure of individual fitness and the size of the foraging group. When group size is too low, animals may have a greater risk of being preyed upon and/or suffer lower feeding rates as more time needs to be spent scanning for predators (Hoogland 1979; van Schaik et al. 1983). When group size increases, competition for food may increase (Janson 1986; Chapman 1988b). Our first three predictions are based on the assumption that calling carries a potential risk of increasing food competition. Feeding competition is thought to occur in spider monkey foraging groups: individuals compete aggressively for access to food trees (Klein 1972; Klein & Klein 1977) and subgroups

\*Present Address: Department of Anthropology, Harvard University, Cambridge, MA 02138, U.S.A.

typically deplete the food trees in which they feed (Symington 1987; Chapman 1988b). Thus, competition for resources and benefits of being in a group may trade off in a way that leads to optimal or stable groups (Giraldeau 1988). When group size goes above the stable or optimal point, mechanisms such as aggression may serve to decrease group size. When group size is too low, recruitment signals may be given to attract conspecifics. This is the framework in which we examine spider monkey food calls. We first provide evidence that whinnies function as conditional recruitment signals, then examine four predictions based on the relationship between subgroup size and assumed measures of individual fitness.

(1) High-ranking individuals may experience less severe food competition than low-ranking individuals as a result of an increase in subgroup size (Whitten 1983; van Noordwijk & van Schaik 1987). Thus, the size of the optimum or stable subgroup will be smaller for a subordinate than for a dominant individual (Giraldeau 1988). We predict that high-ranking individuals should call more than low-ranking animals because the former can displace others from feeding sites and control the higher quality areas in the fruiting tree. (2) When food resources are abundant, feeding competition will be lower than when food is scarce. Thus, we predict that animals should call more frequently when food is abundant. (3) Feeding competition at a single site is inversely related to the size of the site (Chapman 1988b). In small trees, there are fewer feeding positions and less food available than in large trees (Chapman 1988b). Thus, we predict that food calling will increase with the size of the tree in which the spider monkeys are feeding.

The last prediction (4) is based on the idea that male and female spider monkeys may have different objectives in calling. Females may be primarily interested in acquiring food resources to produce and feed infants. In meeting this objective, females should try to minimize feeding competition. In addition to feeding, males must contact females and attempt to mate (Wrangham 1979). For males, the need to attract potential mates may conflict with attempts to minimize feeding competition and instead of withholding information at a newly discovered feeding site to minimize food competition, they may call to attract females. Thus, we predict that subgroups with males should give more food calls than subgroups with only females.

## METHODS

The ecology and behaviour of the free-ranging spider monkeys of Santa Rosa National Park, Costa Rica have been studied since 1983, involving a total of 36 months of field observations. The study area is in a region of tropical dry forest which experiences a long, severe dry season (Janzen 1986; Chapman 1988a). Individual recognition was possible following the darting and tagging of animals, either as a result of the tag placed on the animal ( $N = 13$ ) or by scars and pelage patterns ( $N = 22$ ).

To obtain information on the behaviour and foraging success of known individuals, subgroups containing recognizable individuals were located in the morning or early afternoon, and focal animal data were recorded continuously until the monkeys entered the area of the sleeping site. When possible, the subject chosen for focal animal observation was selected according to a fixed rotation between individual and/or age-sex class. Whenever the focal animal was feeding, the food item and plant species were recorded and the diameter at breast height of the tree was visually estimated. The error in visually estimating the diameter was 3.7% ( $N = 46$ , mean diameter at breast height of the trees used by the monkeys was 43.1 cm).

Information on the frequency with which whinnies were given was collected on an ad libitum basis over an 11-month field season (April 1987–March 1988). Whinnies are expressed as a rate (calls/h). The conspicuous nature of the call minimizes the possibility of missing it. As these animals live in a complex arboreal environment, in which visibility is often limited, individual identification of the caller was difficult. However, over the period of observation, it was possible to identify which individuals were in the subgroup. Thus, results are described as the number of calls per subgroup and not on an individual basis. Whenever a whinny was given in a food tree, the tree species and its size were determined. Only whinnies given in a foraging context were considered in this analysis.

The behaviour of the spider monkeys was recorded during 3-week sampling periods so that at the end of each period approximately an equal number of observations were made in each hour of the day and on all individuals of the community. Over the entire study, 26 sampling periods were completed. During these 3-week observation periods, an attempt was made to search all areas of the community's home range. To facilitate this

search, 25 km of trails were cut throughout the area.

The composition of the subgroup being watched was monitored continuously. With small subgroups, it was relatively easy to see all individuals at one time and monitor changes in subgroup composition. However, as subgroup size increased, it became increasingly difficult to notice all departures and arrivals. Thus, when large subgroups were being followed, one observer would attempt to identify all individuals once every 1/2 h.

The dominance rank for each identifiable adult ( $N=13$ ) was determined for diadic interactions involving displacements observed in the focal-animal sessions ( $N=117$ ) or involving overt aggressive interactions ( $N=38$ ) observed either during focal-animal sessions of the individual involved or at any other time. Since these overt aggressive interactions involved loud vocalizations and often chases, they were very noticeable. Thus, it is probable that all episodes that occurred were recorded. Dominance relationships are difficult to describe for spider monkeys, as some individuals of the community rarely, if ever, meet and because individuals rarely meet alone, and interactions appear to be affected by the presence of others. For individuals that rarely met, dominance rank was assigned according to their interactions with individuals with which they both associated. All statistical tests involving dominance were done with non-parametric statistics and the equivalent parametric test and if the tests agreed, the parametric results were reported (following Conover 1980). All of the probabilities reported are two-tailed.

The density and distribution of the spider monkey's food resources were determined by locating all of the trees containing food items in each of three 4-ha grids approximately once every 3 weeks (Chapman 1988a). The diameter of breast height of these trees was measured. Tree diameter reflects the fruiting capacity of tropical trees (Peters et al. 1988). Thus, tree density weighted by diameter should reflect food abundance more closely than does plant density alone.

## RESULTS

### Function of the Whinny

Before examining the possibility that spider monkeys can selectively manipulate the size of their

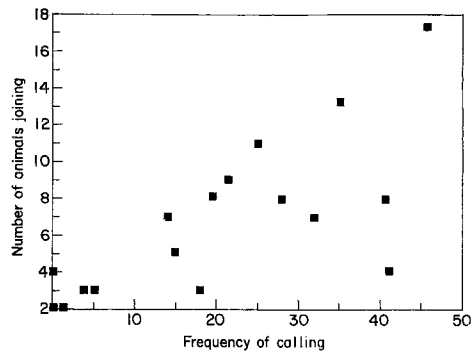


Figure 1. The relationship between the frequency of whinnies (calls/h) and the number of individuals that joined the calling subgroup ( $r=0.71$ ,  $N=17$ ,  $P<0.01$ ).

subgroups by altering the frequency with which they give food calls, it is important to determine that these calls carry information. The number of subgroups joining at a feeding site was dependent upon whether calls were given ( $\chi^2=9.74$ ,  $df=1$ ,  $P<0.005$ ). Subgroups joined in 17 of 101 occasions when calls were given. In comparison, joining occurred on only seven of 145 occasions when a subgroup did not give a call. In addition, subgroups that entered a food tree and were eventually joined, were joined sooner if they had given a whinny ( $\bar{X}=5.6$  min following the call,  $N=17$ ) than if they had not ( $\bar{X}=25.3$  min,  $N=7$ ,  $t=3.29$ ,  $P<0.01$ ).

Subgroups entering a food tree did not always call (41% of the subgroups called) and calling did not always result in joining (joining occurred on 17% of the occasions). When subgroups were joined however, the frequency with which they gave whinnies was strongly related to the number of conspecifics that joined ( $r=0.71$ ,  $P<0.001$ ; Fig. 1). Once the new subgroup had been formed, calling either stopped (65% of the cases) or resumed (35%). In the latter case, continued calling attracted more monkeys 66% of the times. Following this second episode of joining, calling ceased in 33% of the cases and resumed in the other 66%. Resumption of calling was judged to occur if after 10-min following a joining episode, monkeys called again. The 10-min criteria was chosen to eliminate calls given during the excitement of joining. Using a 5-min cut-off point, the percentage of non-callers after a subgroup was first joined was 57%, while using a 15-min level, it was 68%.

Taken together, these results suggest that whinnies do have an attractive function, that the

frequency of calling determines the number of animals that join, and that the decision to continue or to cease calling depends at least in part on the number of arrivals.

### Predictions Concerning Whinny Frequency

As predicted, there was a positive relationship between the rank of the most dominant individual in the subgroup and the frequency of whinnies ( $r = 0.292$ ,  $P < 0.01$ ). Extensive observations on an individual that changed rank provides additional anecdotal support for this point. An adult female dropped in rank subsequent to the birth of a male infant. This drop in rank corresponded to a significant decrease in the frequency with which she gave whinnies ( $t = 3.52$ ,  $P < 0.01$ , 26 h of focal observations on this female; calls/h before decrease in rank = 13.1, after 1.8).

Second, there was a positive relationship between the density of food resources in the spider monkey's home range and the frequency with which whinnies were given ( $r = 0.213$ ,  $P < 0.001$ ). Third, there was a positive relationship between the size of the tree entered and the frequency of whinnies ( $r = 0.568$ ,  $P < 0.001$ ). Thus, when fruiting trees were large, when food was abundant and when subgroups contained high-ranking individuals, spider monkeys called more frequently.

There was no difference in the size of the subgroups in which identifiable adult males and females were observed ( $t = 0.001$ ,  $P = 0.995$ ). Thus, it is possible to examine directly the last prediction. Contrary to what was predicted, the frequency with which food calls were produced by subgroups containing males (5.7 calls/h) was not significantly greater than all-female subgroups (4.3 calls/h,  $t = 0.286$ ,  $P = 0.776$ ,  $N = 246$  subgroups). This suggests that there are no sexual differences in the frequency of whinnies.

In summary, although the frequency with which males and females gave whinnies was not as predicted, there is clearly evidence to suggest that spider monkeys give whinnies in situations where competition for food resources is minimal.

### The Consequences of Too Many Animals Joining

What happens when an individual calls and attracts more animals than its present situation would warrant? Aggression and departure are the two most likely responses to excessive subgroup

size. Symington (1987) studying spider monkeys, *Ateles paniscus*, in Peru, documented that coalitions between females were rare ( $N = 9$ ). Those that did occur were always between females already feeding in a tree and occurred to prevent another female from joining them. In Santa Rosa, nine of the 11 coalitions observed involved females that were feeding in a tree banding together to chase off other approaching females.

It is less probable that low-ranking females could discourage a high-ranking female from entering a tree. Low-ranking females may have had no recourse other than to leave when increasing subgroup size lead to high levels of feeding competition. Consistent with this, we observed that low-ranking females were more likely to leave a subgroup feeding in a food tree than were high-ranking females (females above the average rank versus females below the average,  $\chi^2 = 16.6$ ,  $df = 1$ ,  $P < 0.01$ ).

## DISCUSSION

Our results suggest that the rate with which spider monkeys give whinnies is affected by food abundance and by dominance rank and is correlated with the rate at which conspecifics joined. This implies that individuals have the ability to manipulate the size of the subgroup in which they are members, based on the potential costs and benefits of subgroups of different sizes.

Individual tactics for maximizing fitness will tend to produce stable foraging group sizes that are above the optimum (Sibly 1983; Giraldeau 1988). That is, if there is an optimal group size for the particular ecological pressures that the animals are presently experiencing, animals in groups that are less than the optimum will be under strong pressures to join existing groups, pushing these groups above the optimum. The observation that low-ranking female spider monkeys appear to leave the feeding subgroup more often than high-ranking females suggests that the size of the subgroup may often be above that which would be optimum in terms of their feeding efficiency. Subgroup size may not simply result from individuals below the optimum attempting to join other subgroups, but also from individuals in subgroups below the optimum soliciting others to join.

Our data show that spider monkeys entering a fruit tree call approximately half of the time and

that these calls often produce no joining. The first result is consistent with the idea that calling is withheld in many situations. The second result suggests that calls may not be heard by potential joiners and/or that it may not be advantageous for individuals to join. With respect to the latter argument, there are a number of factors that may lower the benefits of joining. First, if lower ranking individuals join subgroups, they may experience more feeding competition at the site than if they did not join. In addition, if a subgroup is already at the optimal size for its present feeding situation, it may be disadvantageous to join another calling subgroup. The decision to join, like the decision to call, is probably based on a comparison between present and future (post-joining) costs and benefits.

Our results suggest that the exchange of information between members of a spider monkey community depends on social and ecological conditions. Although the precise motivational basis for the manipulation of information is unknown, withholding a food call is potentially an effective means of excluding conspecific competitors from depletable food trees. Although few studies have addressed the issue of whether animals can withhold information and provide it only when they will benefit (see Cheney & Seyfarth 1985; Byrne & Whiten 1986), there is evidence to suggest that this ability is widespread. One of the clearest examples of intraspecific animal deception is seen in descriptions of chimpanzees withholding information (Menzel 1971; Woodruff & Premack 1979; de Waal 1982). De Waal (1982) described a simple experiment in which one chimpanzee was shown the location of hidden food items in an enclosure, then released with other animals into the area. The individual with the knowledge of the food source did not immediately go to the hidden food items, but rather withheld the information about the location from the potential competitors, and waited until they were occupied in other activities before uncovering the food items. Similarly, Cheney & Seyfarth (1985) suggested that vervet monkeys, *Cercopithecus aethiops*, withhold information by not giving alarm calls when they are aware of the presence of a predator. Withholding information thus may be an effective means of manipulating others, since it is difficult to detect cheaters.

Whether conditional calling in spider monkeys should be considered deception depends on whether there is a convention between individuals to provide the information in the first place. If this

convention existed, it would presumably involve some form of reciprocal altruism, with one animal providing information about the location of a food source with the expectation of being repayed in the future. Spider monkeys probably possess the necessary attributes suggested for the evolution of reciprocal altruism: individual recognition and repeated encounters that allow assessment of reciprocates and detection of cheating. Calls do not seem to be specifically given to attract kin since females are thought to disperse (Symington 1987), and young females who are presumed to have recently immigrated and have as of yet no kin in the community, frequently call. Identifying the existence of such a convention is extremely difficult. An anecdotal observation nevertheless suggests that such a convention may exist. A dominant female found a subordinate female who had not been calling in a large fruit tree; the dominant female immediately chased the subordinate female from the tree. On a second occasion when these individuals met, the subordinate had been calling and there was no aggression. There are of course many ways to interpret this observation, but it is conceivable that the dominant female was aggressive because the subordinate had broken a convention by not calling.

Determining whether animals are capable of deception is difficult. It is unlikely that deception will repeatedly involve gross alterations in communicative conventions, because these would presumably be detected (Cheney & Seyfarth 1985, 1988; Byrne & Whiten 1986). We suggest that studying subtle forms of deception, such as withholding information, may be a profitable avenue for future research.

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