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Chapter · January 2008

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8 *Communication in spider monkeys: the function and mechanisms underlying the use of the whinny*

GABRIEL RAMOS-FERNÁNDEZ

Introduction

Several aspects of the biology of spider monkeys (*Ateles* spp.) make their communication system particularly interesting. First, as canopy-dwelling, frugivorous primates, spider monkeys must forage in a complex environment consisting of fruit patches of variable size that are spatially distributed over large areas (Klein, 1972; van Roosmalen and Klein, 1987). Such an environment places a high demand on those mechanisms by which individuals can efficiently coordinate their movements, exploit their food resources and avoid danger (Milton, 2000). Additionally, because of their fluid grouping and association patterns, individual spider monkeys may spend long periods of time away from others in the group (Symington, 1990; Ramos-Fernández, 2005). This implies that at times, long-distance vocalizations, which can overcome spatial separation, or olfactory marks, which can overcome temporal separation, may be the only means by which spider monkeys can locate group members and, in general, maintain their social relationships (Ramos-Fernández, 2005).

This chapter reviews the studies carried out so far on spider monkey communication, placing more emphasis on the vocal mode, as it has received the most attention. The first section reviews the early, more descriptive studies of communication in spider monkeys and provides a set of definitions of the different vocal types used by different species. Among the different vocalizations used by spider monkeys, only the whinny has been studied in any detail. Therefore, in the second section of this chapter I review the studies that have tested specific hypotheses about the proximate mechanisms underlying production, transmission and perception of whinnies in spider monkeys. In the third section I review the studies that have attempted to determine the functional significance of vocal signals. In the final section I place the evidence reviewed into the current framework of communication networks, emphasizing the role that communication may have in the social system of spider monkeys.

Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles ed. Christina J. Campbell
Published by Cambridge University Press. © Cambridge University Press 2008

Background information

After observing a nonhabituated group of *Ateles geoffroyi* in the Coto region in western Panama for one and a half months, Carpenter (1935) published the first account of spider monkey communication. He noted that the most common vocalization was the “terrier-like bark,” which the monkeys gave when approached by an observer on the ground and upon taking defensive action or flight. He proposed that this vocalization functioned as a warning signal to others in the group. The next most common vocalization was the “growl,” which was only heard from “greatly aroused males” or from subgroups that were “contending with each other” (Carpenter, 1935, p. 180). Finally, the “whinny” was reported as a higher pitched, lesser amplitude version of a horse’s whinny, emitted when subgroups or individuals became separated. Carpenter (1935) interpreted that this vocalization functioned to coordinate movements of subgroups and assumed it was equivalent in function to the capuchin’s “caws.”

The first published study to present sonograms of spider monkey vocalization recordings was Klein’s (1972) report of his long-term study of *Ateles belzebuth* in La Macarena, Colombia. Klein used vocalizations to locate spider monkey subgroups and described the use of six vocalization types: “whoops” and “wails,” given in bouts and assumed to be used to locate group members, often followed by a merger of subgroups; “barks,” which were given to predators and conspecific disturbances; “squaks,” given by juveniles that had become separated from the rest of the subgroup; “tschooks,” which were exchanged by spider monkeys after a separation and before joining subgroups; and “whinnys,” emitted by members of approaching and approached subgroups before and during a subgroup merger. Klein (1972) provides a particularly interesting description of subgroup dispersals (fissions) and mergers (fusions) that is very suggestive of the potential role of vocal communication during these important events in the fission–fusion system of *Ateles*. Briefly, during fissions, “tschook” vocalizations from lone juveniles could be followed by “whinny” vocalizations from adult individuals that apparently were waiting for the juveniles to follow them. During fusions, “whinny” vocalizations were almost always heard and “appeared to be initiated when at least one of the members of two different subgroups were first able to see one another directly” (Klein, 1972, p. 179). The exchanges of “whinny” vocalizations during fusions were often reciprocal between individuals in the joined and the joining subgroup. He also noted that the same vocalizations also occurred in contexts that were not related to subgroup fusions.

In 1976, J. F. Eisenberg published the first and only systematic study of the complete communication system of any *Ateles* species. Many of the following

Table 8.1 *Vocal repertoire of spider monkeys with some suggested functions*

Call type	Suggested function	Reference
Long call (harsh)	Position indicator and identifier	Eisenberg 1976
Long call (clear)	Position indicator and potential identifier; may promote assembly	Eisenberg 1976
Bark	Position indicator, promotes assembly; warning signal	Eisenberg 1976; Symington 1987
Chitter	Warns conspecifics about disturbances in the environment	Eisenberg 1976
Tee-tee	Position indicator; friendly greetings	Eisenberg 1976
Whinny	Position indicator; may indicate availability of food; informs others about individual identity	Eisenberg 1976; Chapman and Lefebvre 1988; Teixidor and Byrne 1997, 1999; Ramos-Fernández 2005
Ook-ook-ak-ak	Invitation to play	Eisenberg 1976
Gutural whinny	Friendly approach	Eisenberg 1976
Growl	Hostile approach	Eisenberg 1976
Whoop	Male position indicator	van Roosmalen and Klein 1987

studies have focused only on a single communication mode or a set of vocalizations. This study organized the vocal signals of captive *A. fusciceps* (now classified as *A. geoffroyi fusciceps*) into different types based on acoustic analysis. The study was complemented by a field study of *A. geoffroyi*. Eisenberg (1976) distinguished 13 different vocal types depending their loudness, their tonal quality, the presence of frequency modulation and their length. This classification is based on extensive acoustic analyses and a thorough description of the possible combinations of elements between call types. It also includes the context (in captivity) in which each vocalization type occurs. It is this classification that will be used throughout the rest of this chapter (see Table 8.1).

Adding to Eisenberg's classification, van Roosmalen and Klein (1987) described loud "whoops," long-distance calls performed exclusively by adult males that, although sounding the same, can be given in different contexts: when a male has been recently separated from a subgroup, when monkeys hear a sudden, unfamiliar movement or during agonistic intergroup encounters.

Both Klein's (1972) study and van Roosmalen and Klein's (1987) review include a description of the olfactory communication system in *Ateles*. They suggest that the primary function of the elongated clitoris in spider monkeys is to leave urine marks on branches. Based on the fact that it is mostly males who smelled these marks, these authors inferred that females are announcing their reproductive status in this manner (see Campbell, 2006; Campbell and Gibson,

this volume for additional functions of the clitoris length). Another potential signal may consist of the secretions from the sternal gland, which monkeys rub with saliva (Klein, 1972) or an aromatic leaf–saliva mix (Campbell, 2000; Laska *et al.*, 2007) using their hand. The gland is smelled mutually when two individuals, regularly adults, meet after a separation and engage in a series of embraces, licking and sniffing their sternal gland areas and grunting. The function of this social interaction, which involves several communicative signals, was proposed to be the strengthening of the social bonds (van Roosmalen and Klein, 1987; see also Aureli and Schaffner, this volume).

In describing the communication signals of *Ateles* spp., the studies cited above laid the framework for hypothesis-driven research. Subsequent researchers have asked questions regarding the mechanisms underlying the production, transmission and perception of communication signals as well as the possible functions that these signals may play in the social and ecological environment of spider monkeys. Although vocal signals have received far more attention than olfactory signals, most studies examining vocalizations have focused only on the most frequently heard call type in wild spider monkeys, the whinny. Accordingly, in the next two sections I review what is known about the production and function of this call specifically.

Most studies have made extensive use of field recordings and spectrographic analyses (Chapman and Weary, 1990; Teixidor and Byrne, 1997; Ramos-Fernández, 2000). Briefly, spectrograms are graphic depictions of compound signals indicating variation in their frequency and amplitude with respect to time. They allow researchers to distinguish and measure fine features of vocalizations, quantifying distinctive parameters and studying how they vary among contexts or callers. Another important tool that primatologists use to uncover which aspects of the acoustic variation in natural calls are meaningful to primates are playback experiments (e.g. Waser, 1977; Seyfarth *et al.*, 1980). Using hidden speakers, calls recorded from known subjects in known contexts are played in the field, and the the subjects' behavior before and after the playback is observed and measured. These experiments have been performed only recently on habituated groups of spider monkeys (Teixidor and Byrne, 1997, 1999; Ramos-Fernández, 2005).

The whinny – proximate mechanisms

Questions pertaining to the proximate mechanisms underlying vocal communication in *Ateles* deal with those properties of the vocal organs that produce signals, how the signals transmit through the environment and finally, how they are perceived by the auditory organs of recipients. Although sonograms of

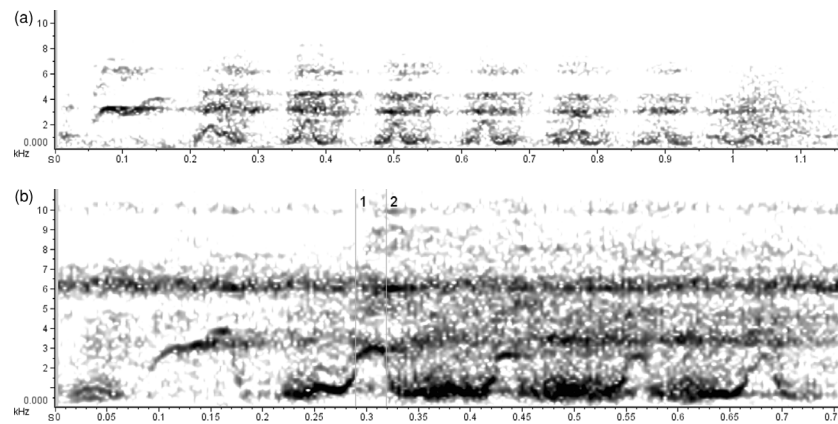


Figure 8.1 Spectrograms of whinny exemplars, recorded in the Yucatán peninsula by the author (see methods in Ramos-Fernández 2005). (a) A typical whinny composed of several elements, in this case two distinct elements at the beginning and then a series of seven “arches” (see text). (b) A whinny composed of two distinct elements up to 0.2 seconds, and then a series of four “arches” and “interarch elements.” Label 1 shows a point of period doubling and label 2 shows the return to the original fundamental frequency at the end of the arch (see text for description). The continuous line at about 6 kHz corresponds to insect noise. Ordinate in kHz, abscissa in seconds.

several of the spider monkey’s calls are presented in many studies, the mechanisms of production and perception of these calls have received very little attention. This is unfortunate, given the fact that the study of these mechanisms may provide important insights into the sources of variation in calls and, therefore, the potential information that recipients may be able to extract from this variation as well as the call’s potential function (Hauser, 1996). This is exemplified by the following analysis of the acoustic structure and the transmission properties of whinnies (M. Y. Liberman, personal communication, 1996).

Whinnies consist of a series of 2–12 rapid rises and falls in pitch, about 100 ms from peak to peak, with a fundamental frequency (F_0) moving from about 1000 Hz to about 2300 Hz and back (Figure 8.1). These “arches” have a fundamental component that is much stronger than the higher harmonics. In between the arches, a typical whinny has other sounds, here called “interarch elements.” These sound (and look, on a spectrogram) quite different. Their pitch is a rise or fall–rise, with a short fall (if any) and a longer rise, all at a much lower fundamental frequency, with a minimum of about 400 Hz and a maximum of about 1000 Hz. The first (and sometimes second) harmonics are just about as strong as the fundamental. The rapid alternation of arches and interarch elements gives whinnies the “grunt-like” quality as well as the similarity to other, higher-pitched calls like trills and tweeters. Because the arches and interarch elements

sound so different, and because they sometimes come and go separately, yielding for instance, calls with no interarch elements (like trills and tweeters), or with intermittent ones, one could think that the two kinds of sounds are produced by different articulatory mechanisms. Alternatively, interarch elements could arise naturally by period-doubling in the lower-frequency regions of a call in which the fundamental frequency of laryngeal oscillation is being rapidly modulated up and down, a phenomenon well known in human phonetics (Herzel, 1993). This is suggested by the fact that the first harmonic of the interarch elements can be seen in spectrograms to be continuous with the fundamental frequency of the arches. That is, near the bottom of the falling limb of the arch, a new fundamental suddenly appears an octave lower, but the former fundamental remains as a strong component of the signal. This period doubling occurs as the fundamental is falling, at or near the bottom of its cycle. As the pitch rises again, the new double-period component vanishes, but this change occurs typically at a much higher frequency than the one at which the double-period component earlier appeared. This hysteresis (Herzel *et al.*, 1995) also seems consistent with the view that the interarch elements are due to a phase transition in laryngeal oscillation. Such phenomena have been observed in human babies' cries and in normal voice characterized as hoarse or creaky and in subharmonic vocalization or "vocal fry" (Herzel, 1993).

Some insight into the functional significance of this alternation of arches and interarch elements in whinnies can be obtained by studying the transmission loss that results from the specific environment in which they occur. Simultaneous observations of two subgroups have determined that spider monkeys can hear whinnies and respond to them when at a distance of up to 300 m from the caller (Ramos-Fernández, 2005). Wahlberg *et al.* (2002) studied the transmission loss exerted by the canopy environment on whinnies using playbacks and recordings of whinnies at different distances from the speaker. These authors found a strong excess attenuation due to friction in the canopy, up to 20 dB per 100 m for the 2000 Hz frequency component of whinnies. This means that a recipient of a whinny located 300 m from the caller can be assumed to obtain much less information in the frequency domain than would a recipient close to the caller. However, if the call contains abrupt changes in fundamental frequency such as those described above, the temporal information will remain despite the loss of energy due to the forest canopy in some frequency bands.

No studies have been carried out on the acoustic perception mechanisms in spider monkeys. However, studies in other nonhuman primate species, like Japanese macaques (*Macaca fuscata*), have shown that their auditory organs are highly sensitive to fundamental frequency modulations such as those found in several of the calls of *Ateles* (Hauser, 1996). Moreover, macaques show categorical perception of calls that grade temporally in the peak frequency

of a modulated call, in a manner akin to humans' speech perception (May *et al.*, 1989). With regard to the localization of long-distance vocalizations in forest environments, the classic playback experiments by Waser (1977) on grey-cheeked mangabeys (*Cercocebus albigena*) showed that these primates were able to localize a single instance of a "whoop-gobble" call at several hundred meters of tropical forest, with a median error of only 6 degrees. Whether spider monkeys can also do this is not known, but anecdotal evidence suggests that they are able to perceive and locate other subgroups in their home range based on their long-distance calls (Ramos-Fernández, unpublished data). Another open question is whether spider monkeys, like other animals, are able to estimate the distance from the source of a call from the acoustic structure as it degrades through their environment (reviewed in Naguib and Wiley, 2001).

Closely related to the production and transmission mechanisms is the search for consistent patterns of variability among signals that could provide recipients with information about the identity of the signaler or other contextual features. Masataka (1986) studied trill vocalizations in a group of captive spider monkeys (*Ateles geoffroyi*) and found that these calls contain information about the caller's identity in the frequencies of the strongest energy band, the second strongest energy band and the lowest energy band. Moreover, trills that had been responded to by particular individuals could be discerned on the basis of their acoustic features. The individual that had originally responded to a trill with another trill of his own could be predicted on the basis of the trill's peak frequency, the amplitude differences between peaks, the frequency modulation of amplitude peaks between 3–5 and 5–8 kHz and the frequency of the strongest energy band (Masataka, 1986). A recorded trill was then played back to those individuals that had originally vocalized after the trill, as well as those that had originally not vocalized. Subjects that originally gave a trill vocalization after the playback call were significantly more likely to vocalize after its played-back version than other individuals. Masataka (1986) interpreted this result as implying that each group member is able to distinguish trills to which they originally responded, so that these vocalizations may indeed consist of "rudimentary" representations for the identity of each group member. If replicated in field conditions, this result could imply that these calls actually consist of labels for one another and that they address each other in this manner.

Chapman and Weary (1990) studied individual differences in the acoustic properties of what seems to be the same vocalization type as Masataka's (1986; based on the sonogram presented), although in this case the authors call it a whinny. Chapman and Weary (1990) found that the duration of the first, middle and ending arches of these vocalizations vary consistently among individuals and that the calls of mothers and their offspring resembled each other more than all other pairwise combinations of calls from different individuals.

Two additional field studies investigating the actual call known by most as the whinny report similar results on the important role of individual identity as a source of consistent variation between calls. Teixidor and Byrne (1999) found significant differences in nine different acoustic parameters among different individuals' calls and then used discriminant function analysis to identify the parameters that best predicted individual identity. These were the maximum peak in the fundamental frequency, the number of frequency modulations and the frequency range of the call. These parameters alone could assign between 50% and 94% of the calls to the correct caller (Teixidor and Byrne, 1999). Similarly, I have found that there are consistent differences between individuals in the call duration, the maximum and minimum frequencies, the frequency range and the duration of the ending element (Ramos-Fernández, 2000). Furthermore, these acoustic parameters could assign 30–70% of the calls to their correct caller using the same discriminant function analysis as the study by Teixidor and Byrne (1999). These results are qualitatively confirmed by the fact that experienced observers of spider monkeys after some time are able to identify some study animals by their whinnies alone (Ramos-Fernández, unpublished data; C. Campbell, personal communication).

Based on the results of these studies, it can be concluded that, among the many vocalizations used by *Ateles*, at least trills and whinnies contain sufficient information to allow identification of the caller. Some of the sources of consistent variation lie in the frequency domain (maximum and minimum frequencies of elements, frequencies of strongest energy bands) and others in the temporal domain (number and duration of elements). The results of the transmission loss experiments cited above, as well as those of perceptual abilities in other primate species, suggest that the individual identity information contained in some of the long-distance calls of spider monkeys would be transmitted successfully even through a closed canopy environment.

The whinny: functional significance

A different question posed by animal communication studies has to do with the function of a communication act; that is, the way in which a signal benefits both signaler and recipients (in the case of cooperative communication acts) or only the signaler (in the case of communication as a manipulation of recipients by the signaler; Dawkins and Krebs, 1978). In primate societies, any communication signal will often have multiple functions, for there are often multiple recipients, each with a different social relationship with the signaler. Thus, in order to understand the function of a communication act, it is important to consider the different social strategies that individuals use to deal with

conflict and cooperation within their group (Walters and Seyfarth, 1987; Aureli and Schaffner, this volume).

The first field study to test an explicit hypothesis about the functional significance of a spider monkey call was performed by Chapman and Lefebvre (1990) on *Ateles geoffroyi* in Costa Rica. Assuming that there is a benefit for spider monkeys to forage with others, mainly by decreasing the risk of predation, these authors postulated that whinnies are used to attract group members to fruiting trees. They predicted that high-ranking individuals should call more than lower-ranking ones and males should call more than females (based on the assumption feeding competition has a stronger effect on low-rank compared with high-rank individuals and on females compared with males). Additionally monkeys should call more when food is abundant than in other times of the year. Indeed, high ranking individuals gave more whinnies than low ranking ones, and there was more calling per subgroup when there was more food in the environment or in the tree they were foraging. However, there was no evidence that subgroups containing only females gave fewer whinnies than mixed-sex subgroups. In addition, other monkeys joined vocalizing subgroups more often (17%) than nonvocalizing subgroups (12%). In those occasions when a subgroup was joined, the more calls there were, the more individuals joined. Subsequently, the whinny of spider monkeys has been cited as an example of a food call used to recruit others to a newly found food source (e.g. Hauser, 1996, p. 449; Heinrich and Marzluff, 1991). However, the fact that there is a very low proportion of subgroups that are actually joined after calling should warn us against concluding that the sole purpose of whinnies would be to recruit others (Cheney *et al.*, 1996, p. 507).

Noting that spider monkeys are considered to be territorial (Klein, 1972; van Roosmalen and Klein, 1987; Symington, 1987), Teixidor and Byrne (1997) proposed that spider monkeys may use whinnies to distinguish among group members and strange individuals from other groups. In order to test this hypothesis, they performed a series of experiments in which whinnies from known and unknown animals were played back to subgroups of *A. geoffroyi*. While the subjects of these experiments responded vocally by giving another whinny in 11/13 trials with stranger whinnies and only in 3/10 trials with familiar whinnies, the frequency of calling per individual did not differ between both trial types. Only in two of the 13 trials with stranger whinnies was there any aggressive response, while none of the 10 trials with familiar whinnies elicited any aggression from the subjects. While these results suggest that spider monkeys are able to distinguish between those in their group and those that are not, this result does not demonstrate conclusively that it is because they are territorial that spider monkeys recognize the stranger whinnies as different from the familiar ones (Teixidor and Byrne, 1997). This is because there was no strong, overt response

toward the stranger whinnies, which would be expected if spider monkeys were in fact detecting an intrusion into their territory (Teixidor and Byrne, 1997).

In their second study, Teixidor and Byrne (1999) searched for the function of *A. geoffroyi* whinnies using observational data as well as acoustic analyses and playback experiments. They found that whinnies emitted when traveling provoked more active responses, such as calling back or approaching the caller, than whinnies emitted when resting or feeding, while whinnies emitted at the presence of an observer did not elicit any active response. This result held true when analyzing the number of responses by any individual to a particular vocalization or the number of responses by a given individual to any vocalization. Next, through acoustic analysis, Teixidor and Byrne (1999) searched for significant sources of variation in the whinny that could inform recipients about what the caller was doing when calling (traveling or feeding). While whinnies emitted when traveling tended to be longer and contained a larger number of elements than those emitted when feeding or resting, there was no consistent difference in the context from which whinnies from different individuals were emitted. In the same study, Teixidor and Byrne (1999) demonstrated that whinnies contain significant acoustic information about the caller's identity (see previous section), but the same was not true for the caller's context. Finally, a series of playback experiments tested the response of subjects to 10 whinnies by 4 different individuals who were moving when vocalizing and to 10 whinnies by 3 different individuals who were feeding when vocalizing. Of all the behaviors observed, scanning was the only behavior to show a difference between the two playback sets. Subjects scanned more when they had heard whinnies emitted while feeding than when they had heard whinnies emitted when traveling.

Recently, I have hypothesized that one of the main functions of whinnies was to maintain contact between individuals in different subgroups (Ramos-Fernández, 2005). To test this I employed simultaneous observations of two different subgroups of *Ateles geoffroyi*. Subgroups that were within 300 m of each other tended to maintain the same distance or come together more often, as well as exchange more whinnies, than subgroups that were farther apart. As reviewed in the previous section, 300 m is close to what can be considered as the active space of the whinny. Also, to test the related hypothesis that whinnies were used to maintain contact between close associates, I included a series of paired playback experiments in which the same whinny was played at the same distance to a close associate and to another, nonclose associate of the caller. While both types of subjects were equally likely to respond to the playback with another whinny, only the close associates ever approached the speaker. This suggested to me that whinnies play a role in maintaining vocal contact between close associates in a loose aggregation system where even monkeys in the same subgroup may lose visual contact with one another.

Another study that touched upon the functional significance of an *Ateles* call was the field study of *A. belzebuth belzebuth* at Cocha Cashu National Park, Peru, done by Margaret Symington (1987). She used the aerial alarm call, Eisenberg's (1976) ook-bark call, to test the hypothesis that these calls are emitted in the presence of aerial predators in order to warn collateral kin about the presence of an aerial predator. Thus, Symington (1987) predicted that males, who are the philopatric sex, would give more calls than females, who disperse upon reaching adulthood (van Roosmalen and Klein 1987). In order to simulate the presence of an aerial predator, she played back the call of a harpy eagle (*Harpia harpyja*), a common primate predator in Cocha Cashu. Contrary to her prediction, females gave more calls than males and neither the number of dependent offspring nor the presence of very young affected females' calling rates. While these alarm calls may not be used to warn particular individuals about the presence of a predator in order to provoke an escape reaction, they could be used to mount a mobbing response. Mobbing congregations have been observed in several studies (van Roosmalen and Klein, 1987; Symington, 1987; Ramos-Fernández, personal observation). In support of this, the distance at which these calls can be heard in the forest is up to 300 m (Symington, 1987), although her observational data did not allow her to determine conclusively whether subgroups are actually joined by others in the group after long bouts of alarm calling.

Synthesis

Traditionally, animal communication acts are considered to occur among dyads of one signaler and one recipient (Smith, 1977; Dawkins and Krebs, 1978; Guilford and Dawkins, 1991; Endler, 1993). However, more recent studies have stressed that most communication acts occur between a signaler and a multiplicity of receivers, each of them holding a different relationship to the caller (McGregor, 1993; McGregor and Dabelsteen, 1996). In this communication network, potential recipients of a signal include all individuals who extract information from a signal and that happen to be within its active space. This includes those recipients who "eavesdrop" on the communication interactions of pairs of others, extracting information about their social relationship (Cheney and Seyfarth, 2004), or even members of other species who detect the presence of the signaler through its communication signal (e.g. predators detecting spider monkeys through their whinnies). It is clear that both the proximate mechanisms and the functional significance of a signal will be determined by the presence of a network of several potential recipients (McGregor and Peake, 2000).

Take the best-studied signal in the spider monkeys' repertoire, for example. In a typical spider monkey habitat, the monkeys can hear whinnies for up to 300 m (Ramos-Fernández, 2005). The average distance between different individuals in the same subgroup is less than 30 m, while the distance between different subgroups is usually between 170 and 370 m (Ramos-Fernández, 2005). This means that most whinnies will reach all individuals in the caller's subgroup and, most of the time, several individuals in other subgroups as well. All the different functions that have been attributed to this call (contact maintenance: Eisenberg, 1976; Ramos-Fernández, 2005; recruitment to food patches: Chapman and Lefebvre, 1990; defense of territory: Teixidor and Byrne, 1997; coordination of group movements: Teixidor and Byrne, 1999; Ramos-Fernández, 2005) are possible if one considers the fact that there are multiple recipients within the communication network of a group of spider monkeys. How these multiple functions have shaped the acoustic design of whinnies and their perception by recipients is still an open question, but they all may be equally important.

The change in emphasis of communication studies from dyads to networks implies that signalers will only provide information when there is an appropriate audience, or will attempt to direct information at suitable recipients. The former situation, known as the "audience effect" (Evans and Marler, 1984) has not been demonstrated in spider monkeys, but the fact that more whinnies are heard in subgroups that have another one within the active space of the whinny (Ramos-Fernández, 2005) is suggestive. As for directing signals at particular individuals, Masataka's (1986) results suggest that whinnies may actually contain information about the intended recipient, which would certainly make communication more specific within the network, permitting monkeys to stay in touch with certain individuals. While suggestive, these experiments need to be replicated in natural conditions, where the social and spatial relationships among different individuals are precisely those in which this individual label would be required.

Another shift in emphasis in communication studies concerns the different perspectives of signalers and recipients, particularly with regard to the information they are able to extract from a signal (Seyfarth and Cheney, 2003). While the information contained in an alarm call, for example, is relatively easy to extract by an observer from the stimulus that elicits the call (i.e. the presence of a predator or a source of danger) and from the responses of recipients (e.g. run for cover), there are other animal signals for which this is not so simple. So called "contact" and "food" calls do not seem to have such a clear external referent as alarm calls do (Cheney *et al.*, 1996). Recipients of these calls may simply keep doing what they were before hearing the call. In such instances, if there has been no overt response how can we know what recipients have been informed about? In dealing with this issue, it becomes crucially important to

distinguish between the cognitive mechanisms that underlie the production and perception of a call. An individual that gives a contact call upon being separated from the group can be said to call regarding its own position with respect to the group. Recipients of this signal, however, are not separated from the group; therefore the information content of the signal cannot be about the separation from the group, unless they are able to place themselves into the signaler's perspective. The available evidence, however, suggests that primates cannot do this (Seyfarth and Cheney, 2003).

What, then, is the information content of whinnies? The only conclusion that can be drawn from the available evidence is that they contain information about the individual identity of the caller. The playback experiments performed by Teixidor and Byrne (1999) demonstrate that recipients use this information and those by Ramos-Fernández (2005) that they respond according to the social relationship they have with the caller. It is possible that, communication being a dynamic phenomenon, the identities of signaler and recipient changing continuously within a network of related individuals, the information content of a signal may not be as "fixed" and may not reside so much in the signal as in the relationship between two or more communicating individuals (Aureli and Schaffner, this volume).

The social system of spider monkeys (and other so-called "fission–fusion" species) has been cited as complex, and as a selective pressure on the evolution of complex cognitive abilities (Milton, 2000; Barrett *et al.*, 2003). However, where this complexity lies is not clear. Societies with "fission–fusion" properties have been found in so many different animal groups, from elephants (*Loxodonta africana*) to dolphins (*Tursiops truncatus*), from hyenas (*Crocuta crocuta*) to bats (*Myotis bechsteinii*), from chimpanzees (*Pan spp.*) to galagos (Galagonidae; ~~F. Aureli, C. Schaffner and C. Boesch, unpublished data~~) that it is hard to define a common evolutionary path and ~~much less~~ a set of cognitive abilities that are necessary for fission–fusion to function properly. In a recent study by Ramos-Fernández *et al.* (2006), a set of simple agents searching for food in a realistic environment are seen to form subgroups and associate among them in ways that resemble the spider monkeys' and other fission–fusion species' grouping and association patterns, without any rules by which they interact among them. The authors suggest that in fission–fusion societies, it is the complexity of the environment that causes variation in the size and composition of subgroups and not the social relationships themselves (Ramos-Fernández *et al.*, 2006). Long-distance vocal and olfactory communication may be used to maintain contact with animals that become separated as they search for food. If they can keep track of their social relationships, the simplest hypothesis to consider is that the signal simply informs them about their own identities.

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