

## Function of loud calls in wild bonobos

**Frances J. White<sup>1</sup>, Michel Waller<sup>1</sup>, Klaree Boose<sup>1</sup>, Michelle Y. Merrill<sup>2</sup>,  
Kimberley D. Wood<sup>3</sup>**

1) Department of Anthropology, University of Oregon, Eugene, Oregon, USA  
e-mail: fwhite@uoregon.edu

2) Cabrillo College, 6500 Soquel Drive, Aptos, California, USA

3) Horizon Research, Inc., Chapel Hill, North Carolina, USA

**Summary** - Under the social origins hypothesis, human language is thought to have evolved within the framework of non-human primate social contexts and relationships. Our two closest relatives, chimpanzees and bonobos, however, have very different social relationships and this may be reflected in their use of loud calls. Much of loud calling in the male-bonded and aggressive chimpanzee functions for male alliance formation and intercommunity aggression. Bonobos, however, are female bonded and less aggressive and little is known on the use and function of their loud calls. Data on frequencies, context, and locations of vocalizations were collected for wild bonobos, *Pan paniscus*, at the Lomako Forest study site in the Democratic Republic of the Congo from 1983 to 2009. Both males and females participated in loud calls used for inter-party communication. Calling and response rates by both males and females were higher during party fusion than party fission and were common at evening nesting. The distribution of loud calls within the community range of loud calls was not random with males calling significantly more towards the periphery of the range and females calling significantly more in central areas. Calling and party fission were common at food patches. Responses were more frequent for female calls than for male calls. Calling, followed by fusion, was more frequent when a small party called from a large patch. We conclude that bonobo females and males loud calls can function in inter-party communication to call others to large food patches. Females call to attract potential allies and males call to attract potential mates. Our results support the social hypothesis of the origin of language because differences in the function and use of loud calls reflect the differing social systems of chimpanzees and bonobos. Bonobo loud calls are important for female communication and function in party coordination and, unlike chimpanzees, are less important in male cooperative aggression.

**Key Words** - *Pan paniscus*, Vocalization, Fission-fusion.

### Introduction

The question of why humans evolved language uses comparisons with the communication systems of our nearest relatives, the non-human primates, to understand the origins of this form of communication. Observations that primates use particular calls to reference specific predators

or food items (Cheney & Seyfarth, 1980; Marler & Tenaza, 1977) led to the referential signaling hypothesis. This hypothesis proposes that human language originated from the value of labeling and identifying important ecological elements. In contrast, the gestural origin hypothesis focused instead on the use of face and body gestures instead of vocalizations in communication.

Gestures were identified as crucial as these more likely to be under earlier voluntary control before speech emerged (Hewes *et al.*, 1973). Other hypotheses have focused on either the underlying cognitive capacities needed for language, such as use of symbols, syntax, or theory of mind (Dunbar, 1998; Ulbaek, 1998), or the anatomical structures necessary for speech production such as the human larynx (Duchin, 1990) or neural control of breathing (MacLarnon & Hewitt, 2004). While important, these hypotheses do not focus on the functional advantage of language and why it evolved. In contrast, the social origin hypothesis proposes that human language evolved in part from our non-human primate ancestor's knowledge of social relationships (Dunbar, 1998; Seyfarth *et al.*, 2005). In a social environment, individuals that could communicate with others on abstract and conceptual issues such negotiating alliances or coordinating activities would be at an evolutionary advantage over those of lesser ability. This hypothesis, therefore, differs from the referential signaling hypothesis in being focused on social advantage rather than on ecological elements.

Studies of the social function of vocal communication in our closest relatives can, therefore, provide information on the circumstances under which language may have evolved. Many studies support the social origin hypothesis which proposes that human language evolved in part from our non-human primate ancestor's knowledge of social relationships. For example, studies of the loud vocalizations of chimpanzees, one of our closest relatives, show complex and varied vocal communications that may show conversational characteristics (Arcadi, 2000; Boehm, 1992). Our two closest living relatives, the chimpanzee and the bonobo, are fission-fusion species where individuals associate in small parties but are also members of a larger community (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Kano, 1980; Nishida, 1979; White, 1988). Separated bonobo and chimpanzee parties can interact through long-range vocalizations, while quiet vocalizations can be used for within-party communication. Both chimpanzees and bonobos

use long-range calls (Goodall, 1986; Mori, 1983; de Waal, 1988) but these calls differ in frequency range and vowel timbre between the two species (de Waal, 1988). Although both species of *Pan* exhibit a flexible fission-fusion social system, there are however important differences between male-bonded chimpanzee (Goodall, 1986) and female bonded bonobo (White, 1996) social systems. As the most notable of these differences involve social patterns within and between the sexes and between different communities, it is to be expected that the function of loud calls will differ with the species differences in social contexts. These species differences in our closest relatives can be used to expand our understanding the range of possible adaptive reasons for origins of human language.

The context of call use has been better studied in wild and captive studies of chimpanzees (Arcadi, 1996, 2000; Clark, 1993; Clark & Wrangham, 1994; Ghiglieri, 1984; Marler, 1976; Marler & Tenaza, 1977; Mitani & Nishida, 1993; Wilson *et al.*, 2007) with fewer studies on bonobos (Hohmann & Fruth, 1992; van Krunkelsven *et al.*, 1996; de Waal, 1988). In chimpanzees, the production of vocalizations varies with rank and social context: at Kibale, high-ranking males call in all social contexts, whereas low-ranking males and females only call in mixed parties (Clark, 1993). At Gombe, all rank and sex classes also call in mixed parties at the provisioning site (Clark, 1993; Marler & Tenaza, 1977). Call production in chimpanzees also varies with ecological context. Captive studies show that production of loud calls (pant-hoots) in feeding contexts differed by the quantity and divisibility of the provisioned food (Hauser *et al.*, 1993). Earlier work on wild chimpanzees at Gombe and Kibale (Ghiglieri, 1984; Wrangham, 1977) suggested that loud calls (arrival pant-hoots, APH) given upon arrival in food patches by male chimpanzees function to attract allies, mates, or both to abundant food sources. Later studies at Kibale and Mahale, however, have shown that production of calls did not correlate with fruit availability, arrival of other parties, party size, and/or location of

estrus females. Instead, these vocalizations were related to the rank of the caller or location of male alliance or association partners (Clark & Wrangham, 1994; Mitani & Nishida, 1993). Studies at Budongo have shown that that food abundance, food patch size and monopolizability as well as proximity and importance of social partners can influence the frequency of production of male food-associated calls (Notman & Rendall, 2005; Slocombe *et al.*, 2010).

Loud calls are also important in inter-community interactions in chimpanzees (Goodall, 1986; Watts & Mitani, 2001). Chimpanzee interactions between neighboring communities are typically aggressive, involving interactions between neighboring males varying from territorial defensive to lethal raiding (as reviewed in Boesch & Boesch-Achermann, 2000; Mitani *et al.*, 2002; Wrangham, 1999). The use of loud calls by chimpanzee males, therefore, changes in complex ways as individuals move from core to peripheral areas of their range. There is evidence of decreased loud calling, presumably to reduce risk of detection when vulnerable in some areas, as well as increasing loud calling, presumably to signal territory ownership under securer situations in other areas (Wilson *et al.*, 2007).

Bonobos, like chimpanzees, exhibit a flexible fission-fusion social system. Communities of both species are composed mostly of related males and unrelated adult females. Unlike chimpanzees, however, bonobo affiliative relationships between the sexes and among females are common (Kano, 1992; White, 1996). The strongest social bonds found in chimpanzees are those among males within a community (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1979). Bonobo males, in contrast, are less cohesive with each other and seldom able to dominate the more cohesive females (White & Wood, 2007), but in chimpanzees males are socially bonded and typically dominant to females (Goodall, 1986; Nishida, 1979; Wrangham *et al.*, 1992). Unlike chimpanzees, bonobo inter-community interactions are rarely hostile and may include vocalizations followed either by avoidance or peaceful association

(Badrian & Badrian, 1984; Furuichi, 1997; Kano, 1992). Lethal raiding and between communities and male territorial patrols observed in chimpanzees have not been observed in bonobos (Kano, 1992; White, 1996). With these differences in social strategies, it is expected that male and female bonobo loud calls, both among parties of the same community and between communities, fulfill different social functions than those of chimpanzee loud calls.

Bonobo vocalizations have been studied in captivity (van Krunkelsven *et al.*, 1996; de Waal, 1988) and the wild (Bermejo & Omedes, 1999; Hohmann & Fruth, 1994; Mori, 1983). It has been suggested that the long range vocalizations of this species, such as the high-hoot, are structurally better for localization of the source than for carrying over distances greater than 500 m (Hohmann & Fruth, 1994; de Waal, 1988). Male and female calls differ in pitch (Hohmann & Fruth, 1994). Krunkelsven *et al.* (1996) found that production of soft, "food peep" vocalizations was related to both social context and food quantity, but did not find sex differences in calling behavior in either context. De Waal (1988) described more than a dozen distinct types of loud and soft calls used by bonobos in captivity. During his study, most loud calls were used in exchanges between parties out of visual contact rather than being directed at individual conspecifics. Loud calls were also given during party movement and were associated with feeding (de Waal, 1988). More recent captive studies have shown that bonobos change their foraging behavior in response to food-associated calls from others (Clay & Zuberbühler, 2009, 2011). Wild studies have found that bonobo loud calls vary through the day and were most frequent in late morning and late afternoon. The later peak was associated with travel to and construction of night nests. Observed parties' most common response to calls of distant parties was to vocalize and/or travel (Hohmann & Fruth, 1994).

We examine the social and ecological contexts and possible functions of loud call vocalizations by wild male and female bonobos. We focus on

two aspects of loud calls: calling for coordination within a community and calling for interaction between communities. We first examine whether sex differences in loud calls function as food calls within a community by examining whether these calls function to attract others to abundant and shareable food sources. We hypothesize that although both sexes will give loud calls, they may function differently and therefore be given in different contexts. Specifically, we hypothesize that wild female bonobos may use loud calls to attract female alliance partners within their community to food sources, and that males may also use loud calls to attract community females into food sources for mating. We predict that both males and females will call from food patches and both will result in party fusion as others are called into food patches. Secondly, we examine whether there are sex differences in loud calls that may be used in inter-community communication, either to attract others or to advertize range occupation. We examine loud call frequency on the periphery of the bonobos range compared to calls made more towards the center of the range. As neighboring females are unlikely to be close allies of resident females, we predict that females will not call more in the periphery than towards the center of the range. However, males may call from the edge to advertize community presence or to attract possible neighboring females from other communities for mating. We therefore predict that males will call more in the periphery of ranges than in the center of the range. If males are calling from the edge to advertize their presence to males in the neighboring community, we predict that they are most likely to call when in larger parties and less vulnerable to aggression from neighboring males. If males are calling more to attract females from neighboring communities, we predict that they will call from the same party sizes as calling in the more central areas.

Calling by females may also be related to group size. As for males, if females call to attract others, we predict that calling will occur at all party sizes with possibly a bias towards calling more in smaller parties when allies are most likely to be absent. It has also been suggested that

bonobo loud calls may be used by females for defense of food patches against other community members (White, 1986; White & Lanjouw, 1992). However, if females are loud calling to advertize their presence in a food patch, we predict that they will call more in larger parties when they are less vulnerable to being supplanted by a larger competing party.

## Methods

Data on vocalizations were taken during approximately 500 hours of focal animal sampling between 1983 and 2009 on non-provisioned bonobos in the Lomako Forest, Democratic Republic of the Congo between 1983 and 2009. Study periods ranged from 6 weeks to 12 months. The study site is located at 0° 51' N 21° 5' E and consists of approximately 40 square kilometers of mapped trails. The study area includes a mosaic of forest types, but is principally climax evergreen, polyspecific rain forest, with some areas of second growth, slope and swamp forest (White, 1992). The study animals were members of two communities (Bakumba and Eyengo) and a small splinter group with consistent composition from 1983 to 1985. By 1991, members of the splinter group were members of the Bakumba community. Data from 2005 to 2009 were from the Eyengo community only.

The data were based on focal animal follows, with 2 minute interval sampling in the 1983 through 1985 observations, and 5 minute intervals for the 1991 through 2009 field seasons. Vocalizations by the focal animal were recorded using continuous sampling whenever calls occurred. Follows lasted until focal animals were lost from sight and averaged 97 minutes ranging from 1 to 545 minutes in length. For each vocalization, we noted the type of vocalization heard, the identity and/or age and sex of the caller, the context of each vocalization including food species and ecological measures of any food patches where calling occurred (DBH for trees, radius and volume estimates for tree and vine canopies), any associated fission or fusion events,

and the location of the caller relative to the trail and transect system. Following Arcadi (2000), calls were considered in “response” to focal animal calls if it was given while another individual was still vocalizing, or within 5 seconds of the termination of the focal animal’s call. We noted the party size before and after the vocalization and if there was a fission or fusion event within 5 minutes of the call. No recordings were made of vocalizations for this study.

Location relative to the trail and transect system was recorded. In 2007 and 2009, the trail and transect system was mapped using a Garmin GPS unit. The borders of the Eyengo and Bakumba community ranges was determined using a Minimum Convex Polygon (MCP) created by plotting all sightings into ArcGIS. All maps and analysis used a Transverse Mercator projection and the WGS 1984 UTM Zone 34N coordinate system. We then measured the distance to the border for each bonobo observation with loud calls.

We calculated predicted frequencies based on loud calls occurring at equal frequencies for each sex or in different contexts such as in or out of food patches using the distribution of focal sampling. The range of the community was approximately 2 km across and approximately circular. Using a circle of radius 1000 m to approximate the range, we calculated the approximate areas contained in concentric annuli in 100 m increments using the formula (see insert in Figure 4). We used these areas to calculate an expected frequency for loud calls based on the assumption that if loud calls occurred randomly throughout the range, the chance of observing a loud call in any annulus was dependent only on its area. We designated the periphery as being the outermost annulus that included all areas within 100 m of the edge of the range.

Frequencies were compared using G tests of Independence with Williams’ correction applied or G tests for Goodness of Fit to predicted distributions (Sokal & Rohlf, 1995). Party sizes were compared using ANOVA and the relationship between party size and patch size was examined using linear regression (Sokal & Rohlf, 1995).

**Tab. 1 - Context of loud calls by focal animals.**

ACTIVITY AND FOOD PATCH CONTEXT	PERCENTAGE OF OBSERVED LOUD CALLS	
	MALES	FEMALES
In feeding tree (feeding or resting)	41.6	56.8
Resting, not in feeding tree	34.8	13.6
Travelling (not in food patch)	22.5	28.4
Meat feeding	1.1	1.1
N	89	88

## Results

A total of 394 loud calls were heard during focal animal sampling. Of these, 190 calls were given by focal animals, 101 by males and 89 by females. The frequency of loud calls by males and females was not significantly different to an expected distribution based on the representation of each in focal sampling ( $G = 0.933$ , not significant). Context was recorded for 331 loud calls and callers were identified to sex for 177 of these calls. There were significant differences in frequencies of loud calls given by males and females in different contexts ( $G = 10.251$ ,  $P < 0.05$ ). Both sexes gave most of their loud calls from within feeding trees (Tab. 1). However, males gave a greater percentage of loud calls outside of food patches, often resting outside of a feeding tree, than did females. Females gave more loud calls when travelling. The rate of loud call production varied with the time of day with loud call production peaking twice, between 1100-1200 h and between 1600-1700 h. The evening calling is a pre-nesting peak in loud calls, as suggested by Hohmann & Fruth (1994).

Focal animals called from food patches that contained fruit, leaves or meat. Four fruit species accounted for 55.4% of loud calls from food

**Tab. 2 - Food patch type or species and frequency of loud calls. Goodness of Fit test to frequencies predicted from focal animal time spent feeding on these species or categories.**

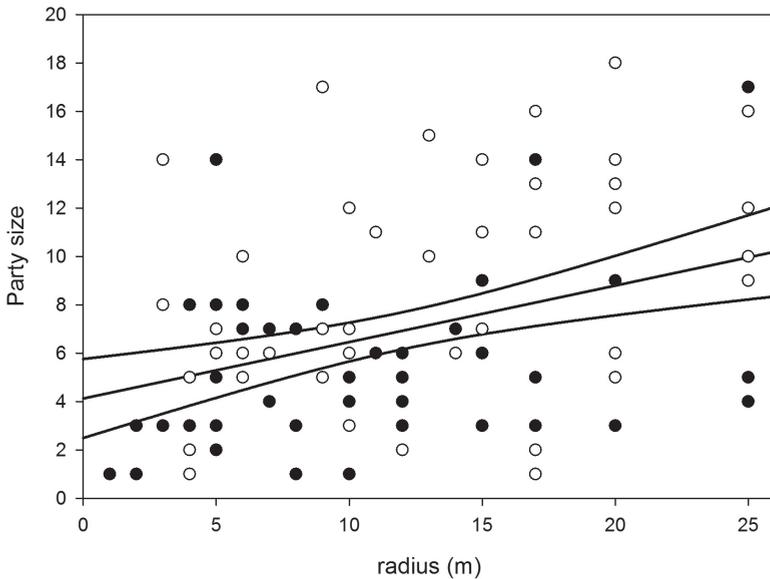
SPECIES OR FOOD TYPE	% OF LOUD CALLS	% PREDICTED FROM FOCAL SAMPLING	G, SIGNIFICANCE	% OF FEEDING FOCAL SAMPLES
<b>Fruit</b>	<b>66.3</b>			<b>71.4</b>
<i>Dialium</i> species	15.4	9.4	G = 20.146, P < 0.001	5.9
<i>Ficus</i> species	18.9	48.6	G = 12.176, P < 0.001	30.5
<i>Nauclea diderichii</i>	10.9	14.0	G = 0.857, not significant	8.8
<i>Antiaris toxicana</i>	10.3	22.7	G = 2.406, not significant	14.2
<b>New leaves</b>	<b>25.6</b>			<b>23.9</b>
<i>Celtis mildbraedii</i>	1.7	20.9	G = 30.096, P < 0.001	13.1
<b>THV</b>	<b>3.4</b>	<b>5.1</b>	<b>G = 0.170, not significant</b>	<b>2.8</b>
<b>Meat</b>	<b>3.4</b>	<b>1.8</b>	<b>G = 6.100, P &lt; 0.05</b>	<b>1.1</b>
<b>Totals</b>	<b>N=175</b>			<b>N=6062 focal samples</b>

patches (Tab. 2). All other food species each accounted for 5% or less of loud calls. The frequency of loud calls was compared to a predicted frequency calculated from the percent of time focal animals spent feeding on that species. Loud calls were significantly more frequent than predicted in *Dialium* and during meat eating, and were less frequent than predicted in *Ficus* and *Celtis*.

Party size was regressed on the radius of the food patch (Fig. 1). There was a significant regression with party size increasing with patch size (Regression  $F = 14.83$ ,  $df 1,102$ ,  $p < 0.001$ , regression line: party size =  $4.1 + 0.23$  radius). The size of parties and the radius of the food patch, as measured by the distance from the tree trunk or center of vine patch to the greatest extent of the canopy, were compared between observations

with loud calls and those without loud calls. Average parties with loud calls were significantly larger (8.82 individuals  $\pm$  SE 0.683) than parties without loud calls (5.41 individuals  $\pm$  SE 0.408; ANOVA  $F=20.09$ ,  $df 1,102$ ,  $p < 0.001$ ) but the average radius of food patches was not significantly different between those where loud calling occurred (13.20 m  $\pm$  SE 1.005) and where it did not (11.05 m  $\pm$  SE 0.781; ANOVA  $F=20.09$ ,  $df 1,102$ ,  $p < 0.001$ ).

Loud calls from one party were often associated with loud calls from other parties (Tab. 3). 36% of loud calls were preceded or followed by loud calls from other parties or lone bonobos out of visual contact. Both males and females were observed to give loud calls that were involved in these vocal exchanges (Tab. 3). The frequency of



**Fig. 1 - Party size and radius of food patch. No loud calls are solid circles and patches with loud calls are open circles. Shows regression of party size on patch size.**

loud calls with and without responses in and out of food patches were compared between males and females using G tests of Independence. Loud calls during meat eating could not be tested because no responses were observed for either sex. Females received significantly more responses than males when in a food patch ( $G=78.221$ ,  $df\ 1$ ,  $p < 0.001$ ), but there was no significant difference when not in a food patch ( $G=3.041$ ,  $df = 1$ ,  $p=0.0812$ ).

Loud calls were also given by lone individuals. Lone males accounted for 3.5% and lone females 2.5% of focal sampling. Lone males were never observed to get a vocal response to their loud calls from others ( $N=27$ ), but lone females received responses for 4 out of 6 observed loud calls; the difference between the sexes was highly significant ( $G=16.738$ ,  $p<0.001$ ). Most of the loud calls during fission and fusion events, however, were made by individuals in mixed-sex parties ( $N=50$  fission or fusion events). About 7% of loud calls were immediately followed by group fusion. No calls were associated with group fusion during nesting. Loud calls followed by group fusion

were most often observed in feeding contexts. 60% of vocal exchanges involving females calling and 61% of vocal exchanges involving male loud calling happened in food patches. Of these vocal exchanges from food patches, 11 resulted in party fusion and 28 did not.

Both males and females were involved in giving loud calls before fission and fusion events (Fig. 2). There was no significant sex difference in frequencies of giving loud calls preceding fusions ( $G=0.081$ , not significant). Loud call production was significantly more frequent when parties were joining than when parties were splitting ( $G = 6.106$ ,  $p<0.05$ ). There was no significant difference in frequencies of loud calls during fission or fusion events between males and females ( $G = 0.393$ , not significant). The average size of parties giving loud calls that were then joined by others was significantly smaller (5.7 individuals not including dependent offspring,  $N=11$ ) than parties that gave loud calls and were not joined by others (9.6 individuals,  $n=30$ ,  $F=4.7203$ ,  $P < 0.05$ ).

We recorded the distance from the edge of the range for 393 loud calls, 100 male focal

**Tab. 3 - Sex and feeding context of focal animal loud calls and frequency of response by others.**

	IN FOOD PATCH	MEAT EATING	NOT IN FOOD PATCH	N
<b>Female</b>				155
No response	18	7	39	64
Response	79	0	12	91
<b>Male</b>				139
No response	61	4	56	121
Response	11	0	7	18

animals and 88 female focal animals. Both males and females showed significant differences to an expected distribution based on the areas calculated from areas of concentric rings (males  $G=38.326$ ,  $df=9$ ,  $p < 0.001$ , females  $G=42.816$ ,  $df=9$ ,  $p < 0.001$ ; Figure 3). The largest deviations from expected were different between the sexes with males giving loud calls more in the area closest to the periphery than called expected, and females calling more in areas more towards central parts of the range.

We recorded complete party size counts for 72 of the observations of the loud calling male focal animals and 33 of these observations occurred within 100 m of the edge of the range. In one of these cases, one unidentified individual joined the calling male. In 5 of the 39 cases when males called in the more central areas, party size increased. Party sizes of calling focal males were significantly smaller within 100 of the edge than towards the center of the range (mean party size near edge  $3.25 \pm SE 0.623$ , mean party size not near edge  $5.60 \pm SE 0.580$ ,  $F = 7.54$ ,  $df 1,70$ ,  $p < 0.01$ ).

## Discussion

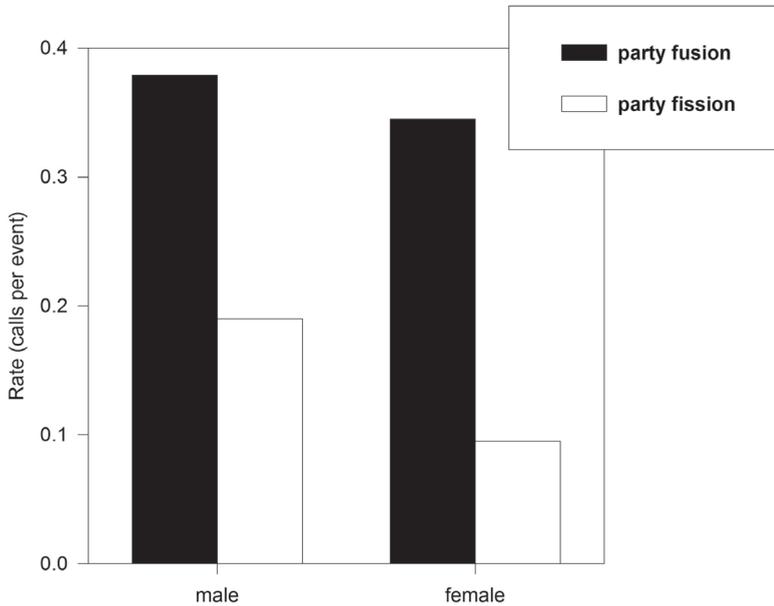
These results demonstrate that bonobo vocalizations do vary with social and ecological contexts but given the limited scope of these

sample sizes, our conclusions are preliminary. As in previous studies (Hohmann & Fruth, 1994), we also found that production of long range calls was most frequent in late morning and late afternoon. The later peak was associated with travel to and construction of night nests.

As found in previous studies of bonobos and in studies of chimpanzees, loud calls of bonobos appear to be important in coordinating the activities of individuals and parties (Clark & Wrangham, 1994; Hohmann & Fruth, 1994; Mitani & Nishida, 1993). There are, however, important differences between the species that may be related to differences in social structure. Studies of chimpanzee vocalizations focused on the importance of male vocalizations in attracting male allies and mates, especially to abundant food sources (Wrangham, 1977), but later studies demonstrated that the rank of the caller or location of male alliance or association partners were more relevant (Clark & Wrangham, 1994; Mitani & Nishida, 1993).

In contrast to chimpanzees, bonobo females were as likely as males to give all types of vocalizations and the vocalizations of both sexes were important in party changes. Loud calls were important in the dynamics of fission and fusion of parties, both males and females were active participants in these dynamics.

Our first hypothesis proposed that female bonobos use loud calls to attract female alliance partners within their community to food sources, and males also use loud calls to attract community females into food sources for mating. We found that loud calls by both males and females were associated with the arrival by other bonobos to abundant and shareable food sources. The importance of females in attracting others to food was indicated by their higher frequency of calling from food patches and the greater frequency of receiving response calls than males. Although sample sizes were small, lone females were also more able to elicit responses from others with loud calls, but lone males were not. These results are supportive of the hypothesis that females use loud calls to attract female alliance partners and suggest that males are attempting to attract others for multiple reasons.



**Fig. 2 - Loud calls given by males and females during party fission or fusion.**

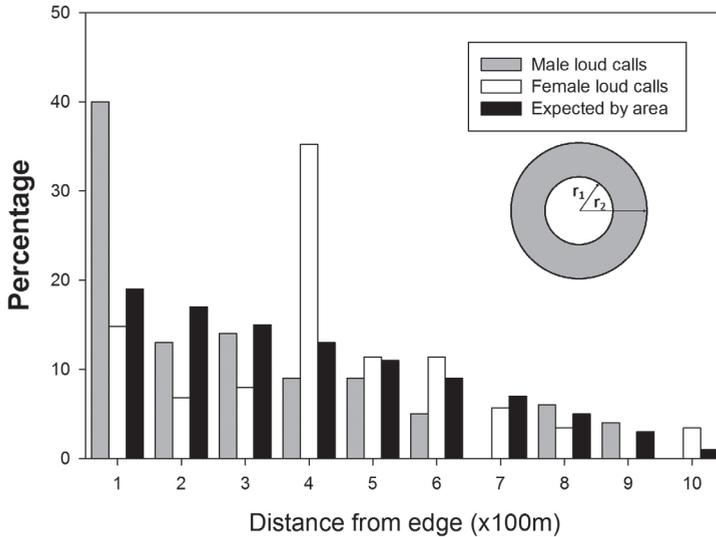
Our second hypothesis examined whether there are sex differences in loud calls that may be used in inter-community communication, either to attract others or to advertize range occupation. We examine loud call frequency on the periphery of the bonobos range compared to calls made more towards the center of the range. The location of individuals influenced frequency of calling differently for males and females. Male calling at the edge of the range does not appear to be related to territorial defense as these loud calls were made from small parties or by lone individuals which would be vulnerable if aggressed against by a larger party. Such calling is, therefore, more consistent with attempts to attract neighboring females, although this did not appear to be successful. Females, in contrast, called more towards the center of the range where they are more likely to be in potential vocal contact with close allies.

The variation in amount of loud calls given by bonobos in different food species indicate that vocalization type and frequency may vary

with food value. Meat-eating is a relatively rare event, but was marked with greater frequencies of vocalizations by both males and females. The high frequency of calling associated with some foods such as figs, however, may simply reflect that these were frequent foods, and actually associated with lower rates of calling. Other species, such as the *Dialium* species, which were relatively large trees, may be more valued resources.

We also predicted that, if females call to attract others, there may be a bias towards calling more in smaller parties when allies are most likely to be absent. We found that calling parties that were joined by others were smaller than calling parties that were not thus providing additional support for the hypothesis that bonobos use food calls to attract allies.

It has been suggested that the bonobo vocalizations may also be used by females to call other females into food patches for cooperative defense of food patches (White, 1986; White & Lanjouw, 1992). This hypothesis was developed from the observation that the frequency



**Fig. 3 - Percentage of calls by males and females by distance from community range edge compared to an expected percentage based on area concentric rings in increments of 100 m. Statistical significance calculated from frequencies. Annulus area (insert shaded area) calculated from  $\pi(r_2^2 - r_1^2)$ .**

of female-female GG rubbing among females as they arrive and enter a food patch was correlated with the amount of food that is going to be removed in the subsequent feeding bout (White & Lanjouw, 1992). If GG rubbing partnerships reflect possible alliances, then more alliances are needed to defend large food patches that contain more food. This study supports the suggestion that loud calls between parties do result in others coming into food patches, and that both males and females are involved in these vocalizations. However, larger parties gave more loud calls than smaller parties, suggesting that individuals in smaller parties are not seeking allies.

All party exchanges of loud calls that were followed by fusion occurred in food patches. There was no direct evidence of female defense of food patches, although anecdotal evidence suggests bonobos may use loud calls to defend more limited resources. In two cases where researchers were tracking two different parties at one time, the approaching party turned away after loud calls were given by another party in a food patch.

It is also possible that bonobos call others into food patches through reciprocal altruism, and that the vocalizations contain information on the quality of the food. Clearly, more information is needed to distinguish between these two hypotheses. Recording and analysis of different loud call types produced in different ecological contexts may help resolve this issue in the future.

The differences in bonobo and chimpanzee social contexts are therefore reflected in differences in the function of loud calls. Under the social origin hypothesis for the evolutionary origin of human language, much has been made of the role of calling among males both for alliance formation and for inter-community aggression as well as communication about food (Wilson *et al.*, 2007). Bonobos similarly use loud calls in food contexts, but females are more active participants in such exchanges and vocalizations by males appear to be directed more towards females and not for behaviors associated with male cooperative aggression. As expected, therefore, including bonobos in any consideration of the possible

evolutionary origins of language greatly expands our range of thinking on sex-based participation and motivation in long distance communication between individuals.

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