

## Contexts and social correlates of long-distance calling by male chimpanzees

JOHN C. MITANI\* & TOSHISADA NISHIDA†

\**Department of Anthropology & Evolution and Human Behavior Program, University of Michigan, Ann Arbor, MI 48109, U.S.A.*

†*Department of Zoology, Faculty of Science, Kyoto University, Kyoto 606, Japan*

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**Abstract.** Chimpanzees, *Pan troglodytes*, live in unstable social groups, whose members associate in temporary parties of varying size and composition. Male chimpanzees utter a long-distance vocalization, the pant-hoot, that has been hypothesized to maintain spatial contact between conspecifics within and between parties. To test this hypothesis, the contexts in which calls by males were produced and the effects several social factors had on pant-hoot production were examined. Males travelled significantly more often before and after hooting than expected by chance. In addition, high-ranking males gave more pant-hoots than lower-ranking individuals, and variation in party size did not affect call production. These data are consistent with the proposed spacing function of pant-hooting, and do not support the suggestion that hooting is a simple manifestation of the high arousal levels caused by social or feeding excitement. Additional observations revealed that subjects called more frequently when alliance partners were nearby, compared with when they were absent. Males also called more when their close associates were nearby relative to situations when those associates either accompanied them or were absent. In contrast, the presence of preferred grooming partners and oestrous females within earshot did not affect the production of pant-hoots by males. These results suggest that males may pant-hoot to particular audiences within their social group, specifically to maintain contact with and to recruit allies and associates. Investigation of how chimpanzees respond to pant-hoots will be necessary to confirm this hypothesis.

Recent research has revealed that the social contexts of signalers influences the vocal production of animals. For example, several birds and mammals vary their alarm calling behaviour as a function of whether particular individuals are present (Sherman 1985; Cheney & Seyfarth 1985; Sullivan 1985; Gyger et al. 1986; Karakashian et al. 1988; Heinrich & Marzluff 1991). These observations suggest that animals can control their vocal output voluntarily, and provide insights into the functional significance of vocalizations.

The unusually fluid nature of chimpanzee, *Pan troglodytes*, society and their long-distance calling behaviour offer an ideal opportunity to explore the effects that variations in social context have on vocal production. In contrast to most other diurnal anthropoid primates, chimpanzees do not live in stable social groups, but instead form loosely organized 'unit groups' or 'communities', comprising 20–105 animals (review in Nishida & Hiraiwa-Hasegawa 1987). Individuals within unit groups

associate in temporary parties that last for as little as a few minutes to several days. Party membership, while variable, is determined in part by a complex set of social interactions within and between the sexes. Within the sexes, strong bonds exist between male chimpanzees (Nishida 1968; Goodall 1986). These bonds are reflected in grooming relationships, association patterns and behaviour in coalitions. Male chimpanzees groom and associate with each other frequently and often form alliances during which individuals cooperate by directing aggression towards conspecifics (Simpson 1973; Bygott 1979; Goodall et al. 1979; Wrangham & Smuts 1980; Nishida 1983; Takahata 1990). Between the sexes, males adopt alternative mating tactics, whose outcomes may influence the structure of heterosexual parties involving oestrous females (Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983). Patterns of association within and between the sexes are also affected by rank of individuals. High-ranking males are more sociable

and are able to follow and monopolize females to a greater degree than lower-ranking animals (Bygott 1979; Halperin 1979; Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983; Takasaki 1985; Takahata 1990).

Chimpanzees utter a species-typical, long-distance call known as the pant-hoot (Goodall 1968; Marler & Hobbett 1975). Previous field work indicates that pant-hooting behaviour may be affected by ecological factors, principally food availability; male chimpanzees tend to call frequently upon arrival at large food sources (Wrangham 1977; Ghiglieri 1984; Clark 1991). Additional observations suggest that social factors, such as party size, may influence pant-hooting behaviour; call production appears to increase in large parties compared with small parties (e.g. Reynolds & Reynolds 1965). These observations have led several researchers to hypothesize that pant-hoots function to establish and maintain parties (Reynolds & Reynolds 1965; Goodall 1968; Wrangham 1977; Ghiglieri 1984; Clark 1991). Two proposed benefits gained by those who maintain or enlarge their social groups by calling include the attraction of potential allies or mates (Wrangham 1977; Wrangham & Smuts 1980). A potential proximate explanation of this behaviour, heretofore not considered, yet consistent with the preceding observations is that the production of pant-hoots is a consequence of the high arousal levels that typically result from large gatherings of chimpanzees. Evaluating these hypotheses is difficult given that no study has focused explicitly on exploring the possible proximate and functional bases of pant-hooting behaviour.

In this paper we investigate the effects several social factors have on the production of pant-hoots. We begin by examining the social relationships among adult male chimpanzees. Observations of grooming, associations and alliances provide the background for an analysis of the contexts and social correlates of pant-hooting behaviour. To test the spacing and arousal hypotheses of pant-hooting, our investigation into the possible social factors influencing calling include party size and those variables hypothesized as important determinants of party membership. We consider the effects of rank, grooming relationships, association partners, alliance partners and oestrous females on pant-hooting.

## METHODS

### Study Site, Subjects and Sampling Protocol

Chimpanzees were observed from January through to June 1990 at the Kasoje Research Station in the Mahale Mountains National Park, Tanzania. The Kasoje site lies along the eastern shore of Lake Tanganyika at the extreme eastern edge of the geographical range of the longhaired chimpanzee, *P. troglodytes schweinfurthii* (Tuttle 1986). Long-term records of the demographic composition and behaviour of the Mahale chimpanzees is available by virtue of previous research (Nishida 1990).

Chimpanzees of the 'M' unit group or community were observed during this study. The group consisted of approximately 90 animals and included 10 adult males. Sampling the behaviour of wild chimpanzees regularly and systematically is difficult due to their fission-fusion society, and as a result, only seven of the 10 adult males in M group were observed as focal subjects. Infrequent sightings of the beta male (DE) and two relatively low-ranking individuals (BA & KZ) forced us to exclude them from the focal sample. Focal animals were followed for 1-h sample periods between 0800 and 1700 hours. Observations of focal subjects were distributed evenly among months of the study and three periods of the day: 0800–1100; 1100–1400; and 1400–1700 hours. Twenty-five sample periods for each focal individual were completed.

### Social Behaviour and Parties

#### Rank

Low-ranking chimpanzees give a distinctive call, known as the 'pant-grunt', to higher-ranking individuals, and the directions of these calls were used along with the outcomes of agonistic interactions between individuals to establish rank relationships among the seven focal males (cf. Bygott 1979; DeWaal 1982; Goodall 1986; Hayaki et al. 1989).

#### Definition of parties

Chimpanzees at Mahale usually form parties whose members are separated by several metres (Nishida 1990). Despite this spatial separation, party members move together in a directed fashion. Individuals who came within visual range of focal

animals during 'following episodes' were recorded in order to establish the number and identity of chimpanzees that subjects contacted during sample periods. The presence of other chimpanzees in the entire party was noted by multiple observers during 'daily follows'. From these data it was possible to estimate (1) daily party size: the total number of animals observed each day; (2) sample party size: the number of chimpanzees observed with the focal male during sample periods; (3) party size of others nearby: daily party size minus sample party size; (4) party size of males: the number of males observed with the focal subject during sample periods; (5) party size of oestrous females: the number of oestrous females observed with the focal subject during sample periods; (6) party size of males nearby: the total number of males observed per day minus party size of males; and (7) party size of oestrous females nearby: the total number of oestrous females observed per day minus party size of oestrous females.

#### *Alliances*

Alliance partners were defined as individuals who jointly displayed aggression toward a third animal. Rates of alliance formation by male A with a second male B were calculated by dividing the number of alliances A formed with B by the number of times B was involved in aggressive interactions with individuals other than A (cf. Cheney 1977).

#### *Associations*

We calculated the proportions of time males spent in associations with each other by dividing the number of observation hours focal animals were seen with others by the number of sample hours. Values from all of the males were used to compute a mean association index between focal subjects and others. We defined association partners as those individuals whose mean proportions of time spent in associations were greater than one standard deviation from the average value.

#### *Grooming*

During observation sessions, the total amount of time focal subjects groomed other males was noted to the nearest minute. We calculated the expected

times focal subjects spent grooming others by assuming that they distributed their grooming randomly among the nine males. We defined grooming partners based on preferential grooming relationships, i.e. whenever two males groomed significantly more than expected on the basis of chance.

#### **Pant-hooting and Its Contexts**

Pant hoots are loud, distinctive vocalizations given by both male and female chimpanzees. Pant hoots are known to vary acoustically between individuals and populations (Marler & Hobbett 1975; Mitani et al. 1992), and Goodall (1986) has suggested that individuals utter acoustic variants of these calls in different behavioural situations. Preliminary analysis based on a small sample of pant-hoots, however, did not reveal consistent acoustic differences between calls used in different contexts (J. C. Mitani, unpublished data), and for this reason, all pant-hoots we heard were included in the following analyses.

During each observation session, the number of pant-hoots uttered by focal subjects, the number of pant-hoots heard in the distance, the pant-hoot responses by subjects to distant pant-hoots, and the pant-hoot responses by others to the focal's calls were recorded. Distant pant-hoots were scored if they were audible to human observers. We assumed that these calls were perceived by focal subjects as well since the hearing capabilities of chimps and humans are similar at 1 kHz (Kojima 1990), the frequency at which spectral energy of pant-hoots is concentrated (Mitani et al. 1992). Chimpanzees will respond quickly to distant pant-hoots at times (Goodall 1986), and vocal responses were recorded if they followed calls delivered by focal animals within 1 min.

To investigate the contexts of pant-hoot utterance, the behaviour of focal animals immediately before and after pant-hooting was noted. Behaviour preceding and following activities included feeding, travelling, and resting. Feeding comprised the handling and processing of food. Travel was scored when subjects engaged in prolonged locomotor bouts, exclusive of movements while feeding. Resting included activity periods in which individuals were not feeding, travelling or taking part in social behaviour. We examined whether the production of pant-hoots was associated with the preceding

behavioural activities by comparing observed calling frequencies with those expected on the basis of chance. Expectations were generated by assuming that call rates were proportional to the time spent by focal subjects in each behavioural state.

### **Social Correlates of Pant-hooting**

We investigated the effects of male rank and party size variables on pant-hooting by correlating these variables with each male's mean frequency of pant-hoot production. The effects of alliance partners, association partners, grooming partners and oestrous females on pant-hooting were examined by comparing the mean frequencies of focal subjects' calling in three conditions: (1) when all the male partner(s) were with focal subjects; (2) when all the partner(s) or female(s) were presumably nearby and within earshot, and (3) when all the partner(s) or female(s) were absent. Only fully swollen females, near or at the peak of their oestrous cycles, were considered in the following analyses. Male alliance, association and grooming partners were scored with focal subjects if they were observed in the focal's party during the entire sample period. This condition occurred infrequently as a result of the constantly changing compositions of chimpanzee parties, and therefore, an adequate sample exists only for the situation in which focal subjects were with their association partner(s). We assumed that specific animals were near subjects if they were not observed with the focal male during sampling hours, but were seen in the focal's party during the hour preceding or following the sample bout. Chimpanzees were considered absent from the focal's party if they were not observed during the entire day on which the sample occurred.

Pant-hoots are often chorused together and given immediately in response to distant calls. Inclusion of these hoots would inflate call rates in the 'with' and 'nearby' conditions relative to the situation in which animals were 'absent', and for this reason, only those pant-hoots initiated by focal animals were used in tabulating calling frequencies. A male already accompanied by an oestrous female may not call to attract additional females, and for comparisons involving oestrous females, we excluded days when focal subjects were accompanied by females in reproductive condition.

Control comparisons were conducted using randomly selected individuals other than partners if our analyses indicated that their presence or absence affected the pant-hooting behaviour of focal subjects. For these comparisons, we examined the mean calling frequencies of focal animals when randomly chosen males were with them, nearby and absent. The number of males selected for these controls equalled the number of association partners, alliance partners and grooming partners for each focal subject.

### **Statistical Tests**

All analyses employed non-parametric statistical procedures and were two-tailed with the criterion of significance set at  $P < 0.05$ .

## **RESULTS**

### **Rank Relationships**

A dominance matrix combining the direction of pant grunting with the outcomes of aggressive interactions revealed a linear rank order among the seven focal subjects (Table I).

### **Alliances, Associations and Grooming**

Table II shows the rates of alliance formation, Table III shows the proportions of time spent in associations, and Table IV shows the grooming distributions among the seven focal animals. Significant positive correlations existed between the proportions of time spent in associations and both the rates of alliance formation and the amounts of grooming received (Spearman rank correlation coefficients: rate of alliance formation and proportions of time spent in association = 0.33,  $N = 63$ ,  $P < 0.01$ ; proportions of time spent in association and rate of grooming received = 0.33,  $N = 63$ ,  $P < 0.01$ ). Measures of alliance formation and grooming showed no apparent association ( $r = 0.19$ ,  $N = 63$ ,  $P > 0.10$ ).

With the exception of one individual (BE), each focal subject either formed or was joined in an alliance with at least two other males (Table II). The number of alliance partners per male ranged from two to four individuals.

The proportions of time the seven focal subjects spent in associations with other adult males ranged from zero to 0.64 ( $\bar{X} = 0.23$ ,  $SD = 0.16$ ; Table III);

**Table I.** Dominance matrix of the seven, focal adult males in the M group chimpanzees

	Pant-grunts received or aggression given	Pant-grunts uttered or aggression received						
		NT	SU	NS	LJ	MU	AJ	BE
Rank	NT	—	31	10	7	6	32	12
	SU	0	—	1	2	3	4	5
	NS	0	0	—	2	1	0	3
	LJ	0	0	0	—	0	0	6
	MU	0	0	0	0	—	1	1
	AJ	0	0	0	0	0	—	1
	BE	0	0	0	0	0	0	—

Entries show the combined number of aggressive acts and pant-grunts given and received by each focal male. Aggression contributed to 25% of all entries (32 of 128), while pant-grunts formed 75% (96).

**Table II.** Rates of alliance formation between males\*

Alliances formed by	Alliances formed with									
	NT	SU	NS	LJ	MU	AJ	BE	BA	DE	KZ
NT	—	0	0	0	<b>0.20</b>	0	0	0	0	0
SU	<b>0.02</b>	—	0	<b>0.20</b>	0	<b>0.33</b>	0	0	0	0
NS	<b>0.02</b>	0	—	<b>0.20</b>	0	0	0	0	<b>0.13</b>	0
LJ	<b>0.08</b>	0	<b>0.17</b>	—	<b>0.20</b>	0	0	0	0	0
MU	<b>0.02</b>	0	0	0	—	0	0	0	<b>0.13</b>	0
AJ	0	0	0	0	<b>0.20</b>	—	0	0	0	0
BE	0	0	0	0	0	0	—	0	0	0

\*See text for an explanation of the calculation of rates. Bold entries indicate those individuals with whom males formed alliances.

**Table III.** Proportions of time spent in associations between adult males

Associations formed by	Associations formed with									
	NT	SU	NS	LJ	MU	AJ	BE	BA	DE	KZ
NT	—	0.36	0.28	<b>0.44</b>	0.32	0.24	0.12	0.16	0	0.12
SU	<b>0.56</b>	—	0.28	<b>0.44</b>	0.24	0.36	0.08	0.12	0.08	0.12
NS	<b>0.44</b>	0.24	—	0.32	0.24	0.12	0	<b>0.40</b>	0.12	0.08
LJ	<b>0.64</b>	0.28	0.28	—	0.36	0.36	0.08	0.12	0.12	0.04
MU	<b>0.64</b>	<b>0.40</b>	<b>0.44</b>	<b>0.48</b>	—	0.08	0.04	0.28	0	0.04
AJ	<b>0.44</b>	0.32	0.20	0.24	0.08	—	0.16	0.08	0.12	0.04
BE	0.32	0.25	0.08	0.16	0.08	0.28	—	0.12	0.12	0.08

Proportions were computed by dividing the number of observation hours focal animals were observed with each male by the number of sample hours. Bold entries indicate association partners, those individuals whose values exceeded 1 SD above the total mean association proportion.

Table IV. The distribution of grooming among adult males

Groomer	Recipient									
	NT	SU	NS	LJ	MU	AJ	BE	BA	DE	KZ
NT	—	21	0	<b>29</b>	<b>30</b>	12	0	19	0	0
SU	14	—	0	4	1	3	0	20	0	<b>72</b>
NS	0	7	—	<b>81</b>	13	0	0	11	24	3
LJ	0	3	0	—	<b>40</b>	0	0	<b>33</b>	15	0
MU	<b>25</b>	0	0	<b>22</b>	—	0	0	<b>31</b>	0	0
AJ	16	<b>22</b>	0	0	0	—	0	0	13	<b>30</b>
BE	0	0	2	0	0	<b>20</b>	—	0	0	<b>11</b>

Cells show the number of minutes each focal male groomed others. Bold entries indicate grooming partners, those males that were groomed significantly more than expected by chance. Chance expectations were computed by assuming that males distributed their grooming randomly among the other nine individuals. See text for further explanation.

using a value one standard deviation above the mean to define association partners revealed that each focal animal associated closely with one to four males.

The grooming distributions among focal subjects and other males showed that males did not distribute grooming randomly; each male had one to three preferred grooming partners (Table IV).

### Contexts of Calling

The production of pant-hoots was associated with one particular activity (Table V). Travelling frequently preceded and followed calling. Small samples precluded comparison of observed call rates with those expected on the basis of chance for all but the two highest ranking males (NT and SU). Travelling preceded calling by these two males more often than expected ( $\chi^2$  test,  $df=2$ ,  $P<0.001$  for both comparisons), a trend consistent for the other five focal subjects as well.

The two highest ranking males fed and travelled more often than expected by chance after giving pant-hoots ( $\chi^2$  test,  $df=2$ ,  $P<0.001$  for both comparisons). The five other focal subjects, however, only showed a tendency to continue travelling after hooting. These males did not consistently feed more than expected after calling.

### Effects of Rank, Party Size and Party Composition on Pant-hooting

Male rank affected the rate of pant-hoot production. High-ranking males called more than

low-ranking animals (Kendall  $\tau = -0.714$ ;  $N=7$ ;  $P=0.05$ ; Fig. 1). In contrast, party size variables were not clearly related to call production. None of the mean party size variables correlated strongly with the mean calling frequencies of individuals ( $N=7$ ;  $P>0.10$  for all seven comparisons). Moreover, party size variables did not show any consistent association with the calling rates of individual males. Party size variables were positively related with the calling rates of some males, but these same variables were negatively associated with the calling rates of other males.

### Effects of Alliance, Association and Grooming Partners on Pant-hooting

Focal subjects called more frequently when alliance partners were nearby compared with when they were absent (Wilcoxon matched-pairs signed-ranks test,  $N=6$ ,  $P<0.05$ ; Fig. 2a). In contrast, a control comparison involving call production by focal animals when randomly selected males were nearby and absent did not reveal any differences between the two conditions (Wilcoxon test,  $N=6$ ,  $P>0.90$ ; Fig. 2b). The mean frequencies with which focal subjects pant-hooted when association partners were with them, nearby and absent showed significant heterogeneity (Friedman two-way analysis of variance,  $N=6$ ,  $P<0.02$ ; Fig. 2c). Pair-wise comparisons revealed that focal males called more frequently when association partners were nearby compared with when partners were absent or with focal subjects (Wilcoxon matched-pairs signed-ranks tests,  $N=6$ ,  $P<0.05$  for both

**Table V.** Contexts of pant-hoot production: activity before and after hooting

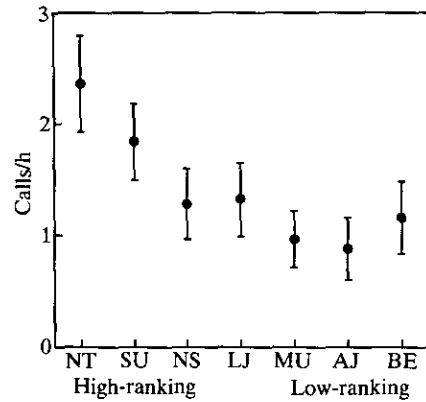
Individual		Rest	Feed	Travel	Other	<i>N</i>
<b>Preceding activity</b>						
NT	Observed	7	11	32	9	59
	Expected	13	22	10	13	
SU	Observed	7	15	17	7	46
	Expected	11	20	6	9	
NS	Observed	9	1	18	4	32
	Expected	14	10	4	5	
LJ	Observed	7	6	15	5	33
	Expected	9	16	4	5	
MU	Observed	7	4	9	4	24
	Expected	7	9	3	5	
AJ	Observed	5	3	9	5	22
	Expected	8	7	2	5	
BE	Observed	4	14	5	6	29
	Expected	7	15	3	5	
<b>Following activity</b>						
NT	Observed	10	30	17	2	59
	Expected	13	22	10	13	
SU	Observed	9	27	10	0	46
	Expected	11	20	6	9	
NS	Observed	10	6	13	3	32
	Expected	14	10	4	5	
LJ	Observed	8	11	12	2	33
	Expected	9	16	4	5	
MU	Observed	7	9	6	2	24
	Expected	7	9	3	5	
AJ	Observed	4	8	7	3	22
	Expected	8	7	2	5	
BE	Observed	5	19	2	3	29
	Expected	7	15	3	5	

The activities preceding and following pant-hoot production are shown for each of the seven focal males. Observed values are shown with those expected on the basis of chance. Chance expectations were calculated by assuming that call rates by subjects in each behavioural state were proportional to the time they spent in that activity.

comparisons, Fig. 2c). A control using the mean call production by focal animals when randomly selected males were with them, nearby and absent did not reveal significant heterogeneity among the three conditions (Friedman two-way ANOVA,  $N=6$ ,  $P>0.70$ ; Fig. 2d). Similarly, the presence of preferred grooming partners within earshot did not affect the frequency of production of pant-hoots by focal animals (Wilcoxon test,  $N=7$ ,  $P>0.05$ ; Fig. 2e).

#### Effects of Oestrous Females on Pant-hooting

The production of pant-hoots by all males was not affected by the presence of oestrous females.

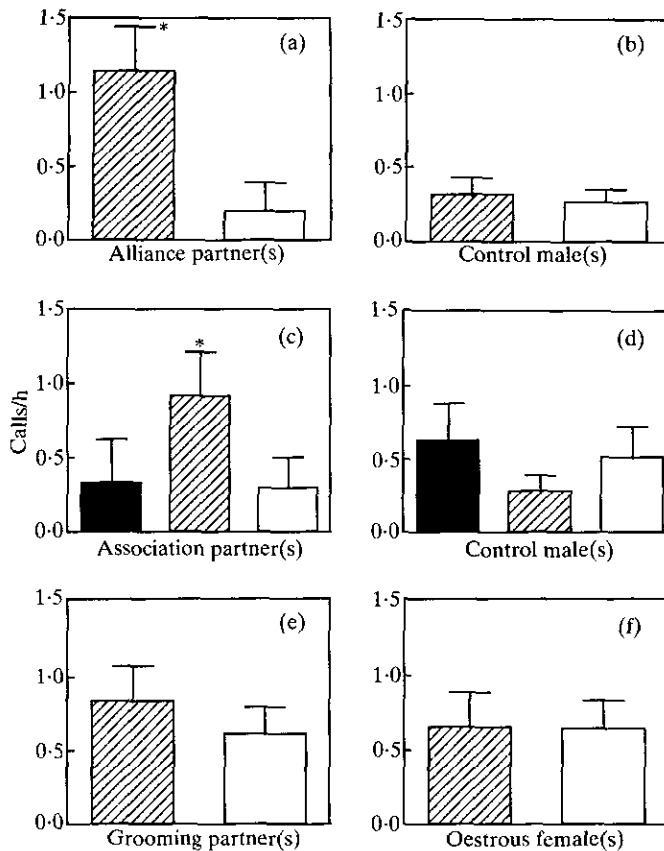


**Figure 1.** The association between pant-hoot production and rank. The mean ( $\pm$ SE) number of pant-hoots produced by each focal male versus male rank are plotted. Calculations are based on 25 h of observation of each male.

Call rates did not differ when oestrous females were nearby compared with when they were absent (Wilcoxon test,  $N=7$ ,  $P>0.70$ ; Fig. 2f). A closer examination of these data, however, indicated variation among males in their tendency to pant-hoot in the two conditions. Two high ranking males, SU and NS, and an additional high-middle ranking male, LJ, called more frequently when oestrous females were nearby compared with when they were absent altogether (see Table I for ranks). The alpha male (NT) and the three lowest ranking males in the sample, MU, AJ and BE, showed the opposite pattern.

#### Responsiveness to Pant-hoots

To investigate variation in the responsiveness to pant-hoots, we examined whether focal subjects responded differentially to the calls of others and whether others responded differently to each focal male's calls. Significant heterogeneity did not exist among the pant-hoot response rates of males to the calls of others (Kruskal-Wallis test,  $H=7.10$ ,  $df=6$ ,  $P>0.30$ ; Fig. 3a). In addition, the rates with which others uttered pant-hoots in response to the focal male's calls did not show significant variation among focal subjects (Kruskal-Wallis test,  $H=10.39$ ,  $df=6$ ,  $P>0.10$ ; Fig. 3b). Graphical illustration of these data, however, revealed distinctive trends in the calling behaviour by and directed towards the alpha male, NT. This male was relatively unresponsive to the pant-hoots of others, yet was answered frequently (Fig. 3).



**Figure 2.** Effects of social context on pant-hoot production. The mean ( $\pm$  SE) number of pant-hoots produced by focal males when: (a) alliance partners were nearby (▨) and absent (□),  $N=6$  focal males; (b) randomly selected males (who were not alliance partners) were nearby and absent,  $N=6$ ; (c) association partners were with them (■), nearby and absent,  $N=6$  focal males; (d) randomly selected males (who were not association partners) were with them, nearby and absent,  $N=6$ ; (e) grooming partners were nearby and absent,  $N=7$ ; (f) oestrous females were nearby and absent,  $N=7$ . \*  $P < 0.05$ , Wilcoxon matched-pairs signed-ranks test between (1) 'nearby' and 'absent' conditions and (2) 'nearby' and 'with' conditions. See text for further explanation.

## DISCUSSION

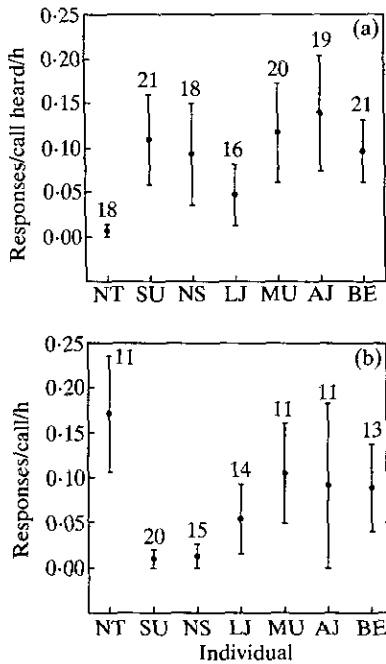
### Contexts of Pant-hooting

Previous studies have emphasized the influence of ecological factors, specifically food availability, on pant-hooting behaviour (Reynolds & Reynolds 1965; Wrangham 1977; Ghiglieri 1984; Clark 1991). These studies suggest that, in addition to having the incidental effect of informing others of the location of food, pant-hooting may play a role in the formation and maintenance of spatially separated parties. Results of our contextual analysis confirm the relationship between hooting and arrival at food sources, at least for two high-ranking males. Our observations also reveal that

male chimpanzees frequently travel prior to pant-hooting, with movement preceding calling more often than expected on the basis of chance. In addition, travelling regularly takes place following pant-hooting. Considered together, these data support the hypothesis that hooting maintains spatial contact between conspecifics. Male chimpanzees who call appear to broadcast information regarding a chance in their positions to other unit group members.

If pant-hooting serves solely to maintain the integrity of chimpanzee parties, one might expect all males to hoot equally often and to call more frequently in large parties, when animals are spread out, than in smaller, more cohesive parties (cf.





**Figure 3.** Responsiveness to pant-hoots. (a) Responsiveness by focal males to the pant-hoots of others. The mean ( $\pm$  SE) number of pant-hoots uttered per hour by focal males in response to those of others. (b) Responsiveness by others to the pant-hoots of focal males. The mean ( $\pm$  SE) number of pant-hoots uttered by others per hour in response to those uttered by focal males. Observation hours for each individual are indicated above error bars.

Reynolds & Reynolds 1965). Results of the preceding analyses, however, indicate variation in pant-hooting as a function of rank and that differences in party size do not affect call production by adult males. An implication of these observations is that hooting cannot be considered a simple involuntary response stimulated by the high levels of social excitement and arousal that are characteristic of large parties.

#### Audience Effects and Social Correlates of Pant-hooting

Recent research indicates that animals modulate their production of calls as a function of the presence or absence of particular individuals (review in Cheney & Seyfarth 1990). Consideration of such audience effects on calling behaviour opens the possibility that males may not direct their calling towards all individuals within their unit group,

but rather to specific chimpanzees. Males may benefit by maintaining contact with two classes of individuals, allies and potential mates. Wrangham (1977) hypothesized that the recruitment of allies would be especially important for males given the high degree of inter-community conflict that typically takes place between chimpanzees (Goodall et al. 1979; Nishida et al. 1985). In addition, Wrangham speculated that by enlarging their social group, males who call would create a forum within which females might be able to choose mates. Overlooked in his discussion was the possibility that males might gain important benefits within their unit groups by pant-hooting.

Chimpanzees may accrue social and reproductive benefits through alliances, associations and grooming. For example, male chimpanzees frequently form coalitions to assist each other in aggressive disputes, whose outcomes have significant reproductive consequences for males. Alliances may play a critical role in determining rank relationships among males (Riss & Goodall 1977; Bygott 1979; Nishida 1983), and rank among the Mahale chimpanzees is positively related to mating success (Hasegawa & Hiraiwa-Hasegawa 1983; Nishida 1983; Takasaki 1985). Considered within the context of the chimpanzee's fluid society where individuals are often spatially separated, these observations lead us to hypothesize that males may pant-hoot to maintain contact with selected animals, such as allies, associates or grooming partners from whom important fitness benefits can be derived (cf. Wrangham 1977; Wrangham & Smuts 1980). Several predictions regarding the acoustic structure of pant-hoots, their production and the responsiveness to calls follow directly from this hypothesis.

An initial requirement is that calls be individually distinctive. Previous research suggests that individual and dialectal differences exist in pant-hoots, thus making it a particularly appropriate call to use in the identification of specific chimpanzees (Marler & Hobbett 1975; Mitani et al. 1992). Second, the hypothesis predicts that the presence or absence of allies, associates and grooming partners will affect pant-hoot production. Our results are consistent with this proposal insofar as males hooted significantly more often when their allies and associates were nearby compared with when they were absent. In contrast, males did not alter their calling frequencies in control comparisons involving randomly selected individuals in the same

two conditions. A logical extension of the hypothesis that males pant-hoot to maintain contact with allies and associates is a third prediction that males should exhibit reduced rates of calling when they are in the company of these same individuals. Our sample did not permit a complete test of this prediction, but nevertheless showed that males called less frequently when they were with associates compared with when associates were nearby.

A strong test of the proposed hypothesis that males pant-hoot to recruit the company and support of allies and associates ultimately depends on an examination of how specific individuals respond to calls. In particular, we require evidence, currently lacking, that males approach and seek out their allies and associates after hearing their pant-hoots. Field experiments using the playback of tape-recorded calls to animals (e.g. Waser 1975), simultaneous observations of multiple animals (Boehm 1989), and a larger data set in which the effects of social factors can be evaluated simultaneously in a multivariate model rather than independently (cf. Heinrich & Marzluff 1991) will provide the empirical means to examine this issue.

Our observations did not support the additional hypothesis that pant-hooting by all males plays a role in attracting potential mates (cf. Wrangham 1977). Adult males as a collective group called equally often when oestrous females were nearby or entirely absent. Female chimpanzees spend considerable time alone and exhibit situation-dependent oestrous cycles (Wrangham & Smuts 1980; Wallis 1985). Given these circumstances, the failure of males to vary their call production may be related to their inability to precisely monitor the locations of females in reproductive condition. Alternatively, our results may reflect the different mating tactics employed by males of varying ranks. Alpha males are able to monopolize matings with females relative to lower-ranking individuals, who must rely on mating either opportunistically or with females who prefer them (Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983; Nishida 1983). Observations indicate that the three males who ranked directly below the alpha male in our sample called more frequently when oestrous females were nearby compared with when they were absent. These data suggest the possibility that only a subset of males of specific rank may pant-hoot selectively to increase their mating opportunities. The alpha male may not alter his calling behaviour in the presence or absence of females

since he is able to control mating opportunities at will; low-ranking males do not increase their production of pant-hoots to attract females because they are neither preferred partners nor able to compete effectively with other males. Additional field observations are needed to evaluate this suggestion.

We conclude by noting two significant limitations of the preceding analyses. First, our field protocol did not permit us to sample the behaviour of all the M group adult males. One of these individuals, DE, was the second-ranking male in the M unit group, and it is unclear whether his exclusion from the focal sample affects the generality of the results presented here. A second limitation of this study, as already noted above, lies in the paucity of robust data regarding the responses of chimpanzees to pant-hoots. Our few observations suggest that calls of the alpha male were attended to more than those of others, and that this male did not respond frequently to the pant-hoots of conspecifics. These data are consistent with the proposition that the alpha male serves as the central focus of chimpanzee societies (cf. Goodall 1986; Kawanaka 1990), and promise that further insights will be derived from study of the responses to calls. Until such research is conducted our conclusions regarding the functional significance of pant-hooting will remain tentative.

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