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Vocal greeting behaviour in wild chimpanzee females

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Chimpanzees, *Pan troglodytes*, are unusual among primates in that they express their social position with a unique vocal signal, the pant-grunt. The call is only produced when encountering a higher-ranking group member and has thus been interpreted as a ‘greeting’ signal. We monitored the calling behaviour of nine adult females in a group of free-ranging chimpanzees, the Sonso community of Budongo Forest, Uganda, when encountering higher-ranking adult males. We found that call production was by no means rigid, but that calls were given only if certain social conditions were met. Although all adult males received pant-grunts from females, the alpha male received a significantly larger proportion of calls. The number of pant-grunts given to males was not correlated with their hierarchical position or with the level of anticipated aggression. Instead, females were significantly more likely to vocalize to other males if the alpha male was absent, suggesting that their calling behaviour was moderated by social inhibition. The presence of the alpha female had a similar yet weaker inhibitory effect. Social inhibition was further increased with increasing numbers of bystanders, especially males. Our results thus demonstrate that chimpanzees use their ‘greeting’ signals flexibly by taking into account the social fabric of their community.

‘Greeting’ behaviour has been observed in a range of social animals, although its biological function appears to vary between species. For example, greeting signals are often produced during intragroup conflicts, either to decrease or increase levels of aggression (e.g. mantled howler monkeys, *Alouatta palliata*: Dias et al. 2008; baboons, *Papio hamadryas* and *P. cynocephalus*: Colmenares 1990; spotted hyaenas, *Crocuta crocuta*: East et al. 1993; spider monkeys, *Ateles geoffroyi*: Aureli & Schaffner 2007; Schaffner & Aureli 2005). Other reported functions have to do with assessing another individual’s willingness to interact socially at that particular moment or with testing long-term bonds between familiar individuals (Guinea baboons, *Papio papio*: Whitham & Maestripieri 2003; black-horned capuchins, *Cebus apella*: Lynch Alfaro 2008). In most species, greeting signals are visual, usually part of an individual’s species-specific communication repertoire. In chimpanzees, *Pan troglodytes*, however, greeting is conducted in the vocal domain, the so-called ‘pant-grunts’ (Bygott 1979; de Waal 1982; Goodall 1986). A remarkable feature of chimpanzee pant-grunts is that the signal is given only by lower-ranking individuals when encountering a more dominant group member, which contrasts with the greeting behaviour of other primates and nonprimates, such as baboons (Colmenares 1990), howler monkeys (Dias et al. 2008) or hyaenas (East et al. 1993). In captive chimpanzees, pant-grunts are often accompanied by ritualized behaviours of subordination, such as bobbing, crouching or presenting (de Waal 1982). In the wild, where individuals are freer in their choosing or avoiding of social interactions, pant-grunts are often given without additional signals, although the acoustic structure can vary from soft grunts to loud pant screams (Goodall 1986).

Although pant-grunts are among the most common signals in the chimpanzee vocal repertoire, the social variables driving their production are not well understood. The notion of rank-related ‘greeting’ is largely uncontroversial, but there are a number of reports in the literature that indicate that the communicative function of pant-grunts is more complex than merely expressing subordination. First, pant-grunts are not compulsory when encountering someone higher ranking (Takahata 1990; Newton-Fisher 1997), suggesting some kind of social assessment by the signaller. Second, although pant-grunts are mostly given to higher-ranking group members, in some social dyads they can temporarily be given in bidirectional ways, perhaps reflecting uncertainties in the callers’ perceived social position (Newton-Fisher 2006; Emery Thompson et al. 2008; Townsend et al. 2008). Third, pant-grunts sometimes trigger aggressive responses from previously calm

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higher-ranking receivers (Hayaki 1990) but they also appear to play some role in reconciliation and appeasement following conflicts (de Waal 1982; Arnold & Whiten 2001). Overall, these observations suggest that call production might be the product of relatively complex social assessments rather than a rigid response to encountering a high-ranking group member.

These reports are relevant for an ongoing discussion about modality and flexibility in primate communication. One dominant argument is that primate vocalizations, including those of apes but not humans, are not very flexible, especially if compared with gestures, and as such not very relevant for understanding human language evolution (Corballis 1992; Pollick & de Waal 2007; Arbib et al. 2008). A key empirical finding is that ape gestures are often socially directed and in this sense intentionally produced. In contrast, primate vocalizations appear to be broadcast in socially less specific and untargeted ways, often to a larger audience, an observation that tends to attract arousal-based interpretations (Pollick & de Waal 2007; Arbib et al. 2008). However, other studies have found that primate vocalizations have directional and intentional components, mainly because production can vary depending on the audience (Mitani & Nishida 1993; Wilson et al. 2001, 2007; Slocombe & Zuberbühler 2007) or the attentional state of a human receiver (Hostetter et al. 2001; Hopkins et al. 2007). Chimpanzee pant-grunts are particularly interesting for this discussion because they represent one of the few vocalization types that are always directed to a specific receiver.

To address the problem of flexibility more systematically, we investigated whether pant-grunt vocalizations were influenced by the presence of bystanders in a group of wild chimpanzees, the Sonso community of Budongo Forest, Uganda. Although audience effects are widespread in animal communication (e.g. yellow mongoose, *Cynictis penicillata*: le Roux et al. 2008; chickens, *Gallus gallus*: Marler et al. 1986; brown capuchins, *Cebus apella*: Pollick et al. 2005), in chimpanzees they seem to be the product of a considerable degree of social awareness and strategic impulse (Slocombe & Zuberbühler 2007; Townsend et al. 2008). We investigated the use of pant-grunts by female chimpanzees to understand the social patterns and motivations that drive call production in this species. We focused on adult females because in chimpanzees they are formally subordinate to all adult males (Noë et al. 1980; Goodall 1986; Reynolds 2005). We were interested in how flexible females were when using this vocal signal, and whether they took the wider audience into account. If pant-grunts merely functioned as a ritualized signal of subordination, call production should be determined by the relative rank of the receiver, regardless of other social factors, such as the composition of the nearby audience, or the nature of the ongoing social interaction.

METHODS

Study Site

Data were collected between August 2007 and February 2008 and between July and December 2008 in the Sonso community of Budongo Forest, Uganda, a 428 km^2 moist, semideciduous tropical forest between 1°35′ and 1°55′N and 31°08′ and 31°42′E at an altitude of 1100 m. In August 2007, the community consisted of 76 individuals (10 males, 25 females, six subadult males, four subadult females, 15 juveniles and 16 infants; categories by Goodall 1986). Permission to conduct the research was given by the Uganda Wildlife Authority (UWA) and Ugandan National Council for Science and Technology. Ethical approval was given by the School of Psychology, University of St Andrews.

Data Collection

Pant-grunt utterances are an acoustically heterogeneous signal, which usually consists of repeated grunts that can be panted and that can grade into barks or screams (Fig. 1). Given in a variety of contexts, such as during travelling, feeding or resting, they are always directed to a specific receiver within a relatively short distance. As mentioned earlier, calling can be accompanied by other behaviours, such as presenting, crouching or bobbing. The calls typically do not result in noticeable responses in the receiver, although sometimes they are followed by agonistic (display, chase, hit) or affiliative (grooming, touching, kissing) interactions.

We used focal animal sampling and 5 min scan samples of focal individuals (Altmann 1974). For each scan sample, the behaviour of the focal animal and target individual was recorded, as was the identity of all individuals within a radius of both 10 m (i.e. the average visual range) and 35 m (i.e. the average spread of the travel party; Newton-Fisher 2004). An ‘encounter’ was defined as any individual entering a 10 m radius surrounding the focal animal. Ten metres were chosen because this roughly corresponded with an individual’s visual range in which most social interactions, such as grooming, competition over food or sexual interactions, took place (Hayaki 1990). The radius was estimated jointly by M.L. and her field assistant for every encounter, regardless of whether or not the focal animal produced pant-grunts. Subsequent encounters with the same individual had to be separated by at least 5 min to be considered as independent events. For each encounter, we noted whether or not the focal animal produced a pant-grunt (within 2 min). We assessed the level of threat experienced by the caller as (1) low (affiliative interactions: present, groom, touch), (2) neutral (no noticeable social behaviour) or (3) high (agonistic interactions: threat posture, display, chase). For the audience effect analyses, we considered all individuals present within a radius of 10 m (roughly corresponding to the average visual range), while male and female presence was assessed separately.

Dominance Hierarchy

In chimpanzees, the social dominance hierarchy is heavily sex biased (de Waal 1982). Males constitute the core of the group and all adult males are dominant over all adult females, as assessed in terms of agonistic interactions (Noë et al. 1980; Takahata 1990). Our aim was to evaluate how females were reacting to the male hierarchy. To increase precision we therefore calculated the dominance indexes separately for males and females. We used M.L.’s own and the project’s long-term data (Zuberbühler & Reynolds 2005) to determine the social status of group members. In natural habitats, rank relations between males are somewhat dynamic and

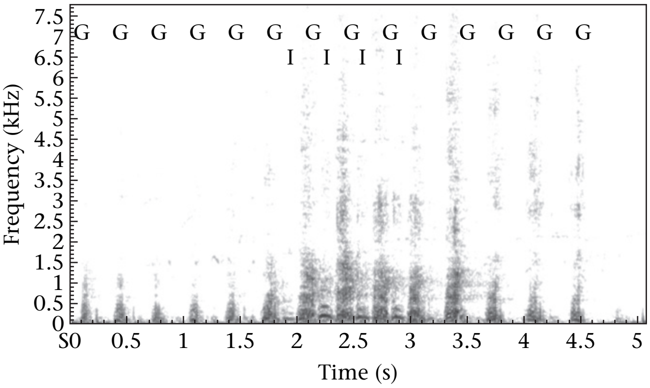

Figure 1. Spectrographic illustration of a pant-grunt vocalization given by the alpha female NB to the alpha male NK, containing voiced inhalations (I) and grunts (G).

Table 1
Demographic data on the males and females of the Sonso community who participated in this study

Sex	Identity	Code	Age (2007)	Status	Rank value	No. of encounters	Observation time (h)
Females	Flora	FL	28	P	N/A	8	4.92
	Harriet	HT	29	P	N/A	4	15.42
	Janie	JN	23	P	−2.35	32	21.00
	Kalema	KL	28	R	−0.11	44	35.83
	Kewaya	KY	24	R	0.45	34	37.58
	Kutu	KU	28	R	0.22	36	46.25
	Kwera	KW	26	R	−0.53	47	37.17
	Mukwano	MK	27	P	−0.19	27	21.33
	Nambi	NB	45	R	2.13	44	30.75
	Ruhara	RH	39	R	1.45	25	20.25
	Sarine	SE	36	R	N/A	0	13.58
	Zimba	ZM	39	R	1.92	12	17.25
Males	Bwoba	BB	20	—	−0.16	26	N/A
	Duane*	DN	41	—	−0.05	19	N/A
	Gashom*	GS	20	—	−1.19	20	N/A
	Maani*	MA	49	—	−1.06	15	N/A
	Musa	MS	16	—	−0.68	42	N/A
	Nick	NK	25	—	3.45	84	N/A
	Squibs	SQ	16	—	−0.99	46	N/A
	Tinka	TK	47	—	−0.97	30	N/A
	Zefa	ZF	25	—	0.16	19	N/A

Identity: * died or disappeared during the study; status (females only): R = resident; P = peripheral. N/A = no focal data on males or because individual was rarely seen or not interacting enough with others during study period.

susceptible to sometimes rapid change (Newton-Fisher 1997), a possible result of their fission–fusion social organization (Muller 2002). For example, three adult males (MA, DN, GS) died during the study period, which appeared to increase the social dynamics between group members. We therefore did not attempt to determine a linear dominance hierarchy for the entire study period. Instead of trying to assign an exact rank to each of the nine adult males, we calculated a relative cardinal rank value for each male while taking into account the total observation time for each dyad, a reflection of his average social position within the community throughout the study period. To this end, we used the 'conferred respect equation' developed by Newton-Fisher (1997, 2004) and based on Fournier & Festa-Bianchet (1995):

$$\text{conferred respect} = \{[N(\text{pant} - \text{grunts received}) \times \text{DC}] + 1\}/\{[N(\text{pant} - \text{grunts performed}) \times \text{DC}\,] + 1\}$$

DC = dyad correction = (*N* scan samples of most seen dyad)/(*N* scan samples of dyad studied). For the males, we used the long-term project data, which consisted of 15 min scan samples, in which the simultaneous presence of two individuals in the same party was recorded. For females, we used M.L.'s own data which were more detailed in that they consisted of 5 min scan samples where the two females were seen within 10 m of each other.

Because we used different dyad correction factors for males and females, rank values are only meaningful in relation to other members of the same sex (Table 1).

Statistical Analyses

Many Sonso females lead relatively solitary lives. As a result the number of encounters remained low for some of them, and as a consequence not all females contributed to all analyses. We required a minimum of 12 male encounters to be included in the analyses, which led to a final sample of nine females (JN, KL, KU, KW, KY, MK, NB, RH, ZM) encountering a total of nine males (BB, DN, GS, MA, MS, NK, SQ, TK, ZF; $N = 301$ encounters). The data of three additional females (FL, HT and SE) contributed to calculations of encounter rates (Table 1). Calling rates during encounters were determined for each female separately. Raw data were transformed (arcsin of square root; Snedecor & Cochran 1980) and checked for normal distribution (Shapiro–Wilk test) and homogeneity of variances (Levene's test). If conditions were met, we used parametric tests, such as paired *t* tests. The data generally did not meet the conditions of normal distribution and homogeneity of variances, in which case we used nonparametric Friedman's ANOVA for multiple matched comparisons, Wilcoxon signed-ranks tests and Spearman correlations. All tests were two tailed with significance levels set at $\alpha = 0.05$. For small sample sizes, we calculated exact *P* values (Mundry & Fischer 1998). All analyses were conducted with SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.). Means are given ± SD.

RESULTS

General Patterns

During 455 h of focal observations, we witnessed 1346 encounters of focal individuals (adult females, subadult and juvenile males or females) with other group members, 211 of which led to pant-grunts (16.4%). During 301 h of focal observations, we recorded 755 encounters of adult females with juveniles ($N = 156$), subadults ($N = 157$), adult females ($N = 129$), adult males ($N = 227$) and the alpha male ($N = 86$).

Effects of Target Individual Identity

Across the 12 adult females, encounter rates with different types of individuals varied significantly (Friedman's ANOVA: $\chi^2_3 = 10.103$, $N = 12$, $P_{\text{exact}} = 0.014$). Encounters with adult males were generally rare (1.02 ± 0.5 encounters/h), but more frequent than encounters with other females (0.41 ± 0.21 encounters/h; Wilcoxon test: $T = -2.903$, $N = 12$, $P_{\text{exact}} = 0.001$), subadults (0.56 ± 0.41 encounters/h; $T = -2.401$, $N = 12$, $P_{\text{exact}} = 0.014$) and juveniles (0.55 ± 0.35 encounters/h; $T = -2.275$, $N = 12$, $P_{\text{exact}} = 0.021$; Bonferroni-adjusted $P = 0.016$). For seven females, we had enough data to compare their behaviour across males. Although all seven females pant-grunted to all nine males, they did so significantly more to the alpha male than the other males (mean probability of calling: alpha: 0.63 ± 0.17; nonalpha: 0.35 ± 0.06; Wilcoxon test: $T = -2.366$, $N_{\text{females}} = 7$, $P_{\text{exact}} = 0.016$; Fig. 2a). Despite this bias towards the alpha male, it was not the case that male social status per se explained the females' pant-grunting behaviour. There was no significant correlation between the average rank value for the nine males and their likelihood of receiving pant-grunts when encountering a female (Spearman correlation: $r_S = 0.293$, $N_{\text{males}} = 9$, $P = 0.444$). Similarly, the rank of the female caller also did not explain her likelihood of giving a pant-grunt when encountering a male (Spearman correlation: $r_S = -0.192$, $N_{\text{females}} = 9$, $P = 0.620$).

Effects of Target Individual Behaviour

Compared to other adult males, the alpha male NK could be very violent towards other group members. We therefore tested whether pant grunting could be explained by the level of threat experienced by the caller during an encounter. During neutral encounters the females' average probability of producing a pant-grunt was relatively low ($N_{\text{females}} = 9$; mean probability of pant grunting = 0.36 ± 0.08). The probability was higher in aggressive contexts ($N_{\text{females}} = 4$; 0.65 ± 0.27) but highest in affiliative contexts ($N_{\text{females}} = 4$; 0.89 ± 0.13), demonstrating that level of threat was not associated with elevated levels of pant grunting.

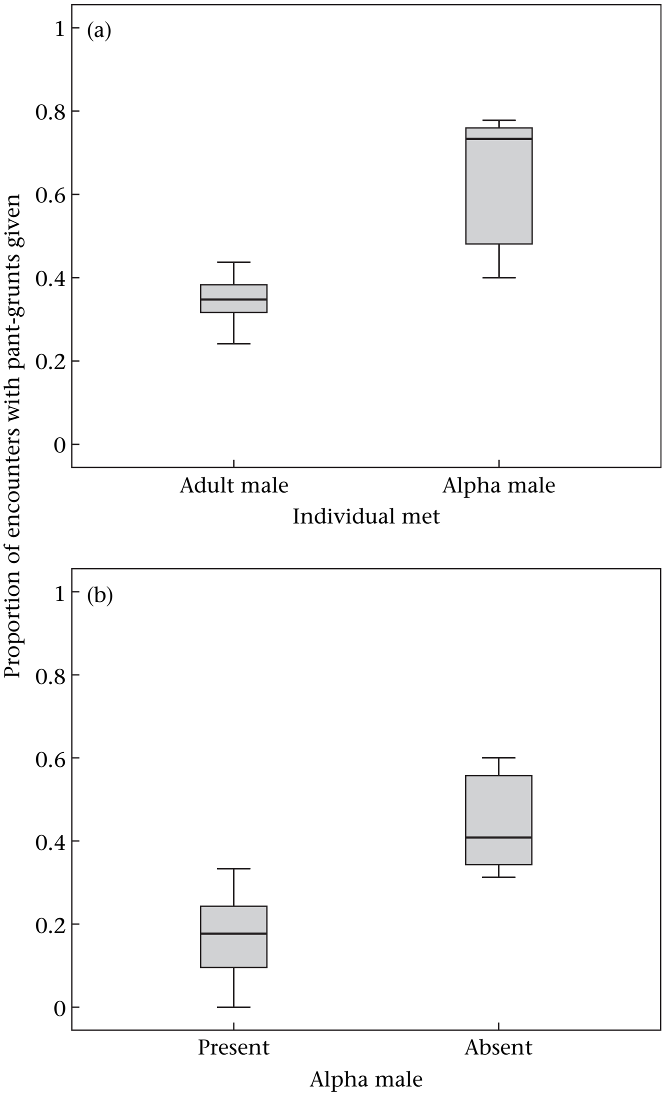

Figure 2. Proportion of pant-grunts given by adult females when meeting (a) the alpha male versus another adult male; (b) one or more adult males in the presence or absence of the alpha male. Boxes show the median values for all females with the upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range.

Audience Effects: Alpha Male and Female

We investigated whether the composition of the audience affected female pant-grunt production. Overall, the presence of the alpha male significantly reduced the likelihood of females pant grunting when encountering another male (*t* test: $t_7 = -4.368$, $N_{\text{females}} = 8$, $P = 0.003$; Fig. 2b). Encounters with males can be single encounters (if a single male joins the female's travelling party) or group encounters (if the female joins a group of males). In both conditions, the alpha male can be present or absent. To investigate further the audience effect of the alpha male, we analysed the single-male encounter subsample only. The effect remained the same, albeit only as a nonsignificant trend (Wilcoxon test: $T = -2.023$, $N_{\text{females}} = 5$, $P_{\text{exact}} = 0.063$).

We also tested whether the presence of the alpha female had an effect on the production of pant-grunts when encountering a male. We managed to compare matched data for four females, with or without the alpha female present within 10 m, while encountering a male. The probability of pant grunting to adult males was about three times higher when the alpha female was absent than present (0.42 ± 0.11 versus 0.14 ± 0.17), suggesting an inhibitory effect comparable to that of the alpha male.

Audience Effects: Group Size

The size of the audience had no effect on the likelihood of females producing a pant-grunt when encountering the alpha male. This was because the mean number of individuals in the vicinity of a female was not different whether she did or did not give a pant-grunt (mean *N* individuals present with calls: 1.136 ± 0.655; without calls: 1.143 ± 0.627; $t_6 = -0.019$, $N_{\text{females}} = 7$, $P = 0.984$). However, when females encountered another male, the size of the audience mattered greatly, and this was not due to the presence of the alpha male within 10 m (mean *N* individuals present with calls: 0.484 ± 0.452; without calls: 1.082 ± 0.454; $t_8 = -3.252$, $N_{\text{females}} = 9$, $P = 0.012$; Fig. 3a). The group size effect on calling behaviour was stronger for male than female audiences. As the number of males increased, the likelihood of females pant grunting to another male decreased (mean *N* males present with calls: 0.052 ± 0.090; without calls: 0.38 ± 0.335; Wilcoxon test: $T = -2.028$, $N_{\text{females}} = 8$, $P_{\text{exact}} = 0.047$; Fig. 3b) while we only found a nonsignificant trend in the same direction for the number of females present within 10 m (mean *N* females present with calls: 0.432 ± 0.442; without calls: 0.702 ± 0.370; $t_8 = 2.218$, $N_{\text{females}} = 9$, $P = 0.057$; Fig. 3c).

DISCUSSION

A key element in the debate over human uniqueness is whether animals are intended addressees or merely accidental eavesdroppers of communication signals produced by conspecifics. We have addressed this problem to some extent with this study on pant grunting in wild chimpanzees. Our results showed that wild chimpanzees adjust the production of pant-grunts in flexible ways. All individuals monitored in this study produced pant-grunts when encountering higher-ranking group members, but call production was not mandatory during such encounters and depended on a number of social variables. The probability of pant grunting was highest during affiliative interactions, compared to agonistic or neutral situations. It is therefore not likely that pant-grunts function specifically to appease aggressively motivated group members or to express fear. Another finding was that the alpha male received a particularly large share of all pant-grunts. However, the relative social position of the call receiver failed to explain the production patterns of pant-grunts. Similarly, the social position of the caller also did not explain individual differences in the likelihood of calling. A further finding was that the presence of the alpha male had a powerful socially inhibitory effect, which might also be the case for the alpha female. In the presence of these individuals, the females typically refrained from greeting other group members, who under other circumstances were regular receivers of pant-grunts.

Although the sample size was too low to make statistical comparisons for the alpha female audience effect, we observed some differences in the likelihood of calling in all individuals. A number of anecdotal observations are in line with this interpretation. Once we observed a low-ranking female (KL) approaching, and pant grunting to, the alpha male, followed by an attempt to groom him. The alpha female was also nearby but was probably not noticed by KL, as they were out of view from each other. While attempting to groom the alpha male the alpha female suddenly approached and aggressively chased KL away, something that probably would not have happened had KL remained silent.

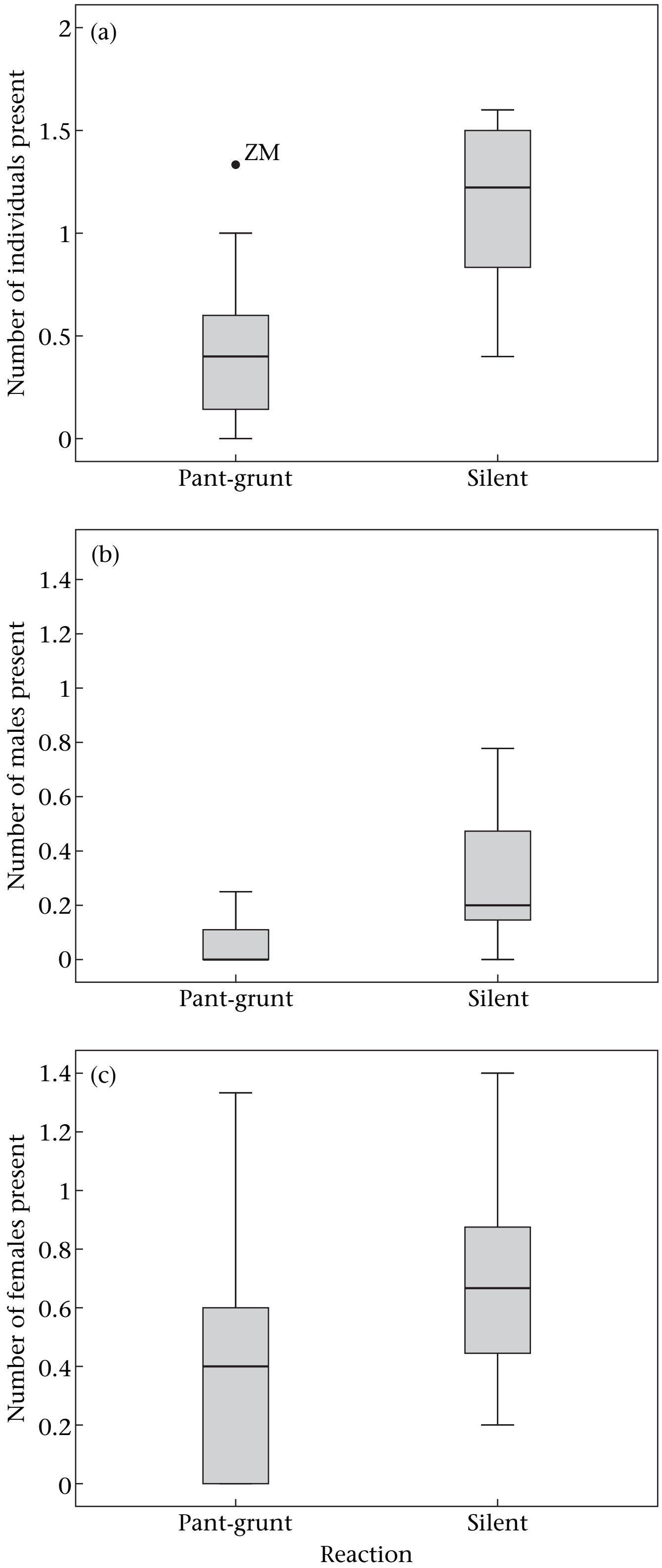

Figure 3. Medians of the average number of individuals present for each focal female when encountering an adult male with or without pant-grunting: (a) all individuals; (b) adult males only; (c) adult females only. Boxes show the median values for all females with upper and lower quartiles; whiskers represent data within 1.5 times the interquartile range; the black circle indicates an outlier.

Chimpanzee females are generally less gregarious than males but nevertheless are confronted with considerable intrasexual social competition (Newton-Fisher 2006; Emery Thompson et al. 2008; Townsend et al. 2008), as indicated by this and other observations.

Previous research has shown that chimpanzee vocal behaviour can be flexible in terms of both acoustic morphology and call use (Slocombe & Zuberbühler 2006). Most chimpanzee vocalizations are acoustically graded and there is evidence that some acoustic variants are meaningful to receivers (Slocombe & Zuberbühler 2005; Slocombe et al. 2009). Another recurrent finding is that callers take into account the identity of all nearby individuals, as well as their potential relevance during an ongoing social event (Slocombe & Zuberbühler 2007; Townsend et al. 2008). In this study, we found further evidence that the presence and identity of bystanders had a significant impact on an individual's willingness to produce a vocal signal.

One consequence of our results is that the notion of pant-grunts as a behaviourally rigid and phylogenetically ritualized signal of subordination in chimpanzees becomes questionable, which is in line with other research (Takahata 1990; Newton-Fisher 1997, 2006; Emery Thompson et al. 2008; Townsend et al. 2008). More likely, pant grunting is a socially flexible behaviour that appears to be the product of a variety of motives (see also Hayaki 1990). It appears to be a reflection of a caller's wish to interact with a socially relevant group member, a way of probing a recipient's mood and motivations, and a vocal tool to make one's presence known and to convey respect. Pant grunting, in other words, is part of a chimpanzee's tool kit to build social relations, rather than a straightforward consequence of a social hierarchy. There are some interesting parallels to human greeting, which has also been argued to serve to attract attention, to signal intent, to enter a relationship, to reduce social anxiety and to mark social status, especially during tense situations (Firth 1972).

Social complexity is thought to be one of the major driving forces of cognitive evolution (Humphrey 1976; Byrne & Whiten 1988;) and our findings fit well with this more general idea. Chimpanzees live in a fluctuating social system where individuals' motives and alliances can change rapidly. This fusion—fission social system, combined with the difficult visual conditions of the forest habitat, has the effect that individuals typically witness only a very small proportion of the ongoing social events, a possible selection factor towards enhanced cognition (Barrett et al. 2003; Aureli et al. 2008;). Female chimpanzees are frequent targets of male aggression, suggesting that they benefit from initiating social interactions strategically to control the possible social consequences. Acoustically, pant-grunts are individually distinct, something that can be discriminated by other chimpanzees (Kojima et al. 2003). In the wild, the calls are audible over a considerable distance of up to 50 m (M. Laporte, personal observation), indicating that they provide a rich source of social information to nearby listeners.

Why should a caller be sensitive to the presence of certain bystanders during encounters with higher-ranking group members? First, greeting others in the presence of the alpha male could be risky if it elicits aggressive behaviour by him. Of 11 cases of females pant grunting to another male in the presence of the alpha male, we observed two cases of aggression towards the female within the next 5 min. On the other hand, pant-grunts sometimes elicited aggressive behaviour from the receiver, especially towards subadult individuals (Hayaki 1990), suggesting that being addressed with pant-grunts is not always perceived as a positive event. Another provocative hypothesis is that females may contribute to the social climbing of their favourite males by allocating their pant-grunting behaviour strategically (de Waal 1982). Although it seems plausible that females are interested in social stability (to raise their offspring successfully), our results cannot really contribute to this debate in a meaningful way.

There is no doubt that apes have demonstrated high levels of flexibility in their gestural communication signals and that they sometimes use them to manipulate the behaviour of others to their own benefits (Pika et al. 2003, 2005; Liebal et al. 2004). Whether this kind of communicative flexibility is entirely restricted to the gestural domain, however, is becoming increasingly more controversial. Our study does not fit well with the notion of structurally rigid, contextually inflexible and cognitively uninteresting vocal communication (Arbib et al. 2008; Tomasello 2008). More likely, both gestural communication and vocal communication are susceptible to the same cognitive processes and architecture that govern social behaviour in primates (Leavens et al. 2004, 2010; Slocombe & Zuberbühler 2007; Townsend et al. 2008).

Overall, pant-grunts are clearly interesting vocalizations because they enable group members to signal, interpret, maintain or potentially even change social relationships with or between other group members. The notion of chimpanzees as strategic individuals who are constantly assessing each other's dominance relationships has largely emerged from research on captive adult males in their relations with each other (de Waal 1982). Our study is in line with this general stance, but highlights that subordinates are possibly as strategic as dominants when interacting with other group members.

Acknowledgments

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