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The development of a greeting signal in wild chimpanzees

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Abstract

Adult chimpanzees produce a unique vocal signal, the pant-grunt, when encountering higher-ranking group members. The behaviour is typically directed to a specific receiver and has thus been interpreted as a 'greeting' signal. The alpha male obtains a large share of these calls, followed by the other adult males of the group. In this study, we describe the development of pant-grunting behaviour from the first grunt-like calls of newborn babies to the fully developed pant-grunts in adults. Although babies produce grunts from very early on, they are not directed to others until about 2 months of age. Subsequently, socially directed grunting steadily increases in frequency to peak around 7 months of age, but then decreases again to reach a nadir in older infants and juveniles, while the specificity in use increases. During adolescence, grunt production increases again with grunts given most frequently to socially relevant individuals. As young chimpanzees are closely affiliated to their mothers for the first decade of their lives, we also compared the grunting patterns of mothers and their offspring, which revealed some influences in pant-grunt production. In conclusion, the acquisition of pant-grunting behaviour in chimpanzees is a long-lasting process with distinct developmental phases in which social influences by the mother and other group members are likely to play a role.

Introduction

Early studies with artificial language systems demonstrated that great apes are capable of using symbolic systems to communicate with humans. One relevant finding here was that paradigms based on vocal signals were less successful than visually based communication systems (Gardner & Gardner, 1969; Hayes & Hayes, 1951; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986). This resulted in a widely accepted notion of gesturally flexible and vocally rigid apes. More recently, however, this strict dichotomy has been challenged on various grounds, for instance due to evidence for flexibility in sound production (Hopkins & Savage-Rumbaugh, 1991; Hopkins, Taglialatela & Leavens, 2007; Leavens, Hostetter, Wesley & Hopkins, 2004; Taglialatela, Savage-Rumbaugh & Baker, 2003). Equally relevant, the natural vocal and gestural behaviour of chimpanzees and other great apes had hardly been studied, with vocal development being especially poorly investigated. One source of information was from early developmental studies with captive apes, which sometimes included observations on vocal behaviour (Hayes, 1951; Jacobsen, Jacobsen & Yoshioka, 1932; Ladygina-Kohts, de Waal & Vekker, 1935/2002). However, they were conducted with single chimpanzees, which were human-raised and had no contact with conspecifics. Mother–infant interactions in the wild were first investigated at Gombe, Tanzania, where socially directed grunts were documented in young infants (van Lawick-Goodall 1968). A subsequent study by Plooij (1984) was the first systematic attempt to describe the development of five wild chimpanzees during their first two years of life, which also generated important information about their vocal behaviour. More recently, Bard (1994a) and van Ijzendoorn and colleagues (2009) studied the development of emotions and cognition in different rearing conditions, while Kojima (2001) described some of the vocalizations produced by a captive chimpanzee during the first 18 weeks of life. Hayaki (1990), finally, reported differences in pant-grunting activity in older individuals, but apart from these reports, we are not aware of any systematic studies of ape vocal development, either in the wild or in captivity.

A dominant theme in studies of vocal development in primates is the question of vocal learning by signallers and receivers. The established view is that non-human primates possess little control over call production, particularly call morphology, which typically results in limited vocal repertoires (Janik & Slater, 1997, 2000). Flexibility is generally greater in other domains of vocal behaviour, such as context-specific call use and call comprehension (Cheney & Seyfarth, 2009; Seyfarth & Cheney, 1986, 1999). Some observations of adult individuals suggest that social and individual learning mechanisms are likely to be involved, but the effects seem

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to be minor and the details are not well understood. For instance, Diana monkeys (*Cercopithecus diana*) of Tai Forest, Ivory Coast, can discriminate between chimpanzee screams given during social conflict and to a leopard, provided they have had sufficient experience with chimpanzees (Zuberbühler, 2000).

As call producers, it has been found that Diana monkeys living on Tiwai Island, Sierra Leone, a habitat with no leopards, give alarm calls to leopard models, but their calls do not differ from the alarm calls given to general disturbances, suggesting that some aspects of call production are also controlled by ontogenetic experience (Stephan & Zuberbühler, 2008). In chimpanzee, there is documented acoustic variability in the pant-hoot vocalizations between communities, which has also been taken as evidence for learning (Crockford, Herbinger, Vigilant & Boesch, 2004; Mitani, Hasegawa, Gros-Louis, Marler & Byrne, 1992). Another line of research comes from vervet monkeys (*Cercopithecus aethiops*). Young monkeys initially produce eagle and leopard alarm calls to a broad range of events and only with experience begin to give these calls to the dangerous predator classes (Cheney & Seyfarth, 1990; Seyfarth & Cheney, 1980). Similarly, the amount of experience with intergroup encounters is closely linked to the onset of ‘wrr’ production in young vervet monkeys, a call type produced when detecting a neighbouring group (Hauser, 1989). Overall, socialization and experience with group members seem to be important in the development of vocal behaviour, suggesting that vocal development should be studied in natural group settings.

In the past, ontogenetic studies have often focused on alarm or separation calls that are expected to be morphologically less flexible than social or affiliative calls (Snowdon, 2004). Here, we focus on a potentially interesting vocal signal in chimpanzees, the pant-grunts, an acoustically heterogeneous and graded call type that serves important social functions. Pant-grunts are exclusively given by individuals when encountering a more dominant group member. Hence, this calling behaviour is usually interpreted as a ‘greeting’ signal, which is commonly used as an indicator of dominance relationships (Goodall, 1986; van Hooff, 1973; Noë, de Waal & van Hooff, 1980). Pant-grunts can also be produced in appeasement and reconciliation contexts (de Waal, 1982). In the laboratory, pant-grunting decreases if groups are kept under crowded conditions where social tension is high (Aureli & De Waal, 1997), suggesting that additional variables govern grunt production. Pant-grunts are produced by all individuals, apart from the alpha male and some high-ranking males (Clark, 1993) and there is evidence that they are individually recognizable (Kojima, Izumi & Ceugniet, 2003). In the wild, callers appear to be aware of the potential consequences of producing pant-grunts to certain group members (Laporte & Zuberbühler, 2010). For example, in the presence of the alpha male, females typically refrain from producing pant-grunts to other high-ranking males, who would normally obtain such calls.

Grunts are some of the first vocalizations produced by chimpanzees in the wild (Plooij, 1984) and in captivity (Bard, 2003; Kojima, 2001). Plooij (1984) reported that first grunts were given as part of physical efforts (the ‘effort grunts’), the result of air release during muscular contraction (Plooij, 1984). Other early vocalizations were staccato grunts and whimpers given in reaction to loss of contact with the mother or to a sudden loud noise (Plooij, 1984; Kojima, 2001). In captivity, Bard (2003) reported both effort grunts and pant-grunts in the first weeks of life while earlier studies did not report them before the second month (Jacobsen *et al.*, 1932), possibly due to differences in rearing conditions or methodology (Bard & Gardner, 1996). Other work has shown that chimpanzees are tuned to conspecific vocalizations from very early on, possibly as a result of prenatal experience (Berntson & Boysen, 1989) and due to the fact that cognitive development in chimpanzees is significantly affected by rearing conditions (van Ijzendoorn *et al.*, 2009). From about 3 to 4 months, chimpanzees begin to produce grunts at the sight of other group members (Hiraiwa-Hasegawa, 1989; Plooij, 1984) or human caretakers in captivity (Jacobsen *et al.*, 1932; Ladygina-Kohts *et al.*, 1935/2000; Bard, 2003). In the wild, the mother–offspring dyad provides a particularly important context for studying the vocal development in chimpanzees as infants stay in constant ventro-ventral contact with their mothers until about 7 months of age (van de Rijt-Plooij & Plooij, 1987). Even after offspring start to move independently, mothers and their offspring usually stay close to each other and travel together for another 10 years or so, until the offspring reach adolescence (Pusey, 1990).

We systematically studied the development of context-specific grunt production from birth to adulthood in a large number of individuals in a free-ranging group of chimpanzees, the Sonso community of Budongo Forest, Uganda. We describe the basic developmental patterns across the different age groups, assuming that both maturation and learning were likely to be involved in this process. Since we were interested in how individuals were socially influenced during the acquisition process we also examined the relationship between the vocal behaviour of the mother and of her offspring.

Methods

Study site

Data were collected during three field periods between January and April 2007, August 2007 and February 2008, and July and December 2008 in the Sonso community of Budongo Forest, Uganda (Reynolds, 2005). Budongo Forest is a 428 km^2 moist, semi-deciduous tropical forest reserve located between 1°35′ and 1°55′ N and 31°08′ and 31°42′ E at an altitude of 1100 m (Reynolds, 2005). At the beginning of the study, the community consisted of 78 individuals (10 males, 25 females, eight subadult males, five subadult females, 13 juveniles 12 infants and five babies) (Table 1).

Data collection

In total, we followed 35 babies, infants, juveniles and subadults belonging to 16 different families (Table 2). Due to the slow development of chimpanzees, we used both cross-sectional and longitudinal data collection, by comparing four major periods of development. These periods are generally determined by major changes in locomotion and other behaviour. At the same time, there is substantial variability in the reported age ranges during which key transitions take place (see van Lawick-Goodall, 1968; Plooij, 1984; Reynolds, 2005). In line with Plooij (1984), we based our analyses on four age categories, although for older individuals we extended the classification by 1 year.

A first dataset consisted of focal animal samples (‘focal’: $N = 501$ hours) and 5 min scan samples of focal individuals (Altmann, 1974). During focal animal samples, we noted all vocalizations produced by the infant and the mother, together with the context of production on an all-occurrence basis. For each scan sample, the behaviour of the focal animal and his or her mother was recorded, as was the identity of all individuals present within a radius of both 10 m (average visual range) and 35 m (average spread of a travel party; Newton-Fisher, 2004).

A second dataset consisted of all individuals remaining within a 10 m radius surrounding the focal animal during at least two consecutive scans (‘focal 10 m’: $N = 531$ hours). To calculate grunt rates and to carry out context analyses, we combined the two datasets (‘focal + focal 10 m’: $N = 1032$ hours; Table 3). All occurrence data were taken for all visible individuals situated further than 10 metres from the focal. For some specific contexts, sometimes involving low numbers of vocalizations, we calculated the proportion of each grunt type produced, relative to all grunts produced, for which we included the data collected during all occurrence sampling.

Vocalizations

Chimpanzee babies produce grunt-like calls and whimpers from their first day of life (Kojima, 2001; Plooij, 1984). These grunts probably serve as the substrate for a wider range of call types, including various grunts, but maybe also hoots and barks. Early grunts produced by babies and infants are produced in a range of situations. Contextually based distinctions were made by Plooij between ‘effort’ grunts and ‘social’ grunts, and these were labelled ‘staccato grunts’ and ‘uh-grunts’. Adult grunts fall into at least three distinct categories, based on acoustic structure and contextual use: rough grunts given to food, travel grunts given in relation to movement, and pant-grunts given when encountering a higher-ranking group member (Goodall, 1986; Clark, 1993; Marler, 1976). However, the relationship between the acoustic morphology of adult and infant grunts has yet to be investigated, a complex task that goes beyond the scope of this study. The grunt-like calls of immature individuals were thus categorized according to their contextual use.

Table 1 *Community size over the 17-month study period, including births, deaths and developmental changes*

Year	Month	AM	AF	SM	SF	JM	JF	IM	IF	BM	BF	Total	D	B	C
2007	JAN	10	25	8	5	4	9	5	7	2	3	78		Karibu, Sharlot	
	FEB	10	25	8	5	4	9	5	7	2	4	79		Kox	
	MAR	10	25	8	5	4	9	5	7	2	4	79			
	APR	10	25	8	5	4	9	6	7	1	4	79			Klauce (B-I)
	MAY–JUL												Bob, Mark, Banura	Rafia	Faida, Sokomoko (B-I)
	AUG	9	23	7	5	4	9	7	10	0	2	76	Zana		Karibu, Sharlot (B-I)
	SEPT	9	23	7	5	4	9	7	11	0	1	76			Kox (B-I)
	OCT	9	23	7	5	4	9	6	11	0	2	76	Sean	Marion	
	NOV	9	23	7	5	5	9	6	11	0	2	77			Zak (I-J)
	DEC	9	23	7	5	5	9	5	11	0	2	76			
2008	JAN	9	22	7	5	5	9	5	12	0	1	75	Lola		Rafia (B-I)
	FEB	7	22	7	5	5	10	5	11	0	1	73	Duane, Gashom		Night (I-J)
	MAR–JUN														Marion (B-I), Monika (I-J), Rachel, Zig (J-S)
	JUL	7	22	8	6	4	10	5	11	0	1	74		Kathy	
	AUG	6	21	8	6	5	10	4	11	0	1	72	Maani, Polly		Kasigwa (I-J)
	SEPT	6	21	8	6	5	11	4	11	0	1	73			Ramula (I-J)
	OCT	6	21	8	6	5	11	4	10	0	2	73		Kaspa	
	NOV	6	21	8	7	5	10	4	10	0	2	73			Rose (J-S)
	DEC	6	21	8	7	5	10	4	10	0	2	73			

AM adult males; AF adult females, SM subadult males, SF subadult females, JM juvenile males, JF juvenile females, IM infant males, IF infant females, BM baby males, BF baby females; D = disappear, B = birth; C = change age group

Table 2 *Adult females and their offspring in the Sonso community during the study period. Mothers: R: residential, P: peripheral (Laporte & Zuberbühler, 2010, and adapted from Williams, Pusey, Carlis, Farm & Goodall, 2002). Offspring: B, babies, I: infants, J: Juveniles, S: Subadults. *: died during the study. Italics: data could not be taken from this individual or family. Bold: alpha female*

Offspring	Gender	DOB	Age class	Mother	Mother status
Fred	M	1994	S	Flora	P
Frank	M	1999	J		
Faida	F	Oct-06	B,I		
Hawa	M	1993	S	Harriet	P
Helen	F	Feb-01	J		
Honey	F	4/10/2005	I		
Janet	F	1/10/1999	J	Janie	P
James	M	4/5/2006	I		
Bahati	F	1/12/1994	S	Kalema	R
Kumi	F	17-09-2000	J		
Klauce	M	5/9/2006	B,I		
Katia	F	30-12-1998	J	Kewaya	R
Kox	F	15-02-2007	B,I		
Kato	M	Sep-93	S	Kutu	R
Kana	F	29-10-1998	J		
Kasigwa	M	15-08-2003	I,J		
Kathy	F	27-07-2008	B		
Kwezi	M	7/1/1995	S	Kwera	R
Karo	F	1/11/2001	J		
Karibu	F	10/1/2007	B,I		
Monika	F	22-06-2003	I,J	Melissa	P
Marion	F	15-09-2007	B,I	Mukwano	P
Nora	F	Feb-95	S	**Nambi**	R
Night	F	6/2/2003	I		
Pascal	M	1998	J	*Polly**	*P*
Rose	F	15-11-1997	S	Ruhara	R
Ramula	F	6/9/2002	J		
Rafia	F	15-06-2007	B,I		
Sharlot	F	6/1/2007	I	Sabrina	P
Simon	M	1993	S	Sarine	R
Sokomoko	M	1/10/2006	I		
Zalu	M	29-06-1995	S	*Zana**	*P*
Zed	M	1/5/2001	I,J		
Zig	M	24-06-1997	J,S	Zimba	R
Zak	M	21-11-2002	I,J		

Context analysis

For offspring grunts, we determined the grunt rates (grunts per hour) of any grunt-like vocalization produced by all offspring. We conducted the following four main analyses of grunt use in four basic and mutually exclusive contexts: (1) no apparent external event, (2) hearing vocalizations only, (3) encountering food with or without hearing vocalizations, with or without other individuals present and (4) encountering group members with or without hearing vocalizations.

Although it was possible to calculate grunt rates per month (0–2 years) and per year of development (2–15 years, i.e. onset of adulthood), it was not possible to conduct meaningful statistical analyses at this level due to the low number of individuals per observation month, the low grunt rates, and the imprecise age estimates of some older individuals. Previous studies differed in how the age classes were assigned. Taking into account these previous studies, we adhered to the general developmental milestones and defined four main age classes as follows: babies (birth to onset of dorsal riding, i.e. 0–6 months), infants (dorsal riding to weaning, i.e. 7–60 months), juveniles (weaning to puberty, i.e. 5–10 years) and subadults (puberty to adulthood, i.e. 11–15 years) (adapted from Hiraiwa-Hasegawa, 1989; van Lawick-Goodall, 1967; Plooij, 1984; van de Rijt-Plooij & Plooij, 1987; Reynolds, 2005; Table 3).

Using this dataset we compared grunt rates and proportional grunt use, per individual and age class, requiring a minimum of 5 hours of observation for an individual to be included in the frequency analyses and a minimum of three calling events to be included in the proportional analyses. The resulting number of individuals per age class varied between 5 and 15.

For analysis 2 (‘hearing vocalizations’), we carried out two additional analyses combining the contexts ‘hearing vocalizations only’, ‘encountering food with individuals around while hearing vocalizations’ and ‘encountering group members with hearing vocalization’. In analysis 2.1, we investigated the role of pant-grunts by other group members as triggers of infant grunts. To this end, we calculated the proportion of pant-grunts (relative to other vocalizations) that triggered grunt-like vocalizations in a focal immature individual.

In analysis 2.2, we determined the influence of age/sex class of the caller (adult male, adult female, mother, subadult, group of at least two individuals or others, e.g.

Table 3 *Observation efforts (hours) for each individual in the different age groups and contribution of individuals to the different analyses. Y: individual participated in the analysis. N: Individual did not participate in the analysis. Individuals who contributed to two adjacent age classes had two letters for each age class (Baby-Infant, Infant-Juvenile, or Juvenile-Subadult). Frequency analyses (general context): 1, 2, 3, 4, 4.1; Frequency analyses (similarity with mother): 4.2, 4.3; Proportional analyses (vocalizations); 2.1, 2.2; Proportional analyses (similarity with mother): 4.4.*

	Age class					Analysis			
Individual	Baby	Infant	Juv.	Subad.	Total	1-4, 4.1	2.1, 2.2	4.2, 4.3	4.4
Kathy	42.25				42.25	Y	Y	Y	Y
Faida 0*	1.08	6.33			7.42	N-Y	N-Y	N-Y	N-Y
Klauce	15.50	66.75			82.25	Y-Y	Y-Y	Y-Y	Y-Y
Kox	6.92	48.08			55.00	Y-Y	Y-Y	Y-Y	Y-Y
Karibu	16.33	65.17			81.50	Y-Y	Y-Y	Y-Y	Y-Y
Marion	10.00	11.33			21.33	Y-Y	Y-Y	Y-Y	Y-Y
Rafia 0	7.00	25.00			32.00	Y-Y	N-Y	Y-Y	N-Y
Honey		15.42			15.42	Y	Y	N	N
James		46.33			46.33	Y	Y	Y	Y
Sokomoko 0		17.50			17.50	Y	N	Y	N
Sharlot 0*		3.00			3.00	N	N	N	N
Night 0		18.50	31.92		50.42	Y-Y	Y-N	Y-Y	N-Y
Kasigwa		30.25	31.00		61.25	Y-Y	Y-Y	Y-Y	Y-Y
Zak 0		10.58	21.92		32.50	Y-Y	N-Y	Y-Y	N-Y
Ramula 0			15.67		15.67	Y	N	Y	N
Monika 0*			4.33		4.33	N	N	N	N
Zed!			30.91		30.91	Y	Y	N	N
Helen |0			10.00		10.00	Y	N	N	N
Karo 0			24.50		24.50	Y	N	Y	Y
Kumi			26.42		26.42	Y	Y	Y	Y
Janet			14.50		14.50	Y	Y	Y	Y
Pascal!			21.65		21.65	Y	Y	N	N
Frank			15.75		15.75	Y	Y	Y	Y
Katia 0			33.58		33.58	Y	N	Y	Y
Kana			23.25		23.25	Y	Y	Y	Y
Zig 0			7.75	17.75	25.50	Y-Y	N-Y	Y-Y	Y-Y
Rose 0			7.00	6.17	13.17	Y-Y	N-N	Y-Y	Y-N
Nora				31.67	31.67	Y	Y	Y	Y
Zalu!				40.08	40.08	Y	Y	N	N
Bahati				28.67	28.67	Y	Y	Y	Y
Kwezi				37.25	37.25	Y	Y	Y	Y
Fred				20.50	20.50	Y	Y	Y	Y
Kato				27.50	27.50	Y	Y	Y	Y
Hawa!				28.33	28.33	Y	Y	N	N
Simon				10.83	10.83	Y	Y	Y	Y
Total	99.08	364.25	320.14	248.75	1032.23				

! no mother; 0 grunt number too low; * focal time too low

juvenile or younger individuals or not determined) to assess their relative importance of the social identity of the caller in eliciting grunt-like responses.

For the main analysis 4 ('encountering another group member'), we conducted the following four follow-up analyses. In analysis 4.1, we compared the grunt rates to different group members over the course of development. Socially directed grunts ('social grunts') are relatively easy to identify, even in very small babies who are difficult to observe within their mother's hair. At this early age, grunt production requires considerable efforts, both in terms of attention and physical strength. It was not rare to see a baby seemingly preparing for a grunt, with body and lip posture directed towards a specific individual over several seconds before attempting to produce a grunt, with sometimes no audible sound generated. Using all grunting events during which grunts were directed to another individual ('encountering group members with or without hearing vocalizations'), we calculated the grunt rates directed to the alpha male, other adult males, adult females and subadults. We then compared the immatures' grunt rates with the pant-grunt rates of the mother's family group given to the same target individual ($N_{\text{mothers}} = 11$).

In analysis 4.2, we investigated if grunting behaviour of immatures was more generally influenced by the vocal behaviour of their mothers, particularly whether more vocal mothers had more vocal offspring. Hence, we compared the mothers' overall pant-grunting activity with the grunting activity of their offspring, regardless of the targeted individual.

In analysis 4.3, we assessed the influence of the mother on their offspring's choice of targeted individuals. We first checked whether mothers and their offspring correlated in the number of group members that received grunts for each age class.

In analysis 4.4, finally, we tested whether the target individuals selected by the offspring for social grunts were part of the mother's portfolio by calculating the proportion of offspring social grunts directed to group members that were part of their mother's portfolio.

Figure 1 provides a summary of the 10 different analyses carried out in this study. The contributions of each individual to the different analyses are listed in Table 3.

Statistical analysis

All proportional data were transformed using an arcsine of square root function. For $N < 50$, it is recommended to apply a $1/4N$ or $1\text{-}1/4N$ transformation for proportions = 0 or 1 with N = total number of occurrences (Snedecor & Cochran, 1980). As not all individuals contributed to the different situations, sample sizes varied between analyses. Raw data per individual were subsequently checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene's test). If conditions were met, we used parametric tests (ANOVAs, Student *t*-tests, Pearson correlations). The data, however, did not always meet the conditions of normal distribution and homogeneity of variances, in which case we used non-parametric Kruskal-Wallis tests for multiple unmatched comparisons with Jonckheere-Terpstra tests, Mann-Whitney tests and Spearman's correlations. The Kruskal-Wallis test determines if there is an overall difference among groups, akin to an ANOVA, while the Jonckheere-Terpstra procedure tests if significant differences are linear, i.e. whether there are ordered patterns across the medians (akin to a trend analysis in an ANOVA). *Z*-scores > 1.65 indicate a significant increase across categories, while *z*-scores < −1.65 indicate a significant decrease across categories. All tests were two-tailed with significance levels set at $\alpha = 0.05$, or stated otherwise. For small sample sizes, we calculated exact *p*-values (Mundry & Fischer, 1998). Post-hoc comparisons were carried out using a Sidak corrected alpha set at $\alpha = 1 - (1-\alpha)$^1/n. All analyses were conducted with SPSS 17.0.

Results

1. Analysis of context: Grunts produced with no external reason

As noted by Plooij (1984), we observed that most grunts of chimpanzee babies were given with no apparent external reason, apparent by-products of physical effort when moving on their mother's body. As infants started to move independently we found that such 'effort grunts' became more rare, but they remained in the vocal repertoire, even as adults. In older individuals, grunts produced for no apparent reason did not seem to be the result of physical effort any more; they were often produced when sitting or lying down. Overall, we observed a significant change in the production of grunts produced for no apparent external reason (H (3) = 12.586, $p = .006$, Kruskal-Wallis test, two-tailed; Figure 2a), which was not the result of an overall decrease with increasing age (J = 297, $z = -0.848$, $r = -0.129$, Jonckheere's test) but was due to a significant decrease between babies and infants (U = 6, $z = -2.816$, $p_{\text{exact}} = .003$, Mann-Whitney test, Sidak-corrected $\alpha = 0.017$).

2. Analysis of context: Grunts produced to other vocalizations

A first indicator of grunts as communication signals was when babies responded with grunts to the vocalizations of other group members. We found a significant negative relationship with age for grunts given in response to vocalizations by other group members (H (3) = 9.141, $p = .027$, Kruskal-Wallis test, two-tailed; J = 250, $z = -1.916$, $r = -0.29$, Jonckheere's test; Figure 2b).

2.1. Analysis of call types: Grunts in response to pant-grunts

Not all call types were equally effective in eliciting grunts in young chimpanzees. Vocally elicited grunting was first observed in older babies and infants, but these individuals were already selective. They did not respond to all vocalizations but preferred pant-grunts produced by other group members (babies: 47% ± 34%, $N = 5$; infants: 69% ± 20%, $N = 11$; juveniles: 82% ± 14%, $N = 8$; subadults: 87% ± 9%, $N = 9$; ANOVA, $F(3, 29) = 5.097$, $p = .006$). There was a significant linear trend (ANOVA, $F(1, 29) = 15.10$, $p = .001$), indicating that the proportion of pant-grunts preceding grunt-like vocalizations increased with age within this age group (Figure 3). Sidak-corrected post-hoc tests revealed significant differences between babies and juveniles ($p = .032$) and between babies and subadults ($p = .006$).

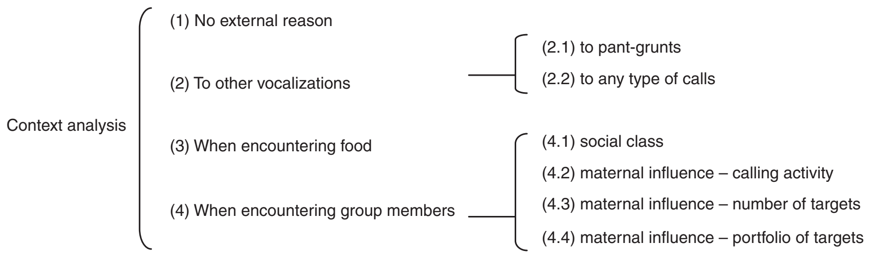


Figure 1 *Overview of the analyses carried out in this study.*

2.2. Analysis of social class: Grunts produced to other group members' vocalizations (any type of calls)

The largest percentage of grunts produced by young chimpanzees was in response to vocalizations produced by their mothers. This pattern remained until subadulthood, when subjects began to respond equally strongly to other subadults (Figure 4). The relative importance of the mother's calls as triggers of offspring grunts significantly decreased with age (H (3) = 13.316, $p = .004$, Kruskal-Wallis test, two-tailed; J = 91.00, $z = -3.302$, $r = -0.584$, Jonckheere's test, Figure 4a) while the opposite pattern was observed for subadults as triggers of grunts (H (3) = 18.047, $p = .0004$, Kruskal-Wallis test, two-tailed; J = 312.00, $z = 4.183$, $r = 0.740$, Jonckheere's test, Figure 4b). In contrast, the proportion of calls of adult males and other adult females triggering grunts remained relatively low with no significant changes throughout the age groups (H (3) = 4.574, $p = .206$, and H (3) = 0.707, $p = .872$, Kruskal-Wallis tests, two-tailed, Figure 4c and 4d).

3. Analysis of context: Grunts produced when encountering food

We found positive relations between caller age and the propensity to produce grunts to food. However, grunts to food (the likely precursors to chimpanzee 'rough grunts') did not appear regularly until the second year of life (Figure 2c) but from then on these calls occupied a significant amount of all grunts produced, significantly increasing with age (H (3) = 18.778, $p = .0003$, Kruskal-Wallis test, two-tailed; J = 517, $z = 3.986$, $r = 0.607$, Jonckheere's test).

4. Analysis of context: Grunts produced when encountering group members

Grunts to other group members ('social grunts', the likely precursors of adult 'pant-grunts') was the most common context of grunt production but it developed in a peculiar non-linear way (Figure 2d). Initially, grunt rates were very high but they subsequently decreased to a nadir at around 5 years of age. Afterwards, grunt rates increased again steadily until reaching adult levels. Analysis at the age class level revealed an overall significant variation, but the increase was not significant as a result of this non-linear development (H (3) = 8.664, $p = .034$, Kruskal-Wallis test, two-tailed; J = 374, $z = 0.842$, $r = 0.128$, Jonckheere's test; Figure 2d).

4.1. Analysis of social class: Social grunts produced to other group members

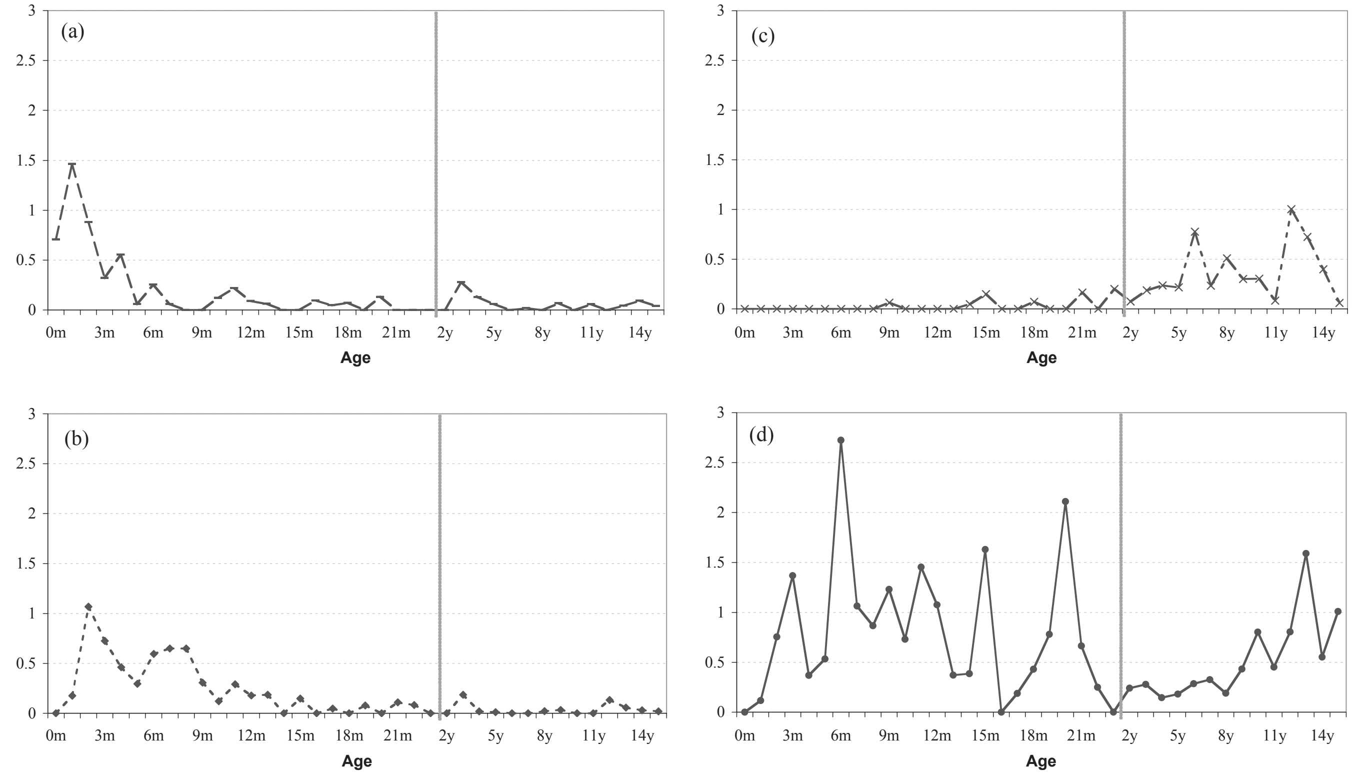
For three families, we were able to extensively monitor very young babies during their first 2 months of life. In all three individuals, the first social grunts (i.e. grunts given to a target individual) were directed to a sibling. In adults, the alpha male attracts the largest proportion of all pant-grunts, but in young chimpanzees the alpha male does not appear as a relevant recipient until subadulthood (see Figure 5a). This was revealed in terms of the similarity between the subadult's and mother's choice of targets, although there was a significant increase with age in the frequency of social grunts directed to him (H (4) = 28.604, $p = .00001$, Kruskal-Wallis test, two-tailed; J = 870.5, $z = 4.594$, $r = 0.625$, Jonckheere's test; Figure 5a). In contrast, grunt rates to adult males remained low in all age groups, despite relatively high grunt rates by the mothers and significant variability across all age groups (H (4) = 18.785, $p = .001$, Kruskal-Wallis test, two-tailed; J = 733.00, $z = 2.488$, $r = 0.339$, Jonckheere's test; Figure 5b). Call rates to adult females were uniformly low with no significant changes over time (H (4) = 7.886, $p = .096$, Kruskal-Wallis test, two-tailed; J = 506.00, $z = -1.100$, $r = -0.150$, Jonckheere's test; Figure 5c). Call rates to subadults, finally, were also low but showed significant variation across age (H (4) = 12.919, $p = .012$, Kruskal-Wallis test, two-tailed; J = 610.5, $z = 0.604$, $r = 0.0821$, Jonckheere's test; Figure 5d).

4.2. Maternal influence: Comparison between maternal pant-grunts and offspring grunts

Females differed in their overall sociability and willingness to produce pant-grunts to other group members (mean 1.15 pant-grunts/h; range 0.34–2.08). Using non-parametric paired comparisons, we compared the pant-grunt rates of each mother with the grunt rates of their offspring and found significant differences in infants ($p = .006$), juveniles ($p = .000$) and subadults ($p = .038$; Wilcoxon test) but not babies ($p = .064$). As data did not meet parametric requirements, we carried out non-parametric correlations between the mothers' and their offspring's grunt rates, which did not reveal any significant relationships in any of the four age groups ($\sigma_{\text{babies}} = -0.486$, $p = .329$, $N = 6$; $\sigma_{\text{infants}} = -0.009$, $p = .979$, $N = 11$; $\sigma_{\text{juveniles}} = 0.225$, $p = .481$, $N = 12$; $\sigma_{\text{subadults}} = 0.476$, $p = .233$, $N = 8$, Spearman correlation; Table 4).

4.3. Analysis of maternal influence: Number of targets

We tested whether there was a relation between the number of individuals targeted with grunts by the mothers and their offspring. For data that met the parametric requirements, we found significant correlations in the younger, but not older age groups ($R_{\text{babies}} = 0.839$, $p = .037$, $N = 6$; $R_{\text{infants}} = 0.707$, $p = .015$, $N = 11$; $R_{\text{juveniles}} = 0.356$, $p = .256$, $N = 12$; $R_{\text{subadults}} = 0.229$, $p = .585$, N = 8, Pearson correlations; Table 5), indicating that mothers and offspring became increasingly different in the group members targeted with grunts.



Time focal hours	14.2	17.1	15.9	12.4	10.8	16.9	11.8	16.9	9.3	16.3	16.4	13.8	11.2	16.2	20.8	6.8	10.6	21.4	13.9
Number of individuals	2	3	3	3	3	4	3	4	3	3	4	5	3	3	3	2	1	3	2
Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	MONTHS																		
Period of develoment	BABIES							INFANTS											

Time focal hours	12.8	7.6	18.1	12.0	5.0	66.8	10.8	54.9	82.8	24.5	55.3	47.2	59.9	46.2	35.4	59.8	70.5	32.6	50.5
Number of individuals	2	2	3	1	1	5	1	3	5	4	4	3	5	4	3	4	4	4	3
Age	19	20	21	22	23	2y	3y	4y	5y	6y	7y	8y	9y	10y	11y	12y	13y	14y	15y
						YEARS													
Period of develoment									JUVENILES						SUBADULTS				

Figure 2 *Frequency of grunt-like vocalizations produced in four basic contexts: (a) no apparent external reason, (b) in response to vocalizations, (c) in response to food, (d) in response to individuals. For the first 2 years, average hourly call rates were calculated for each month of development; from years 2 to 15, average hourly call rates were calculated for each year of development (total number of vocalizations produced by all individuals divided by the total number of hours focal for the different periods). The number of individuals and the number of focal observation hours are noted for each point in the supplemental information.*

4.4. Analysis of maternal influence: Portfolio of targets

Finally, we determined, for each mother separately, her typical portfolio of individuals targeted with pant-grunts. We then assessed the proportion of grunts produced by young chimpanzees of different age classes corresponding to those of the mother. Proportions of similarity in the portfolio of targets significantly increased with age (proportion of targets similar to mother: babies 62% ± 26%, $N = 5$; infants: 87% ± 14%, $N = 11$; juveniles: 90% ± 14%, $N = 7$; subadults 96% ± 4%, $N = 9$, ANOVA, $F(3, 27) = 6.066$, $p = .003$, with a significant linear trend, ANOVA, $F(1, 27) = 16.652$, $p = .0003$; Figure 6, Table 6).

Discussion

Pant-grunts are an interesting example of chimpanzee vocal behaviour because they require a considerable amount of social cognition during production (Laporte & Zuberbühler, 2010). The calls are only given to higher-ranking group members, but call rates are determined by various additional social factors, suggesting that learning of social patterns and sensitivity to context is required. Our primary goal was to document the emergence and growth of this social signal in free-ranging chimpanzees from the first days of life to adulthood. Our second goal was to assess the potential role of the mother in the development of grunting behaviour of young chimpanzees.

Early stages: birth to weaning

The first grunts by chimpanzee babies were produced with no external reason. As already reported by Plooij (1984), we observed that they seem to be linked to moving on the mother's body, apparently as a mere by-product of physical activity. These 'effort grunts' (Plooij, 1984) were not produced in a socially targeted or voluntary way, but when the infant was trying to meet a locomotor goal (changing position, reaching the mother's nipple, grasping to prevent fall and so on). How the transition to communicatively active signals takes place is unclear. It is interesting that older infants, who are producing socially directed grunts, often try to touch their targets or extend their bodies towards them. This suggests that social grunts could be action-based signals that later become ritualized. Interestingly, similar arguments have been made for the development of human grunts from early infancy (McCune, Vihman, Roug-Hellichius, Bordenave, Delery & Gogate, 1996).

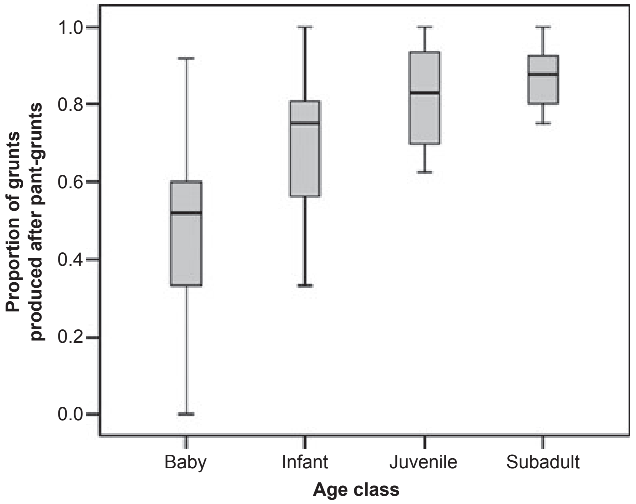


Figure 3 *Proportion of grunts given after adult pant-grunts in the four developmental stages ($N_{babies} = 5$, $N_{infants} = 11$, $N_{juveniles} = 8$, $N_{subadults} = 9$). Box plots represent medians with upper and lower quartiles; whiskers represent data located within 1.5 times the inter-quartile range.*

Socially directed grunting appears around 2 months of age in free-ranging chimpanzees (Plooij, 1984), roughly when other social activities, such as social smiling, emerge in captivity (Tomonaga, Tanaka, Matsuzawa, Myowa-Yamakoshi, Kosugi, Mizuno, Okamoto, Yamaguchi & Bard, 2004). These grunts are typically produced when encountering other group members or in response to vocalizations by the mother. It is often difficult to get a sense of the motivation underlying grunt production in babies, as hearing vocalizations and seeing an individual can act in synergy to trigger these grunt-like calls. The grunting rates in this context increase over the following months with a peak around the seventh month, coinciding with Goodall's (1986) observation of the onset of greeting grunts. Recognition of and interest in other group members thus emerges early and develops rapidly in chimpanzees. However, it should be noted that no grunts were directed at the mother while looking at her, suggesting that these social grunts are not part of mother–infant communication and might thus develop independently. Also, it has been noted that human-reared

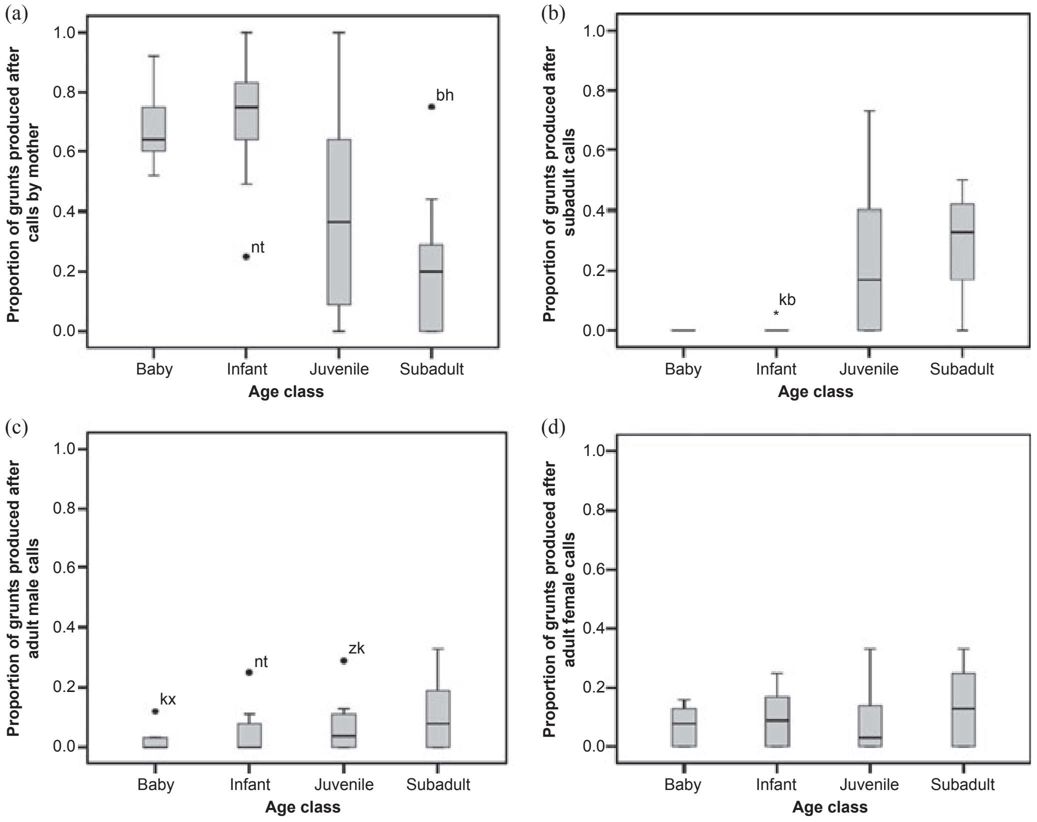


Figure 4 *Grunts produced after vocalizations by members of different social groups: (a) mother, (b) subadults, (c) adult males, (d) adult females. Box plots represent medians with upper and lower quartiles; whiskers represent data located 1.5 times within the inter-quartile range; black circles indicate outliers that are further than 1.5 inter-quartile ranges from the nearer edge of the box, and a star to denote outliers that are further than three inter-quartile ranges from the nearer edge of the box. Individuals' codes: bh: Bahati, kb: Karibu, kx: Kox, nt: Night, zk: Zak.*

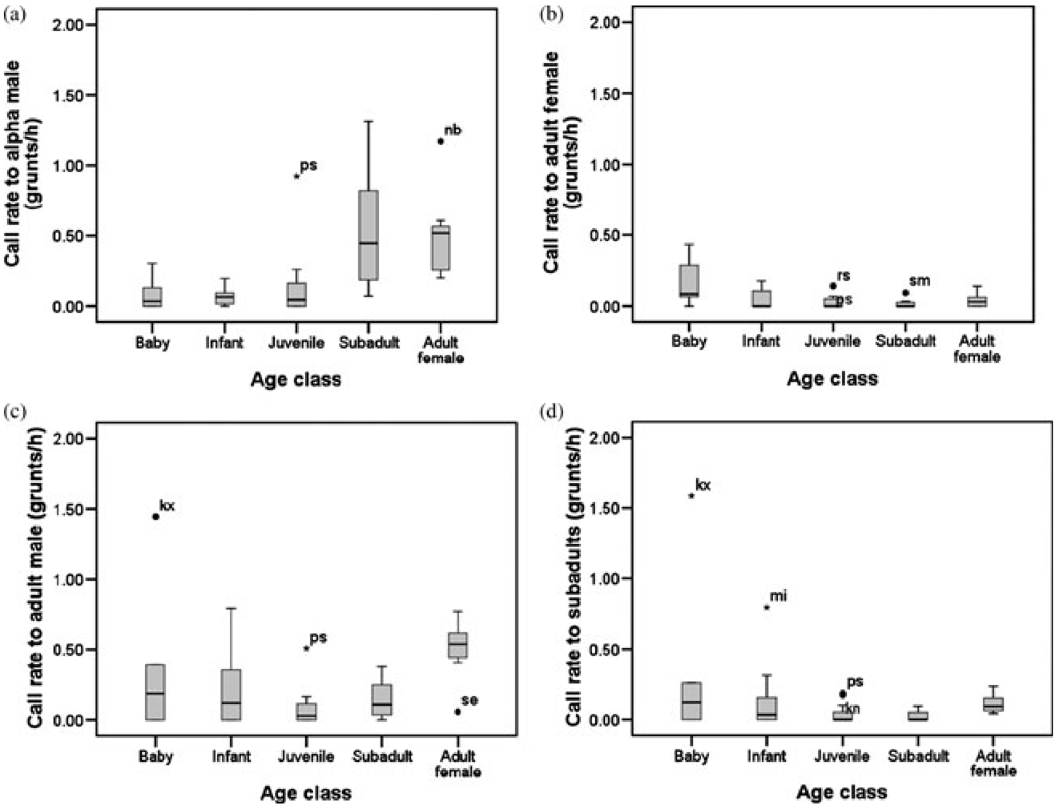


Figure 5 *Grunts produced to different social classes during development: (a) to the alpha male, (b) to adult males, (c) to adult females and (d) to subadults. Box plots represent medians with upper and lower quartiles; whiskers represent data located 1.5 times within the inter-quartile range; black circles indicate outliers that are further than 1.5 inter-quartile ranges from the nearer edge of the box, and a star to denote outliers that are further than three inter-quartile ranges from the nearer edge of the box (Individuals' codes: kn: Kana, kx: Kox, mi: Marion, nb: Nambi, ps: Pascal, rs: Rose, se: Sarine, sm: Simon).*

chimpanzees have no trouble adapting their social grunt production to human carers (Hayes, 1951; Jacobsen *et al.*, 1932; Ladygina-Kohts *et al.*, 1935/2002), suggesting that the signal becomes part of interacting with socially relevant partners. Human infants are sensitive to faces from birth and remain attracted to them during later development (Johnson, Dziurawiec, Ellis & Morton, 1991; Lewis, Mondloch, Budreau, Maurer, Dannemiller, Stephens & Kleiner, 1998). However, they start using grunts communicatively somewhat later than chimpanzees, at around 12 months of age. Interestingly, human grunt production peaks during the second year of life, coinciding with the onset of referential word production, and some authors have argued that grunts constitute an important step toward language acquisition (McCune *et al.*, 1996; Roug-Hellichius, 1998).

A characteristic feature at this early stage in chimpanzees is that, although grunt production can be considerable, there are no visible patterns in selecting targets. Nearly half of all grunts are directed to adult males, but they are also given to a wide range of other individuals (Figure 5). As a result, there are considerable differences between the mothers and their offspring in terms of which group members are addressed vocally (Figure 6). Our general impression was that chimpanzee babies were keen to acknowledge the presence of *any* group member with a grunt, regardless of their identity, as also reported from captivity (Jacobsen *et al.*, 1932; Ladygina-Kohts *et al.*, 1935/2002). A potentially interesting parallel is young vervet monkeys who initially produce alarm calls to a wide range of disturbing events and only with experience learn to narrow call production to the few relevant predator classes (Hauser, 1989; Seyfarth & Cheney, 1986).

Why are young chimpanzees so interested in interacting with other group members vocally at such an early age? In the wild, mothers can receive significant aggression from other group members when returning to the group after parturition, especially from the alpha male (observed for Kewaya/Kox, Kutu/Kathy and Kigere/Kaspa). Moreover, infants under the age of 3 are exposed to considerable risks of infanticide by both male and female group members, although the mechanisms of such events are poorly understood (Clark & Wrangham, 1999; Townsend, Slocombe, Emery Thompson & Zuberbühler, 2007). One possibility is that an infant's efforts to interact with other group members could function in lowering infanticide risk. The prediction here is that vocal infants receive less aggression compared to silent ones, which would suggest that natural selection has favoured social grunting in infants. The fact that cases of infanticide in chimpanzees tend to be committed

Table 4 *Frequency of production of mother pant-grunts and offspring social grunts. Offspring are ranked by age and in ascending order of their mothers' pant-grunt rates*

Class of dev caller	Immature name	Mother name	Immature social grunt rate	Mother pant-grunt rate
Infant	Sokomoko	Sarine	0.00	0.34
Subadult	Simon	Sarine	0.28	0.34
Infant	Zak	Zimba	0.09	0.77
Juvenile	Zak	Zimba	0.23	0.77
Juvenile	Zig	Zimba	0.00	0.77
Subadult	Zig	Zimba	0.45	0.77
Baby	Kox	Kewaya	3.47	0.85
Infant	Kox	Kewaya	0.96	0.85
Juvenile	Katia	Kewaya	0.09	0.85
Baby	Rafia	Ruhara	0.29	0.91
Infant	Rafia	Ruhara	0.20	0.91
Juvenile	Ramula	Ruhara	0.00	0.91
Juvenile	Rose	Ruhara	0.29	0.91
Subadult	Rose	Ruhara	0.16	0.91
Infant	James	Janie	0.82	1.17
Juvenile	Janet	Janie	0.21	1.17
Infant	Faida	Flora	0.47	1.21
Juvenile	Frank	Flora	0.32	1.21
Subadult	Fred	Flora	0.73	1.21
Baby	Marion	Mukwano	0.70	1.22
Infant	Marion	Mukwano	1.85	1.22
Baby	Klauce	Kalema	0.84	1.30
Infant	Klauce	Kalema	0.21	1.30
Juvenile	Kumi	Kalema	0.04	1.30
Subadult	Bahati	Kalema	0.21	1.30
Baby	Karibu	Kwera	0.12	1.35
Infant	Karibu	Kwera	0.46	1.35
Juvenile	Karo	Kwera	0.08	1.35
Subadult	Kwezi	Kwera	1.83	1.35
Baby	Kathy	Kutu	0.38	1.42
Infant	Kasigwa	Kutu	0.17	1.42
Juvenile	Kana	Kutu	0.34	1.42
Juvenile	Kasigwa	Kutu	0.19	1.42
Subadult	Kato	Kutu	0.36	1.42
Infant	Night	Nambi	0.00	2.08
Juvenile	Night	Nambi	0.09	2.08
Subadult	Nora	Nambi	0.82	2.08

Table 5 *Number of individuals addressed with pant-grunts by the mother or social grunts by her immature offspring*

Period of development	Mother-Offspring dyad	Number of targets mother	Number of targets offspring
Babies	Kalema -Klauce	11	9
	Kutu - Kathy	14	13
	Kwera - Karibu	7	3
	Kewaya - Kox	7	10
	Mukwano - Marion	5	4
	Ruhara - Rafia	5	2
Infants	Flora - Faida	4	3
	Janie - James	15	15
	Kalema-Klauce	11	8
	Kutu - Kasigwa	13	3
	Kwera - Karibu	12	14
	Kewaya - Kox	12	20
	Mukwano - Marion	8	9
	Nambi - Night	9	0
	Ruhara - Rafia	5	1
	Sarine - Sokomoko	4	0
	Zimba - Zak	1	0
Juveniles	Flora - Frank	5	2
	Janie - Janet	15	2
	Kalema - Kumi	15	0
	Kutu - Kana	15	6
	Kutu - Kasigwa	9	2
	Kwera - Karo	13	2
	Kewaya - Katia	15	2
	Nambi - Night	9	1
	Ruhara - Ramula	10	0
	Ruhara - Rose	10	1
	Zimba - Zig	8	0
	Zimba - Zak	8	1
Subadults	Flora - Fred	5	3
	Kalema - Bahati	15	3
	Kutu - Kato	15	1
	Kwera - Kwezi	13	9
	Nambi - Nora	13	5
	Ruhara - Rose	10	0
	Sarine - Simon	4	2
	Zimba - Zig	8	3

mainly on the offspring of newly immigrated and poorly integrated females (Townsend *et al.*, 2007) supports this hypothesis.

Intermediate stages: after weaning

Weaning usually coincides with the arrival of a new sibling, generally when the previous offspring is between 4 and 6 years old. Older infants continue to spend much time with their mothers, but increasingly also with peers. During this prolonged period, a key observation was that although youngsters were grunting a lot to food (Figure 2c), they were very reluctant to give grunts to group members, which resulted in very low rates of social grunting (Figure 2d). If social grunts were produced then it was only in special circumstances, such as when separated from the mother by a more dominant individual or when encountering an adult male in the absence of the mother, presumably because they perceived the situation as dangerous (see also van Lawick-Goodall, 1967). Apart from such instances, individuals generally remained silent during encounters, while their mother produced pant-grunts at normal rates, suggesting that the lack of production was not due to a lack of opportunities because they travelled together and thus experienced the same situations. If grunts were given, then they were already produced in an adult-like way, with juveniles often showing the same individual preferences as their mothers (Figure 6). Hence, although young chimpanzees possessed a tool to interact and explore their social world, they made little use of it. Our observations suggest that the lack of use was not the result of incompetence but could be explained with changes in motivation, similar to the patterns of vocal development in human infants that are not straightforward to interpret (Locke, 1993).

Later stages: subadulthood

As subadults, both sexes produced social grunts that were used frequently and in socially competent ways, and (to humans) were indistinguishable from adult pant-grunts (Hayaki, 1990; Hiraiwa-Hasegawa, 1989). A detailed acoustic study would be necessary to determine more quantitatively when the grunts of immatures

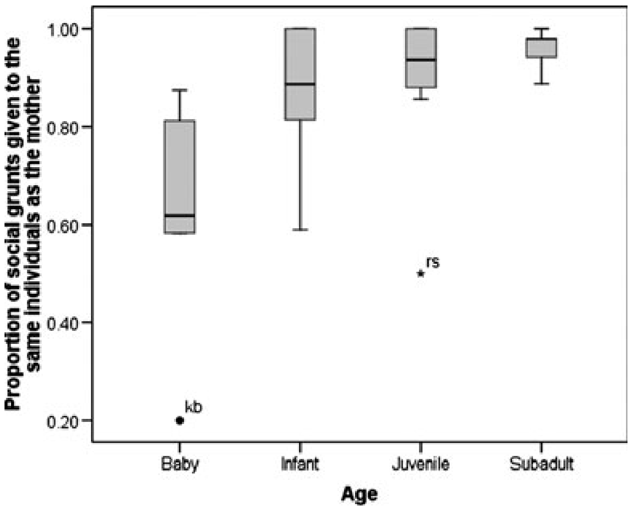


Figure 6 *Proportion of social grunts given to the same individuals as the mother. Box plots represent medians with upper and lower quartiles; whiskers represent data located 1.5 times within the inter-quartile range; black circles indicate outliers that are further than 1.5 inter-quartile ranges from the nearer edge of the box, and a star to denote outliers that are further than 3 inter-quartile ranges from the nearer edge of the box. Individuals' codes: kb: Karibu, kx: Kox, nt: Night, zk: Zak.*

Table 6 *Proportion of social grunts produced by immatures directed to individuals also targeted by their mothers*

	Proportion targets of grunts same as mother	
	Mean	SD
Baby *N* = 5	61.80%	26.45%
Infant *N* = 8	87.43%	14.16%
Juvenile *N* = 11	90.12%	14.41%
Subadult *N* = 7	95.90%	3.77%

become acoustically indistinguishable from adult pant-grunts. At this stage, individuals were very interested in the social fabric of the group, their encounters with other group members multiplied, and they became socially active members with their own independent positions within the community (Pusey, 1980, 1983). The change in social behaviour coincided with physiological changes, such as descended testes in males and sexual swellings in females (Pusey, 1980, 1983). Subadult males no longer behaved in a relaxed manner around the adult male but produced frenzied submissive responses (Hayaki, 1990; Pusey, 1990), a behaviour also present in our study group, which coincided with an increase in social grunt production. Perhaps this was in response to higher rates of aggression, or perhaps they were simply more interested in interacting with adult males, which increased the likelihood of aggressive responses (as suggested by Hayaki, 1990). Although most subadults overlapped largely with their mothers in terms of the preferred individual grunt targets (Figure 6), they differed in the overall grunting activity and in the absolute number of targets. At this age, they might prefer to narrow down their grunt production to specific targets.

Maternal influence

Vocal development in non-human primates, and especially apes, remains a poorly researched area of science. Chimpanzees are famously unable to acquire speech (Hayes & Hayes, 1951), although they can learn other communicative systems based on gestures or visual symbols (Gardner & Gardner, 1969). In terms of vocal behaviour, most complexities so far have been found as context-specific acoustic modifications of basic call types, which often appear to be meaningful to receivers (barks: Crockford & Boesch, 2003; screams: Slocombe, Townsend & Zuberbühler, 2009; food grunts: Slocombe & Zuberbühler, 2005; copulation calls: Townsend, Deschner & Zuberbühler, 2008) or as a result of interactions with humans carers (Hopkins & Savage-Rumbaugh 1991; Hopkins *et al*., 2007; Leavens *et al*., 2004; Taglialatela *et al*., 2003). How these patterns are acquired and whether social learning from the mother and other group members plays a key role is largely unknown.

We did not observe any vocal interactions involving mutual gaze between mothers and their offspring (ML, personal observation), a behaviour thought to facilitate communicative learning in humans (Bard & Leavens, 2009; Papousek, Suomi & Rahn, 1991; Trevarthen & Aitken, 2001). Thus, chimpanzee social grunts do not seem to be acquired within the mother–infant dyad, but develop externally to it. As noted by others, chimpanzee mothers paid little attention to their babies' faces until the babies started touching the mothers' faces, roughly from the second month (Plooij, 1979, 1984). In captivity, face-to-face interactions are observed more often and can involve mutual gaze, possibly the result of decreased physical contact between mothers and infants and more observation efforts relative to the wild (Bard, 1994b, 1998; Bard, Myowa-Yamakoshi, Tomonaga, Tanaka, Costall & Matsuzawa, 2005). The fact that affiliative mutual gaze has also been reported in rhesus macaques (Ferrari, Paukner, Ionica & Suomi, 2009) and that face-to-face interaction can be rare or absent in human societies (Ochs & Schieffelin, 2009) further emphasizes the diversity of mother–infant interactions within and between species.

In chimpanzees, a striking behavioural change was in the juveniles' overall decrease in grunt production during adolescence (Figure 2d). This change took place despite the fact that other crucial social features remained unchanged, such as the close bond to the mother or opportunities to interact with others. This prolonged period of under-using grunts lasted several years, and was succeeded by appropriate signal production during adolescence (Figures 2d and 6), a pattern also seen during the acquisition of a social signal in vervet monkeys. Vervet monkeys produce 'wrr' calls from birth when in distress, but only produce them in the appropriate adult context (in response to other groups) after a temporary gap in production from 3 to 10 months of age (Hauser, 1989). Hauser (1989) suggested that this phenomenon could be the result of interference caused by the integration of other vocalizations into the repertoire. Another hypothesis is that during this period of low social grunt production, young chimpanzees begin to understand the social organization of their community together with appropriate adult grunt use. They may inhibit grunt vocalization until they feel ready to integrate themselves into the social group as independent group members.

In conclusion, during chimpanzee childhood socially directed grunting changes from high production frequency with low social specificity (babies, infants) to low production frequency with high social specificity (juveniles) to high production frequency with high social specificity (subadults), compared to adult female behaviour (Figures 2d and 6). Babies' and infants' vocal behaviour resembles that of their mothers in the *number* of individuals targeted but not in the identity of individuals targeted, suggesting that, despite similar experiences, mothers and offspring assess the same social situations differently or that the grunts serve different functions.

As always, it is difficult to assess the underlying motivation and meaning of these signals and any interpretations should be done in reference to the context of emission and direction (Smith, 1965). The problem becomes even more complex if callers are not yet in full control of their social behaviour which may serve several functions or which may still be subject to maturational processes. For example, visual acuity increases tenfold in the first 8 months of life (Bard, Street, McCrary & Boothe, 1995), suggesting that babies and infants may not have a deep understanding of the social fabric of their community, including the fact that social grunting functions as a submissive signal in adults.

Our study is in line with the interpretation that social grunts produced by young chimpanzees develop into pant-grunts produced by adults, suggesting that an increasingly enhanced understanding of the social relationships between group members progressively aids full adult competence. This transition from initial social interest to recognition of rank relations may not take place in a replacing but in a complementary way. This suggests, supporting Hayaki (1990) and Laporte and Zuberbühler (2010), that chimpanzee pant-grunting should not be conceptualized as a simple ritualized expression of submission but also as a desire to interact with another group member who is higher ranking.

Acknowledgements

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