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ORIGINAL ARTICLE

Between-group variation in production of pant-grunt vocalizations by wild bonobos (*Pan paniscus*)

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Abstract

The potential for aggression is inherent in social interaction, and strategies to reduce the costs of aggression are ubiquitous among group-living animals. One strategy employed by lower-ranking individuals in a variety of species is the production of subordination signals, which are formal signals that communicate the signaler's inferior status relative to the recipient of the signal. Here, we report the results of our investigations into (1) the presence and usage of the pant-grunt vocalization in two populations of wild bonobos; (2) the relationship between the production of pant-grunts and agonistic predictability across the genus *Pan*. We find stark differences in production of pant-grunts in the two populations: bonobos at the LuiKotale field site regularly used pant-grunts as a signal of subordination (primarily, though not exclusively, among male-male dyads); in contrast, at the Kokolopori field site, adult bonobos were never observed producing pant-grunts. Across *Pan*, we find weak support for an association between agonistic predictability and production of pant-grunt vocalizations.

Significance statement

There have been conflicting reports on whether bonobos, like chimpanzees, produce the submissive pant-grunt vocalization. We confirm the presence of the pant-grunt in the bonobo vocal repertoire, and document variation in its production across communities. We also suggest that variation in pant-grunt production across the genus *Pan* may be explained by the predictability of dominance interactions.

Keywords Bonobos · Bonobo communication · Bonobo vocal repertoire · Chimpanzees · Animal communication · Formal signal of subordination · Agonistic predictability

Introduction

Aggression—and the accompanying risk of serious injury—is one of the principal costs of social interactions. Strategies to reduce the costs of aggression are ubiquitous in animals, and, in many species, vocal or visual signals allow individuals to negotiate tense interactions without escalation into aggression or physical contact (e.g., Clutton-Brock and Albon 1979; Kitchen et al. 2013). In some social groups, low-ranking individuals "greet" higher-ranking individuals by producing signals that announce their subordinate status. These signals appear to facilitate peaceful interactions between disparately ranked individuals by reaffirming existing dominance relations, reducing the risks of physical aggression. Such signals of subordination, which do not reflect the outcome of a specific interaction, but instead indicate a signaler's generally inferior status, have been documented in many species, including the "chatter" vocalization of Verreaux's

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Sifaka (*Propithecus verreauxi*) (Lewis 2019), the erect pseudo-penis of spotted hyenas (*Crocuta crocuta*) (East et al. 1993); the grimace and spat call of ring-tailed lemurs (*Lemur catta*) (Jolly 1966; Pereira and Kappeler 1997); hindquarter presenting in hanuman langurs (*Semnopithecus entellus*) (Lu et al. 2008); and mouth licking in arctic wolves (*Canis lupus arctos*) (Cafazzo et al. 2016).

Under which conditions should we expect to observe the production of such signals of subordination? Preuschoft and van Schaik (2000) proposed that subordination signals should be found in societies in which dominance interactions are highly predictable. In other words, when dyadic aggression is unidirectional—i.e., one individual wins all observed contests over another individual—it may benefit lower-ranking individuals to preemptively announce their subordinate status and avoid potential injuries resulting from physical contests with dominant individuals. (Note: we use the term "subordinate" to refer to an individual's current status relative to a higher-ranking individual; it does not imply any intrinsic or permanent status.) However, if dominance interactions are less predictable, it may no longer benefit lower-ranking individuals to preemptively concede contests they could plausibly win.

The strongest evidence in support of Preuschoft and van Schaik (2000)'s proposal, termed here the *Predictability Framework*, comes from a comparison of the signaling behavior across the genus *Macaca*, whose members vary in the predictability of their dominance interactions. In the two species with the most predictability of power asymmetries, rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*), lower-ranking individuals produce formal signals of subordination (de Waal and Luttrell 1985; Preuschoft et al. 1995). In contrast, among their less predictable congeners, stump-tailed macaques (*Macaca arctoides*), barbary macaques (*Macaca sylvanus*), lion-tailed macaques (*Macaca Silenus*), and tonkean macaques (*Macaca tonkeana*), such signals are absent (Deag 1974; Thierry et al. 1989 Tennemann 1992; Preuschoft 1995; Beckmann 1997).

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), who share a common ancestor only 1–2 million year ago (Prüefer et al. 2012), but display differences in social structure and dominance relationships (Gruber and Clay 2016), represent another opportunity to investigate the association between agonistic predictability and production of a formal signal of subordination. Across chimpanzee populations and communities, male-male and male–female dominance interactions are highly predictable. One way to measure agonistic predictability is to categorize each dyad in social group according to the directionality of their dominance interactions: in *one-way dyads*, one individual is always the aggressor while the other individual is always the victim; in *two-way dyads*, both individuals perform aggressive and submissive behaviors to one another. Among adult male chimpanzees, the percentage of two-way dyads is consistently (though not uniformly) low across study sites, indicating a high degree of dyadic predictability (e.g., Ngogo: 0–12% [Watts 2018]; Kanyawara: 5% [Muller and Wrangham 2004]; Tai 25% (Boesch and Boesch-Achermann 2000); see Table S5 for complete list). Female-female interactions are less-well understood and appear to exhibit considerable variation in predictability across communities (Wittig and Boesch 2003; Murray 2007).

The production of a subordination signal among chimpanzees is similarly clear. Lower-ranking individuals produce *pant-grunts*—breathy vocalizations consisting of voiced inhalations and exhalations—which signal their subordination to the individual that is the target of the call (Marler 1976). Pant-grunts are produced by male and female chimpanzees of all ages, directed unilaterally towards individuals of higher rank than the caller (and especially to the very highest-ranking males, who receive a disproportionate proportion of the calls) (Fedurek et al. 2019). Pant-grunts have been observed in all chimpanzee communities studied by researchers, regardless of subspecies, habitat, observation time, or group size (Hayaki et al. 1989; Laporte and Zuberbühler 2010; Sakamaki 2011).

In contrast to chimpanzees, the incidence of two-way dyads varies enormously across study populations of bonobos, ranging from 0% in Lomako and the Wuppertal Zoo to 40% at the Plankendal Zoo, with many communities exhibiting intermediate values (Stevens et al. 2007; White and Wood 2007; Surbeck and Hohmann 2013).

There are also contradictory reports on the use a signal of subordination in bonobos. At the San Diego Zoo, de Waal (1988) observed so-called greeting grunts, a call type exclusively given by two adolescent males to the group's sole adult male in a variety of contexts, including "aggression received; sudden approach; just out; post-conflict, [and] assertive wrestle" (p 207). Pant-grunts have also been observed in all three bonobo groups at the Lola ya Bonobo Sanctuary, though not formally investigated (ZC, unpublished data). In contrast, however, other studies have reported that bonobos do not produce pant-grunts (Ihobe and Furuichi 1994; Furuichi 1997; Stevens et al. 2005, 2007; Paoli et al. 2006; Sakamaki 2013). While a number of previous studies have reported on the presence/absence of pant-grunts, it is worth noting that none of these studies had the occurrence of pant-grunts as their primary focus.

In conducting the present study, we had two goals: (1) to report on the presence/absence of pant-grunt vocalizations, and the relationship between pant-grunt production and age, rank, and sex, in two populations of bonobos (Lui Kotale and Kokolopori) where pant-grunting has not yet been studied; and (2) using these new and previously published data from multiple bonobo and chimpanzee groups to examine

the relationship between pant-grunt production and agonistic predictability across the genus *Pan*. For this comparative analysis, we predict that in high-predictability groups, lower-ranking individuals will produce pant-grunts, while in low-predictability groups, pant-grunts will be absent.

Methods

We collected data for this study at two field sites: LuiKotale and Kokolopori. Details of each field site are given below.

LuiKotale field site

For 13 months between July 2011 and March 2014, IS and ZC sampled behavior and recorded vocalizations from 19 adults (7 males and 11 females, aged ≥ 11 years) and 5 juveniles (3 males and 2 females, aged 5–10 years) from a single group of wild bonobos (the Bompusa community) at the LuiKotale field site in the Mai-Ndombe province of the Democratic Republic of Congo (DRC). Individuals in this community have been studied continuously since 2002 and were fully habituated and identified at the beginning of the study. The subjects' home range was located in dense rainforest consisting of large patches of both *terra firma* and swamp forest (Hohmann and Fruth 2003).

Kokolopori field site

From January to May 2018, IS sampled behavior and recorded vocalizations from two groups of wild bonobos (the Ekalakala and Kokoalongo communities) at the Kokolopori field site in Equateur, DRC. The Ekalakala community consisted of 3 adult males, 6 adult females, and 1 juvenile male. The Kokoalongo community consisted of 27 adults (10 males and 17 females, aged ≥ 11 years), and 7 juveniles (5 males and 2 females, aged 5–10 years). Bonobos in these communities have been studied continuously since 2016 and were fully habituated from the beginning of the data collection period. Home ranges for both communities were located in dense rainforest consisting of large patches of both terra firma and swamp forest (Surbeck et al. 2017).

Data collection

Observers recorded vocalizations and accompanying behavior with an audio recorder (Marantz PMD 660; Sennheiser directional microphone) and later transcribed the recordings. Data were collected over the course of 1515 observation hours (1224 h at LuiKotale and 291 h at Kokolopori). It was not possible to record data blindly because our study involved focal animals in the field.

Observers recorded all instances of pant-grunts, and noted the following information: (1) the identity of the caller; (2) the identity of target of the call; and (3) the context in which the call was produced (contexts included resting, feeding, traveling, aggression, branch dragging, approaching another individual, and being approached by another individual).

For data on agonistic predictability, observers noted the occurrence of dominance interactions that met the following two criteria: (1) an individual ("the aggressor") performed one of the following dominance-related behaviors: arm wave, bipedal swagger, lunge, directed charge, chase, hit, bite, or supplant; and (2) the target of the aggressor's behavior ("the victim") exhibited one of the following subordinate behaviors: fleeing, screaming, or clearly avoiding the aggressor (de Waal 1988).

IS and ZC conducted inter-rater reliability tests in the field with 92% agreement on classification of behavior (based on simultaneous focal-animal sampling, the two observers agreed on 116/126 recorded behaviors).

A note on LuiKotale pant-grunt dataset

Given that the central research question of this study concerns whether bonobos produce pant-grunts *at all*, rather than the rate at which they are produced, our main results are based on a dataset consisting of all observations of pant-grunts collected during focal-animal and all-occurrence sampling. Due to the rarity of the data and to maximize the data available for analysis, we combined our observations from both focal and all-occurrence into a single dataset. However, to calculate sex-specific rates of pant-grunting, we exclusively used focal data; and rates were calculated by averaging each individual's rate.

Dominance ranks

For LuiKotale subjects, individual ranks were based on previously published mixed-sex dominance hierarchies, which were calculated with MatMan (version MfW 1.1, Noldus Information Technology, Wageningen, The Netherlands) using data on agonistic dominance interactions (Surbeck and Hohmann 2013; Douglas et al. 2017).

Dominance ranks for Kokolopori subjects were not calculated because we were only interested in dominance rank in relation to the production of pant-grunts among adults. We did not observe any adult-produced pant-grunts at Kokolopori, so it was not possible to test the association between rank and production of pant-grunts. Therefore, there was no need to calculate dominance ranks for these subjects.

Dyadic directionality

Using our observations of dominance interactions, we categorized all dyads as one of three following three dyad types (and then calculated the proportion of each dyad type in each community):

One-way dyad: the dominant individual was the "aggressor" for all observed dominance interactions, and never the "victim."
Two-way dyad: both individuals in a dyad acted as the "aggressor" in at least one dominance interaction. Two-way dyads, in which each individual was observed acting as the "aggressor" an equal number of times, were further classified as *tied dyads.*
Unknown dyad: no dominance interactions between two individuals were observed.

Dyads for which only one agonistic interaction was observed were categorized as *one-way dyads*. Categorizing such dyads as *one-way dyads* has the potential to artificially inflate the number of one-way dyads relative to the number of two-way dyads because, by definition, they cannot be classified as *two-way* dyads. To assess the influence of this potential bias, we ran two additional analyses based on our model of agonistic predictability (detailed below).

Directional Consistency Index

In addition to the measures of dyadic directionality, we also calculated a measure of overall agonistic predictability: the Directional Consistency Index (DCI) (van Hooff and Wensing 1987). The DCI is calculated using the equation $DCI = (H - L)/(H + L)$, where H is the number of dominance interactions in which a dominant individual was observed acting as the aggressor towards a lower-ranking individual, and L is the number of dominance interactions in which a lower-ranking individual acted as an aggressor. DCI ranges from 0 to 1. A DCI of 0 would indicate that dominants and subordinates acted as aggressors an equal number of times. A DCI of 1 would indicate subordinates never acted as aggressors towards dominants.

A note on datasets comparing agonistic predictability across *Pan*

In order to examine the relationship between agonistic predictability and production of pant-grunts across both bonobo and chimpanzee communities, we supplemented our datasets from LuiKotale and Kokolopori with previously published data. Such a process necessarily means compiling heterogenous datasets collected by different observers, for different purposes, and under different living conditions (captive vs. wild) (see Table S2 for details of each field site/zoo). To avoid the potential confounding effect of comparing mixed-sex and single-sex datasets, we limited our analysis to data on male-male dyads only (and removed the data on female subjects from the mixed-sex datasets).

Acoustic classification

Classification of pant-grunts followed de Waal's (1988) original description of "greeting grunts" as "a rhythmic series of brief, grunt-like, vocalized air expulsions sounding like 'eh-eh-eh'. The grunts are breathy and moderately loud, with an abrupt onset over a broad frequency range… uttered in a rhythm of one or two grunts per second" (p. 207). Observers initially identified pant-grunts in the field during observations. These live classifications were subsequently confirmed via visual examination of spectrograms (Fig. 1; see Supplementary Information for audio recordings).

Statistical analyses

All statistical analyses were conducted in R 3.6.1 GUI 1.70 El Capitan build (R Development Core Team 2019).

Model 1: Relationship between pant-grunts, rank, and sex

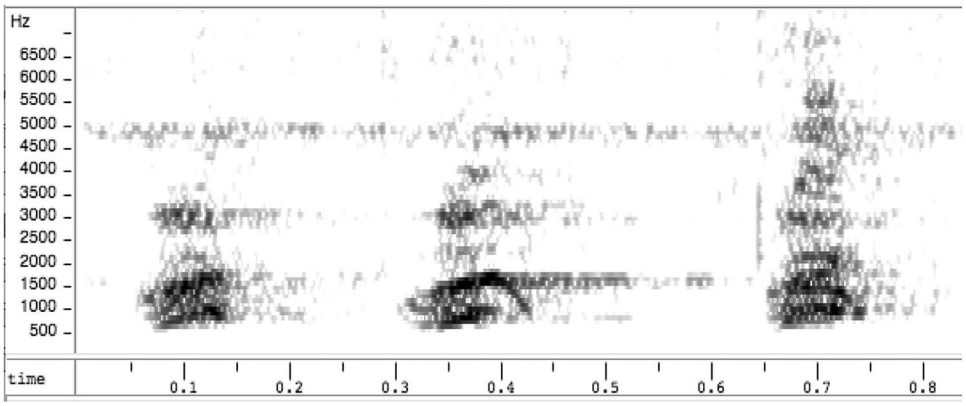

Fig. 1 Spectrogram of a pant-grunt produced by an adult male at the LuiKotale field site

To examine the influence of rank and sex on the production of pant-grunts, we fitted a generalized linear mixed model with binomial error structure and logit link function using the function "glmer" in R package "lme4" (lme4 (version 1.1–27.1). The response variable was a binary observation: did Individual A produce pant-grunts directed at Individual B (0/1). Because we were interested in the directionality of pant-grunts, each dyad is represented by two separate datapoints in this analysis (however pseudo-replication was avoided as individual was entered as a random effect). For example, the dyad consisting of Individuals A and B is included in the model twice: once noting whether Individual A pant-grunted to Individual B; and again noting whether Individual B pant-grunted to Individual A.

The predictor variables we tested were the following: the rank difference between Individuals A and B; the sex of individual A; the sex of individual B; and the interaction between the sex of Individuals A and B. We included "rank difference" in the model to examine whether pant-grunts are produced up the hierarchy. We included the sex of Individual A as a predictor variable to test if males or females are more likely to produce pant-grunts. We included the sex of Individual B as predictor to test if males or females are more likely to be the target of pant-grunts. We examined the interaction between Individual A's sex and Individual B's sex to test whether production of pant-grunts is associated with particular dyad types (i.e., male-male, male–female, or female-female dyads).

To control for repeated contributions per individual and the possibility that some individuals were driving apparent patterns, we entered the identity of Individual A and a Dyad ID that was associated with both the A + B and B + A dyads as random effects.

Model 2: Agonistic predictability and pant-grunt production in the genus *Pan*

To test the association between agonistic predictability and pant-grunt production among male-male dyads at the community level across *Pan*, we fitted a generalized linear model with a binomial error structure and logit link function using the R package "stats" (version 3.6.2). The response variable was the presence or absence (0/1) of pant-grunts in a particular community—i.e., each chimpanzee or bonobo community represented a single datapoint in this model. The predictor variables (defined above) were DCI, the proportion of two-way dyads in the community, and the number of male subjects. Pant-grunts were not used to calculate any of these predictor variables. We included the number of male subjects as a predictor variable to control for the variation in number individuals across communities.

To assess the influence of dyads with only one observed interaction, we ran two modified versions of Model 2 (Model 2a and Model 2b). In Model 2a, we re-ran the Model 2 analysis with all 1-interaction dyads excluded from the analysis. Datasets for which the number of 1-interaction dyads was unknown—i.e., datasets that only included descriptive statistics of dominance interactions, but did not include dominance matrices—were also excluded. In Model 2b, we recategorized all known 1-interaction dyads as either 1- or 2-way dyads according to the cross-community mean proportions of 1- and 2-way dyads. Datasets for which the number of 1-interaction dyads was unknown—i.e., datasets that only included descriptive statistics of dominance interactions, but did not include dominance matrices—were also excluded. Because Models 2a and 2b had significantly reduced sample sizes ($n = 10$ communities, compared to $n = 16$ for Model 2), it was not possible to include three predictor variables; we, therefore, did not include *number of subjects* as a predictor variable in these additional analyses.

Results

Production of pant-grunt vocalizations

LuiKotale field site

We observed 166 pant-grunts produced by adult subjects (27 observed during focal-animal sampling; 139 observed during all-occurrence sampling) (Table 1). Males produced pant-grunts at a mean ± SD rate of 0.45 ± 0.42 per hour ($N = 7$ males; mean number of focal hours per male = 6.5), and all adult males except the most dominant male-produced pant-grunts. Females produced pant-grunts at a mean ± SD rate of 0.10 ± 0.14 per hour ($N = 11$ females; mean number of focal hours per female = 6.5), and 8/13 females were observed to produce pant-grunts. Males were the primary producers and receivers of pant-grunts: 67% (112/166) occurred within male-male dyads (which were 11% of total dyads), 27% (44/166) within mixed-sex dyads (which were 48% of total dyads), and 5% (9/166) within female-female dyads (which were 41% of all dyads). Ninety-nine percent (116/117) of male-produced pant-grunts and 90% (44/49) of female-produced pant-grunts were directed up the hierarchy—i.e., the caller was lower ranking than the receiver (see Fig. 2 for a summary of these data at the dyadic level).

We also observed 9 instances of pant-grunts produced by 5 different juveniles (4 males, 1 female). Eight out of nine juvenile pant-grunts were directed towards adult males; in one instance, the pant-grunt was directed towards a juvenile female (Table S1).

Table 1 Pant-grunts produced by a) male and b) female bonobos at the LuiKotale field site in DR Congo. Data in the table combines focal-animal sampling and ad libitum observations. Individuals are listed in order of rank. Asterisks are next to juveniles; all other individuals are adults (note: individual ZD was a juvenile when he produced 2/28 of his observed pant-grunts)

a)

	Male recipients							Female recipients		
Male callers	CA	BE	JA	AP	EM	RO	ZD	PA	RI	PG*
CA										
BE	24							1		
JA	12	5		1						
AP	5	3	5							
EM		2	4					1		
RO	14	5								
ZD	28		2	2	2	1			2	
UL*	3	1								
GU*			1							
HG*										1

b)

	Male recipients							Female recipients			
Female callers	CA	BE	JA	AP	EM	RO	ZD	PA	MA	OL	GW
PA											
IR											
MA	1										
OL	6	2	1	1	1			2			
RI	1								1		
ZO								1			
GW											
UM	1	1									
WI	1		1					1		1	
LU											
NI	10	4	4			3	1				1
SU	1								1		
PO										1	
RT*	1										

Kokolopori field site

We observed 16 pant-grunts produced by males (12 from the Kokoalongo [KKL] community and 4 from Ekalakala [EKK] community). In all but one case, we could exclude adult individuals as the caller. In 4/16 instances, it was possible to identify the caller. These four cases came from two immature males (one aged ~ 10 and the other ~ 5). In 11/16 instances, it was only possible to identify the caller as an infant or juvenile. In one instance, it was not possible to determine whether the caller was a juvenile or an adult. Adult males were the most frequent recipients of pant-grunts: 6/16 directed to adult males; 6/16 directed to unknown individuals; 2/16 directed to adult females; 2/16 directed to juvenile males. All pant-grunts were observed during all-occurrence sampling (we did not conduct focal follows on juveniles). It was, therefore, not possible to calculate rate of pant-grunts.

We did not observe any pant-grunts produced by Kokolopori females.

Adjusting for differences in time spent on focal-animal sampling and total observation (see Supplementary Information S.1 for details focal hours per individual), if adult bonobos in Kokolopori produced pant-grunts with the same frequency as adult subjects at LuiKotale, we would expect to observe approximately 10 pant-grunts during focal-animal sampling and 40 pant-grunts during the entire period of observation at Kokolopori.

Model 1: Relationship between pant-grunts, rank, and sex

Across dyads, rank difference, the sex of Individual B, and the interaction between the sexes of the two individuals were significantly associated with production of pant-grunts (Table 2). These results indicate that (1) pant-grunts were overwhelmingly produced by lower-ranking individuals towards higher-ranking individuals (Fig. S1), (2) males are more likely to be recipients of pant-grunts than females, and (3) pant-grunts occur more within male-male dyads than male–female or female-female dyads. As adults were not observed to produce pant-grunts at the Kokolopori field site, this analysis only includes individuals from the LuiKotale field site, where adults regularly produced pant-grunts.

Agonistic predictability

Data on Dyadic Directionality and the Directional Consistency Index (DCI) for all three communities are presented in Table 3. As measured by both Dyadic

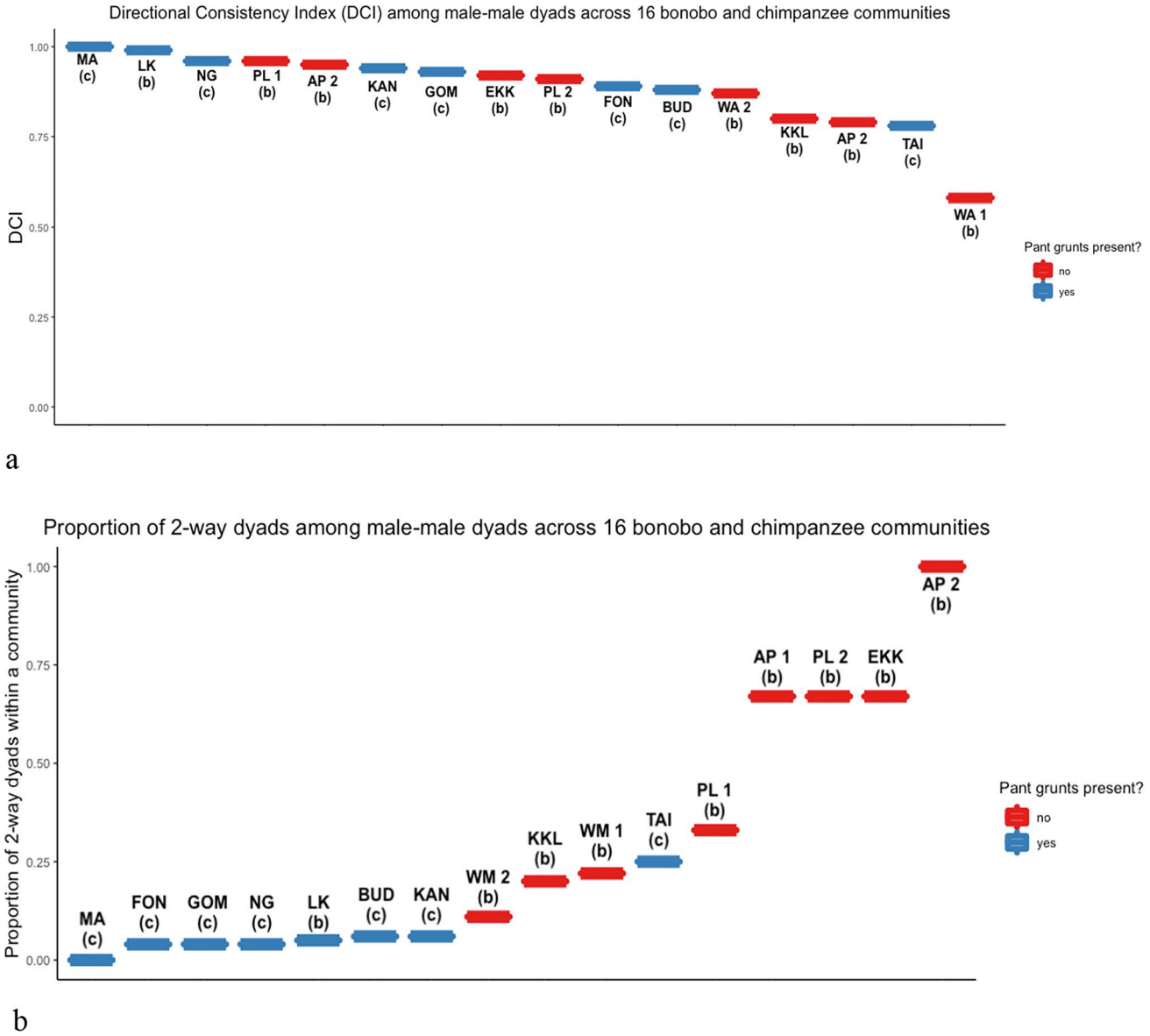

Fig. 2 Two measures of agonistic predictability among male-male dyads: **a** Directional Consistency Index (DCI) and **b** proportion of two-way dyads. "Present" and "absent" refer to whether pant-grunts are observed among adults in a given community (note: juveniles were observed to produce pant-grunts in two "absent" communities: EKK and KKL). Abbreviations above and below bars refer to the following communities: AP Apenheul, BUD Budongo, EKK Ekalakala, FON Fongoli, GOM Gombe, KAN Kanyawara, KKL Kokoalongo, LK LuiKotale, MA Mahale, NG Ngogo, PL Planckendael, TAI Tai, WA Wamba. Letters in parentheses indicate species: c = chimpanzee, b = bonobo

Directionality and DCI, dominance interactions were most predictable in the LuiKotale community, followed by the Ekalakala community, and were least predictable in the Kokoalongo community. The same pattern of relative agonistic predictability was stable across all dyad types (see Table S4 for Tables presenting results separately for male-male, female-female, and male–female dyads).

Model 2: Agonistic predictability and production of pant-grunts across *Pan*

To compare our results to those from other bonobo and chimpanzee communities, we extracted the same measures of dominance predictability for male-male dyads from previously published research from seven wild chimpanzees communities (Ngogo: Watts 2018; Budongo: Newton-Fisher 2004; Kanyawara: Muller and Wrangham 2004, Mahale: Hayaki et al. 1989; Fongoli: Wessling 2011; Tai: Boesch and Boesch-Achermann 2000; Gombe: Bygott 1974) and six bonobo communities (Planckendael1: de Vries et al. 2006; Planckendael2: Vervaecke et al. 2000: Appenheul1 and 2:

Table 2 Results of GLMM testing the relationship between pant-grunt production within a given dyad and the rank and sex of each individual in the dyad among adult individuals at the LuiKotale field site. Bolded *p*-values indicate significance at the $p < 0.05$ level

Model 1	Production of pant-grunts within a dyad (AB)				
Full model	Pant-grunt in dyad (0/1) ~ (1| Individual A) + (1| dyad A + B) + Rank difference + A sex + B sex + A * B sex				
Null model	Pant-grunt in dyad (0/1) ~ (1| Individual A) + (1| Dyad A + B)				
Full-null comparison	$df = 4, \chi^2 = 87.61, p < 0.0001$				
	Estimate	SE	95% CI	*z*	*p*
(Intercept)	−1.63	0.29	(−4.81, −2.30)	−5.57	**< 0.001**
Rank difference	0.26	0.05	(0.16, 0.37)	4.87	**< 0.001**
Indiv. A sex (male)	−1.20	0.95	(−3.07, 0.66)	−1.22	0.206
Indiv. B sex (male)	1.19	0.48	(0.25, 2.13)	2.48	**0.013**
A * B (male*male)	3.07	0.86	(1.39, 4.75)	3.58	**< 0.001**

Table 3 Measures of agonistic predictability in three communities of wild bonobos (key measures highlighted for emphasis). *LK* LuiKotale, *KKL* Kokoalongo, *EKK* Ekalakala. *DCI* Directional Consistency Index. See "Methods" for descriptions of DCI, *1-way*, *2-way*, *unknown*, and *tied dyads*

Bonobo community	LK	KKL	EKK
# of dyads	190	253	45
# of observations	267	432	338
DCI	0.96	0.81	0.87
1-way dyads	41%	48%	51%
2-way dyads	2%	11%	33%
Tied dyads	1%	7%	4%
Unknown dyads	57%	42%	16%

Paoli and Pagali 2008; Wamba 1: Furuichi 1997; Wamba 2: Ihobe 1992).

In pant-grunt-present communities, the incidence of two-way dyads ranged from 0 to 25%; in pant-grunt-absent communities, the range was 11 to 100% (Tables S3, S4). With one exception—the Tai chimpanzees—all pant-grunt-present communities had lower proportions of two-way dyads than pant-grunt-absent communities (Fig. 2b). A model including 2-way dyads, DCI, and number of subjects explained significantly more of the between-group variance in pant-grunt production than a null model including only the number of subjects (Table 4), indicating that together the variables of proportion of 2-way dyads and DCI explain a significant portion of the variation production of pant-grunts across the 16 communities of chimpanzees and bonobos.

Discussion

Our results demonstrate the presence of a formal signal of subordination, the *pant-grunt*, in the bonobo vocal repertoire. This vocalization, similar in acoustic form to the call type of the same name in chimpanzees, was shown to be reliably produced by lower-ranking individuals towards higher-ranking individuals. Given the similarities in both acoustic structure and social usage, the bonobo pant-grunt appears to be homologous to the chimpanzee pant-grunt in form and function.

However, in contrast to the ubiquitous chimpanzee pant-grunt (Crockford 2019), the bonobo pant-grunt was not produced by adults in all communities. In our study, we observed marked differences in the production of pant-grunts across social groups: at the LuiKotale field site, lower-ranking individuals regularly produced pant-grunts towards dominant individuals, while at the Kokolopori field site, no adults were observed to produce pant-grunts.

Table 4 Results of Model 2, testing the relationship between production of pant-grunts within a community and proportion of two-way dyads, DCI, and number of subjects

Model 2	Production of male-male pant-grunts across 16 communities of chimpanzees and bonobos				
Full model	Pant-grunts present in group (0/1) ~ prop. 2-way dyads + DCI + number of subjects				
Null model	Pant-grunts present? (0/1) ~ number of subjects				
Full-null comparison	$df = 2, \chi^2 = -6.52, p = 0.038$				
Predictors	Estimate	SE	95% CI	*z*	*p*
(Intercept)	−2.74	9.96	(−35.31, 16.86)	−0.28	0.783
Proportion 2-way dyads	−14.06	10.87	(−44.89, 2.31)	−1.29	0.196
DCI	5.78	9.54	(−13.11, 34.69)	0.61	0.545
# of subjects	0.04	0.24	(−0.28, 1.03)	0.15	0.882

As predicted by the Predictability Framework (Preuschoft and van Schaik 2000), this variation in production of a formal signal of subordination was associated with underlying variation in the agonistic predictability. As measured by the Directional Consistency Index (an indicator of how frequently dominant individual win agonistic interactions) and 2-way dyads, the pant-grunt-producing LuiKotale bonobos had more predictable dominance interactions than either community in Kokolopori, where no adults were observed to produce pant-grunts.

Our results provide tentative support for the Predictability Framework's predicted association between dominance predictability and production of a subordination signal. With one exception (the Tai chimpanzees), all pant-grunt-present communities have a lower incidence of 2-way dyads than pant-grunt-absent communities (Fig. 2b), though the relationship between two-way dyads and pant-grunt production was not significant (Table 4). Our other measure of agonistic predictability, the Directional Consistency Index (DCI), did not appear to correlate at all with pant-grunt production (Fig. 2a), suggesting DCI and incidence of 2-way dyads may measure different aspects of agonistic predictability.

Data from both the present study and de Waal (1988) are consistent with the possibility that juvenile males (aged 5–10) may produce pant-grunts more consistently than other age-sex classes. The Predictability Framework may also shed light on this curious observation. Though we do not have data on dominance interactions involving juveniles, interactions between juvenile and adult males are likely extremely one-sided. Producing a formal signal of subordination, then, would be an advantageous strategy for juvenile males to reduce unnecessary aggression. A recent report on the high cost of severe aggression directed at juvenile males highlights the potential benefit of avoiding such aggression (Hohmann et al. 2019).

Limitations

We would like to address several potential limitations of the current study. First, our conclusion that pant-grunts are not produced by adults at the Kokolopori field site is based on relatively low number of hours of focal-animal sampling (mean ± SD of 1.7 ± 1.1 h/individual). While we acknowledge that this merits a cautious interpretation our results, we also believe there are several reasons to have confidence in the reliability of our finding that juveniles, but not adults, produce pant-grunts at the Kokolopori field site. First, observers were recording audio for 291 h of observation. Using these recordings, it is possible to observe all (or very nearly all) the pant-grunts occurring during that time regardless of the observation condition. Thus, the total hours of observation is a more accurate measure of research effort than focal hours alone. Second, the fact that pant-grunts were quickly observed among juveniles strengthens the case that adults were not producing pant-grunts as it demonstrates that the calls are relatively easy to observe when they are, in fact, being produced (even when produced by individuals that observers were not actively observing). Thus, it is very unlikely that observers would have recorded the pant-grunts of juveniles, but missed those of the carefully observed adults. Lastly, at LuiKotale, pant-grunts produced by adults were quickly observed by two trained researchers before the lead researcher visited Kokolopori (just as for the juveniles at Kokolopori). Again, we believe this strengthens the case for the non-observation of adult pant-grunts at Kokolopori because it demonstrates the observers can reliably record the vocalization with relative ease with essentially the same observation conditions.

Second, some of the previously published datasets we analyzed came from wild communities; others were from captive groups. It is possible that captivity may distort patterns of dominance interaction, and a perfect comparison would only use datasets from the wild. However, we do not believe using data from captivity presents a significant problem for the current study because we are interested in the consequences of agonistic predictability, not its proximate or ultimate causes. Thus, if captivity tended to produce less predictable interactions, we would expect to see fewer groups in captivity producing pant-grunts.

Future directions

Our results, given their preliminary nature, raise more questions than they answer, and we want to briefly mention two issues we hope future research might address: first, agonistic predictability at the *dyadic* level appears to influence *group-wide* production of pant-grunts. Even in communities with highly unpredictable dominance interactions, there are many one-way dyads (i.e., dyads where one individual is always dominant to the other). Why is it that lower-ranking individuals in highly predictable dyads do not produce pant-grunts? One possibility is the pant-grunt is a signal that not only reflects dyadic dominance relations, but is also contingent upon group-wide behavioral tendencies (i.e., something analogous to a social norm). A similar phenomenon was recently observed in chimpanzee call sequences (Girard-Buttoz et al. 2022).

Second, future research should test alternative hypotheses for the variation in pant-grunt production across *Pan*. One such alternative worth investigating is the relationship between cohesiveness (i.e., the degree of fission–fusion dynamics) and production of pant-grunts. Pant-grunts are often observed during fusion events when individuals are reuniting, suggesting that pant-grunts may be especially beneficial for low-ranking individuals negotiating their interactions

with higher-ranking individuals whom they have not seen for some time (Fedurek et al. 2021). There is also evidence for significant variation between communities in the frequency with which individuals separate into distinct parties and then subsequently reunite (i.e., variation in community cohesiveness) (Furuichi 2009). One possibility, then, is that the variation in pant-grunt production across communities can be explained by the degree of fission–fusion dynamics in different communities—i.e., there is stronger selection pressure on lower-ranking individuals to produce pant-grunts in communities with a high degree of fission–fusion dynamics, compared to individuals in more cohesive communities.

Conclusion

The bonobo vocal repertoire includes the *pant-grunt*, a call type that signals a caller's subordinate status vis a vis the recipient of the call. Based on acoustic and functional similarity, it is likely homologous to the chimpanzee pant-grunt. In contrast to observations from chimpanzees, the pant-grunt is not universally produced across communities. In our study, we observed one community (LuiKotale) in which adults regularly produced pant-grunts in one community, and two communities (Ekalakala and Kokoalongo) in which adults were not observed producing pant-grunts. Our results do not provide a definitive explanation for the variation in the presence of pant-grunts across bonobos and chimpanzees. However, they are consistent with the prediction of the Predictability Framework (Preuschoft and van Schaik 2000) that pant-grunts (and other signals of subordination) are likely to be present in societies with highly predictable dominance interactions, and, conversely, likely to be absent in societies with unpredictable dominance interactions.

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Data availability All datasets analyzed in the current study are presented in either the "Results" section or Supplementary Information.

Declarations

Ethics approval The study was conducted in accordance with the current laws in the Democratic Republic of the Congo, Switzerland, and the USA. The research was approved by the Animal Care and Use Committee of the University of Pennsylvania (Protocol no. 804117) and also adhered to the guidelines set forth by the Animal Behaviour Society. Furthermore, observers took the following precautions to minimize stress for subject animals: (1) maintaining at least 7 m of distance from animals; (2) remaining as quiet as possible and never interacting in any way with the bonobos; (3) wearing surgical facemasks at all times to reduce the risk of zoonotic transmission.

Conflicts of interest The authors declare no competing interests.

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