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Begging and social tolerance: Food solicitation tactics in young chimpanzees (*Pan troglodytes*) in the wild

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ABSTRACT

The substantial role of food sharing in human evolution has been widely recognized, and food-soliciting tactics may have been critical in facilitating these transfers. Great apes, our closest living relatives, also use different food-soliciting tactics to obtain food from both kin and non-kin. However, the individual and social factors involved in requests for and subsequent transfers of food have been relatively little studied. Here, we examined which tactics (e.g., tactile gestures, taking actions, and vocalizations) infant chimpanzees (*Pan troglodytes*) employ to solicit food as well as the success of obtaining food from their conspecifics. Using a multimodal approach, we focused on food-related interactions in 14 chimpanzee infants of two different subspecies (*P. t. schweinfurthii/verus*) living in the communities of *Kanyawara*, Uganda, and *Taï South*, Côte d'Ivoire. Overall, we found that infants' solicitation tactics included mainly visual or tactile gestural requests and taking attempts, while vocalizations and gestures involving auditory components were rarely used. With increasing age, infants used more visual gestures when soliciting food from conspecifics other than the mother. If food was solicited from mothers or maternal kin, infants predominantly begged for food via (mechanically effective) taking attempts. In terms of subsequent food transfers, taking attempts were more successful than gestures. In light of the prevalent use of non-contact begging despite low rates of success, food solicitation in young great apes might also function to facilitate social tolerance and gain social information. We thus conclude that the food sharing context might represent a critical platform to learn and practice social rules underlying cooperative interactions, which can later be generalized across collaborative domains.

1. Introduction

Humans have evolved highly specialized forms of food sharing, which enabled them to live in large social groups and probably selected for sophisticated cognitive skills (Isaac, 1978). Food sharing in humans has been considered unique in the animal kingdom as it is often associated with the concepts of cooperation, fairness, and punishment (Fehr & Schmidt, 1999; Gintis, 2000), and developed into central place foraging and central place provisioning (Isaac, 1978; Lovejoy, 1981). Food transfers play a larger role in human society compared to other primate species, occurring frequently among related and unrelated individuals in both hunter–gatherer and industrialized societies (Boyd & Richerson, 2009; Kaplan, Hill, Hawkes, & Hurtado, 1984). Favoring reproductive success by facilitating faster reproduction and greater survival, it represents a critical element of allo-parenting and vertical (i.e. intergenerational) cooperation (Jaeggi & Gurven, 2013). Thus, intergenerational transfers among kin have become one of the key features of human social organization (Kaplan, Gurven, Hill, & Hurtado, 2005; Kaplan, Hooper, & Gurven, 2009) and are inseparably linked to humans' phylogenetic history and success (Isler & van Schaik, 2012; Kaplan, Hill, Lancaster, & Hurtado, 2000). Hallmarks of human cooperative psychology such as sensitivity to signals of need and audience effects supposedly have played a major role for this reliance on provisioning, signalling, and social exchange (Gurven, 2004; Jaeggi & Gurven, 2013). Specifically, enhanced prosociality linked to the human cooperative breeding system has been argued as one of the important psychological preconditions for the evolution of honest, low-cost communication and enhanced cognitive abilities (Burkart, Hrdy, & van

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Schaik, 2009; but see Lukas & Clutton-Brock, 2012; Thornton & McAuliffe, 2015 for different views). Therefore, the evolutionary roots of cooperative forms of food sharing have attracted increasing research attention in recent years (e.g. Burkart, Guerreiro Martins, Miss, & Zuercher, 2018; Jaeggi & van Schaik, 2011; Samuni et al., 2018)

Active food solicitation in the form of requests has been of special interest to developmental and comparative research, as this comprises a crucial platform for early social communication during hominid development (Bard, 1992). The earliest (pre-linguistic) gestures of humans are requests used to manipulate another's behaviour in food or object transfer interactions (Acredolo & Goodwyn, 1988; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979). For example, 15–16-month-old human infants reliably understand begging gestures (i.e. hand palm turned up) as requests and respond to them appropriately (e.g., by handing over an object to the requesting individual; Rheingold, Hay, & West, 1976; Rossano & Liebal, 2014). Rather than using begging gestures in isolation to request objects, they produce multimodal combinations involving reaching gestures (i.e. arm and hand extended towards the food) and short vocalizations towards the target (Rossano & Liebal, 2014).

In the middle of the last century, food sharing was still attributed to humans only and tightly linked to the emergence of cooperative hunting (Tiger & Fox, 1971; Washburn & Lancaster, 1968). However, this might have been due to a narrow use of the term, as it is now well-understood that food sharing is not necessarily cooperative. Defined as relinquishing control of a food item by one individual (the owner) in favour of another (Feistner & McGrew, 1989; Gurven, 2004), food sharing can also be classified according to the increasing level of sharing intention in the food possessor: theft, recovery from ground, passive sharing, active-passive sharing, active sharing, and gift (Boesch & Boesch, 1989; for more details, see below). Today, we know that this behaviour is widespread across the animal kingdom. Food-sharing interactions have been reported from various taxa, including insects (e.g. Mas & Kölliker, 2008; Rauter & Mooref, 1999; Vahed, 1998), birds (e.g. Kilner, 2002; Sacchi, Saino, & Galeotti, 2002; Villaseñor & Drummond, 2007), bats (e.g. Carter & Wilkinson, 2013), cetaceans (e.g. Wright, Stredulinsky, Ellis, & Ford, 2016) and primates (e.g. Feistner & McGrew, 1989; Jaeggi & van Schaik, 2011). It occurs among both kin and non-kin, although regular sharing beyond the bonds with offspring and mates is restricted to few mammalian taxa, such as primates and bats (Stevens & Gilby, 2004).

In this context, signals (i.e. acts or structures that alter the behaviour of others; e.g. Maynard Smith & Harper, 2003) of need by dependent offspring have evolved, allowing parents to provide their young with an optimal level of resources (Godfray, 1991, 1995). Because several studies in birds and mammals demonstrated an empirical link between food solicitation effort (e.g. call amplitude) and levels of hunger (= need), begging is thought to qualify as honest, costly signalling (Godfray, 1991; Villaseñor & Drummond, 2007). Surprisingly, even insect larvae deploy an impressive variety of tactile, vibrational, or chemical signals to solicit food from parents (Mas & Kölliker, 2008). For example, ant larvae beg by waving their heads and mandibles, and waving rate is correlated with hunger level (Hölldobler, Stanton, & Markl, 1978). Similarly, burying beetles (*Nicrophorus* spp.) larvae solicit food by head raising, leg waving and touching the mouth parts of the parents (Rauter & Mooref, 1999). However, begging signals inducing feeding from parents have been most extensively studied in altricial birds (i.e. with young that are hatched in a very immature and helpless condition, e.g. all passerine species). They are remarkably similar across species, as they usually consist of multimodal signals involving forceful postural movements, brightly coloured beak gapes (sometimes including patterns acting as supernormal stimuli) and repetitive vocalizations (Kilner, 2002). Different signal components (e.g. call amplitude, gape size) seem to provide different kinds of information about the nestlings (hunger levels, offspring quality) (Kilner, 2002; Sacchi et al., 2002; Villaseñor & Drummond, 2007). Hence, begging in birds can be considered as *multiple-message* signals (Bradbury & Vehrencamp, 2011), with "message" defined in the sense of Smith (1965) as the information that the sender encodes. Studies on vocal begging in several mammal species (e.g., meerkats *Suricata suricatta*, and piglets *Sus scrofa domesticus*) also revealed that parental provisioning was associated with need or quality. Specifically, it was shown that call rate affects feeding rate in meerkats (Manser & Avey, 2000), whereas call pitch and amplitude was associated with offspring hunger levels and parental feeding investment in piglets (Weary & Fraser, 1995; Weary, Lawson, & Thompson, 1996).

In non-human primates, our main models for the study of human social evolution, food sharing from adult individuals to immature ones occurs very frequently (see for review Jaeggi & van Schaik, 2011) and has been shown to be often independent from the nutritional value of food items (Jaeggi, van Noordwijk, & van Schaik, 2008; Nishida, 1996; Silk, 1978). There is ample evidence that social actions like gesturing in a food-related context are probably deeply rooted in humans' evolutionary past (Holler & Levinson, 2019): some gesture types that have been described in great apes (Rossano & Liebal, 2014; Wilkinson, Leudar, & Pika, 2012) resemble to a large extent those gestures young children deploy to request (e.g. reaching) or offer food (e.g. holding out hand with object).

A recent study of Liebal and Rossano (2017) on captive chimpanzees (*Pan troglodytes*) and orang-utans (*Pongo abelii*) showed that taking, as opposed to requesting or offering, was the initiation type that most commonly led to transfers of food. The researchers explained the low rates of overall food sharing with the food items being easy to obtain by other individuals in the group, and concluded that monopolizability of food determines to a large extent the rate of food requests. Other studies with easy-to-monopolize food items revealed that food transfers in orang-utans and chimpanzees were generally preceded by begging gestures (Kopp & Liebal, 2016; Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013). Silk and colleagues (2013) showed that producing begging gestures resulted in higher transfer rates in captive chimpanzees; low frequencies of begging were likely to be ignored, while higher levels of begging received more active responses "that seemed to reflect the possessors desire to resist solicitations" (Silk et al., 2013). Moreover, previous work has shown that gestural requests play a role in food solicitations of young apes in natural environments, including orang-utans (Bard, 1992) and chimpanzees (Fröhlich, Müller, Zeiträg, Wittig, & Pika, 2017). The transition from intentional action to intentional communication—when infants start to direct their behaviour to a social agent in addition to a desired item ("coordinated person-object sequences") (Bretherton & Bates, 1979; Sugarman, 1983)—is thus evident both in human and great ape infants, pointing towards an evolutionary basis for communicative competence (Bard, 1992; Plooij, 1978).

However, the communicative acts used to initiate food transfers in great apes have not received much research attention thus far (but see Liebal & Rossano, 2017; Rossano & Liebal, 2014; Wilkinson et al., 2012), especially with regards to effects of modality, age and social relationship. In the evolution of human communication, predicting outcomes in the interaction with our social environment was probably critical (de Lange, Heilbron, & Kok, 2018; Kilner, Friston, & Frith, 2007), but little is known about the origins (or presence) of this cognitive ability in other primates (however, see e.g. Schmelz, Call, & Tomasello, 2013; Waller, Whitehouse, & Micheletta, 2016). Considering that food transfers are probably tightly linked to cooperative tendencies (Jaeggi, Burkart, & van Schaik, 2010), we would also expect familiarity and kin relationships to play a profound role in food solicitation tactics. Studying the influence of familiarity on communicative output in great apes represents an interesting parallel to politeness theory in linguistics, in which recipients are considered "as to how they should be interactionally treated, including behaving in a manner that demonstrates appropriate concern for interactors' social status and their social relationship" (Brown, 2015, p. 326).

Concerning primate food-sharing, one of humans' closest living

relatives, the chimpanzee has received the majority of research attention, assuming that chimpanzee behaviour can provide crucial insights into our own evolution. Moreover, chimpanzees hunt and feed on a large variety of plant and animal species, some of which represent high-energy, monopolizable food sources in the wild (Boesch & Boesch-Achermann, 2000; Gilby, 2006; Goodall, 1986; Mitani & Watts, 2001; Nishida, 1996). The evolutionary forces shaping food transfers have been heavily debated. Currently—and due to the large variation between research groups and populations—hypotheses center around reciprocity, harassment and social bonding (e.g. Gilby, 2006; Gomes & Boesch, 2009; Mitani & Watts, 2001; Samuni et al., 2018; Silk et al., 2013; Wittig et al., 2014). The role of communicative tactics employed to solicit food has, however, received very little attention in these studies, and the repertoire of communicative acts initiating food transfers in chimpanzees might be considerably larger than previously recognized (e.g., Gilby, 2006; Nissen & Crawford, 1936; Silk et al., 2013). Early ethograms from various field sites of wild chimpanzees described different begging gestures involving the hand(s) or the mouth (e.g. "extend hand") (Goodall, 1986; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999; Plooij, 1984). Focusing specifically on meat sharing, a recent study on the *Ngogo* community in the Kibale National Park, Uganda described gestures such as "HAND CUPPED", "HOVER" and "PALM UP" (Wilkinson et al., 2012). However, systematic and quantitative studies focusing on communicative acts in chimpanzee food sharing are still limited to great apes living in captivity (Liebal & Rossano, 2017; Rossano & Liebal, 2014).

Fröhlich and colleagues recently carried out one of the first systematic investigations of communicative complexity in chimpanzees living in their natural environments with a special focus on development (Fröhlich et al., 2017; Fröhlich, Wittig, & Pika, 2016a, 2016b; Fröhlich, Wittig, & Pika, 2019; Pika & Fröhlich, 2019). A major conclusion deriving from these studies was that social exposure and interactional experiences play a critical role for the communicative development of chimpanzees. Moreover, their study on play solicitation revealed that the use of sensory modality (visual versus tactile gestures) was affected both by infant age and kin relationship with the recipient (Fröhlich et al., 2016a). Specifically, the use of visual (and also audible) signals by chimpanzees increased throughout infancy. While visual signals were mainly directed towards interaction partners other than the mother, tactile play solicitations were in the majority of interactions directed at mothers (Fröhlich et al., 2016a). In line with an early study of Bard (1992) on young free-ranging orang-utans, a recent cross-contextual study on gestural development indicated that food sharing is an important context for gestural practice in young chimpanzees (Fröhlich et al., 2017). Chimpanzee mothers regularly share food with their offspring, particularly foods that are difficult for offspring to process on their own (McGrew, 1975; Nishida, 1996; Silk, 1978). However, infants will also attempt to acquire food from other individuals, such as siblings, peers and adults. In light of accumulating evidence for social learning in chimpanzee societies (Whiten et al., 1999), it remains critical to disentangle effects of age, kin relationship and group affiliation on communication efforts. Despite the great intra-specific variability in chimpanzee behaviour (Boesch, Hohmann, & Marchant, 2002), we still know next to nothing about the existence of between-group differences in communicative behaviour (however, see Fröhlich & Pika, 2019; Pika & Deschner, in press). While there is, to date, only limited evidence for cultural variants of communicative acts (e.g. leaf-clipping; Boesch, 1996), an in-depth understanding of chimpanzee communication has probably been hampered by overlooking the role of context- and group-specific usage learning underlying communication (Fröhlich & Hobaiter, 2018; Pika & Deschner, in press). In addition, the influence of social and individual factors involved in requesting and receiving food in infant chimpanzees is poorly understood.

Here, we aimed to shed light on the solicitation tactics and success in chimpanzees living in their natural environments by focusing on gestures, vocalizations and actions used in the context of food sharing. Our goal was to disentangle the individual, social and communicative factors influencing the deployment of solicitation behaviours as well as the success of obtaining food from social partners. We studied the behaviour of chimpanzee infants living in two communities (*Kanyawara*, Kibale National Park, Uganda, and *Taï South*, Taï National Park, Côte d'Ivoire) comprising two different subspecies (*Pan troglodytes schweinfurthii, Pan t. verus*).

Specifically, we investigated three questions: First, which solicitation tactics do infant chimpanzees use to elicit food transfers? To address this question, we examined the variety of gestural, vocal, and mechanically effective (i.e. including forceful actions) behaviours employed. We analysed whether instances of food solicitation were purely visible (no physical contact to food owner, no vocalization), tactile (involved physical contact but no vocalization), audio-visual (vocalization without physical contact) and audio-tactile (vocalization with physical contact).

Second, to what extent do (maternal) kin relationship and age affect the production of gestures and taking attempts? We did not consider paternity, since evidence for paternal kin recognition in chimpanzees with their promiscuous mating system seems very limited (however, see Lehmann, Fickenscher, & Boesch, 2006; Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016). Chimpanzee mothers have been reported to be generally tolerant towards their offspring, often sharing food passively and allowing 'theft' (van Lawick-Goodall, 1968). Given that less familiar, unrelated conspecifics may be more reluctant to share their food, we predicted that infants would employ considerably more non-physical communicative effort in interactions with food owners other than the mother (Wilkinson et al., 2012). Moreover, we predicted to find effects of infant age on the type of food requests, since a developmental trajectory from actions and tactile signals to visual signals had been found in previous studies in the contexts of mother-infant joint travel and social play (Fröhlich et al., 2016a, 2016b).

Third, which individual, social and communicative factors predict the successful initiation of food transfers? We predicted that mothers and maternal kin would be more likely to share food with infants than other conspecifics. In addition to the effects of kin relationship and age discussed above, we examined whether the food solicitation tactic, such as visual and tactile requests as well as taking attempts (i.e. mechanically effective acts), affected the success in eliciting food sharing. Recent work on captive chimpanzees and orang-utans demonstrated that taking attempts more often resulted in obtaining food than gestural requests (Liebal & Rossano, 2017). However, the drivers of various begging tactics and food sharing might differ substantially between groups living in wild and captive settings.

2. Methods

2.1. Study sites and subjects

The study was carried out on two communities of chimpanzees: *Kanyawara* in the Kibale National Park, Uganda, and *Taï South* in the Taï National Park, Côte d'Ivoire. Detailed information on study sites and communities has been provided elsewhere (Boesch & Boesch-Achermann, 2000; Wilson, Kahlenberg, Wells, & Wrangham, 2012; Wittig, 2018; Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996). We observed food-related interactions of 14 chimpanzee infants, comprising seven individuals living in the *Kanyawara* and seven in the *Taï South* community. Ages ranged from nine to 78 months (see Table 1 for detailed information on subjects and recorded interactions).

2.2. Data collection

Focal observations of chimpanzee mother-offspring pairs were conducted during two three-month periods at both *Kanyawara* and *Taï South* between October 2012 and May 2014 (*Kanyawara*: March–May 2013 and 2014; *Taï South*: October–December 2012 and 2013). We

Table 1
Details on study subjects and recorded interactions.

Group	ID	Age (min)	Age (max)	Sex	*N* solicitations	*N* transfers
Kanyawara	LL	15	18	F	9	1
	MM	13	27	F	17	1
	OB	13	28	M	84	11
	OL	48	60	F	17	0
	TR	15	30	F	105	21
	WC	55	68	M	47	11
	WZ	9	23	M	113	36
Tai South	BL	48	61	F	28	0
	IN	10	12	M	119	28
	IT	64	78	M	47	3
	JF	15	15	M	2	0
	KY	19	33	F	149	16
	MH	12	24	F	121	23
	SL	15	29	M	339	67
Total	**14**	**9**	**78**	**7:7**	**1197**	**211**

followed infants and their mothers on average five days per week between 0700 and 1800 (dawn to dusk), using an integrated focal-behavioural sampling approach (Altmann, 1974). Social interactions between chimpanzee infants and their conspecifics in the behavioural context of feeding were recorded using a digital High-Definition camera (Canon Legria HF M41) with an externally attached unidirectional microphone (Sennheiser K6). The use of these devices enabled the collection of high-quality footage combined with observer comments and broad categories of vocalizations (Fröhlich et al., 2016a, 2016b). During 1154 hrs (*Kanyawara*: 556.5 h, *Taï South*: 597.5 h) of focal observation, we collected a total of 16.7 hrs (*Kanyawara*: 6.5 h, *Taï South*: 10.2 h) of video footage capturing social interactions in the context of food solicitation.

2.3. Coding procedure

To enable statistical analyses, a total of 310 high-quality recordings of food-related interactions (i.e. all video files with clear visibility of our target behaviours) were coded using the program Adobe Premiere Pro CS4 version 4.2.1. We coded food-related interactions from when the solicitor started to show interest in the food until a piece of food was transferred or the solicitor did not show interest for at least 5 s or left (see also Kopp & Liebal, 2016). Interactions usually comprised a request and/or a taking attempt, as well as a resistance behaviour (or, ignorance/tolerance) and/or a food transfer. Based on previously established coding schemes on chimpanzee communication (e.g., Fröhlich et al., 2016a; 2017; Pika, Liebal, & Tomasello, 2003, Pika & Mitani 2006) and published work on great ape food sharing (Liebal & Rossano, 2017; Rossano & Liebal, 2014; Wilkinson et al., 2012), we differentiated between requests and taking attempts. A *gestural request* was defined as socially directed, mechanically ineffective movement of the extremities or body, including body postures, enabling a voluntary response (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2011a; Pika, 2008). In contrast, a *taking attempt* was defined as any behaviour where food was solicited (i.e. either successfully or unsuccessfully) through direct manipulation of another's body or hand-held items, without a "request" involved (Halina, Rossano, & Tomasello, 2013). We also coded the sensory modalities employed, accounting for the fact that great ape close-distance communication is inherently multimodal (Fröhlich & van Schaik, 2018; Hobaiter, Byrne, & Zuberbühler, 2017; Liebal, Waller, Burrows, & Slocombe, 2013; Wilke et al., 2017). Since all audible and many tactile signals also have a salient visual component, for each instance of begging we specifically coded whether it was purely visible (no physical contact to food owner, no sound), tactile (physical contact but no sound), audio-visual (sound without physical contact) and audio-tactile (sound with physical contact). In addition, we coded food solicitor's age (in months), sex (male, female) and kin relationship between food solicitor and owner (mother, maternal kin or "non-kin"). Distance between food solicitor and food owner was coded in terms of physical contact present or absent before an act of food solicitation. For the accessibility of the food source, we differentiated between easily accessible food parts (e.g. small fruits, leaves) and food that is difficult to access for infants (Silk, 1978) (e.g. hunted meat; fruit pulp, *Treculia africana*, and nuts, *Coula edulis*). Finally, sharing events were coded based on six levels defined by Boesch and Boesch (1989): theft, recovery from ground (in vicinity of food owner who dropped it), passive sharing (excluding facilitating actions), active-passive sharing (including facilitating actions), active sharing (offering), and gift (offering piece that is larger than the one which is kept). Rather than looking at the sequence leading to food transfers in a qualitative way (Rossano & Liebal, 2014), for this study we coded the production of and responses to individual cases of food solicitation.

About 15% of coded interactions were coded by a second observer and tested using the Cohen's kappa coefficient (κ) to ensure inter-observer reliability (Altman, 1990; Bakeman & Quera, 2011). A 'very good' level of agreement was found for sensory modality (κ = 0.815), while a 'good' agreement was obtained for solicitation tactic (κ = 0.760).

2.4. Statistical analyses

To investigate the sources of variation in the production of different food solicitation tactics in the first three models (response variables: (1) visual gesture, (2) tactile gesture, (3) taking attempt; the sample size of other communicative behaviours was too small to conduct inferential analyses), we used Generalized Linear Mixed Models (GLMM; Baayen, 2008) with a binomial error structure and logit link function. Each instance of food solicitation was thus treated as a separate data point. Into these three models, we included *kin relationship* (3 levels: mother, maternal kin, non-kin) and *signaller's age* (in months, range = 9–78) as key test predictors. Since age varied considerably between infants, we used the method of within-subject centering (van de Pol & Wright, 2009) to determine whether the effect of age was particularly relevant within and/or between infants. Specifically, we included into the model the average age of each infant ('between-age') and the difference between the infant's actual age and its average age (mean-centred or 'within- age'). We assumed that over the course of ontogeny specific types of food requests might play a larger role for interactions with non-kin conspecifics, and thus also included the two-way interactions between two levels of kinship (mother and maternal kin) and the variables representing age (within- and between-age) into the models. For the fourth and final model with the response variable (4) 'success in eliciting food transfers', we included *solicitation tactic* (3 levels: visual gesture, tactile gesture, taking attempt) as key test predictor in addition to the fixed effects mentioned above (i.e. kin relationship and signaller's age).

To control for confounding effects in all four models, we always included *sex* (2 levels: female, male), *distance* (2 levels: physical contact, no physical contact), *accessibility* of food item (2 levels: high, low) and *study site* (2 levels: *Kanyawara*, *Taï South*) as further fixed effects. As random effects (intercepts) we included signaller, recipient and dyad identity, bout ID (accounting for the fact that behaviours of the same interaction are non-independent) as well as the relevant random slope components. The models were implemented in R (version 3.4.1; R Development Core Team, 2017) using the function *glmer* of the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014). To firstly test the overall significance of our key test predictors (Forstmeier & Schielzeth, 2011), we compared the full models to the respective null models comprising only the control predictors (i.e. sex, distance, food accessibility and study site) and random effects using a likelihood ratio test (Dobson, 2002). Tests of the individual fixed effects were also derived using likelihood ratio tests (R function *drop1* with argument 'test' set to 'Chisq'). For further details regarding model specification and

implementation (e.g. collinearity checks, transformations), we here refer to previous work (e.g. Fröhlich et al., 2016a; Fröhlich et al., 2017).

3. Results

3.1. Overview of food solicitations and transfers

First, we looked at the sensory modalities employed in food solicitation behaviours, irrespective of whether they qualified as gestural request or taking attempts (i.e. actions). Overall, we coded a total of 1134 instances of food solicitation, with 360 instances observed in the *Kanyawara* and 774 cases observed in the *Taï South* community. When controlling for individual observation time, we found that interactions regarding hard-to-access food items were significantly more common in *Taï South* (mean ± SD = 0.71 ± 0.46 solicitations/h observed) as compared to *Kanyawara* (0.17 ± 0.26 solicitations/h; $F[1,9] = 6.056$, $P = 0.036$, $N = 11$). There was no difference between the two communities for easy-to-access food items (*Kanyawara*: 0.46 ± 0.3; *Taï South*: 0.56 ± 0.35; $F[1,9]) = 0.236$, ($P = 0.639$, $N = 11$).

Food solicitations consisted of 586 visual/non-contact, 387 cases of tactile, 29 cases of visuo-vocal and only 2 instances of tactile-vocal acts. On average, 68.6 ± 24.4% of infants' food solicitations were purely visual, involving neither contact nor vocalizations. Food solicitations involving physical contact (without vocal or other auditory components) were identified in 31.1 ± 24.2% of instances, while in only 2.7 ± 7.6% food solicitations involved vocalizations but no physical contact. Due to the relatively low proportion of food-related gestures and actions involving audible components, our inferential statistics focused on the production of visual/non-contact and tactile/contact gestural requests as well as taking attempts.

In mother-infant interactions, we observed a total of 190 sharing events (*Kanyawara*: $N = 85$; *Taï South*: $N = 105$), out of which six (*Kanyawara*: $N = 2$; *Taï South*: $N = 4$) qualified as "thefts" (S1 in the framework of Boesch & Boesch, 1989), 44 were recoveries from the ground (S2; *Kanyawara*: $N = 3$; *Taï South*: $N = 41$), 56 cases were classified as passive sharing (S3; *Kanyawara*: $N = 31$; *Taï South*: $N = 25$), 74 cases as active-passive sharing (S4; *Kanyawara*: $N = 43$; *Taï South*: N = 31) and 10 cases as active "offers" (S5; *Kanyawara*: $N = 6$; *Taï South*: N = 4). We observed no cases of "gifts" (S6). In 56 sharing events involving conspecifics other than the mother (*Kanyawara*: $N = 10$; *Taï South*: $N = 46$), we observed 3 "thefts" (*Kanyawara*: $N = 2$; *Taï South*: $N = 1$), 25 ground recoveries (*Kanyawara*: $N = 2$; *Taï South*: $N = 20$), 21 cases of passive sharing (*Kanyawara*: $N = 2$; *Taï South*: $N = 19$), 5 cases of active-passive sharing (*Kanyawara*: $N = 0$; *Taï South*: $N = 5$) and 2 "offers" (*Kanyawara*: $N = 1$; *Taï South*: $N = 1$).

3.2. Food-soliciting behaviours

We then tested whether individual and social factors influenced the production of visual and tactile gestural requests, as well as taking attempts. Overall, the full models fitted the data better than the null models, as the Likelihood ratio tests [LRT] revealed a significant effect of the key test predictors for all three response variables (LRT for visual gesture: $\chi^2_8 = 27.732$, $P < 0.001$; tactile gesture: $\chi^2_8 = 17.74$, $P = 0.023$, taking attempt: $\chi^2_8 = 23.126$, $P = 0.003$, $N = 1121$). For visual gestural requests (1) we found a significant interaction between kin relationship and within-age, indicating that visual gestures were increasing with age in food interactions with conspecifics other than the mother, but decreasing in mother-infant interactions (Table 2-a, Fig. 1). Moreover, visual gestures were significantly more frequent if the food owner was a conspecific other than the infant's mother (Fig. 2). None of the other effects in the model were significant (see Table 2-a).

In terms of tactile gestures (2), we found that the production was significantly more likely in younger individuals (Table 2-b, Fig. 3). Moreover, results showed that males produced more tactile gestures than female infants (Table 2-b, Fig. 3). None of the other effects in the model turned out to be significant (see Table 2-b).

For food solicitation via taking attempts (3), we found these actions to be significantly more often employed in interactions with kin, including both mothers and other maternal kin (Table 2-c, Fig. 2). Moreover, with increasing age infants more frequently solicited food via taking attempts (Table 2-c). None of the other effects in the model were significant (see Table 2-c).

Table 2
Effects of kinship, age and control predictors on the employment of (a) visual requests, (b) tactile requests, and (c) taking attempts derived using GLMMs with a binomial error structure and logit link function. Significant effects ($P < 0.05$) are marked in bold.

a) Visual requests	Estimate	SE	χ^2	P
Intercept	1.619	0.400	—	—
Kinship (mother)	−1.867	0.352	—	—
Kinship (maternal kin)	−0.443	0.545	—	—
Within-age	0.402	0.229	—	—
Between-age	0.248	0.252	—	—
Sex (male)	−0.347	0.327	1.144	0.285
Distance	−0.120	0.085	1.885	0.170
Accessibility (high)	0.102	0.212	0.228	0.633
Site (Taï)	0.036	0.351	0.010	0.919
Mother:within-age	**−0.522**	**0.251**	**4.205**	**0.040**
Mother:between-age	0.069	0.272	0.061	0.805
Maternal kin:within-age	−0.735	0.402	2.860	0.091
Maternal kin:between-age	0.085	0.491	0.028	0.867
b) Tactile requests				
Intercept	−2.001	0.374	—	—
Kinship (mother)	0.167	0.268	0.393	0.531
Kinship (maternal kin)	−1.064	0.725	3.018	0.082
Within-age	−0.200	0.116	2.437	0.119
Between-age	**−0.374**	**0.120**	**8.132**	**0.004**
Sex (male)	**0.767**	**0.236**	**8.580**	**0.003**
Distance	0.113	0.134	0.803	0.370
Accessibility (high)	0.152	0.247	0.363	0.547
Site (Taï)	−0.252	0.256	1.046	0.307
c) Taking attempts				
Intercept	−3.330	0.643	—	—
Kinship (mother)	**2.677**	**0.467**	**15.387**	**<0.001**
Kinship (maternal kin)	**1.437**	**0.644**	**4.089**	**0.043**
Within-age	**0.199**	**0.095**	**4.480**	**0.034**
Between-age	−0.147	0.319	0.236	0.627
Sex (male)	0.424	0.478	0.876	0.349
Distance	0.103	0.088	1.391	0.238
Accessibility (high)	−0.371	0.231	1.724	0.189
Site (Taï)	0.027	0.536	0.003	0.960

3.3. Success in soliciting food transfers

Finally, we examined the effects of individual, social and communicative variables on the successful initiation of food transfers (4). We found that the full model with the test predictors solicitation tactic, kinship and age was clearly significant as compared to the null model (LRT: $\chi^2_{10} = 61.054$, $P < 0.001$, $N = 1031$). After removal of the non-significant interaction terms, we found that kin relationship with the food owner and the solicitation tactic best predicted successful transfers: mothers were significantly more likely to share food than other conspecifics including siblings. Success in obtaining food was significantly higher when solicitations involved physical contact or when food transfers were initiated by taking attempts (Table 3, Fig. 4). Moreover, food was more likely to be transferred if it was easy to access for the infants (Table 3). The other variables had no significant effect on successful food solicitations (Table 3).

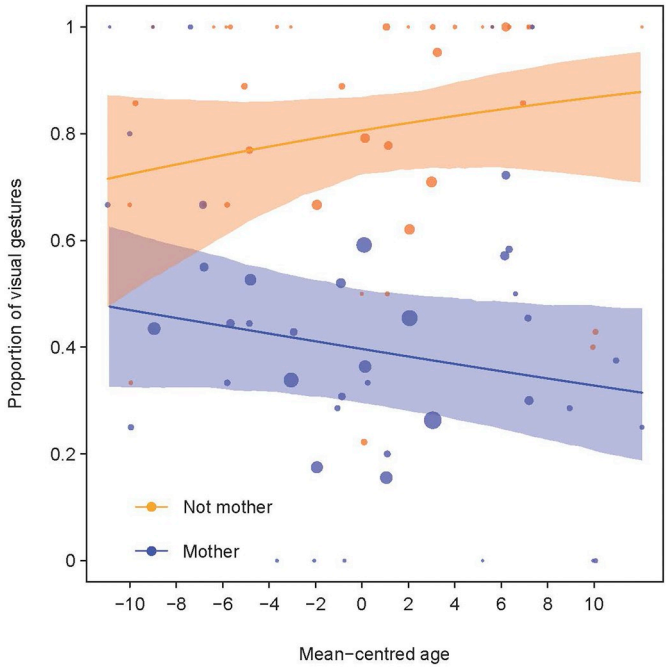

Fig. 1. Effects of kin relationship with food owner and mean-centred age ('within-age') on the proportion of visual food requests in chimpanzee infants. Depicted are raw proportions, with the dot area corresponding to the sample size per individual. The solid lines and shaded areas represent the fitted GLMM and confidence intervals, respectively, based on all other covariates and factors centred to a mean of zero.

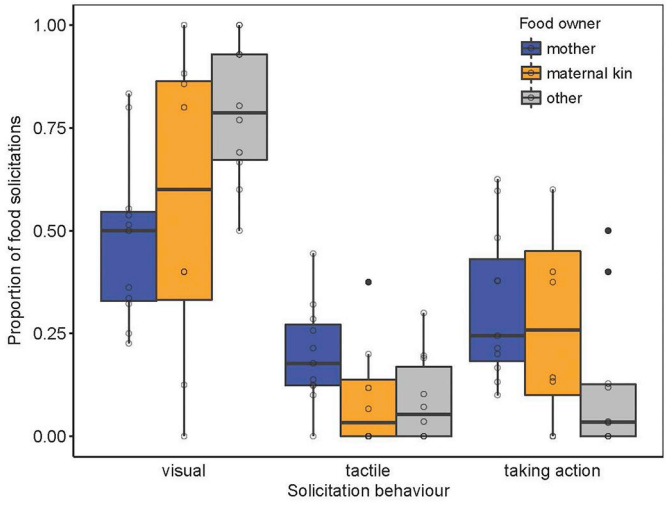

Fig. 2. Proportion of three different tactics of food solicitation (visual gesture, tactile gesture, taking attempt) as a function of kin relationship with the food owner. Indicated are individual means (circles), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots).

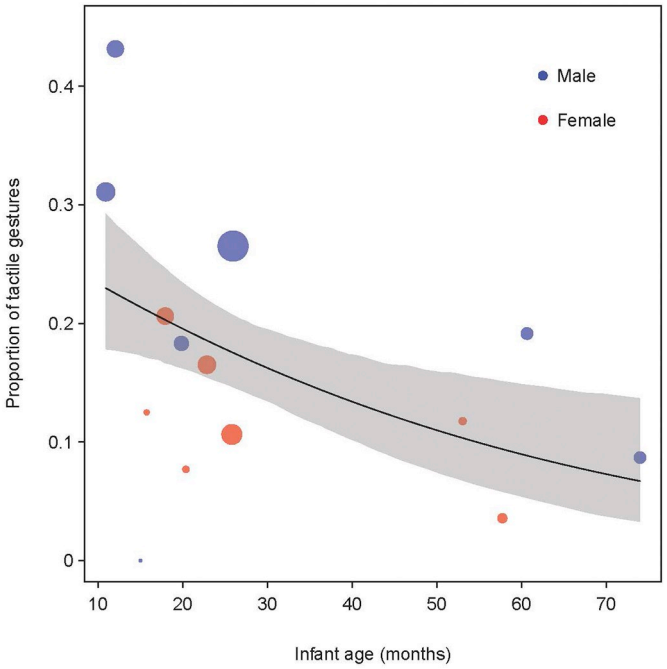

Fig. 3. Effect of age ('between-age') on the proportion of tactile food requests in chimpanzee infants. Depicted are raw proportions, separately for each infant against its mean age, with different colours for both sexes. The area of the dots corresponds to the sample size per individual. The solid line and shaded area represent the fitted GLMM and confidence interval, respectively, based on all other covariates and factors centred to a mean of zero.

Table 3
Effects of solicitation tactic, kinship, age and control predictors on the success of soliciting food transfers derived using GLMMs with a binomial error structure and logit link function. Significant effects ($P < 0.05$) are marked in bold.

Successful food solicitation	Estimate	S.E.	χ^2	P
Intercept	−3.147	0.582	—	—
Tactic (visual gesture)	**−1.992**	**0.347**	**25.351**	**<0.001**
Tactic (taking attempt)	**0.779**	**0.241**	**10.737**	**0.001**
Kinship (mother)	**1.712**	**0.492**	**14.643**	**<0.001**
Kinship (maternal kin)	−0.352	1.311	0.085	0.771
Within-age	0.019	0.117	0.027	0.871
Between-age	0.133	0.156	0.716	0.397
Sex (male)	0.316	0.269	1.382	0.240
Distance (no contact)	**−0.293**	**0.102**	**5.561**	**0.018**
Accessibility (high)	**0.692**	**0.279**	**5.107**	**0.024**
Site (Taï)	−0.127	0.284	0.202	0.653

4. Discussion

In this study, we examined the solicitation tactics infant chimpanzees employ to obtain food from others. Our goal was to disentangle the individual, social and communicative factors influencing the deployment of communicative requests and taking attempts as well as the success of obtaining food from social partners. We addressed the following three questions: First, which solicitation tactics do infant chimpanzees employ to initiate food transfers? Second, to what extent do maternal kin relationship and age predict the production of visual and tactile food requests, as well as taking attempts? Third, do individual, social and communicative variables (e.g. visual versus tactile gestures) predict the successful initiation of food transfers? Our results showed that most food solicitations involved either taking attempts or gestures in the visual or tactile modality, whereas vocalizations and other audible communicative acts were rarely used in this context. Moreover, we found that chimpanzee infants employed non-contact (i.e. purely visual) gestural requests to solicit food transfers more often with increasing age, but only if the food owner was a conspecific other than the mother. In interactions with mothers, taking attempts were the major solicitation tactic, which is reflected in a higher success in obtaining food from mothers compared to maternal kin or non-kin conspecifics. In general, taking attempts represented the most effective solicitation tactic, whereas purely visual solicitations were least likely to result in a successful food transfer. In the following paragraphs, we will discuss our findings in more detail.

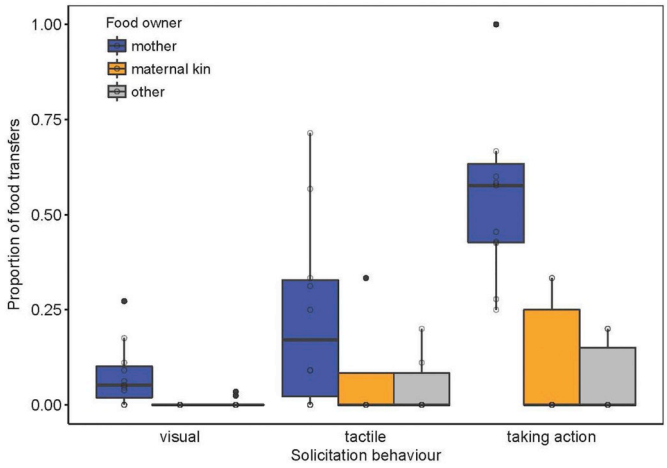

Fig. 4. Proportion of food transfers following different solicitation tactics as a function of kin relationship with the food owner. Indicated are individual means (circles), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots).

4.1. Food solicitation from mothers

We found that taking attempts were predominantly employed in interactions with mothers and maternal kin compared to those with other conspecifics, therefore it is not surprising that food was mostly (albeit passively) shared in mother-infant interactions. Contrary to unrelated individuals in the community, mothers gain direct fitness benefits by sharing food with their offspring. Chimpanzee mothers are generally highly tolerant towards their young infants and regularly share monopolizable food items (Nishida, 1996; Silk, 1978; van Lawick-Goodall, 1967). Maternal tolerance thus seems to explain why infants in our study used significantly more forceful actions to obtain food if the food owner was their mother. Due to high familiarity and predictable outcomes, "riskier" tactile forms of communication might be more pervasively used in these interactions (Fröhlich et al., 2016a; Fröhlich et al., 2017).

4.2. Effects of sex and age

With regard to tactile gestural requests, we found that frequencies were higher in males than in female infants, and were mainly used by younger as opposed to older infants. Only few studies have addressed age and sex differences in communicative strategies used by great apes, especially in natural environments (but see Hobaiter & Byrne, 2011b). However, previous research in the contexts of social play (Fröhlich et al., 2016a) and mother-infant joint travel (Fröhlich et al., 2016b) are consistent with these findings regarding tactile signal use. Our results suggest that a sex difference in signal directness specifically (in terms of physical contact involved) and gestural communication generally is evident beyond the play context in chimpanzees (Fröhlich et al., 2017). Hence, a divergent use of communicative modalities by males and females seems to be more pervasive in chimpanzee communication than hitherto assumed. These findings are consistent with evidence for chimpanzee's sex differences in early socialization (Murray et al., 2014). At the chimpanzee community of *Gombe*, male chimpanzees seem to exploit social opportunities more than females from a very early age, with the number of social partners of males increasing with offspring age and distance to the mother (Lonsdorf et al., 2014; Lonsdorf et al., 2014). We speculate that similar studies on other primate species in the future might reveal that the sex difference in communicative behaviour is a feature characterizing un-egalitarian societies, such as the patriarchal system of chimpanzees and the matriarchal system of vervet monkeys (*Cercopithecus aethiops*) (Horrocks & Hunte, 1983).

Moreover, our results regarding age effects (specifically, an increase in visual signalling at the expense of tactile forms of communication, including physical actions) mirror previous results of Fröhlich and colleagues in the contexts of play (Fröhlich et al., 2016a) and joint travel (Fröhlich et al., 2016b), as well as those of Schneider and colleagues studying different ape species in captivity (Schneider, Call, & Liebal, 2012). Interestingly, there seems to be a general pattern of using more non-contact (i.e. visual) gestures towards conspecifics other than the mother throughout early age (Fröhlich et al., 2016a; Fröhlich et al., 2019; Pika & Fröhlich, 2019).

4.3. "Begging for tolerance" and social learning

Successful food transfers were less likely to be elicited by purely visual requests than by contact forms of food solicitation (i.e. tactile requests and taking attempts). In terms of food solicitation types leading to successful transfers, our findings are thus consistent with a recent study of Liebal and Rossano (2017) on captive chimpanzees and orang-utans. However, the captive studies discussed above differ vastly in the use of observational and analytical procedures, and is thus difficult to relate them to our findings. Moreover, it is important to acknowledge that the need and "evolutionary urgency" to solicit food in captivity is considerably lower compared to individuals in the wild. Captive apes do not face the same ecological challenges and constraints of wild individuals (Boesch, 2007), and it is thus likely that the drivers influencing food transfers are highly different between the research settings. Captive settings represent stable environments where food is always abundant (Lehner, Burkart, & van Schaik, 2010; van Schaik, 2016), with a lesser need to obtain high-quality and energy-rich food items. Currently it is still unclear whether captive and wild chimpanzees differ in the extent to which they beg for specialized or rarely available food items.

An important question arising at this point is: if non-contact food solicitations are less likely to result in successful food transfers than contact requests, why do we still find these communicative acts to be pervasive in food-related interactions? One possible explanation may be that co-feeding tolerance differs among the various social partners of young chimpanzees. Unrelated conspecifics might respond aggressively to touching or stealing food, ranging from mild threats to severe physical attacks (Goodall, 1986), although this was only observed occasionally in the present study. Especially in situations of high arousal during interactions involving food of high value such as meat, food owners might be prone to strong aggression and violence (Goodall, 1986; Stevens & Gilby, 2004; Wrangham, 1975). Requesting from some physical distance is therefore a less risky strategy to obtain high-value food from other conspecifics, although likelihoods of success might be considerably lower. In this study, taking attempts were more frequently used to solicit food from mothers and maternal kin than from non-kin, despite success rates for solicitations from maternal kin (i.e. excluding mothers) not being higher than for those from non-kin food owners. Chimpanzee mothers are hardly reluctant to share with their younger offspring and attempts of food takings will seldom be punished, albeit they might be resisted occasionally (van Lawick-Goodall, 1967). Our conclusion is also supported by findings of Nishida (1996) who showed that with increasing age, infants increased the distance between themselves and mothers as the latter became more defensive in food sharing interactions. The difference between kin and non-kin interactions revealed in our study might also relate to the level of experience with the infant. While mother and siblings are intimately familiar with the infant's communicative intentions, other conspecifics may be less able to anticipate (or inclined to please) infants' needs (Fröhlich et al., 2019, Goodall, 1986). Purely visual, non-contact communication is thus more suitable to perform lower-risk requests towards less familiar conspecifics (e.g. unrelated adults) that will be less tolerant to attempts of obtaining their monopolizable food items. Nonetheless, these interactions might represent a critical niche for social learning, since

younger individuals might beg for specific food items where the visual signalling results in being tolerated. Hence, immatures have the opportunity to remain in the immediate vicinity of the food-processing conspecific and gain insight into how to access and process food. The food sharing context might represent a crucial platform to practice and learn the social rules critical for cooperation.

For begging by immatures in primates, both nutritional and informational functions of mother-offspring food transfers have been discussed (Jaeggi et al., 2008). By soliciting food from other individuals, immatures acquire information about the value and processing of food items, which in turn supports social learning (Jaeggi et al., 2008; Schuppli et al., 2016). It is also possible that our study demonstrated a learning effect of "inhibitory control" towards unrelated conspecifics. The ontogenetic phase in which social tolerance exhibited by kin and non-kin towards a young chimpanzee decreases might be tightly linked to the developmental stage at which the intentional, context-appropriate use of communicative signals via "social negotiation" develops (Fröhlich et al., 2019; Pika & Fröhlich, 2019). In other words, rather than begging for food from conspecifics, what we might often see is "begging for tolerance" as well as "begging for information". In any case, sensitivity to social inputs seems to play a substantial role throughout development and across social roles, which change across lifetimes of great apes (Fröhlich & Hobaiter, 2018). Our results seem to suggest that intentional, gestural communication is less relevant in highly predictable interactions with close kin that are highly tolerant, whereas gestural requests are favourable in less predictable interactions with unfamiliar peers and adults. We are just at the beginning to understand the precise social inputs and learning mechanisms underlying gestural production. Is the presence of specific social partners sufficient to elicit a particular communicative behaviour, or is there a specific interactive component (and if so, which?) that supports usage learning in gestural communication?

4.4. Effects of food accessibility and study site

We also found that accessibility had an effect on elicited food transfers, with easy-to-access food items more readily shared with infants than difficult-to-access items. This finding seems to contradict the early study of Silk (1978) on the *Gombe* chimpanzees, which showed that foods infants could find and process on their own were not shared by mothers as frequently as foods infants could not obtain independently. However, this may be due to infants merely soliciting fewer food transfers if food accessibility is high, or due to Silk's restriction to mother-offspring interactions. Notably, lower rates of food solicitation by infants were observed at *Kanyawara* where the accessibility of food items is thought to be generally higher due to the absence of percussive tool use as common in *Taï*. In contrast, there was no difference in the proportion of interactions related to food of low accessibility at the respective study sites. Since easy-to-access food was shared more readily with infants, it is however not surprising that the proportion of food transfers (successful solicitations) in *Taï* was not higher than in *Kanyawara*. The sample sizes in our study may have been too small to detect a significant statistical interaction between the effects of kin relationship and food accessibility (or between study site and food accessibility) on food sharing; this would be surely an exciting avenue for further research.

4.5. Conclusion

In sum, our findings constitute further evidence that communicative effort, in the form of gestural requests, might be particularly relevant in interactions with less familiar and less tolerant conspecifics (see also Fröhlich et al., 2016a; Fröhlich et al., 2017). When outcomes are more predictable, riskier food solicitation tactics involving physical contact will be used and vice versa. This might explain why visual food requests were among the most frequent tactics observed despite lower success rates compared to other forms of solicitation, such as taking or stealing. Our findings suggest that food solicitation in young great apes may also function to facilitate social tolerance and information transfer. We thus conclude that the food sharing context might represent a critical platform to learn and practice social rules underlying cooperative interactions, which can later be generalized across collaborative domains. Sensitivity to social inputs is critical not only throughout development, but also across social roles in great ape society. A fruitful avenue of research would be to address the precise social and interactive inputs (e.g. interaction frequency, interaction "space", social network, audience composition, role of innovations) that play a role in great ape communication; and to account for the interaction sequence (did taking attempts follow requests or not?) to make conclusions about which solicitation tactic is more successful. In turn, we can gain more insight into the mechanisms of usage learning underlying the communication systems of our closest living relatives.

Humans have evolved highly differentiated forms of food sharing, facilitating to live and survive in relatively large social groups and thus probably selecting for and enforcing specialized cognitive skills (Isaac, 1978). To better understand the origins of these behaviours and their role in the dawn of human evolution, we have to look at our closest living relatives, the great apes. Our findings on chimpanzees are relevant to human behavioural evolution for (at least) two reasons: First, our results corroborate previous work suggesting that there is a strong evolutionary foundation of intentional communication in requesting interactions (Bard, 1992; Rossano & Liebal, 2014). Similar to studies on pre-linguistic human children (Bates et al., 1979), we showed that chimpanzees are able to deploy the appropriate communicative tools to solicit objects or food. Second, we presented further evidence that social distance has a profound effect on great apes' interactions from early age, with social tolerance possibly driving communicative acts. Studying the effect of social tolerance on tactics of food solicitation might ultimately help to understand precursors of human social rules, including politeness (Brown, 2015): in great apes, food-sharing situations may serve as a platform to acquire the social rules critical for cooperation, whereas politeness (i.e. demonstrating appropriate concern for interactors' social status and their social relationship expressed in speech) is thought to be a critical precondition for human cooperation in general. Studies on drivers of food sharing in natural environments, where great apes are faced with active selection pressures, are important to gain insight into the evolutionary origins of the human cooperative psychology. This will enable us to draw conclusions about the extent to which the emergence of prosociality and high sharing motivation played a role in cooperative breeding systems, including humans (Jaeggi & Gurven, 2013). More studies on the links between communication, coordination and cooperation from a comparative perspective will hopefully reveal further insights into the role of cooperation in human evolution.

Data availability

All data are availabale from the corresponding author upon request.

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Declaration of Competing Interest

None.

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