

# The ontogeny of intentional communication in chimpanzees in the wild

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## Abstract

The onset of intentional communication in children's first year of life represents a major milestone in human cognitive development. Similarly, it is well established that our closest living relatives, the great apes, communicate with signals characterized by at least first-order intentionality. Despite the well-documented influence of developmental experiences on socio-cognitive abilities in apes, the developmental trajectory of intentional signal use as well as effects of social exposure remain poorly understood under naturalistic conditions. Here, we addressed these issues by studying the ontogeny of intentional communication in chimpanzee infants of two subspecies (*Pan troglodytes schweinfurthii/verus*) and communities living in their natural environments. Overall, we found that gestures and bimodal signal combinations were most commonly accompanied by markers of intentional communication: audience checking, persistence to the goal, and sensitivity to recipient's attentional state. Within individuals, the proportion of communicative behaviours associated with goal persistence and sensitivity to attention increased with age. Cross-sectional comparisons between infants revealed an age effect on the use of audience checking. Context, interaction partner and site affiliation affected the production of specific markers irrespective of infants' age. The present study provided hitherto undocumented evidence for the development of three important markers of intentional communication in great apes. Moreover, our results suggest that social exposure impacts early intentional signal use.

## 1 | INTRODUCTION

Language is one of the most characteristic traits distinguishing humans from the rest of the animal kingdom (Christiansen & Kirby, 2003b; Hauser, Chomsky, & Fitch, 2002). Intentionality is commonly regarded as one of its cornerstones (Dennett, 1983; Grice, 1957; Tomasello, 2008). Broadly defined as acts or thoughts produced voluntarily and in a goal-directed way (Dennett, 1983; Grice, 1957), intentionality has attracted research attention from a wide range of disciplines, including the cognitive sciences, philosophy, psychology and linguistics (e.g. E. Bates, Camaioni, & Volterra, 1975; Dennett, 1983; Leavens, Russell, & Hopkins, 2005; Scott-Phillips,

2015; Townsend et al., 2017). In human development, intentional communication is distinguished from intentional action in that it involves the ability to coordinate actions on objects with actions on social agents (also labelled illocutionary acts by E. Bates et al., 1975; Sugarman, 1983). Around the age of 10 to 12 months (E. Bates et al., 1975; Bruner, 1981a; Sugarman, 1983), human infants start to communicate in goal-oriented (i.e. intentional) ways with their caretakers by using gestures and bimodal signal combinations (vocalization plus visual gesture; E. Bates et al., 1975). This transition has been associated with the ability to understand others as social agents (E. Bates et al., 1975). It has also been linked with the onset of true symbolic communication, the capacity for linking sounds or gestures

arbitrarily to specific concepts and/or percepts (Christiansen & Kirby, 2003a). Importantly, the acquisition of communicative intentions and the development of their linguistic expression crucially relies on the interactional usage of language in early childhood. Vygotsky's (1962) theory of socio-cultural development postulates that social interaction plays a fundamental role in the development of cognition. Building on this premise, in the social interactionist theory of language development Bruner (1985) emphasizes the social and interpersonal nature of language. Children acquire language in the context of meaningful parent–infant interaction, with formats used in indicating and requesting. These are designed to achieve joint attention and joint action, serving essential linguistic functions (Bruner, 1981a, 1981b).

In interactions with their caretakers, human children use gestures before their first words (E. Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; E. Bates et al., 1975). Hewes (1973) proposed that this early ontogenetic phase in humans recapitulates phylogeny, with gestures preceding spoken language evolutionarily (however, see e.g. Liebal, Waller, Burrows, & Slocombe, 2013, for a review of different theories of language evolution). In subsequent decades, considerable research effort has been dedicated to the question of whether great apes also use their signals in intentional ways (e.g. Bard, 1992; Call & Tomasello, 2007; Leavens et al., 2005). Comparative research, using data from extant non-human species, may present one of the most powerful tools to draw conclusions regarding the evolutionary origins of distinct components of language, including intentionality (Arbib, Liebal, & Pika, 2008). To operationalize 'intention' in non-human species, Dennett (1983) distinguished different orders of intentionality depending on the degree of mental state attribution involved: *zero-order* intentionality does not assume any thoughts or beliefs in a signaller, such as a chimpanzee female's conspicuous sexual swellings of the perineal skin signalling fertility. *First-order* intentionality requires that a signaller holds beliefs or desires. For instance, the signaller intends a begging gesture to produce a response in the recipient, namely a food transfer. In contrast, *second-order* intentionality requires that the signaller ascribes thoughts and beliefs to the recipient and vice versa. In our example, the recipient would recognize the signaller's communicative intention, namely manipulating the recipient's behaviour to obtain food (see also Sperber & Wilson, 1986, 2002).

To investigate intentional communication in non-human primates (hereafter primates), different research labs have operationalized distinct behavioural criteria (Leavens et al., 2005; Pika, Liebal, & Tomasello, 2003; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; Tomasello et al., 1997) based on research on pre-linguistic communication in human children (E. Bates et al., 1979; E. Bates et al., 1975). Among others, these three criteria have been proposed to qualify as reliable markers to discriminate intentional from unintentional signals: audience checking, persistence to the goal, and sensitivity to the recipient's attentional state (Leavens et al., 2005; Townsend et al., 2017). First, visual checking and monitoring of the recipient's behaviour has been repeatedly highlighted as an indicator of the socially directed nature of a signal

## RESEARCH HIGHLIGHTS

- We examined the ontogeny of intentional communication in wild chimpanzees of two different subspecies (*Pan troglodytes schweinfurthii/verus*).
- The study presents hitherto undocumented evidence for the development of three established behavioural markers of intentional communication in apes.
- We found that proportions of audience checking, goal persistence and sensitivity to the recipient's visual orientation increase with infant age.
- Our results suggest that context, interaction partner and study site (and thus, social environment) impact intentional signal usage.

(e.g. Leavens et al., 2005; Liebal, Call, & Tomasello, 2004; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013). Second, persistence to the goal implies that the signaller would stop if the goal is achieved, but persist (by means of response waiting and repeating, exaggerating or modifying the initial signal) if unsuccessful (Leavens et al., 2005). Third, sensitivity to the recipient's attentional state (i.e. communicating more or only when the audience is receptive to the signal) also suggests that the sender has a goal-directed intention to communicate (Liebal et al., 2013).

To date, studies have provided evidence for first-order intentionality, as demonstrated by flexible and voluntary communication, in a large variety of non-human taxa from fish to great apes (e.g. coral trouts/groupers, *Plectropomus leopardus/pessuliferus*: Vail, Manica, & Bshary, 2013; common ravens, *Corvus Corax*: Pika & Bugnyar, 2011; domestic dogs, *Canis familiaris*: Miklosi, 2008; barbary macaques, *Macaca sylvanus*: Hesler & Fischer, 2007; olive baboons, *Papio anubis*: Meunier, Prieur, & Vauclair, 2013; orangutans, *Pongo pygmaeus*: Bard, 1992; chimpanzees, *Pan troglodytes*: Leavens et al., 2005). While the existence of first-order intentionality in animals is now relatively well established (Maynard Smith & Harper, 2003), little agreement exists concerning the presence of second-order intentionality in non-human species (Hare & Tomasello, 2005; Scott-Phillips, 2015; Townsend et al., 2017). Since we are not able to directly observe animals' and pre-linguistic children's psychological states (Scott-Phillips, 2015; but see Krupenye, Kano, Hirata, Call, & Tomasello, 2016, for evidence of false-belief understanding in apes), it remains an inherently challenging task to determine if communication is goal-oriented or not. However, this problem also applies to observations of communicative behaviour in pre-linguistic children, and it is crucial to devise the same objective measures for non-human and human testing groups to enable comparability (Leavens, Bard, & Hopkins, 2017). The fine-grained study of proximate mechanisms in communication, such as underlying developmental processes, might shed some light on the extent to which human intentionality truly differs from other animal species.

To make meaningful comparisons with the development of intentionality in humans, we need to take a closer look at the well-cited notion of ontogeny recapitulating phylogeny during language evolution. However, the impact of development on intentional communication has received surprisingly little research attention in ethology and comparative psychology (Bard & Leavens, 2014; Pika & Fröhlich, 2018). This is despite the fact that a developmental approach is indispensable for an in-depth understanding of how intentional communication emerges and develops in non-human species. Only by observing how communicative behaviour unfolds throughout ontogeny can we draw inferences about the extent to which communication relies on input from the socio-ecological environment. Given the growing evidence for a strong impact of social experiences on socio-cognitive (for reviews see Bard & Leavens, 2009; Leavens & Bard, 2011) and communicative development in great apes (Bard et al., 2014; Fröhlich, Müller, Zeiräg, Wittig, & Pika, 2017; Katsu, Yamada, & Nakamichi, 2017; Laporte & Zuberbühler, 2011; Snowdon & Hausberger, 1997), it is vital to understand the role of learning processes for signal usage (Fröhlich et al., 2017; Higham & Hebets, 2013). In his pioneering studies, Plooiij (1978, 1979) described the naturally occurring communicative interactions between mother–infant dyads of eastern chimpanzees (*Pan troglodytes schweinfurthii*) at the Gombe community, Tanzania. He showed that the onset of intentional communication takes place at a similar age as in human infants, that is around 9 to 12 months. Moreover, Plooiij reported a developmental shift from perlocutionary acts to intentional signalling (Plooiij, 1978). In perlocutionary acts, communication occurs only because the receiver is adept at interpreting the behaviour of the 'sender'. In contrast, illocutionary acts are used to carry out a socially recognized function ('intentional signals'). Since Plooiij's studies, it has been well established that social experiences during ontogeny (e.g. rearing histories) substantially affect the development of social-cognitive skills in primates (for review see Bard & Leavens, 2014). Recently, the criticism has been put forward that comparative research on social cognition has mostly ignored the detrimental effect of impoverished social and physical environments on cognitive development (Leavens et al., 2017). The failure to examine groups in the same testing settings may have led to the universal conclusion that humans' enhanced task performances are due to evolutionary rather than developmental histories (Leavens et al., 2017).

Given that the most influential comparative research on communicative development was carried out in the wild (Plooiij, 1978, 1979; van Lawick-Goodall, 1967, 1968), it seems surprising that the majority of subsequent studies in great apes have been conducted in captive settings (e.g. Halina, Rossano, & Tomasello, 2013; Schneider, Call, & Liebal, 2012; Tomasello et al., 1994; Tomasello et al., 1997). Moreover, work on communicative development in general is heavily biased towards the acoustic modality (reviewed in Partan, 2013). Longitudinal studies allowing for both a between- and a within-subject design enable researchers to gain detailed insight into subtle developmental changes (Halina et al., 2013; Pika

et al., 2003; Tomasello et al., 1997) but are still rare outside of captive settings (but see Fröhlich et al., 2017; Fröhlich, Wittig, & Pika, 2016b). However, to unravel the impact of learning through social exposure, we first need to understand the ontogeny of intentional communication in groups living in their natural environment, where they are exposed to active selection pressures (Boesch, 2007). Although very suitable for fine-grained analyses, the generalizability of findings from captive apes is inevitably limited due to human influence on the social and physical environment. Due to the large inter-site variability reported for chimpanzee social behaviour in natural environments (Boesch, 2007; Doran, Jungers, Sugiyama, Fleagle, & Heesy, 2002), there is also a pressing need to distribute research efforts to multiple communities living in different ecological settings to ensure the analyses of samples representative of whole species.

Diverging methodologies have thus far prevented researchers from drawing firm conclusions about the role intentional communication plays for different communicative modalities (e.g. gestural vs. vocal), taxa (e.g. primate vs. non-primate species), and research settings (e.g. captive vs. wild). Moreover, primate communication has rarely been studied holistically, with most studies focusing on either gestures or vocalizations alone (Slocombe, Waller, & Liebal, 2011; but see e.g. Genty, Clay, Hobaiter, & Zuberbühler, 2014; Hobaiter, Byrne, & Zuberbühler, 2017; Wilke et al., 2017). This bias resulted in the dominance of different behavioural criteria in gestural and in vocal research (for review see Liebal et al., 2013). Thus, a multimodal approach and a wider comparative perspective are crucial to enable a consistent use of behavioural criteria to infer intentional communication across species and communicative channels (Townsend et al., 2017).

In this study, we used a within-/between-subject design to investigate the development of intentional communication in chimpanzees living in two communities of different subspecies (*Pan troglodytes schweinfurthii/verus*) in their natural environments, by focusing on the influence of age, context and interaction partner. We aimed to expand Plooiij's (1978, 1979) early descriptive work by conducting the first systematic, quantitative study on behavioural markers of intentional communication and taking into account potential within-species variability. Recent work on chimpanzees living in different study populations has shown that social factors such as context, familiarity and social bond (Fröhlich et al., 2017; Fröhlich, Wittig, & Pika, 2016a; Luef & Pika, 2017; Roberts & Roberts, 2016; Schel et al., 2013), and also individual or demographic factors (mother's experience in rearing offspring, sex and study site) can have a profound influence on signal production (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a, 2016b). We therefore need more systematic data on the communicative behaviour of great apes in the wild to better understand how communicative development relates to social opportunities in the environment. Chimpanzees have been the main model system for research on non-human intentional communication, justified by the relatively recent divergence of humans from the *Pan* lineage around five to eight million years ago (Langergraber et al., 2012;

Prufer et al., 2012), and their complex social relationships that are navigated by means of a large signal diversity (De Waal, 1988; Goodall, 1986).

In accordance with the framework proposed by Townsend and colleagues (2017), we aimed to take a first step into using transparent and comprehensible behavioural markers to infer intentional communication, enabling subsequent comparisons between species, communities and settings. To understand the 'base of the iceberg' of non-human intentional signalling, we examined the development of three established markers that have been highlighted as valuable means to determine communicative intent in non-human species: audience checking, persistence to the goal, and sensitivity to the recipient's attentional state (Leavens et al., 2005; Liebal et al., 2013; Townsend et al., 2017). We observed communicative interactions during three frequently occurring communicative contexts—food sharing, mother–infant joint travel, and social play. These contexts were selected since they occur frequently and comprise fruitful candidates for communicative exchanges (Fröhlich et al., 2017; Goodall, 1986).

Specifically, we addressed three questions. First, how frequently are different communicative behaviours, like gestures, vocalizations and bimodal signal combinations, accompanied by markers of intentionality? To address this question, we investigated whether communicative, socially directed behaviours were associated with audience checking, persistence to the goal and sensitivity to the recipient's visual orientation. In light of previous findings on early intentional communication in great apes (Bard, 1992; Fröhlich, Wittig et al., 2016b; Halina et al., 2013), we expected that intentionality markers would mainly accompany gestures and bimodal signal combinations.

Second, to what extent are markers of intentional communication influenced by development? To address this question, we examined the effect of age on the use of the three behavioural criteria (see above). Previous work has shown that there is a developmental shift from physical, non-intentional acts to intentional

signals in young chimpanzees (Fröhlich, Wittig et al., 2016b; Plooi, 1978), but the effect of age on single behavioural parameters used to identify intentional communication has not been systematically studied. We predicted that the use of each marker would increase with age both within and between individuals.

Third, do specific social circumstances of the interaction affect markers of intentional signal usage? We examined to what extent communicative context and the relation to recipients (maternal or non-maternal recipient) influenced the use of the above-mentioned markers. While a distinction into mother and non-mother conspecifics appears relatively superficial given the complex relationships young chimpanzees have with individuals in their community, we explicitly wanted to address the specificity of the mother–infant relationship. Due to the exceptionally large degree of familiarity within the dyad, mother–infant interactions have highly predictable outcomes compared to interactions with other conspecifics such as unrelated adult males. They most likely represent less risky interactions with a lesser need to employ visual behavioural signals (Fröhlich, Wittig et al., 2016a). Moreover, gestural production for play solicitation does not appear to differ profoundly in interactions with siblings (maternal kin) as compared to those with non-kin (Fröhlich, Wittig et al., 2016a). In a previous study, we thus argued that interactional experiences beyond the mother–infant relationship might play a larger role in communicative development than hitherto acknowledged (Fröhlich et al., 2017). Hence, here we also wanted to test whether the interaction partner (i.e. the recipient) had an effect on the proportion of use and/or number of markers of intentional communication. Because this receiver effect might not be constant throughout ontogeny, we also investigated whether the influence of the interaction partner on the use of markers depends on infant age. More specifically, we expected that older infants in particular would use intentionality markers more commonly with non-maternal conspecifics.

Group	ID	Sex	Infant age P1 [months]	Infant age P2 [months]	Observation time [h]	Interaction time [h]
Kanyawara	WZ	M	9–11	21–23	105.5	17.7
	OB	M	13–15	25–27	119	23.0
	MM	F	13–15	25–27	87.5	8.6
	LL	F	N/A	15–17	60.5	8.0
	TR	F	16–18	28–30	112	23.0
	OL	F	48–50	60–62	45	10.0
	WC	M	55–57	67–69	73	13.2
Tai South	MH	F	10–12	22–24	150.5	17.7
	IN	M	N/A	10–12	91	14.0
	SL	M	15–17	27–29	148.5	22.9
	KY	F	19–21	31–33	147	23.8
	IT	M	64–66	76–78	41	17.7
Total	12	6:6	10	12	1,180.5	199.6

**TABLE 1** Information on observed infants with respective observation time and recorded interaction time. The bottom line provides a summary for each column (P1/P2: first/second period of data collection)

## 2 | METHODS

### 2.1 | Study sites and subjects

The study was conducted with two different communities of chimpanzees (*Pan troglodytes*): *Kanyawara* in Kibale National Park, Uganda (eastern chimpanzee, *P. t. schweinfurthii*), and *Tai South* in Tai National Park, Côte d'Ivoire (western chimpanzee, *P. t. verus*). Detailed information on study sites and community sizes has been provided previously elsewhere (Fröhlich, Wittig et al., 2016a, 2016b). We observed communicative interactions of a total of 12 chimpanzee infants. Seven infants were observed at *Kanyawara*, and five at the *Tai South* community. Infant ages ranged from 9 to 78 months (see Table 1 for detailed information on subjects and datasets).

### 2.2 | Data collection

Focal observations of chimpanzee mother–infant pairs were conducted during two three-month periods in *Kanyawara* and *Tai South*, respectively, between October 2012 and June 2014 (*Kanyawara*: March–May 2013 and 2014; *Tai South*: October–December 2012 and 2013). All interactions of the infants (that is, those with the mother and other conspecifics) in the three contexts of feeding, travel and social play were recorded using a digital high-definition camera (Canon Legria HF M41) with an externally attached unidirectional microphone (Sennheiser ME64/K6). The use of these devices enabled the collection of high-quality footage combined with observer comments and broad categories of vocalizations (Fröhlich, Wittig et al., 2016a, 2016b). During 1,180 hours of observation, we collected a total of 199.6 hours of video footage that captured social interactions of chimpanzee infants (*Kanyawara*: 103.5 h, mean  $\pm$  SD per infant =  $14.8 \pm 6.5$  h; *Tai South*: 96.1 h; mean  $\pm$  SD per infant =  $19.2 \pm 4.1$  h; see also Table 1).

### 2.3 | Coding procedure

We specifically focused on communicative behaviour that elicited the transfer of food ('food sharing'; Fröhlich et al., 2017), the initiation of maternal transport or joint travel ('joint travel'; Fröhlich, Wittig et al., 2016b) and the solicitation of social play ('social play'; Fröhlich, Wittig et al., 2016a). A total of 826 high-quality recordings of infant-initiated interactions in these three different contexts (food sharing:  $N = 330$ , joint travel:  $N = 122$ ; social play:  $N = 374$ ) were coded using the program Adobe Premiere Pro CS4 version 4.2.1. Based on parameters used in previous work on great ape communication (Pika et al., 2003; Pika, Liebal, & Tomasello, 2005), a coding scheme was developed to enable the analysis of the following communicative behaviours and signals (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a): (i) physical actions, (ii) gestures, (iii) vocalizations, and (iv) bimodal signal combinations. A *physical action* was defined as any socially directed behaviour that led to the perceived goal through direct manipulation of another's body or the movement of one's own

body (Halina et al., 2013). *Gestures* were defined as directed, mechanically ineffective movements of the extremities or body, or body postures, allowing for a voluntary response of the recipient (Pika, 2008). They were coded based on parameters described in detail elsewhere (Fröhlich, Kuchenbuch et al., 2016; Fröhlich, Wittig et al., 2016b). *Vocalizations* were coded based on ethograms established for chimpanzees living in wild populations, and included hoo-whimpers and play-panting (Goodall, 1986; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999; Plooij, 1984). *Bimodal signal combinations* were defined here as a synchronous combination of gesture and vocalization (Luef & Pika, 2017). For each instance of communicative behaviour, we specifically coded whether it was accompanied by the following key criteria (or 'markers') of intentional communication: audience checking via eye gaze, persistence to the goal, and sensitivity to recipient's attentional state. For each marker, we built upon the definitions of previous work on prelinguistic human children and great apes (E. Bates et al., 1979; E. Bates et al., 1975; Call & Tomasello, 2007; Fröhlich, Wittig et al., 2016b; Leavens et al., 2005)

*Audience checking via eye gaze*: Signaller visually orients towards and monitors the recipient before and during producing a signal (hence, mere bodily orientation towards recipient was not sufficient). Gaze alternation between the recipient and a third entity may occur if applicable (e.g. in food sharing context). Clear visibility of the signaller's head and gaze was presupposed to code this behaviour.

*Persistence to the goal*: Signaller waits for a response and elaborates if the initial signal was presumably unsuccessful, e.g. by repeating/exaggerating the signal or by switching to a different modality. Goal persistence was only coded for those cases where an immediate response (i.e. within 2 seconds) by the recipient did not follow.

*Sensitivity to the recipient's attentional state*: Signaller adjusts to the recipient's state of attention, that is, by employing visual behaviour only when the recipient is entirely visually oriented towards the signaller and pays attention. In the absence of recipient's visual attention, signallers adjusted only if they produced tactile and/or audible signals.

Finally, we coded the responses of recipients with regard to the presence or absence of an apparently satisfactory outcome (Hobaiter & Byrne, 2014). We particularly focused on the occurrence of communicative failure, that is, behaviours that lacked an adequate response or were ignored. Response coding was necessary to rule out that variation in goal persistence is merely linked to variation in responsiveness towards signallers of different ages.

About 15% of coded interactions were coded for accuracy by a second observer and tested using the Cohen's Kappa coefficient to ensure inter-observer reliability (Bakeman & Quera, 2011). A 'very good' or better level of agreement was found for signal modality ( $\kappa = 0.815$ ), audience checking ( $\kappa = 0.817$ ) and recipient's visual orientation ( $\kappa = 1.000$ ), while a 'good' agreement was obtained for persistence to the goal ( $\kappa = 0.746$ ) and recipient's response ( $\kappa = 0.719$ ).

**TABLE 2** Information on the association of markers of intentional communication with different types of communicative behaviours, and the occurrence of immediate and lacking responses. Percentages refer to the total number of coded communicative behaviours ( $N = 2711$ )

Type of commun. behav.	Audience checking	Persistence to goal	Sensitivity to orientation	No marker	Immediate response	No response	Total
Action	9.4% (254)	11.1% (300)	14.7% (398)	15.1% (409)	16.3% (441)	24.1% (652)	1,441
Gesture	25.3% (685)	24.3% (658)	37.7% (1022)	0.1% (4)	12.1% (328)	18.1% (490)	1,158
Vocalization	0.4% (10)	0.5% (13)	0.3% (8)	0.0% (1)	0.2% (6)	0.4% (12)	34
Bimodal	2.6% (71)	2.1% (57)	1.0% (26)	0.0% (0)	0.6% (16)	0.7% (18)	78
Total	37.7% (1020)	38.0% (1028)	53.7% (1454)	15.2% (414)	29.2% (791)	43.3% (1172)	2,711

## 2.4 | Statistical analyses

For our inferential statistics, we used the entire dataset with all types of communicative behaviours (i.e. actions, gestures, vocalizations and bimodal combinations). In a first step, we used Generalized Linear Models (GLM; McCullagh & Nelder, 1989) with binomial error structure and logit link function for each marker of intentionality (audience checking, persistence to the goal, sensitivity to attentional state) to analyse whether they differ in their association with distinct types of communicative behaviours. To then test whether the three criteria of intentionality were influenced by age, interaction partner and communicative context, we used Generalized Linear Mixed Models (GLMM; Baayen, 2008) with a binomial error structure and logit link function. Additionally, we tested the effect of the same variables on communicative failure. Into these models, we included age (in months, range = 9–78), interaction partner (two levels: mother, non-mother) and communicative context (three levels: food sharing, joint-travel initiation, play solicitation) as fixed effects (key test predictors). Since age varied considerably between infants, we used the method of within-subject centring (van de Pol & Wright, 2009) to determine whether the effect of infant age was relevant within and/or between infants. Specifically, we included in 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 age or 'within-age'). Because we assumed that over the course of ontogeny interactions with non-maternal conspecifics might play an increasing role for intentional signalling, we also included the two-way interactions between interaction partner and the two variables representing age in the models (Figures 1 and 2). As control predictors and further fixed effects in the model, we included mother's parity (number of offspring reared at least until juvenility plus present infant; range = 1–5), sex (two levels: female, male) and study site (two levels: *Kanyawara*, *Tai South*). As random effects (intercepts) we included signaller, recipient and dyad identity in the model, as well as the relevant random slope components. The models were implemented in R (version 3.4.2; R Development Core Team, 2017) using the function *glmer* of the package 'lme4' (D. Bates, Maechler, Bolker, & Walker, 2014). To test the overall significance of our key test predictors (Forstmeier & Schielzeth, 2011), we compared these full models with the respective 'null models' comprising only the control predictors (i.e. mother's parity, sex, study site) and all random effects using a likelihood ratio test (Dobson, 2002). This test revealed

whether the full model including the key test predictors fits the data significantly better than the null model. Subsequently, tests of the individual fixed effects were derived using likelihood ratio tests (R function *drop1* with argument 'test' set to 'Chisq'). If the interaction terms (i.e. partner\*within-age and partner\*between-age) were non-significant, they were removed so that estimates were only derived for the main effects. For further details regarding model specification and implementation (e.g. collinearity checks, model stability) see electronic supplementary material, Table S1.

## 3 | RESULTS

### 3.1 | Overview of communicative events used for the analysis of markers

Overall, we coded a total of 2,711 communicative behaviours with regard to association with three specific markers of intentional communication. Out of these cases, we were able to reliably analyse 2,359 cases with regard to occurrence of audience checking behaviour, 1,919 cases in terms of goal persistence, and 2,566 cases for sensitivity to the recipient's attentional state. Note that cases where the signaller's or recipient's visual orientation was not clearly visible, or where the response followed the signal immediately, could not be considered for the analysis of markers.

### 3.2 | Communicative behaviours accompanied by markers

The 2,711 coded behaviours consisted of 1,441 cases of physical actions, 1,158 cases of gestures, 34 cases of vocalizations and 78 cases of bimodal signal combinations. Gestures (estimate  $\pm$  standard error =  $1.868 \pm 0.095$ ,  $z = 19.620$ ,  $p < 0.001$ ) and bimodal signal combinations ( $3.766 \pm 0.431$ ,  $z = 8.742$ ,  $p < 0.001$ ) were significantly more often associated with audience checking than actions (reference level) or vocalizations ( $0.553 \pm 0.391$ ,  $z = 1.415$ ,  $p = 0.157$ ). The same results were obtained for the association with goal persistence (gesture:  $2.188 \pm 0.11$ ,  $z = 19.889$ ,  $p < 0.001$ ; bimodal:  $3.279 \pm 0.471$ ,  $z = 6.959$ ,  $p < 0.001$ ; vocal:  $0.638 \pm 1.682$ ,  $z = 1.681$ ,  $p = 0.093$ ). Gestures ( $2.968 \pm 0.111$ ,  $z = 26.796$ ,  $p < 0.001$ ), bimodal combinations ( $2.364 \pm 0.457$ ,  $z = 5.176$ ,  $p < 0.001$ ), and also vocalizations ( $2.977 \pm 1.062$ ,  $z = 2.803$ ,  $p = 0.005$ ) were significantly more often adjusted to recipients' visual orientation than actions. In Table 2, proportions of association with

**TABLE 3** Effects of age, context, interaction partner and control predictors (mother's parity, sex and study site) on the proportion of communicative behaviours associated with (a) audience checking, (b) persistence to goal, and (c) sensitivity to recipient's visual field, derived using GLMMs with a binomial error structure and logit link function. Effects with  $p$ -values < 0.05 are depicted in bold

	Estimate	SE	$\chi^2_1$	$p$
<b>(a) Audience checking</b>				
Intercept	-1.052	0.167	(1)	(1)
Within-age	0.145	0.076	3.724	0.054
<b>Between-age</b>	<b>0.194</b>	<b>0.100</b>	<b>5.405</b>	<b>0.020</b>
Partner [non-maternal]	-0.253	0.201	1.613	0.204
<b>Context [joint travel]</b>	<b>0.863</b>	<b>0.208</b>	<b>9.714</b>	<b>0.002</b>
<b>Context [play]</b>	<b>1.717</b>	<b>0.253</b>	<b>27.126</b>	<b>&lt;0.001</b>
Mother's parity	0.117	0.080	2.057	0.152
Infant sex [male]	0.274	0.169	2.766	0.096
Site [Tai]	0.001	0.161	0.000	0.996
<b>(b) Persistence to the goal</b>				
Intercept	0.544	0.235	(1)	(1)
<b>Within-age</b>	<b>0.180</b>	<b>0.073</b>	<b>5.005</b>	<b>0.025</b>
Between-age	0.162	0.082	3.821	0.051
<b>Partner [non-maternal]</b>	<b>1.424</b>	<b>0.217</b>	<b>29.276</b>	<b>&lt;0.001</b>
Context [joint travel]	0.032	0.381	0.007	0.932
<b>Context [play]</b>	<b>-1.129</b>	<b>0.168</b>	<b>27.207</b>	<b>&lt;0.001</b>
Mother's parity	-0.025	0.090	0.074	0.786
Infant sex [male]	-0.234	0.186	1.652	0.199
<b>Site [Tai]</b>	<b>-0.624</b>	<b>0.197</b>	<b>9.39</b>	<b>0.002</b>
<b>(c) Sensitivity to attentional state</b>				
Intercept	-0.070	0.170	(1)	(1)
<b>Within-age</b>	<b>0.298</b>	<b>0.105</b>	<b>6.624</b>	<b>0.010</b>
Between-age	-0.019	0.112	0.024	0.877
<b>Partner [non-maternal]</b>	<b>1.608</b>	<b>0.191</b>	<b>30.301</b>	<b>&lt;0.001</b>
Context [joint travel]	-0.030	0.650	0.002	0.964
Context [play]	0.092	0.204	0.201	0.654
Mother's parity	0.113	0.069	2.179	0.140
Infant sex [male]	0.371	0.135	2.679	0.102
<b>Site [Tai]</b>	<b>-0.909</b>	<b>0.153</b>	<b>21.116</b>	<b>&lt;0.001</b>

different markers are summarized for each type of communicative behaviour. More detailed results concerning the production of gesture types and bimodal signal combinations are presented elsewhere (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a, 2016b).

### 3.3 | Audience checking via eye gaze

Overall, the full model was highly significant as compared to the null model, thereby revealing a significant effect of the key test predictors on audience checking (Likelihood ratio test [LRT]:  $\chi^2_7 = 47.308$ ,  $p < 0.001$ ). After removal of the two non-significant interaction terms, we found significant age effects: the proportion of communicative behaviours associated with audience checking was significantly higher in older infants (between-infants age, see Table 3a; Figure 2). Moreover, audience checking was significantly more frequent in the joint travel and play contexts compared to the reference category of food sharing (Table 3a, Figure 3). None of the other effects in the model were significant (Table 3a).

### 3.4 | Persistence to the goal

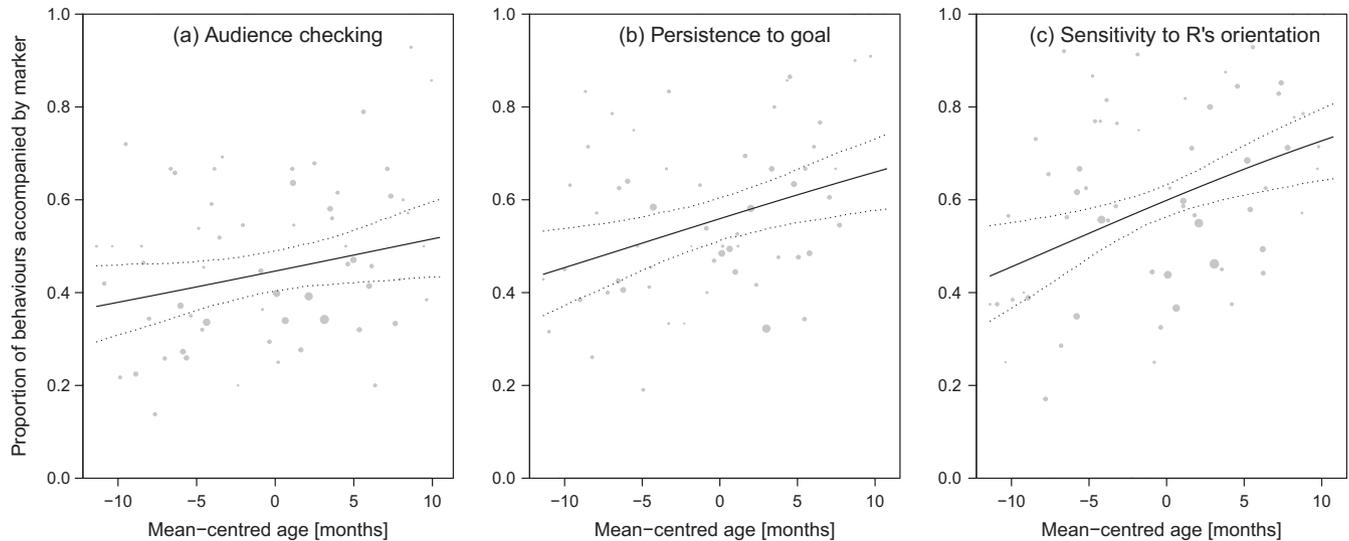
For the marker of goal persistence, we found that the full model was highly significant as compared to the null model (LRT:  $\chi^2_7 = 61.238$ ,  $p < 0.001$ ). Once again we found effects of age after the non-significant interaction terms were removed: Goal persistence increased significantly with age (within-infants age, see Table 3b, Figure 1). In addition, goal persistence was significantly less likely if the recipient was the mother (Table 3b; Figure 4), and when the interaction took place in the context of social play compared to the other two behavioural contexts (Table 3b; Figure 3). In terms of site affiliation, we found that individuals from the *Kanyawara* community showed higher proportions of goal persistence than individuals from the *Tai South* community (Table 3b; Figure 5). None of the other effects in the model were significant (Table 3b).

### 3.5 | Sensitivity to the recipient's attentional state

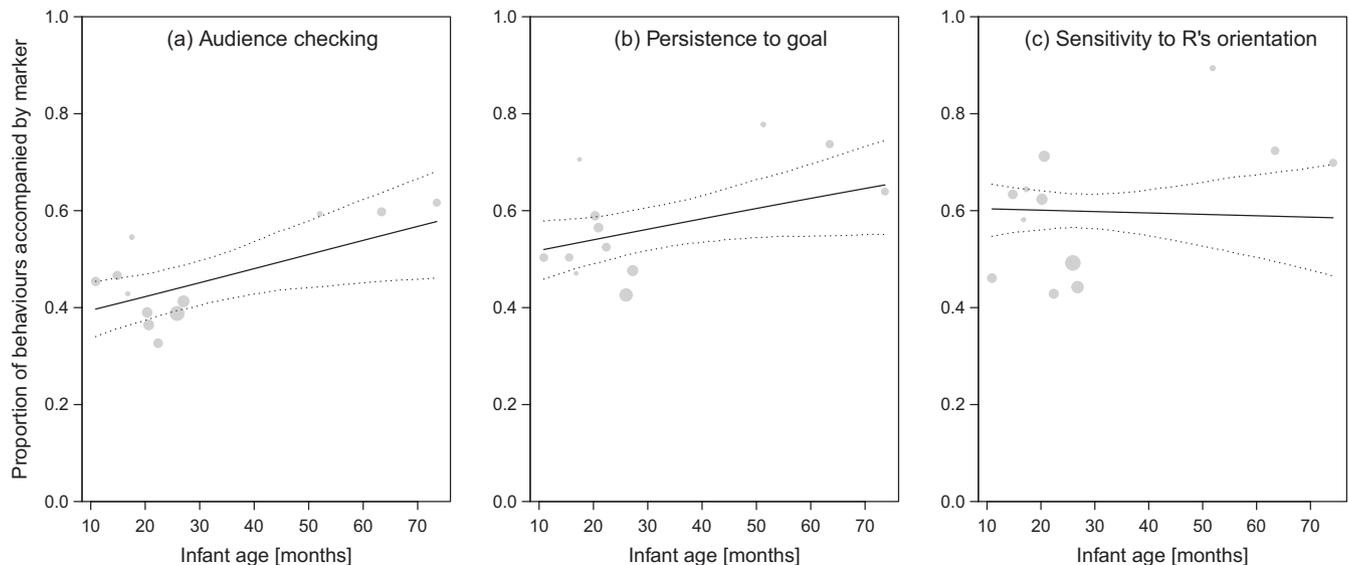
Overall, the full model was highly significant compared to the null model for the third marker (LRT:  $\chi^2_7 = 44.027$ ,  $p < 0.001$ ). After both non-significant interaction terms were removed, we found that signallers adjusted to the recipients' visual field significantly more often with increasing age (within-infants age, see Table 3c; Figure 1) and that this marker was more likely in interactions with non-maternal individuals (Table 3c, Figure 4). Moreover, adjustment to the recipient's attentional state was significantly more likely in chimpanzees of the *Kanyawara* than in those of the *Tai South* community (Table 3c; Figure 5). Between-age and the other effects in the model were not significant (Table 3c, Figure 3).

### 3.6 | Lack of response

The full model was clearly significant compared to the null model (LRT:  $\chi^2_7 = 60.317$ ,  $p < 0.001$ ). After removing the two non-significant interaction terms, we found that the proportion of behaviours lacking an appropriate response was significantly higher in interactions with non-maternal conspecifics (Table 4). Moreover, communicative failure of signals was significantly less likely in the joint travel and play contexts



**FIGURE 1** Effect of mean-centred age ('within-age') on the proportion of communicative behaviours associated with (a) audience checking, (b) persistence to the goal, and (c) sensitivity to the recipient's visual orientation in chimpanzee infants. Depicted are raw proportions, separately for each centred month of age of a given individual; thus individuals can be represented more than once. The area of the dots corresponds to the sample size per centred month of age ( $\text{range}_a = 1\text{--}190$ ;  $\text{range}_b = 1\text{--}155$ ;  $\text{range}_c = 1\text{--}210$ ). The solid and dashed lines represent the fitted model and confidence interval based on all other covariates and factors centred to a mean of zero. The effect on audience checking was not significant ( $\chi^2_1 = 3.724$ ,  $p = 0.054$ )



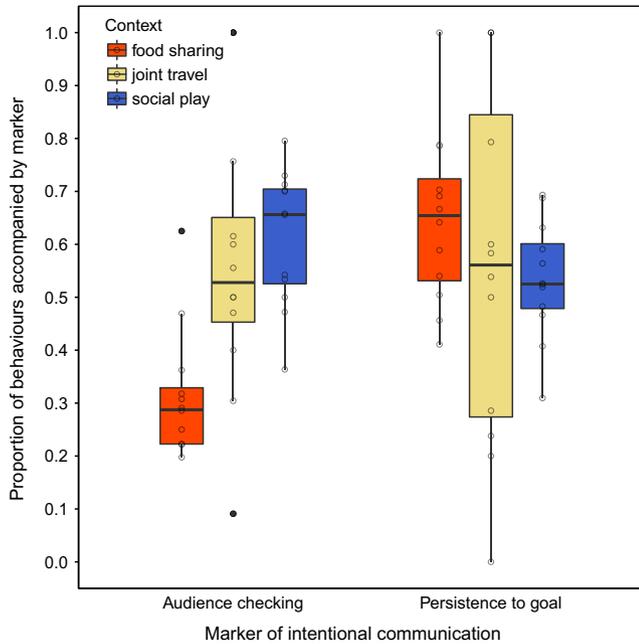
**FIGURE 2** Effect of age ('between-age') on the proportion of communicative behaviours associated with (a) audience checking, (b) persistence to the goal, and (c) sensitivity to the recipient's visual orientation in chimpanzee infants. Depicted are raw proportions, separately for each infant against its mean age. The area of the dots corresponds to the sample size per individual ( $\text{range}_a = 42\text{--}518$ ;  $\text{range}_b = 34\text{--}413$ ;  $\text{range}_c = 43\text{--}575$ ). The solid and dashed lines represent the fitted model and confidence interval based on all other covariates and factors centred to a mean of zero. The effects on goal persistence ( $\chi^2_1 = 3.821$ ,  $p = 0.051$ ) and sensitivity to recipient's orientation ( $\chi^2_1 = 0.024$ ,  $p = 0.877$ ) were not significant

compared to the reference level of food sharing (Table 4; Figure 6). The other effects in the model were not significant (see Table 4).

## 4 | DISCUSSION

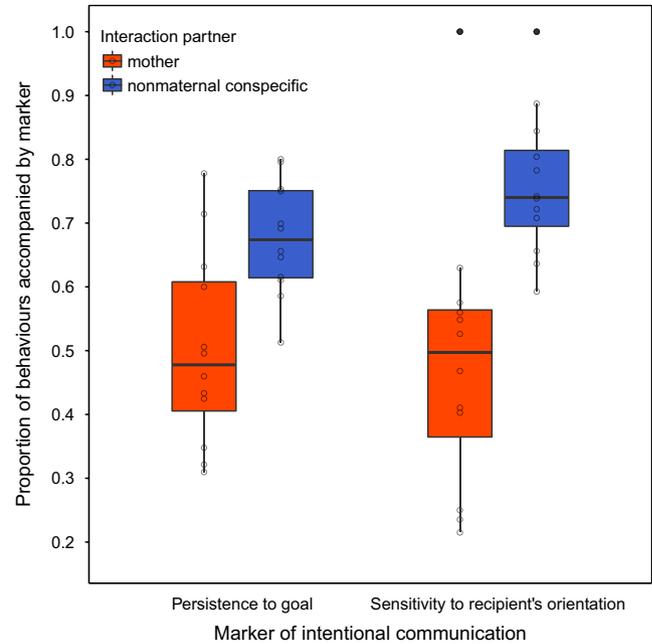
In the present study, we investigated the development of intentional signal usage in chimpanzee infants of two different subspecies living

in their natural environments. As such, the present study broadens our comparative dataset on the gestural communication of young chimpanzees in the same communities (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a, 2016b). Specifically, we focused on the effects of age, context and interaction partner on the use of three established markers of intentional communication: audience checking, goal persistence and sensitivity to the recipient's attentional state (E. Bates et al., 1975; Leavens et al., 2005; Townsend et al., 2017).



**FIGURE 3** Proportion of communicative behaviours accompanied by audience checking (left) and persistence to goal (right) in relation to context. Dots represent mean proportions per subject (food sharing:  $N = 12$ ; joint travel:  $N = 12$ ; social play:  $N = 12$ ). Indicated are median (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots)

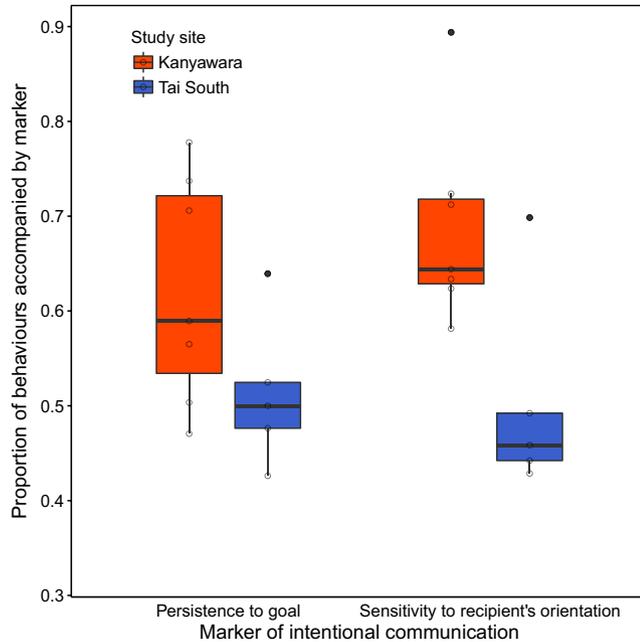
Overall, gestures and bimodal combinations were more commonly accompanied by markers of intentional communication in the examined communicative contexts than actions or vocalizations. We found an impact of age on the use of all markers used to identify intentional communication. Between the ages of 9 and 78 months, chimpanzee infants significantly increased their use of audience checking. Within subjects, we found that infants increased their use of persistence and sensitivity to attention markers. Moreover, either context (audience checking), interaction partner (sensitivity to the recipient's attentional state), or both factors (goal persistence) played a crucial role for the association of a given marker with a communicative behaviour. Audience checking was relatively more frequent in social play and joint travel than in food sharing, whereas persistence to the goal was relatively less frequent in social play than in food sharing. Concerning the role of recipients, infants showed considerably less often sensitivity to the attentional state and persistence in interactions with mothers than in interactions with non-maternal conspecifics. Site affiliation (subspecies) also seemed to have an influence on the association of communicative behaviours with markers, with persistence and sensitivity to recipients' attention employed more in *Kanyawara* (eastern chimpanzee) than *Tai South* (western chimpanzee) infants. With regard to the link between persistence and communicative failure, we found that lack of responsiveness was not significantly affected by age in the subjects of our study. Communicative failure was more common in interactions with non-maternal individuals and in the food sharing context. In the following paragraphs, we will discuss our findings in depth.



**FIGURE 4** Proportion of communicative behaviours accompanied by persistence to goal (left) and sensitivity to recipient's visual orientation (right) in relation to interaction partner. Dots represent mean proportions per subject (non-maternal:  $N = 12$ ; mother:  $N = 12$ ). Indicated are median (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots)

We aimed to examine the ontogeny of communicative abilities in chimpanzees by means of a multimodal approach. The finding that gestures and bimodal signal combinations were more frequently accompanied by markers of intentional communication than other communicative behaviours might be a consequence of the chosen social contexts, in which dyadic, close-up interactions fostering visual and tactile communication are most common. In addition, we assume that results presented in this study apply particularly to gestures and actions, as sample sizes for the other observed types of communicative behaviour (vocalizations and bimodal signal combinations) were comparatively small.

Our study provided hitherto undocumented evidence for the development of three crucial markers of intentional signal usage. While controlling for age differences between subjects, we demonstrated that infants increased their use of goal persistence and sensitivity to attention during the observation period. The proportion of communicative behaviours accompanied by audience checking was significantly higher in older infants. Although we did not grasp the onset of these markers, our results suggest that audience checking and persistence play a larger role in older infants. While sensitivity to the recipient's visual orientation is already crucial from the earliest developmental stages in mother-infant coordination (van Lawick-Goodall, 1967), the need for consistent audience checking and goal persistence increases during infant development. This can be explained by means of the chimpanzee's general developmental trajectory: after breaking the constant association with the mother, and when faced with situations where social partners are



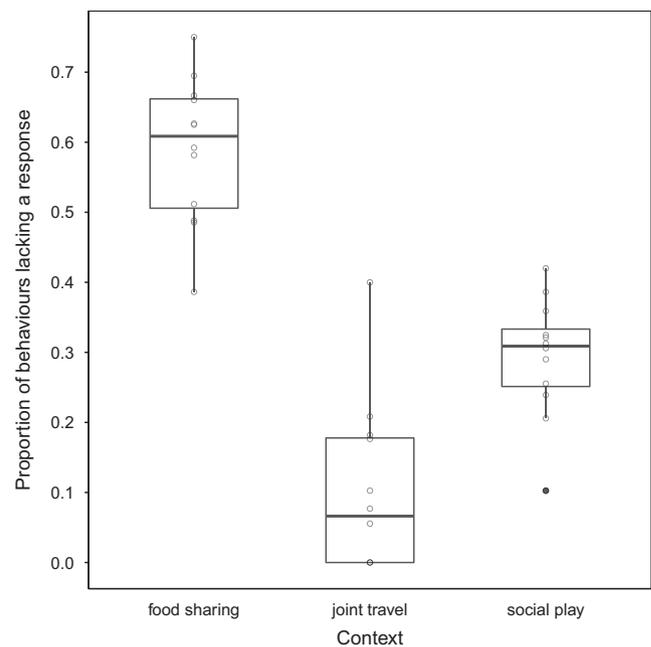
**FIGURE 5** Proportion of communicative behaviours accompanied by persistence to goal (left) and sensitivity to recipient's visual orientation (right) in relation to study site. Dots represent mean proportions per subject (*Kanyawara*:  $N = 7$ ; *Tai South*:  $N = 5$ ). Indicated are median (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots)

not responsive (e.g. resulting in a higher urgency for visual communicative behaviour), recipient monitoring and persistence play an increasing role for young chimpanzees. Importantly, by demonstrating that the responsiveness of interaction partners was not affected by infants' age, we ruled out that higher levels of goal persistence were merely due to decreasing responsiveness of conspecifics towards signallers of increasing age. To be able to show that chimpanzees learn to persist during ontogeny (and rule out the possibility that age differences in the use of markers were merely due to maturation processes), we would have needed to demonstrate an effect of interactional experiences on signal use as in our recent study on gesture development (Fröhlich et al., 2017). The fitted model curves run approximately parallel to each other, showing that age seems to have the same effect on all three measures of intentional signal use. This finding suggests that all behavioural criteria underlie the same domain of intentional communication, as they appear to develop at the same pace. Nonetheless, it also demonstrates how critical it is to implement a developmental approach in studies of comparative social cognition (Bard & Leavens, 2014).

By observing how intentional communication unfolds over time in individuals living in their natural environment, we can decipher to what extent the developmental trajectory of intentional communication (measured via established behavioural markers) in ape infants mirrors that of human infants. Since all three markers are already present at 9 months of age, our findings suggest that chimpanzees have an earlier onset age of intentional communication than humans. However, because no comparable studies exist on developmental trajectories

**TABLE 4** Effects of age, context, interaction partner and control predictors (mother's parity, sex and study site) on the proportion of communicative behaviours lacking a response from the recipient, derived using GLMMs with a binomial error structure and logit link function. Effects with  $p$ -values  $< 0.05$  are depicted in bold

Lack of response	Estimate	SE	$\chi^2_1$	$p$
Intercept	-0.321	0.268		
Within-age	0.059	0.058	1.085	0.298
Between-age	-0.013	0.077	0.030	0.863
<b>Partner [non-maternal]</b>	<b>0.857</b>	<b>0.234</b>	<b>9.666</b>	<b>0.002</b>
<b>Context [joint travel]</b>	<b>-2.075</b>	<b>0.257</b>	<b>22.568</b>	<b>&lt;0.001</b>
<b>Context [play]</b>	<b>-1.459</b>	<b>0.176</b>	<b>27.162</b>	<b>&lt;0.001</b>
Mother's parity	-0.116	0.112	1.102	0.294
Infant sex [male]	0.169	0.224	0.414	0.520
Site [Tai]	0.451	0.322	2.291	0.130



**FIGURE 6** Proportion of communicative behaviours lacking a response in relation to context. Dots represent mean proportions per subject (food sharing:  $N = 12$ ; joint travel:  $N = 12$ ; social play:  $N = 12$ ). Indicated are median (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (dots)

of specific markers in humans, we can only speculate about similarities to and differences from human intentional development. Our findings suggest that the developmental patterns of markers in chimpanzees mirror to some extent findings generated for human infants. From the earliest use (i.e. 9 months of age), intentional acts such as pointing, showing and offering were only produced if the caretaker



was attentive towards the infant (Bakeman & Adamson, 1986). Human infants start to use gestures associated with visual checking around 10 months of age (E. Bates et al., 1975) and shift from looking after pointing to looking before gesture execution around 16 to 18 months (Franco & Butterworth, 1996). This shift might be specifically linked to the declarative function of pointing, with the communicative goal concerning the social partner rather than an object (Franco & Butterworth, 1996). Finally, persistence in the form of communicative negotiation and modification has been shown to occur from the beginning of the second year of life, around 13 to 14 months of age (E. Bates et al., 1975; Golinkoff, 1986, 1993). 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—is thus evident both in human and great ape infants (Bard, 1992). Since we lack studies using a similarly integrative developmental approach for markers of intentional communication in human infants, we are prevented from drawing final conclusions. Our results nevertheless demonstrate the importance of a mixed longitudinal/cross-sectional approach, thereby taking into account within- and between-subject effects in studies of communicative intent in both captive and wild great apes.

With respect to the influence of interaction partner, the low overall proportion of intentional signal usage towards mothers compared to other conspecifics presents another conspicuous finding of this study. In particular, chimpanzee infants showed less sensitivity to the attentional state and showed lower proportions of goal persistence in maternal as compared to non-maternal interactions. In our recent study on play-soliciting gestures in chimpanzees, we also demonstrated that visual and audible gestures are predominantly directed at conspecifics other than mothers (Fröhlich, Wittig et al., 2016a). Moreover, this result is in line with recent findings suggesting that interactional experience with conspecifics outside the mother–infant bond crucially impacts communication skills, while within the mother–infant dyad—due to the high familiarity and predictable outcomes of interactions—mutual understanding is achieved via relatively few signals (Fröhlich et al., 2017). The difference between infants' interactions with the mother and those with non-maternal partners in our study might also relate to other specificities of the mother–infant relationship. As a consequence of the high levels of familiarity discussed above, the mother is particularly apt to recognize her infant's needs and intentions in relation to its developmental stage (see Boesch, 1991; Fröhlich, Wittig et al., 2016b, for similar conclusions). In contrast, other individuals in the infant's social environment will be less responsive or capable of understanding. This might be especially valid for the context of food sharing: chimpanzee mothers have been reported to be generally tolerant towards their offspring, often share food passively and allow 'thefts' (van Lawick-Goodall, 1968). However, infants might be required to employ considerably more communicative effort (i.e. goal persistence) if the targeted recipients are other individuals in the community that are more reluctant to share their food (Fröhlich, Müller, Zeiräg, Wittig, & Pika, in prep.; Wilkinson, Leudar, & Pika, 2012). This notion is corroborated by the result that communicative failure was more likely to occur in interactions with non-maternal conspecifics and in the food sharing context. Along with these findings, we also showed that the three markers were used in different proportions across behavioural

contexts. Specifically, audience checking accompanied play-soliciting behaviours more often than food-requesting behaviours throughout the age range examined, whereas goal persistence was associated more frequently with food- than with play-soliciting behaviours.

In terms of inter-site differences, we found an effect of site affiliation (subspecies) on the use of two of the examined markers of intentional communication. While there was no site difference for the use of audience checking, *Kanyawara* (eastern) chimpanzees seemed to exhibit more often sensitivity to recipients' visual orientation and higher proportions of goal persistence than *Tai* (western) chimpanzees. It has been shown that western chimpanzees exhibit greater male–female gregariousness than eastern chimpanzees (Doran et al., 2002; Surbeck et al., 2017). Thus, the social environments of the two subspecies seem to differ in crucial respects, with stronger bonds between males and females and possibly lower risks of infanticide in *Tai* compared to *Kanyawara* (Gruber & Clay, 2016). In light of the smaller community size of *Tai South*, ranging between 26 and 33 as compared to 53–56 at *Kanyawara*, we speculate that this difference might have resulted in a smaller proportion of communicative behaviours associated with intentionality markers. In the *Tai South* community, signals might have more predictable outcomes due to a large number of repeated interactions (i.e. high degrees of familiarity) among the same individuals. As argued for our findings regarding signal use in mother–infant interactions (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a), it is likely that infants rely particularly on intentionally produced signals to enable mutual understanding with less familiar (non-maternal) conspecifics. Therefore, chimpanzee infants of *Tai* and *Kanyawara* seem to grow up in very different social settings. However, it is also possible that these differences are partly caused by diverging habitat characteristics and average distances between signaller and recipient. Since we do not have detailed data for party sizes and visibility during interactions, we can only speculate about the social or ecological factors causing the effect of site affiliation on communicative behaviour. Moreover, the site differences might point to the variability in signal characteristics across the different places where chimpanzees live. Intentional communication in chimpanzees has been intensively studied both in captivity (e.g. Leavens et al., 2005; Roberts, Vick, Roberts, & Menzel, 2014; Tomasello et al., 1994; Tomasello et al., 1997) and in the wild (e.g. Fröhlich et al., 2017; Hobaiter & Byrne, 2014; Roberts, Roberts, & Vick, 2014), but it is difficult to relate our specific results to previous findings. On one hand, most of the existing studies differ with regard to the type and number of criteria that were used to infer intentionality (reviewed in Waller, Caeiro, & Davila-Ross, 2015). On the other hand, the family and group structures in wild groups differ crucially from those of chimpanzees living in captive settings (not living in large groups or in fission-fusion groups), and in sanctuaries (living in 'wild' ecologies, but without family or group structures). It is important to acknowledge this variability when looking for the factors driving differences in intentional signal use (as suggested by Bard & Leavens, 2014). Notably, site differences have also been found with regard to some gestural parameters in our previous work (Fröhlich et al., 2017; Fröhlich, Wittig et al., 2016a). This highlights the need to control for

social and ecological variables in future studies to disentangle the source of inter-site variation and the possibility of 'communicative culture' (Pika & Fröhlich, 2018).

The field of primate communication is still faced with a shortage of studies implementing multimodal paradigms (Fröhlich & van Schaik, 2018; Slocombe et al., 2011). Most of the studies aiming to operationalize intentionality have been limited to one modality only hampering systematic cross-modal comparisons that are indispensable to gain insight into intentional communication as a whole (reviewed in Townsend et al., 2017). If research efforts focus on single modalities only, we might be missing much of the complexity ingrained in a communicative system and thus not be able to recognize primary functions of communicative acts (Fröhlich, 2017; Liebal et al., 2013). There has been a large discrepancy in using behavioural criteria for intentional communication in vocal, facial and gestural research (Liebal et al., 2013; Schel et al., 2013; Waller et al., 2015). Previous research focusing on intentional communication in primates predominantly focused on gestural signals: out of 24 studies reviewed by Liebal and colleagues (2013), all included gestural signals, while only nine and seven were additionally concerned with vocal and facial signals, respectively. This review stressed the large discrepancy across studies related to both number and type of criteria used to identify intentional signalling (Liebal et al., 2013). We hope that our study will stimulate future work taking into consideration the effects of age and development on communication, including contexts involving long-distance communication and limited visibility.

Taken together, this study expands Plooi's findings on chimpanzees' communicative development by providing hitherto undocumented evidence that markers of intentional communication undergo developmental trajectories, since the use of all three behavioural markers was affected by infant age. By using a systematic within-/between-subject approach in great apes living in their natural habitat, we showed that the onset of intentional communication in ape infants might precede that in human infants. Nonetheless, we also demonstrated that specific social factors, such as communicative context, interaction partner and group affiliation, might also play a crucial role for the use of intentional communication, and urgently need to be considered in comparative studies. In addition, we hope to have opened the stage for future studies involving carefully chosen representatives of the more than 50 genera of primates, but also more distantly related taxa living in complex social settings such as elephants, cetaceans and corvids. This might provide further insight into the linkage between social, ecological and communicative complexity (Bradbury & Vehrencamp, 2011; Freeberg, Dunbar, & Ord, 2012; Pika, 2017).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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