

The ontogenetic ritualization of bonobo gestures

Marta Halina · Federico Rossano · Michael Tomasello

Received: 5 June 2012/Revised: 29 December 2012/Accepted: 15 January 2013/Published online: 31 January 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Great apes communicate with gestures in flexible ways. Based on several lines of evidence, Tomasello and colleagues have posited that many of these gestures are learned via ontogenetic ritualization—a process of mutual anticipation in which particular social behaviors come to function as intentional communicative signals. Recently, Byrne and colleagues have argued that all great ape gestures are basically innate. In the current study, for the first time, we attempted to observe the process of ontogenetic ritualization as it unfolds over time. We focused on one communicative function between bonobo mothers and infants: initiation of “carries” for joint travel. We observed 1,173 carries in ten mother–infant dyads. These were initiated by nine different gesture types, with mothers and infants using many different gestures in ways that reflected their different roles in the carry interaction. There was also a fair amount of variability among the different dyads, including one idiosyncratic gesture used by one infant. This gestural variation could not be attributed to sampling effects alone. These findings suggest that ontogenetic ritualization plays an important role in the origin of at least some great ape gestures.

Keywords Bonobo · Communication · Gesture · Great ape · Ontogenetic ritualization · *Pan paniscus*

Introduction

Although apes are quite flexible in their comprehension of some vocalizations—even comprehending the alarm calls of other species (Zuberbühler 2000)—their production of vocalizations is mostly inflexible. For example, although chimpanzees may produce several acoustic variants of their “rough grunt” food call (Slocombe and Zuberbühler 2005, 2006), they seem quite incapable of producing a “rough grunt” in the absence of food (Goodall 1986). And although Crockford et al. (2012) found that chimpanzees produce quiet “alert hoos” more often when others have yet to see the eliciting snake, it is difficult to imagine them producing the call for a completely different function.

In contrast, great apes use their gestures—that is, some of their gestures—quite flexibly. The same individual will routinely use multiple gestures for the same function (e.g., multiple gestures for play or travel or begging for food) and also can use the same gesture for multiple functions (e.g., attention-getting gestures such as ground-slap to initiate both play and nursing) (Tomasello et al. 1985, 1989, 1994, 1997; Pollick and de Waal 2007; see papers in Call and Tomasello 2007). Moreover, individuals sometimes persist in using their gestures until others react as they want them to, even producing sequences of gestures until they achieve the intended outcome (Liebal et al. 2004; Cartmill and Byrne 2007).

Such flexible usage is most typically characteristic of learned behavioral strategies (Tomasello and Call 1997). A number of other pieces of evidence suggest that apes learn their gestures. First, there is great variability among individuals in which gestures they use, something that is not true of their vocalizations (see the papers in Call and Tomasello 2007). Second, there are some gestures that are idiosyncratic to individuals, which suggest something other

M. Halina (✉)
Department of Philosophy, University of California, San Diego,
9500 Gilman Drive, La Jolla, CA 92093-0119, USA
e-mail: mhalina@ucsd.edu

F. Rossano · M. Tomasello
Department of Developmental and Comparative Psychology,
Max Planck Institute for Evolutionary Anthropology,
Deutscher Platz 6, 04103 Leipzig, Germany

than species-wide hardwiring. For example, Tomasello et al. (1994) observed five idiosyncratic gestures in a study of eight captive juvenile chimpanzees and Pika et al. (2005) observed three idiosyncratic gestures in a study of seven subadult captive bonobos. Lastly, studies on human-enculturated apes have shown that they are capable of learning new gestures with relative ease (Gardner and Gardner 1969; Fouts 1973; Savage-Rumbaugh et al. 1986) and non-enculturated captive apes acquire novel gestures without training (Leavens et al. 2005).

The type of learning involved is almost certainly not social learning or imitation, as social learning could not produce idiosyncratic gestures. Moreover, observational studies of both captive and wild apes have revealed few group-specific gestures (bonobos: Pika et al. 2005; chimpanzees: Call and Tomasello 2007; Hobaiter and Byrne 2011; gorillas: Pika et al. 2003; Genty et al. 2009; orangutans: Liebal et al. 2006). The group-specific gestures that have been found can for the most part be explained by environmental factors. Tomasello et al. (1994) also systematically compared the gestural repertoires of two chimpanzee groups and found that the best explanation of their distribution was individual differences, not group differences. In a second study, these investigators introduced a novel gesture to one individual in the group experimentally, and others did not learn it socially (Tomasello et al. 1997).

Following Plooj (1979), Tomasello and colleagues proposed that the learning process involved in great ape gestural development was ontogenetic ritualization, in which individuals learn their gestures in the context of regularly occurring dyadic interactions such that parts of fully functional social behaviors become ritualized. Thus, using the “arm-raise” play gesture as an example:

1. initially one youngster approaches another with rough-and-tumble play in mind, raises his arm in preparation to play-hit the other, and then actually hits, jumps on, and begins playing;
2. over repeated instances, the recipient learns to anticipate this sequence on the basis of the initial arm-raise alone, and so begins to play upon perceiving this initial step; and
3. the communicator eventually learns to anticipate this anticipation, and so raises his arm, monitors the recipient, and waits for her to react—expecting this arm-raise to initiate the play (Tomasello 2008, p. 23).

Ontogenetic ritualization holds that the forms that gestures take derive directly from the social interactions in which an individual participates (like the phylogenetically ritualized displays of the birds studied by Tinbergen 1959). Thus, one should expect variation in individual gestural repertoires insofar as individuals participate in social

interactions that differ in their regularly recurring elements or insofar as individuals ritualize different aspects of the same interaction. However, although the occurrence of idiosyncratic gestures is evidence for ontogenetic ritualization, ontogenetic ritualization does not predict that idiosyncratic gestures will be the norm. The reason for this is that gesture forms are constrained by the forms of actions found in regularly occurring social interactions; thus, one should expect similar gestures to become ritualized in individuals that participate in similar social interactions (Tomasello et al. 1994). Moreover, gesture forms are further constrained by the fact that the behavior subject to ritualization must be a part of the action sequence from which it is drawn. If a behavioral fragment were not co-occurrent with the functionally effective action itself, then a recipient would not be able to anticipate this action on the basis of the fragment alone.

Recently, Byrne and colleagues have argued that ape gestures are innate or genetically canalized rather than ontogenetically ritualized (Genty et al. 2009; Hobaiter and Byrne 2011). Their claim is that the forms of gestures are innate, but that these gestures are used intentionally and flexibly. Byrne and colleagues give two main reasons for thinking that ape gestures are innate based on their observations of captive and wild gorillas and wild chimpanzees. First, they hold that the variation observed across individual gestural repertoires (including idiosyncratic gestures) can be largely attributed to sampling effects. Second, they categorize those gestures that do not take the form of intention-movements or truncated actions (and thus could not possibly have been ontogenetically ritualized) as innate and point out that these innate gestures are produced as intentionally and flexibly as those gestures that are potentially ritualized. Thus, it is possible that all ape gestures are innate no matter how intentionally or flexibly they are used.

But it is not quite right to categorize those gestures that do not take the form of intention-movements as innate. Attention-getters, for example, do not take the form of intention-movements, but may be individually learned through a process slightly different than ontogenetic ritualization (Tomasello 2008). In this process, a signaler learns that when he performs a certain action (such as one that produces noise), this has the effect of drawing the attention of a nearby agent. This then leads the signaler to later produce that action intentionally with the purpose of drawing attention. Such learned attention-getters might include gestures such as *clap*, *slap object*, and *tap other*, which Genty et al. (2009) characterize as species-typical. However, the fact that gestures such as these do not take the form of intention-movements and are used intentionally and flexibly is not clear evidence that innate gestures are used intentionally and flexibly.

Moreover, with respect to gorillas, the findings of Genty et al. (2009) are consistent with the earlier conclusions of Pika et al. (2003) and Call and Tomasello (2007). Gorilla gestures seem to be subject to greater phylogenetic constraints than the gestures of other great apes. Alternatively, Pika (2002) has argued that this lack of gestural variability in gorillas may be a product of the cohesiveness of their social system. Unlike gorillas, however, the individual gestural repertoires of chimpanzees and bonobos show high levels of variability. Thus, we suspect that ontogenetic ritualization plays a larger role in the gestural development of these two species than Byrne and colleagues acknowledge. Here, we focus on bonobo gestural development. Studies on wild bonobos have described the form and use of a number of gestures (Kano 1980; Kuroda 1980, 1984; Ingmanson 1996) and work on captive bonobos has added significantly to this knowledge (de Waal 1988; Pika et al. 2005; Pollick and de Waal 2007; Schneider et al. 2011). However, little is still known about bonobo gestural communication and much less about its development. This study aims to fill part of that gap.

The most glaring weakness of the ontogenetic ritualization hypothesis is that its occurrence, which takes place over some considerable time, has never been directly observed. The evidence is all indirect. In the current study, therefore, we attempted to document at a level of detail never before attempted the emergence of gestures for a single communicative function in bonobos. Our focus was the mother–infant carry; that is, the infant becoming somehow attached to his or her mother for the purpose of joint travel. We examined the actions and gestures used to initiate carries in ten captive bonobo mother–infant dyads over many months. On the assumption that ontogenetic ritualization plays a role in the development of bonobo carry gestures, we predicted that if the actions used to initiate carries differ between mothers and infants, then the gestures used by mothers and infants to initiate carries should differ as well. We also expected that the gestures used by infants to initiate carries would structurally resemble the particular role that infants play in the carry interaction and likewise for mothers. Though the structural resemblance of actions and gestures is expected under ontogenetic ritualization, it is also consistent with phylogenetic ritualization. Thus, we further hypothesized that we should find variability among individual gestural repertoires. In order to ensure that such variability could not be attributed to sampling effects alone, we studied two dyads for an extended period of time (over 100 h each). We expected that this observation period would allow us to catalog the full set of carry-initiating gestures used by these two dyads, thus leaving any gestures not found in these repertoires as difficult to account for without appealing to social or environmental effects. Lastly, we investigated

some general factors that might affect bonobo gestural development: we looked at whether there is a relationship between an infant's motivation to initiate carries and that infant's gestural repertoire size, and if an infant's motivation to initiate carries is affected by the number of carries that infant's mother initiates per hour.

Methods

Subjects

We examined the carry interactions of 10 mother–infant bonobo dyads from six zoos (Table 1). During the observation period, the age of the infants ranged from 10 to 24 months. All of the infants were born in captivity and reared by their mothers from birth. Each dyad was videotaped using focal animal sampling with the infant serving as the focal subject (Martin and Bateson 2007). Recordings were made throughout the day and occurred over a minimum observational period of 5 months and a maximum observational period of 11 months. All dyads were videotaped for at least a total of 10 h and two dyads (infants Fimi and Loto) were recorded for over 100 h. The total amount of video collected for all dyads was 410 h.

Identifying carry events

Following the methods of Johnson, Zastrow, and Halina (see Hutchins and Johnson 2009 for a qualitative account), we documented all instances in which a mother carried her infant, excluding only those events in which the infant already had his or her body on the mother for more than 10 s before the carry took place. In the 410 h of video reviewed, we found 2,042 mother–infant carries. Out of these events, 1,173 were ones in which the mother and infant were both clearly visible before the carry took place and it was possible to identify which agent initiated the interaction. These 1,173 carries served as the basis for our analysis.

Coding procedures

We coded all agent-initiated carries according to whether they were initiated by an action or a communicative gesture. We defined an action as any behavior that succeeded in initiating a carry through direct physical force—that is, through the manipulation of another's body or the movement of one's own body into a carry position. Broadly, we defined a gesture as any mechanically ineffective behavior that succeeded in bringing about a carry by providing a recipient with visual or tactile information expressing one's intention to initiate a carry. We required that the signaler

Table 1 Subject information

Group	Infant	Mother	Infant sex	Infant age (months)	Hours observed	Carries per hour ^a
Leipzig	Luiza	Ulindi	Female	10–17	35.8	3.4
	Loto	Ulindi	Male	14–24	132.8	3.9
	Fimi	Yasa	Female	15–21	102.0	5.6
Planckendael	Habari	Djanao	Male	10–17	16.2	6.0
	Hongo	Hortense	Male	10–17	18.3	4.5
	Huenda	Hermein	Female	10–14	10.2	4.8
Apenheul	Nayembi	Liboso	Female	10–17	13.8	6.2
Berlin	Kivu	Yala	Male	10–18	19.1	5.1
San Diego park	Kalli	Loretta	Female	10–20	33.5	8.6
San Diego zoo	Kesi	Lana	Female	10–19	28.6	4.8

^a Based on the total number of carries observed (regardless of pre-carry visibility)

show signs of intending to initiate a carry by (1) appearing satisfied when the recipient responded in accordance with this goal and (2) waiting for a response from the recipient if the goal was not attained immediately. In order to count as a gesture, a behavior that met these criteria had to be observed at least three times in one or more individuals. Given the functional nature of our definition, for any sequence of gestures, only the final one (the one that succeeded in initiating a carry) counted as a gesture. We did not document audible gestures unless they also had a salient visual component, as we did not have auditory access to all of our subjects.

Lastly, we coded each initiating behavior according to its form. Table 2 lists the categories in which we were able to exhaustively classify all initiating actions and gestures. For each action and gesture, we also specified the body part used by the signaler, and for tactile actions and gestures, the body part of the recipient that was contacted. Body-part categories included the following: hand/arm, hands/arms, foot/leg, feet/legs, head, lips, back/shoulder, side/venter, and body. The final category “body” was applied when many body parts were involved in the production of the action or gesture.

Statistical analyses

Bonobo mother–infant carry interactions are asymmetrical because for a mother to successfully initiate a carry, she must get the infant on her venter or dorsum, while for an infant to successfully initiate a carry, he must get his mother moving and climb on. Given this, we predicted that the carry-initiating actions of mothers and infants would differ to a greater degree than the initiating actions of infants compared together and mothers compared together. In order to test this, we calculated and compared DICE-coefficients—which measure the similarity between action

repertoires—for every possible dyad in our subject pool (see “Appendix” for explanation).

We ran two Generalized Linear Mixed Models. The first analysis was run in order to establish if the frequencies of mother and infant carry initiations change as a function of infant age. We ran this test in order to determine whether we needed to control for changes in the frequency of carry initiations over time when conducting the second analysis. The second analysis was run in order to test whether there was a correlation between an infant’s gestural repertoire size and an infant’s “motivation” to initiate carries. We defined infant motivation as the proportion of infant-initiated carries relative to all agent-initiated carries in a dyad (see “Appendix” for explanation). We ran Spearman’s correlations to determine the relationship between an infant’s motivation to initiate carries and (1) that infant’s gestural repertoire size and (2) the average number of carries initiated by that infant’s mother per hour.

We ran two tests in order to determine whether the final gestural repertoires identified in this study depended on the time spent observing subjects. First, we ran Pearson’s correlations to measure the relationship between an individual’s final repertoire size and the total time that individual was observed. Second, we tested whether we had observed the complete repertoires of the two dyads for which we had over 100 h of observation time. We did this by plotting the cumulative number of gesture types observed over time and determining whether an asymptote was approached for each dyad.

Interobserver reliability

One of the authors (MH) coded nine out of ten dyads. To assess interobserver reliability, an assistant independently coded 20 % of these events. This same assistant coded the final dyad (Ulindi and Loto), while MH independently

Table 2 Definitions of initiating behaviors

Type	Form	Definition
Action	Climb on	Climb, drop, or jump onto the recipient's back or venter
	Gather	Bring a hand, arm, foot, or leg around the recipient's body; gather or turn the recipient toward oneself by applying pressure to their body
	Pull	Grab the recipient's hair, skin, or body and exert a force (pull) so as to move the recipient toward oneself
	Push	Use limbs or body to forcefully move a recipient away from oneself
Gesture	Grab	Grab the recipient's hair, skin, or body. Exert either no force or a pulling force that is mechanically ineffective
	Present back	Display or offer one's back to the recipient
	Present venter	Display or offer one's venter to the recipient
	Raise limb(s)	Stretch a limb or limbs upward and/or toward a recipient
	Silent pout	Extend lips toward the recipient in the expression of a pout
	Spin body	Rotate one's body approximately 360°
	Spread legs	Spread legs outward in a scissor-like fashion, positioning them from perpendicular to parallel to the ground
	Step foot	Step on the ground in an exaggerated manner
	Touch	Use hands or feet to come into contact with some part of the recipient's body

Table 3 Carry initiation information

Dyad (infant/mother)	Infant initiations		Mother initiations	
	Total number of carries initiated	Percentage of gesture initiated carries (%)	Total number of carries initiated	Percentage of gesture initiated carries (%)
Luiza/Ulindi	36	50.0	38	13.2
Loto/Ulindi	258	14.3	101	40.6
Fimi/Yasa	200	8.5	109	30.3
Habari/Djanoa	9	55.6	33	15.2
Hongo/Hortense	22	4.5	23	13.0
Huenda/Hermein	6	50.0	21	0
Nayembi/Liboso	10	20.0	30	33.3
Kivu/Yala	14	28.6	33	6.1
Kalli/Loretta	79	13.9	87	8.0
Kesi/Lana	49	49.0	15	33.3

coded 20 % of this dyad's events. The level of agreement between coders was measured using Cohen's Kappa coefficient (κ). There was a good level of agreement for initiating agent ($\kappa = 0.72$), initiation type (action or gesture) ($\kappa = 0.61$), and the specific action or gesture used ($\kappa = 0.73$). The level of agreement for event (ventral or dorsal carry) was perfect ($\kappa = 1$) (Altman 1991).

Results

Out of the 1,173 carries analyzed, 490 were initiated by mothers and 684 were initiated by infants. Table 3 lists the number of carries initiated by each mother and infant, as well as the percentage of carries that were initiated by

gestures. The remaining carries (those not initiated by gestures) were initiated by actions.

Are the gestural repertoires found here due to sampling effects?

With respect to infant gestural repertoires, we found no correlation between the number of hours that each dyad was observed and the final gestural repertoire of each infant (Pearson $\rho = 0.506$, $P = 0.135$). With respect to mother gestural repertoires, there was a correlation between gestural repertoire size and observation time (Pearson $\rho = 0.831$, $P = 0.003$). Given this, we focused on infant gestures in our analyses.

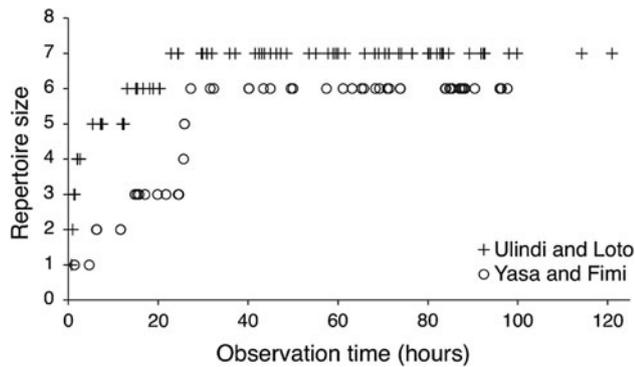


Fig. 1 The gestural repertoire size over time for those dyads observed for over 100 h. Each *symbol* represents one observed gesture

For the two dyads that we observed for over 100 h (Ulindi and Loto at 132.8 h; Yasa and Fimi at 102.0 h), we found that the gestural repertoires approached an asymptote at around the first quarter of the observation period for Yasa and Fimi and the first fifth for Ulindi and Loto. Specifically, the last new gesture type was observed at 27.3 observation hours for Yasa and Fimi and at 22.9 observation hours for Ulindi and Loto (Fig. 1). This suggests that we observed the full gestural repertoires used by these four individuals to solicit carries during this period.

How different are the initiating actions of mothers and infants?

Action repertoires were more similar between dyads from the same class (infant–infant and mother–mother) than between dyads from different classes (infant–mother) (test-statistic = 0.24, $N = 20$, $P = 0.001$; see “Appendix”). Thus, infants resemble each other in the actions that they take to initiate carries more than they resemble mothers, while mothers resemble each other more than they resemble infants.

How different are the initiating gestures of mothers and infants? Do these gestural differences reflect the forms of the actions used to initiate carries?

We observed 245 instances of gesture use (135 by infants and 110 by mothers), which could be exhaustively categorized into nine types (Table 4). Out of these nine gesture types, both mothers and infants employed the visual gesture *raise limb(s)* and the two tactile gestures *grab* and *touch*. Out of the remaining gesture types, only infants employed the four visual gestures *silent pout*, *spread legs*, *step foot*, and *spin body* and only mothers employed the two visual gestures *present venter* and *present back*. With the exception of one gesture (*silent pout*), the forms of the gestures differentially employed by mothers and infants

Table 4 Carry gestures exhibited by mothers and infants

Gesture modality	Gestures	Mothers ($N = 10$)	Infants ($N = 10$)
Tactile	Grab	✓	✓
	Touch	✓	✓
Visual	Raise limb(s)	✓	✓
	Silent pout		✓
	Spin body		✓
	Spread legs		✓
	Step foot		✓
	Present back	✓	
	Present venter	✓	

resembled the forms of the actions used by mothers and infants to initiate carries.

Both mothers and infants employed the gestures *grab*, *touch*, and *raise limb(s)*. We examined the form of these three gestures in greater detail in order to determine whether mothers and infants used them in the same way. For the tactile gestures *touch* and *grab*, we examined which part of the recipient’s body the signaler contacted. We found two main differences in the way in which mothers and infants employed these gestures (Fig. 2). In the case of *touch*, nine mothers employed *touch back/shoulder*, while only three infants used this gesture (Fisher Exact Test, $P = 0.02$). With respect to *grab*, infants used *grab side/venter* to initiate carries, while no mothers employed this gesture (Fisher Exact Test, $P = 0.03$).

The gesture *touch back/shoulder* structurally resembles the action *gather*. Out of all of the carries initiated by mothers by means of an action, 87.3 % were initiated through the use of *gather*. Mothers generally employed the action *gather* by placing a hand or arm on or around an infant’s back or shoulder (94.0 % of mother *gathers* took this form). The form of the gesture *grab side/venter* resembles the act of an infant clinging to the mother’s venter. Out of the 1,173 agent-initiated carries analyzed here, 75.2 % resulted in the infant clinging to the mother’s venter, while 24.8 % resulted in the infant riding on the mother’s back. Whether initiated by the mother or infant, a ventral carry requires that an infant grab onto his mother’s sides or venter, so that the mother’s hands are free for walking and climbing. It is also worth noting here that the infant who participated in the greatest percentage of dorsal carries (Loto at 54.5 %) was the one subject that was observed using the gesture *grab back/shoulder*.

We sorted the visual gesture *raise limb(s)* into three categories: *raise one hand/arm*, *raise two hands/arms*, and *raise one foot/leg*. Each of these three gestures was employed by a greater number of infants than mothers; however, we found no significant differences in their use.

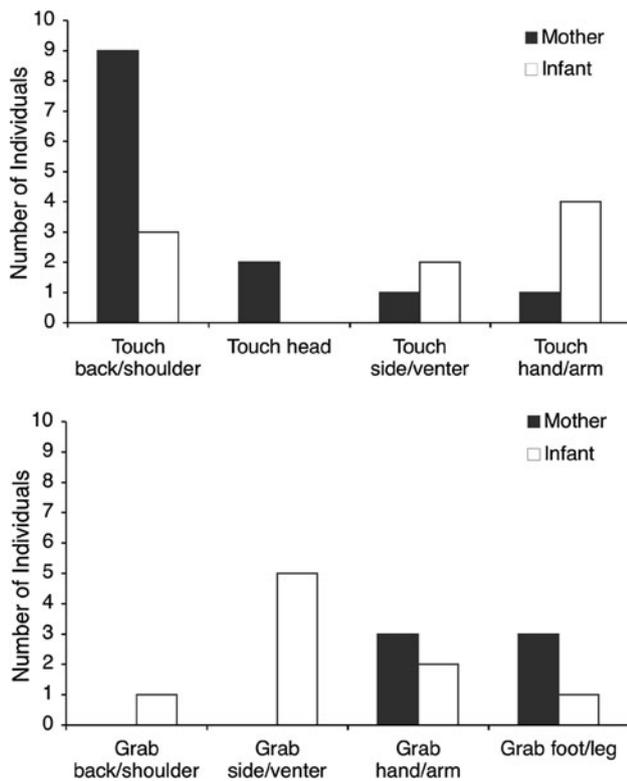


Fig. 2 A comparison of the specific forms that the tactile gestures *touch* and *grab* took in mothers and infants. Gestures are categorized according to the body part contacted by the signaler

The remaining six visual gestures were employed either only by mothers or only by infants. Two mothers (Ulindi and Yasa) employed the gestures *present venter* and *present back*; seven infants used *silent pout* (all except Hongo, Nayembi, and Kalli); three infants employed *spread legs* (Luiza, Loto, and Fimi); two infants exhibited *step foot* (Kesi and Kalli); and only one infant (Kesi) used the gesture *spin body*.

The gesture *spread legs* was used by all and only the three infants in the Leipzig group. Indeed, we did not observe the other seven infants employ this gesture, even on a single occasion. *Spread legs* takes the form of extending and opening one's legs in the air in a scissor-like fashion and resembles the act of an infant wrapping her free legs around her mother for either a ventral or dorsal carry. Given that *spread legs* was found only in the Leipzig infants, we examined if the Leipzig environment afforded the development or use of this gesture in the carry context more than the environments of the other bonobo groups. In order to do this, for every agent-initiated carry, we recorded whether or not one of the participants was hanging before the carry took place, where hanging was defined as having one's body suspended above ground, such that both feet are dangling in the air (that is, not resting on or touching anything) before the initiating move is made. As

shown in Table 5, the three Leipzig infants participated in the highest percentage of carries preceded by hanging by the infant.

Two infants exhibited the gesture *step foot*. This gesture resembles the act of an infant taking one or two steps away from her mother. The two infants that employed *step foot* did not share any apparent environmental features that might have led them to use this gesture more frequently than the other infants. Also, the two infants whose full gestural repertoires we almost certainly observed (those with over 100 h of focal observations) did not exhibit this gesture during the study.

Only one infant employed the gesture *spin body*. The form of this gesture resembles the act of an infant turning from her mother to the direction to be traveled and then back toward her mother. As with *step foot*, this gesture was not exhibited by the two infants observed for over 100 h. Furthermore, though this particular infant has been observed using this gesture before (Christine Johnson, personal communication), the *spin body* gesture has not been observed in any other bonobo in either this or others studies (Table 6). Thus, this gesture appears to be unique to this infant, suggesting that it was individually learned. Generally, a gesture that is ontogenetically ritualized will be directed at only the individual with whom it was ritualized and will have the function of initiating the interaction from which it originated. In this case, if *spin body* was ritualized in the context of an infant initiating travel with her mother, then that infant should generally direct this gesture at her mother for the purpose of initiating travel. In order to determine whether this was the case, we reexamined the 28.6 h of video on Kesi (continuous recording, focal sampling), documenting every use of this gesture by this infant, regardless of the context or potential function.

We found nine additional instances in which Kesi performed *spin body*. In all nine cases, *spin body* was directed at Kesi's mother. In eight cases, *spin body* was used in conjunction with other gestures. Table 7 presents descriptions of the situations in which Kesi used *spin body*, along with a list of the other gestures that were used during the event (that is, those that occurred within <10 s of *spin body*). Eight of the nine occurrences of *spin body* were used in the general context of travel and appeared to serve the specific function of requesting the mother to travel with the infant. Moreover, all of the other gestures that Kesi employed during the events in which *spin body* occurred were ones that she had used to initiate carries. Thus, though these instances of *spin body* did not lead to successful carries, they resemble this infant's typical requests for carries (that is, those that had succeeded in initiating carries at other times).

Two mothers employed the gestures *present venter* and *present back*. The forms of these gestures resemble the act

Table 5 Carries preceded by hanging

Infant	Percentage of agent-initiated carries in which the infant is hanging prior to initiation (%)
Luiza	21.6
Loto	8.9
Fimi	7.4
Kivu	6.4
Habari	4.8
Nayembi	2.5
Hongo	2.2
Kalli	1.8
Huenda	0
Kesi	0

Table 6 Comparing the gesture forms found here with other studies

This study	de Waal (1988)	Pika et al. (2005)	Pollick and de Waal (2007)	Schneider et al. (2011)
Grab		Grab, Grab-push-pull	Grab	Pull
Present back	Rump present	Present	Rump present	Offer body
Present venter	Ventral present	Present	Ventral present	Present genitals
Raise limb(s)	Hand-up begging, hand-side begging, leg-out begging	Reach	Arm-raise, beckon, reach out down, reach out side, reach out up, foot/leg gesture	Arm-raise, extend arm
Silent pout	Silent pout		Silent pout face	
Spin body				
Spread legs				
Step foot		Stomp	Stomp	Foot stomp
Touch		Touch	Gentle touch, hard touch	Gentle touch, nudge

of a mother approaching her infant in a way that facilitates the infant's ability to climb on the mother's venter or back. The two mothers that employed these gestures were the ones that we observed for over 100 h. Thus, it is possible that the variable use of these gestures was an effect of sampling.

Silent pout was observed in seven out of the ten infants studied here, including the two infants that were observed for over 100 h. It was the only gesture found in this study

that was differentially used by mothers and infants, but did not take the form of a truncated carry action.

Do the number of mother and infant carry initiations change as a function of infant age?

Overall, the full model was highly significant compared to the null model (likelihood ratio test: $c^2 = 181.62$, $df = 3$, $P < 0.0001$). There was a clear interaction between the effects of age and the initiator (estimate \pm SE = -0.772 ± 0.065 , $z = -11.81$, $P < 0.0001$). While the number of carries initiated by the infant increased over time, the number of carries initiated by the mother decreased over time (Fig. 3).

The relationship between infant motivation, infant gestural repertoire size, and the frequency of mother-initiated carries

We found that infants with higher motivation to initiate carries had more gesture types than less motivated infants (Spearman's $Rho = 0.72$, $N = 10$, $P = 0.024$). We also found an inverse correlation between infant motivation and the average number of carries initiated by that infant's mother per hour (Spearman's $Rho = -0.794$, $N = 10$, $P = 0.006$). Infants that had higher motivation to initiate carries tended to have mothers who initiated fewer carries per hour, while infants that had lower motivation to initiate carries tended to have mothers that initiated more carries per hour.

Discussion

The purpose of this study was to determine whether ontogenetic ritualization plays a role in bonobo gestural development. Ontogenetic ritualization predicts that if mothers and infants use different actions to accomplish carries, then they should differ in the types of gestures that they use to initiate carries as well. In accordance with this prediction, we found that whereas mothers use gestures such as *touch back/shoulder*, *present venter*, and *present back* to initiate carries, infants use gestures such as *grab side/venter*, *spread legs*, *step foot*, and *spin body*. Moreover, the forms of these gestures resemble the differential roles that mothers and infants play in the carry interaction. Under ontogenetic ritualization, one would further expect that there would be variability across individual gestural repertoires. We found such variability here: there were no gestures shared by all individuals in the class of mothers or infants and very few gestures found in more than two or three individuals in a class. Though we cannot completely rule out the possibility that some of this variability is due to

Table 7 All instances of the *spin body* gesture used by Kesi that do not lead to a successful carry

#	Function	Event description	Other gestures used during event
1	Travel request	Other group member on the move; infant gestures at mother and follows group member; mother responds by following infant	
2	Travel request	Infant gestures at mother who is sitting; mother responds by placing a hand on the infant's back, gathering the infant toward her venter, moving one step, and sitting back down	Grab side/venter (×2)
3	Unclear	Infant gestures at mother, sees other infant nearby, runs toward this other infant to initiate play	Silent pout
4	Request to stand or move	Infant gestures at mother who is laying down; mother responds by sitting up and placing a hand on the infant's back	Grab side/venter, touch side/venter (×2)
5	Travel request	Other group member on the move; infant gestures and follows group member; mother does not respond, but watches infant and other who remain nearby	Touch side/venter
6	Request to stand or move	Infant gestures at mother who is laying down; mother responds by sitting up and placing a hand on the infant's back	Touch side/venter
7	Travel request (failed carry attempt)	Other group member on the move; infant gestures at mother who is laying down; mother responds by getting up, placing a hand on the infant's back, and taking two steps while the infant climbs on; mother does not move further and infant drops off	Touch side/venter
8	Travel request (failed carry attempt)	Infant gestures at mother who is sitting; mother responds by getting up and taking two steps while the infant begins to climb on; mother stops and sits; infant gets off	Touch side/venter (×2)
9	Request to stand or move	Infant gestures at mother who is sitting; mother responds by placing a hand on the infant's back and gathering the infant toward her venter	Silent pout, grab side/venter

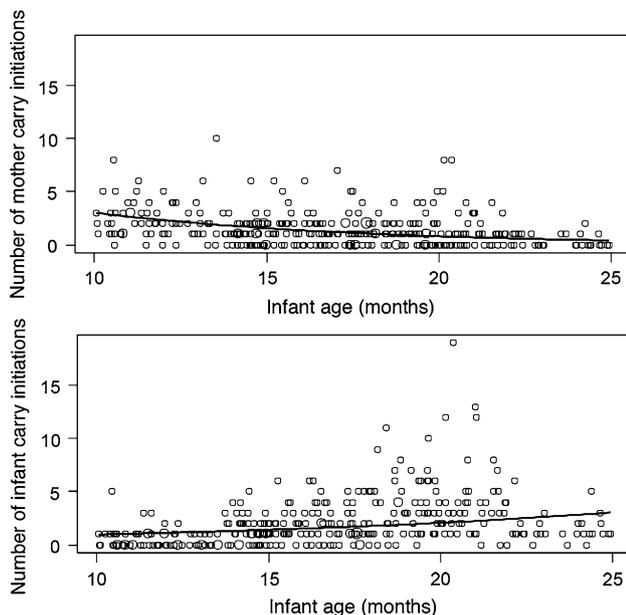


Fig. 3 Frequency of carry initiations by infants and mothers. Shown are the total numbers of initiations per recording session (lasting from <1 h to >5 hs). *Dot sizes* indicate the number of infants that fell into the respective combination of age (i.e., recording session) and number of initiations (maximum: 3). *Lines* depict the result as estimated by a Generalized Linear Mixed Model

sampling effects, this is very unlikely for the gestures *step foot* and *spin body* because they were not employed by those infants that we observed for over 100 h. *Spin body* represents an especially strong case of an ontogenetically

ritualized gesture, as it was used idiosyncratically and dyadically.

In addition to the above analyses, we examined the relationships between an infant's motivation to initiate carries, an infant's gestural repertoire size, and the frequency of carries initiated by that infant's mother. We found that those infants that were highly motivated to initiate carries had larger gestural repertoires than less motivated infants. We also found that those infants that were highly motivated to initiate carries tended to have mothers that initiated fewer carries per hour than those infants less motivated to initiate carries.

Out of the eight gestures differentially employed by mothers and infants, seven took the form of actions used to initiate carries (all except *silent pout*) and thus could have been ritualized from those actions during ontogeny. For example, more mothers used the gesture *touch back/shoulder* than infants and mothers tended to initiate carries using the action *gather*. Familiarity with the *gather* action could lead an infant to anticipate that a mother is potentially preparing to pick the infant up from the first step of perceiving the mother's hand or arm come into contact with the infant's back. More infants used the gesture *grab side/venter* than mothers. Ventral carries require that an infant hold onto a mother's side or venter; thus, the act of an infant grabbing this area can serve as a cue to the mother that the infant is prepared to be carried. Similar analyses can be given for the remaining five visual gestures used exclusively by either mothers or infants (see Table 8).

The Leipzig infants participated in the highest percentage of carries beginning with the infant hanging (from a branch or rope, for example) with legs suspended in the air, and they were the only three infants that employed the *spread legs* gesture. There are two possibilities concerning how this environmental difference might have led to the use of *spread legs* in these infants alone. First, it may be that all of the infants studied here had *spread legs* in their gestural repertoires but that the opportunities to use it were so rare that we did not observe it (as the innateness hypothesis might maintain). Second, it is possible that the environment that the Leipzig dyads inhabited made the likelihood of ritualizing *spread legs* over ontogeny higher than for the other dyads. In this case, the other infants would not be able to use *spread legs* in order to request a carry even if their legs were free for gesturing and they had the goal of initiating a carry. As the dyads studied here performed an average of 3.4–8.6 carries per hour (Table 1), an environmental difference that results in a handful of carries per day beginning from a hanging position could plausibly lead to the ritualization of a gesture that is unique to this type of carry interaction.

Many of the gestures found here resemble gestures described in previous studies on bonobo gestural communication (Table 6). *Step foot*, for example, resembles what others have described as *stomp*. However, these similarities are consistent with ontogenetic ritualization because the raw materials from which gestures are ritualized are social interactions. Detailed comparisons of gestures are needed similar to the analysis of the *touch* and *grab* gestures done here. Such comparisons may reveal, for example, that the *step foot* used to request co-travel differs subtly from the *stomp* used to request play in the same way that the *touch* used by mothers to initiate carries differs from the *touch* used by infants.

A limitation of this study is that we focused on a social interaction that is highly invariant across dyads. Such an interaction should lead to the ritualization of similar gestures; thus, the gestural variation found here is likely lower than that which would be found in a study that focused on an interaction that varied widely across dyads. This suggests that novel gestures may be more prevalent than previously thought, given our identification of two (*spin body* and *spread legs*) here. The ideal conditions for observing the effects of ontogenetic ritualization would be an interaction that is both invariant within dyads (so that co-anticipation of actions can be achieved) and variable across dyads (so that different gestures are ritualized). Nishida et al. (2009) describe non-typical carrying behavior in wild chimpanzees, such as a mother carrying her infant in her mouth by the nape. Comparing the gestures used to initiate these non-typical carries with the ones found here could shed further light on the role of ontogenetic ritualization in gestural development.

The results of this study might be viewed at odds with the recent findings of Hobaiter and Byrne (2011). Hobaiter and Byrne investigated the question of whether some chimpanzee gestures are ritualized from actions using a similar approach to the one taken here, comparing gestures to the actions from which they have potentially been ritualized. They analyzed two gestures: a *reach* gesture that serves the function of begging, which they hypothesize originated from the action of “taking” and a *position* gesture that serves the function of positioning another for grooming, which they hypothesize originated from the act of “positioning” another for grooming. On the basis of their analysis, they conclude that these two gestures differ too greatly in form from their corresponding actions and thus could not have plausibly been ritualized from them. Thus, in contrast to the results of this study, Hobaiter and

Table 8 Visual gestures used exclusively by mothers or infants: function and potential origin

Gesture	Used by	Function	Interaction from which gesture is potentially ritualized
Spin body	Infants	Request that a mother begin locomoting	Infant turns from the mother toward the direction to be traveled and back to the mother
Spread legs	Infants	Request that a mother place herself in a position that will allow the infant to climb on the mother’s venter or back	Infant attempts to wrap legs around the mother; mother responds by drawing closer to the infant
Step foot	Infants	Request that a mother begin locomoting	Infant begins walking or running away from the mother; mother responds by following the infant
Present back	Mothers	Request that an infant climb on the mother’s back	Mother brings her back near the infant; infant responds by climbing on the mother
Present venter	Mothers	Request that an infant climb on the mother’s venter	Mother brings her venter near the infant; infant responds by grabbing or climbing on the mother

Byrne find no evidence for ontogenetic ritualization by comparing gestures and social actions.

However, there are plausible alternative explanations for the lack of correspondence between the gestures and actions analyzed by Hobaiter and Byrne. First, with respect to *reach* and “taking,” it seems unlikely that the *reach* gesture could have been ontogenetically ritualized from the action of “taking” because chimpanzees do not respond to the initial sequence of behaviors involved in taking by handing an object over to the taker. In general, it is difficult to imagine that successful taking will depend on the actions of another individual in chimpanzees; thus, this is not a good candidate action from which communicative signals might be ritualized.

In contrast, the gesture *position* does have the potential to be ritualized from the action of “positioning” another. If individual A often positions individual B for grooming, then B can learn to anticipate what A is about to do from the initial touch and respond appropriately; and A can then learn that a touch is enough to get B to respond appropriately. In fact, this ritualization process is similar to the one that we posit for the *touch back/shoulder* gesture observed here in mothers to request the infant to climb on. The problem with Hobaiter and Byrne’s analysis of this gesture is that they only examine which part of the signaler’s hand comes into contact with the recipient’s body, not which part of the recipient’s body the signaler contacts. However, it is this latter property that is likely important to preserve in order to request a recipient to position himself a certain way. If I want you to raise your arm, for example, I will likely not use a *touch back* gesture, unless pushing on your back has caused you to consistently raise your arm in the past. However, what is less important is what part of my hand I use to touch you. In fact, one would expect that this property might change, as a tactile gesture requires less pressure than an action aimed at manipulating an individual’s body. As it turns out, this is precisely the change that Hobaiter and Byrne’s comparison reveals. Position actions were predominantly performed with the palm of the hand, while position gestures were predominantly performed with the palmer side of the fingers.

We found that those infants that were highly motivated to initiate carries had larger gestural repertoires than infants that were less motivated to initiate carries. We also found that an infant’s motivation to initiate carries negatively correlated with the average number of carries initiated per hour by that infant’s mother. That is, an infant with a mother who initiated very few carries per hour was more highly motivated to initiate carries himself than an infant with a mother who frequently initiated carries. There are many factors that might lead to this kind of trade-off (see Hinde and Atkinson 1970). For example, a mother might exhibit the maternal style of protectiveness, which involves

approaching, making contact with, and restraining the infant (de Lathouwers and van Elsacker 2004). Such a mother might often initiate carries, but leave the infant little freedom to do so himself. Alternatively, a mother might exhibit the maternal style of distance, frequently breaking contact and leaving the infant (de Lathouwers and van Elsacker 2004). An infant with such a mother might be highly motivated to initiate carries (even in the form of just climbing on the mother) so as to stay near her.

The question remains, however, why would an infant who is both highly motivated to initiate carries and has a mother who initiates few carries herself develop new gesture types? In order to address this question, it would be helpful to look at the specific situation between Kesi and her mother. Kesi was highly motivated to initiate carries, but her mother often resisted these initiations. It was common to observe this infant spending long periods of time attempting to get her mother to move (through the use of ineffective actions and gestures) before finally succeeding. The emergence of idiosyncratic gestures in individuals highly motivated to attain a thwarted goal has been observed before. For example, Tomasello et al. (1994) note that one of their chimpanzee infant subjects, Natasha, developed several idiosyncratic gestures as requests for nursing. They hypothesize that the reason for this is that Natasha’s mother was uncharacteristically resistant in allowing Natasha to nurse.

These observations suggest that individuals who are highly motivated to attain a thwarted goal develop new gestures for attaining that goal. Why would this be? In the case of *spin body*, we believe that the answer is two-part: first, Kesi needed a solution to the problem of getting her mother to travel; second, mother–infant carries generally occur frequently. Concerning the latter, even though Kesi’s mother often resisted her infant’s attempts to initiate travel, this dyad participated in approximately five carries per hour. Thus, mother and infant had ample opportunity to anticipate the standard behavioral sequences involved in this interaction. In the course of participating in this interaction many times per day, the infant could have learned that when she turns from her mother to the direction to be traveled and then back toward her mother, her mother often responds by rising and/or moving in the desired direction. Later, faced with the situation of wanting to travel with her mother, but her mother not acting in accordance with this goal, this infant would be able to draw on her knowledge of those actions that caused her mother to behave in the desired way in the past; in this case, turning away and then toward her mother.

The important point here is that ontogenetic ritualization is a process of mutual anticipation that, for highly flexible and cognitively sophisticated organisms, creates learned communicative signals between individuals that one can

later draw on in order to obtain social goals. In some respects, ontogenetic ritualization is similar to the account of ape gestural communication advanced by King (2004). Under King's view, behaviors become communicative when the participants of a social interaction "co-regulate" or continuously adjust to each other's actions. Similarly, in order for a gesture to become ontogenetically ritualized, the members of a dyad must anticipate and adjust to each other's behavior. However, King's view also maintains that the forms and communicative functions of ape behaviors are continuously renegotiated (Shanker and King 2002; King and Shanker 2003). In contrast, under ontogenetic ritualization, behaviors are ritualized into gestures with relatively stable forms and communicative functions. Indeed, it is the stability of a gesture that allows a signaler to use it to satisfy a particular goal in a wide variety of contexts. If the immediate context affected the communicative message of a gesture in major ways, then an individual would not be able to use that gesture to attain her goal unless the context was right. This problem is especially acute for those situations in which an individual is facing a context that is not conducive to her goal—for example, in the case of an infant trying to get her mother to change her behavior from resting supine to walking.

In recent years, it has been established beyond a reasonable doubt that great apes are not only themselves intentional agents, but that they understand others as intentional agents as well (Call and Tomasello 2008). There is thus no doubt that they are cognitively capable of the kind of mutual anticipations necessary for the ontogenetic ritualization of specific communicative signals. It is possible that when interacting with one another communicatively, they might suddenly turn these skills off, but that seems unlikely. Indeed, in the current study, for the first time, we have observed the process of ontogenetic ritualization unfold over time for one communicative function for one great ape species, thus establishing its formative role in at least some important cases.

Acknowledgments We thank Maria John for coding assistance, Roger Mundry for statistical assistance, and the staff of the Wolfgang Köhler Primate Research Center for their help and support in collecting video. We also thank Christel Schneider and Christine Johnson for generously sharing their video material with us. This research was conducted in association with the Evolutionary Roots of Human Social Interaction (ROSI) group and was supported in part by a German-American Fulbright Full Grant.

Appendix

A DICE-coefficient (D_C) measures the similarity between the repertoires of two individuals: $D_C = (2C_{xy}) / (R_x + R_y)$, where C_{xy} is the number of initiating behaviors common to

two individuals (x and y), R_x is the number of initiating behaviors in the repertoire of individual x , and R_y is the number of initiating behaviors in the repertoire of individual y . A DICE-coefficient ranges from 0 to 1, where a value of 0 means that two individuals have no initiating actions in common and a value of 1 means that they have identical repertoires.

We tested whether the level of similarity in the action repertoires of dyads in the same class (mother–mother and infant–infant) differed from the level of similarity in the action repertoires of dyads in different classes (mother–infant). To do this, we first averaged the DICE-coefficients for each of the three groupings of dyads and used as a test-statistic the sum of the squared deviations of these averages from the mean of the averages. To test whether this test-statistic was significantly larger than chance expectation, we used a permutation procedure (using 1,000 permutations) applying the same randomization technique as in a Mantel test (Sokal and Rohlf 1995). The P value was determined as the proportion of permutations revealing a test-statistic at least as large as that of the original data. This test was run using a function written for R (R Development Core Team 2011) by Roger Mundry.

We ran a Generalized Linear Mixed Model (GLMM) in order to determine whether there were any trends in the frequencies in which mothers and infants initiated carries (Baayen 2008). Into this model, we included age (z-transformed to a mean of zero and a standard deviation of one), initiator (levels mother or infant), and their interaction as fixed effects. We included the particular day and the identity of the mother and infant as random effects. To account for varying observation times per day (ranging from less than 1 h to more than 5 h), we included it (log-transformed) as an offset term in the model. The model was fit assuming a Poisson error structure and with a log link function. Overdispersion was no obvious issue (dispersion parameter: 1.04; $c^2 = 668.5$, $df = 642$, $P = 0.227$). We established the significance of the full as compared to the null model (comprising only the random effects and the offset term) by using a likelihood ratio test (Dobson 2002). The model was fit in R using the function `lmer` of the R package `lme4` (Bates et al. 2011).

We ran a second GLMM in order to determine whether there was a correlation between an infant's gestural repertoire size and an infant's "motivation" to initiate carries, which we defined as the proportion of infant-initiated carries relative to all agent-initiated carries in a dyad. As presented in the results, the infants' tendencies to initiate carries increased with their age and hence needed to be controlled. Thus, we ran the GLMM with the infants' age as a predictor and their frequency of initiation as a response. To further control for observation effort and the total number of initiations per mother–infant dyad and day,

we included these two variables (log-transformed) as effort terms into the model. For such effort terms, no coefficient was estimated (but was just set to one) because their effect is trivial. We also included the identity of each infant as a random effect to avoid confounding the effect of age with differences between infants.

We used the derived coefficient for age as well as the respective total number of initiations and the observation effort per infant and day to determine the expected number of initiations per infant and day. We then used the average differences between its actually observed and expected numbers of initiations, averaged across the period until its final repertoire was reached. Also, we residualized the final repertoire size as it weakly related to the total observation time per infant (Spearman's $\rho = 0.51$). Hence, we first estimated the relationship between total observation time and final repertoire size assuming the relationship to be: $\text{final repertoire} = c_1 \times (1 - \exp(c_2 \times \text{observation time}))$. We then took the difference between observed and expected final repertoire as a measure of repertoire size. The GLMM was fitted in R using the function `lmer` of the R package `lme4` with Poisson error structure and log link function. The relationship between total observation time and final repertoire size was estimated using the R-function `nls`. For the correlation between residualized initiation rate and residualized final repertoire size, we used Spearman's correlation coefficient.

References

- Altman DG (1991) Practical statistics for medical research. Chapman and Hall/CRC, Boca Raton
- Baayen RH (2008) Analyzing linguistic data. Cambridge University Press, Cambridge
- Bates D, Maechler M, Bolker B (2011) lme4. linear mixed-effects models using Eigen and Eigen++. R package version 0.999375-42
- Call J, Tomasello M (eds) (2007) The gestural communication of apes and monkeys. Lawrence Erlbaum Associates, Hillsdale, NJ
- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn Sci* 12(5):187–192
- Cartmill EA, Byrne RW (2007) Orangutans modify their gestural signaling according to their audience's comprehension. *Curr Biol* 17:1345–1348
- Crockford C, Wittig RM, Mundry R, Zuberbühler K (2012) Wild chimpanzees inform ignorant group members of danger. *Curr Biol* 22:142–146
- de Lathouwers M, van Elsacker L (2004) Comparing maternal styles in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). *Am J Primatol* 64:411–423
- de Waal FBM (1988) The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behav* 106:183–251
- Dobson AJ (2002) An introduction to generalized linear models. Chapman and Hall/CRC, Boca Raton
- Fouts RS (1973) Acquisition and testing of gestural signs in four young chimpanzees. *Science* 180(4089):978–980
- Gardner RA, Gardner BT (1969) Teaching sign language to a chimpanzee. *Science* 165(3894):664–672
- Genty E, Breuer T, Hobaiter C, Byrne R (2009) Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Anim Cogn* 12:527–546
- Goodall J (1986) The Chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, MA
- Hinde RA, Atkinson S (1970) Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim Behav* 18:169–176
- Hobaiter C, Byrne RW (2011) The gestural repertoire of the wild chimpanzee. *Anim Cogn* 14:745–767
- Hutchins E, Johnson CM (2009) Modeling the emergence of language as an embodied collective cognitive activity. *Topics Cogn Sci* 1:523–546
- Ingmanson EJ (1996) Tool-using behavior in wild *Pan paniscus*: Social and ecological considerations. In: Russon AE, Bard KA (eds) Reaching into thought: the minds of the great apes. Cambridge University Press, Cambridge, pp 190–210
- Kano T (1980) Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: a preliminary report. *J Hum Evol* 9:243–260
- King BJ (2004) The dynamic dance: nonvocal communication in African great apes. Harvard University Press, Cambridge
- King BJ, Shanker SG (2003) How can we know the dancer from the dance?: the dynamic nature of African great ape social communication. *Anthropol Theory* 3(1):5–26
- Kuroda SJ (1980) Social behavior of the pygmy chimpanzees. *Primates* 21:181–197
- Kuroda SJ (1984) Rocking gesture as communicative behavior in the wild pygmy chimpanzee in Wamba, Central Zaire. *J Ethol* 2:127–137
- Leavens DA, Hopkins WD, Bard KA (2005) Understanding the point of chimpanzee pointing: epigenesis and ecological validity. *Curr Dir Psychol Sci* 14(4):185–189
- Liebal K, Call J, Tomasello M (2004) Use of gesture sequences in chimpanzees (*Pan troglodytes*). *Am J Primatol* 64:377–396
- Liebal K, Pika S, Tomasello M (2006) Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* 6:1–38
- Martin P, Bateson P (2007) Measuring behavior: an introductory guide. Cambridge University Press, Cambridge
- Nishida T, Matsusaka T, McGrew WC (2009) Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates* 50:23–36
- Pika S (2002) The gestural communication of subadult gorillas (*Gorilla gorilla*) and subadult bonobos (*Pan paniscus*) in captivity. Dissertation, Westfälische Wilhelms-Universität Münster
- Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *Am J Primatol* 60:95–111
- Pika S, Liebal K, Tomasello M (2005) Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *Am J Primatol* 65:39–61
- Ploof F (1979) How wild chimpanzee babies trigger the onset of mother-infant play and what the mother makes of it. In: Bullowa M (ed) Before speech: the beginnings of interpersonal communication. Cambridge University Press, Cambridge, pp 223–243
- Pollick AS, de Waal FBM (2007) Ape gestures and language evolution. *Proc Natl Acad Sci USA* 104:8184–8189
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Savage-Rumbaugh S, McDonald K, Sevcik RA, Hopkins WD, Rubert E (1986) Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *J Exp Psychol Gen* 115(3):211–235

- Schneider C, Call J, Liebal K (2011) Onset and early use of gestural communication in nonhuman great apes. *Am J Primatol* 73:1–12
- Shanker SG, King BJ (2002) The emergence of a new paradigm in ape language research. *Behav Brain Sci* 25:605–656
- Slocombe KE, Zuberbühler K (2005) Functionally referential communication in a chimpanzee. *Curr Biol* 15:1779–1784
- Slocombe KE, Zuberbühler K (2006) Food-associated calls in chimpanzees: responses to food types or food preferences? *Anim Behav* 72:989–999
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. Freeman and Co, New York
- Tinbergen N (1959) Comparative studies of the behaviour of gulls (*Laridae*): a progress report. *Behavior* 15:1–70
- Tomasello M (2008) *Origins of human communication*. MIT Press, Cambridge, MA
- Tomasello M, Call J (1997) *Primate cognition*. Oxford University Press, New York, NY
- Tomasello M, George B, Kruger A, Farrar J, Evans E (1985) The development of gestural communication in young chimpanzees. *J Hum Evol* 14:175–186
- Tomasello M, Gust D, Frost G (1989) A longitudinal investigation of gestural communication in young chimpanzees. *Primates* 30:35–50
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M (1994) The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates* 35(2):137–154
- Tomasello M, Call J, Warren J, Frost GT, Carpenter M, Nagell K (1997) The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evol Commun* 1:223–259
- Zuberbühler K (2000) Interspecies semantic communication in two forest primates. *Proc R Soc Lond B* 267:713–718