

RESEARCH ARTICLE

Onset and Early Use of Gestural Communication in Nonhuman Great Apes

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The early gesturing of six bonobos, eight chimpanzees, three gorillas, and eight orangutans was systematically documented using *focal animal sampling*. Apes' were observed during their first 20 months of life in an effort to investigate: (i) the onset of gesturing; (ii) the order in which signals of different sensory modalities appear; (iii) the extent to which infants make use of these modalities in their early signaling; and (iv) the behavioral contexts where signals are employed. Orangutans differed in important gestural characteristics to African ape species. Most notably, they showed the latest gestural onset and were more likely to use their early signals in food-related interactions. Tactile and visual signals appeared similarly early across all four species. In African apes, however, visual signaling gained prominence over time while tactile signaling decreased. These findings suggest that motor ability, which encourages independence from caregivers, is an important antecedent, among others, in gestural onset and development, a finding which warrants further investigation. *Am. J. Primatol.* 74:102–113, 2012. © 2011 Wiley Periodicals, Inc.

Key words: gesture; onset; bonobo; chimpanzee; gorilla; orangutan

INTRODUCTION

Gesturing is integral to human communication and plays a vital role in children's early language, cognitive, and social development [Bates et al., 1979; Capone & McGregor, 2004; Goldin-Meadow, 1999; Gullberg et al., 2008; Kendon, 1988; McNeill, 1992]. To further our understanding of the origins of gestural behavior, increasing attention has been paid to our closest living relatives, the four nonhuman great ape species.

What we currently know about gesturing in great apes stems from research that has spanned several decades. Pioneers working mainly with wild and, to a lesser extent, captive populations identified naturally occurring gestures in bonobos, chimpanzees, gorillas, and orangutans [de Waal, 1988; Goodall, 1986; MacKinnon, 1974; Rijksen, 1978; Schaller, 1963; van Hooff, 1973; van Lawick-Goodall, 1968]. Gestures were found to be employed in complex ways in various behavioral situations. With the knowledge that apes regularly gesture to communicate with their conspecifics, subsequent researchers turned their focus to the extent that apes were able to use linguistic symbols in the form of American Sign Language or computer lexigrams [e.g., Fouts et al., 1982; Gardner et al., 1989; Greenfield & Savage-Rumbaugh, 1990; Miles, 1990]. It seems that apes are capable of learning linguistic signs, but are, for example, limited in the number they assimilate and their ability to

syntactically combine them. More recently, attention has returned to natural gestural communication among conspecifics and its systematic study in captive and wild settings [e.g., Cartmill & Byrne, 2010; Genty & Byrne, 2010; Genty et al., 2009; Hobaiter & Byrne, 2011; Liebal, 2004; Nishida et al., 1999; Pika et al., 2003; Pollick, 2006; Tanner, 2004; Tomasello et al., 1985, 1994].

For a gesture to occur, a signal has to be directed toward a social partner and the sender needs to show anticipatory behavior of a response [Call & Tomasello, 2007b]. Through moving limbs, head, or the whole body, apes demonstrate a pursuit of a goal with their signaling, as well as an understanding of the signal's potential influence within a given context [Call & Tomasello, 2007b]. A variety of gesture types in the tactile (incorporating bodily contact), visual (perceived over distance), and auditory (incorporating a nonvocal sound) sensory domains have been reported—although across all four species it is the tactile and

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visual that are the more dominant [Tomasello et al., 1997; van Lawick-Goodall, 1967]. Auditory gestures have been observed less in the African species and not at all in orangutans [Liebal et al., 2006; Pika et al., 2005a]. The majority of gestures initiate or announce a forthcoming action [Call & Tomasello, 2007b; cf., Schneider et al., 2010] and are adapted to a number of different behavioral contexts, most notably play in African species and food-related interactions in orangutans [Call & Tomasello, 2007a].

Only a few studies have paid attention to the emergence and early characteristics of infant signaling and most of what we know stems from chimpanzees. In her pioneering work, van Lawick-Goodall [1967, 1968] provided extensive descriptions of wild chimpanzee mother–infant interactions that gave us important insights into how early gestures are established and used. She observed gestures to first appear in the second half of infant’s first year [van Lawick-Goodall, 1968]. Plooiij [1978, 1984] was the only researcher to date to systematically study the onset age and early use of gestural signaling. Observing six wild mother–infant chimpanzee dyads with infants’ ranging from 0–30 months, he found first gestures to appear around 9 months of age.

Although not specifically focused on onset age, reports of early gesturing do exist in other ape species. Bard [1988, 1992] observed free-ranging orangutans and their gesturing in the context of food sharing within mother–infant dyads. Five infants (aged from 1 month to 5 years) were followed for 9 consecutive months. The author reported gestures from 2 years on; note, however, no infant was observed between 11 months and 2 years of age. Liebal et al. [2006], while studying gestural communication in a predominantly adult group of captive orangutans, reported gesturing in an 11 month old infant. Finally, Pika et al. [2003, 2005b] observed a single bonobo (aged 13 months) and two gorillas (aged 16 and 20 months) employ gestures in their social interactions. The authors concluded that the ability to communicate via gestures was fully developed in captive bonobos and gorillas between 1 and 2 years of life. Broadly speaking, these observations suggest that gestural behavior manifests in apes between the end of the first and second year of life.

Although all great apes share slow life histories (i.e., the time frame for important ontogenetic markers that characterize a course of life) and long periods of dependency for offspring when compared with other primates [Kelley, 1997; Read & Harvey, 1989], research suggests that developmental trajectories still differ among species. Orangutans are the slowest among all four species to achieve important developmental milestones; for example, the age an infant is weaned and independence from the mother is achieved [van Schaik, 2004; Wich et al., 2004,

2009]. Gorillas, on the other hand, are the fastest, showing the shortest infancy and juvenile stages [Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009]. We propose that the onset of gestural communication in nonhuman great apes is inextricably linked with their underlying life histories. The ability for individuals to produce gestures will rely heavily on species-specific maturation processes and the socio-organizational constraints and opportunities that are available to them.

To date, no comparative study has been carried out on the early gestural interactions in all four ape species. This is surprising, given that for several decades authors have considered such an approach to be essential to our overall understanding of communication and its evolutionary roots [Cheney & Seyfarth, 1990; Marler, 1976; Plooiij, 1979]. We performed a longitudinal, observational study of bonobos, chimpanzees, gorillas, and orangutans, and systematically documented their gesturing during the first 20 months of life. More specifically, our aim was to investigate: (i) when infants started to gesture; (ii) the order in which signals of each sensory modality (tactile, visual, auditory) appeared; (iii) the extent to which infants made use of these modalities in their early signaling; and (iv) the behavioral contexts where signals were employed. Given the varying life histories in the four species, we expected the ages of gestural onset to differ; with gorillas showing the earliest and orangutans the latest onset across species, whereas no differences were expected for the two *Pan* species. No predictions were made concerning infants’ early use of signal modalities or the behavioral contexts where signals were employed.

METHODS

The research adhered to the legal requirements of the countries in which it was conducted and to the principles of “Ethical Treatment of Nonhuman Primates,” as stated by the American Society of Primatologists.

Subjects

We observed six bonobos (*Pan paniscus*), eight chimpanzees (*Pan troglodytes*), three gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo pygmaeus*), ranging between 1 and 20 months of age. They were born in captivity and lived in socially housed groups in six European zoos. All infants were reared by their biological mothers, with the exception of the orangutan Dayang who was raised by a foster mother from the group. The zoos shared similar organizational and animal husbandry protocols. Although the housing facilities varied, all enclosures contained materials and structures suitable for foraging (including extractive foraging), climbing, and resting. The daily routines of the apes were not disrupted by

TABLE I. Infant Characteristics

Species	Infant	Sex	Date of birth	Zoo
Bonobo	Habari	Male	29/01/06	Dierenpark Planckendael (B)
	Hongo	Male	25/02/06	Dierenpark Planckendael (B)
	Huenda	Female	06/07/06	Dierenpark Planckendael (B)
	Kivu	Male	24/02/07	Berlin Zoo (D)
	Luiza	Female	27/01/05	Leipzig Zoo (D)
Chimpanzee	Nayembi	Female	26/04/06	Apenheul (NL)
	Gihneau	Male	29/12/05	Burgers' Zoo (NL)
	Kara	Female	23/06/05	Leipzig Zoo (D)
	Kofi	Male	07/07/05	Leipzig Zoo (D)
	Lobo	Male	21/04/04	Leipzig Zoo (D)
	Lome	Male	11/08/01	Leipzig Zoo (D)
	Mora ^a	Female	23/06/07	Leipzig Zoo (D)
	Nafia	Female	10/06/06	Allwetterzoo Münster (D)
Gorilla	Tai	Female	12/08/02	Leipzig Zoo (D)
	Kibara	Female	13/01/04	Leipzig Zoo (D)
	Louna	Female	13/07/06	Leipzig Zoo (D)
Orangutan	Shaila	Female	25/12/06	Burgers' Zoo (NL)
	Dayang ^b	Female	01/12/05	Apenheul (NL)
	Güsa	Male	09/06/06	Burgers' Zoo (NL)
	Ito	Male	26/12/06	Allwetterzoo Münster (D)
	Kila	Female	02/06/00	Leipzig Zoo (D)
	Maia	Female	07/12/07	Leipzig Zoo (D)
	Merah	Female	27/03/06	Apenheul (NL)
Pagai	Male	06/12/03	Leipzig Zoo (D)	
Raja	Female	26/09/03	Leipzig Zoo (D)	

^aInfant died after suffering a bone fracture during observations.

^bInfant was rejected by her mother soon after birth and was raised by a foster mother.

the present research. Table I presents the sex, date of birth, species, and zoo affiliation of each infant.

Observational Procedure

The authors C.S., J.C., and research assistants videotaped the observations between July 2001 and August 2008. We observed each infant for four sessions per month (4 calendar weeks) using *focal animal sampling* [Altmann, 1974]. A session lasted 5 min and was undertaken either once every week or twice every second week. This resulted in 20 min of video footage per individual per month. The time of observations varied throughout the day (between 08:30 a.m. and 7 p.m.), with sessions for every subject distributed across the apes' diurnal activity. Infants were followed for a minimum of 4 consecutive months and a maximum of 20, i.e., the total observation time per infant ranged between 1.33 and 6.67 hr. On average, we observed each species for 27 hr. Table II presents detailed information of the protocol for observations and the analyses in which infants were included.

Operational Definitions and Coding Procedure

Our operational definition of communication was adopted from Kimura [1933; p 3] and refers to "... the behaviors by which one member of a species

conveys information to another member of the species." We thereby focused on nonvocal signals that served to achieve a social goal and aimed to change the immediate behavior of the recipient. A gesture constituted the sender directing a motoric action (using head, limb, or body movements) toward a recipient with apparent anticipation of a reaction [adopted from Call & Tomasello, 2007b; Wetherby et al., 1988]. The senders' action was accompanied by orienting their body toward the recipient, gazing at them (before, during, or after signal), or by physical contact with them. The senders' anticipation of a reaction was evidenced by gaze alignment, waiting, or persisting in the communicative interaction [Bates et al., 1975; Bruner, 1981; Tomasello et al., 1994]. This definition excludes simple mechanical actions produced to complete a desired outcome without leaving the recipient the choice of action, e.g., to relocate another individual by applying physical force [Call & Tomasello, 2007b]. Gestures were clustered into three sensory categories [Tomasello et al., 1997]: tactile (signals were transferred by sharing body contact with recipient, e.g., nudging), visual (signals were realized over distance via particular body movements or postures, e.g., arm raising), and auditory (signals were transmitted via an acoustic yet nonvocal sound, e.g., chest beating). If a gesture incorporated more than one sensory

TABLE II. Protocol for Observations and Analyses

Species	Infant	Frequency of observation	Observation period (initial–final age, in months)	Total observation time in hours	Analyses considered	
					General and modality onset	Modality and context use over time
Bonobo	Habari	Biweekly	13–20	2.7		✓
	Hongo	Biweekly	12–20	3		✓
	Huenda	Biweekly	7–16	3.3	✓	✓
	Kivu	Biweekly	2–20	6.3	✓	✓
	Luiza	Weekly	2–20	6.3	✓	✓
Chimpanzee	Nayembi	Biweekly	12–19	2.2		✓
	Gihneau	Biweekly	14–19	2		✓
	Kara	Weekly	2–20	6.3	✓	✓
	Kofi	Weekly	2–20	6.3	✓	✓
	Lobo	Weekly	1–20	6.7	✓	✓
	Lome	Weekly	2–20	6.3	✓	✓
	Mora	Weekly	1–11	3.7	✓	✓
	Nafia	Weekly	10–20	3.7	✓	✓
	Tai	Weekly	1–20	6.7	✓	✓
	Gorilla	Kibara	Weekly	2–20	6.3	✓
Louna		Weekly	1–20	6.7	✓	✓
Shaila		Biweekly	2–10	3	✓	✓
Orangutan	Dayang	Biweekly	17–20	1.3		✓
	Güsa	Biweekly	8–13	2	✓	✓
	Ito	Weekly	3–20	6	✓	✓
	Kila	Weekly	16–19	1.3	✓	✓
	Maia	Weekly	2–8	2.3		
	Merah	Biweekly	13–20	2.7	✓	✓
	Pagai	Weekly	4–20	5.7	✓	✓
	Raja	Weekly	6–19	4.7	✓	✓

mode, the tactile or auditory category was assigned rather than visual, i.e., these gestures could be perceived even if the recipient was not visually attending to them [Liebal, 2004].

For analysis, we played the footage through media player software and recorded the coding in a spreadsheet application. The applied coding scheme was based upon Tomasello et al. [1985] and Liebal et al. [2006], but was further adapted in respect to the current research objectives. For each gesture, we gathered the following information: sex of sender, sex and age–class (infant: 0–2.5 years; juvenile: 2.6–5 years; subadult: 6–9 years; adult: ≥ 10 years) of recipient, gesture modality (tactile, visual, and auditory), gesture type, and behavioral context as judged by the available pre- and postinformation that accompanied the senders’ signal. Table III presents detailed descriptions of gesture types identified and the behavioral contexts in which they were observed.

Interobserver Reliability and Analysis

The first author coded all video footage. To ensure reliability, 20% of the data were randomly chosen and coded by a naïve second person. We used Cohen’s κ to measure the degree of concordance

between the two observers for gesture modality, type, and behavioral context [Altman, 1991]. The resulting κ values of 0.89 (modality), 0.84 (type), and 0.79 (context), according to Altman [1991], equate to a “good” and “very good” level of agreement.

To analyze the order in which signal modalities appeared, we used a ranking procedure. We assigned the ranks 1–3 to African apes (with “1” being the earliest and “3” the latest) and ranks 1 and 2 to orangutans (because they displayed no auditory signals). This also ensured that infants who had not displayed gestures in all possible modalities were incorporated in the analysis. If an African infant only showed a single sensory domain while being observed, we assigned the unseen modalities tied ranks. For example, gorilla Shaila (observed between 2 and 10 months) showed visual but no tactile or auditory signals. We ranked her as: visual = 1, tactile and auditory = 2.5.

We used nonparametric tests for analyses. The Friedman and Wilcoxon tests compared dependant samples, whereas the Kruskal–Wallis and Mann–Whitney U tests compared independent groups [Siegel & Castellan, 1988]. All P -values were two-tailed and a null hypothesis was rejected at an α -level of 0.05. As sample sizes were small, we reported

TABLE III. Gesture Types Identified and Behavioral Contexts Distinguished Across the Four Ape Species

Coding category	Associated subcategories	Description
Modality and Gesture		
Tactile	Arm on	Finger(s), hand(s), arm(s) were placed on any body part of the recipient; possibly holding on to recipients' body
	Body beat	Repeated, consecutive hits (see "hit" description) executed with the same body part (i.e., hand(s), arm(s), or foot (feet))
	Formal bite	Gentle bite of recipients' body (executed with mouth)
	Gentle touch	Very gentle touch or hold of recipients' body with finger(s) or hand(s)
	Hit	Single and forceful hit of recipients' body with hand(s), arm(s), or foot (feet)
	Lip-lip touch	Touch recipients' mouth with one's own mouth
	Nudge	Brief movement toward recipients' body with single finger(s), hand, or foot; also kind of pinch
	Push	Exert pressure on recipients' body with hand(s), arm(s), or foot (feet)
	Rest head	Place one's own head on recipients' body
	Touch with genitals	Touch recipients' body with genital region
Visual	Arm raise	Lift arm(s) up in the air, approximately perpendicular to the ground
	Extend arm	Hold out one's hand(s) or arm(s) to recipient
	Hands around head	Lift arms up and place them around the head
	Head shake	Move head or head and upper part of body rhythmically or only once (either vertical or horizontal; including nodding and bowing)
	Lay back	Lay down on the ground and raise limbs in the air
	Move object	Move object (e.g., jute bag) on the ground
	Peer	Closely approach recipient and stare at its mouth or hands (while recipient is holding something of interest, e.g., food or performing a certain action)
	Running back	Move backwards
	Shake	Shake limb(s) or whole body rhythmically; includes kind of swinging around rope or bar
	Shake object	Wave object (e.g., rope) mainly with one's hand(s)
Somersault	Turn a somersault on the ground	
Swagger	Move body rhythmically sidewise or back and forth while standing or sitting	
Auditory	Beat object	Repeated, consecutive hits on ground, wall, or object (see "hit object" description) executed with the same body part (i.e., hand(s), arm(s), or foot (feet))
	Body slap	Single hit of one's own body (except chest region) with hand(s)
	Chest beat	Repeated hits with alternating hand(s) on one's own chest
	Foot stomp	Single and forceful step on the ground with one foot or both feet
Hit object	Single and forceful hit on ground, wall, or object with hand(s) or arm(s)	
Behavioral context	Access	Requesting, offering, or preventing contact or possession of an object, e.g., hold out hand ("extend arm") to request an object
	Affiliation	Approaching and establishing body contact with another individual, greeting events, e.g., place hand on mothers body ("arm on") to request "body closeness"
	Agonism	Inflicting bodily harm or simply threatening to do so resulting in an increase in distance between individuals, e.g., display behavior in form of "swagger"
	Ingestion	Requesting the transfer of food or liquids for the individual's consumption, e.g., hold out hand ("extend arm") to request food
	Locomotion	Requesting a partner to carry or move together with the individual to a different location in the enclosure, e.g., place hand on the mother's back ("arm on") to initiate locomotion
	Play	Requesting the initiation or reengagement of a partner in joint physical activities, such as wrestling, chasing, or rough-and-tumble, which are often accompanied by play face facial expression, e.g., throw both arms in the air ("arm raise") to initiate play
	Sexual	Inspecting other's genitalia or presenting genitalia as a way to engage in behavior related to mating, e.g., touch another individual with genitalia ("touch with genitals")

exact significances [Mundry & Fischer, 1998]. Moreover, we reported effect sizes (using Pearson's correlation coefficient r) for the Wilcoxon and Mann-Whitney U tests [Field, 2005]. An effect size of 0.10 represents a small effect, 0.30 a medium effect, and 0.50 a large effect [Cohen, 1988].

Sample sizes differed for particular analyses (see Table II); more detailed information about these variations and their rationale is given in each respective results subsection. The median was the chosen form of central tendency unless otherwise stated.

RESULTS

Overview of Gestures

We identified 27 gesture types (10 tactile, 12 visual, and 5 auditory) incorporating 298 gestures across all four ape species. No orangutan utilized any auditory signal. Because the auditory mode has also not been observed in older orangutans [Liebal et al., 2006; Pika et al., 2005a], we did not include this species in any analyses considering this domain. One out of the eight orangutans, Maia, observed from 2 to 8 months, did not show any signals. Table IV presents the individual use of gesture types and their overall occurrences in the observed time frames over the first 20 months of life.

Gestural Onset

To determine the gestural onset, we considered only subjects observed for at least 2 consecutive months before their potential first gesture. This subsample included 19 subjects (3 bonobos, 7 chimpanzees, 3 gorillas, and 6 orangutans; see Table II).

Figure 1 presents the age of each infant when their first gesture appeared (irrespective of sensory modality). We found differences between species (Kruskal–Wallis test: $H(3) = 10.59$, $P = 0.004$; $N = 19$). Post hoc examinations yielded a significantly delayed onset in orangutans when compared with the three African ape species (Mann–Whitney U tests: gorilla, $U = 0$, $P = 0.012$, $r = -0.80$; chimpanzee, $U = 4$, $P = 0.012$, $r = -0.69$; bonobo, $U = 0.5$, $P = 0.024$, $r = -0.75$). The three African species displayed, however, their first gesture at a similar age (bonobo vs. chimpanzee: $U = 6.5$, $P = 0.467$, $r = -0.30$; chimpanzee vs. gorilla: $U = 9$, $P = 0.800$, $r = -0.11$; bonobo vs. gorilla: $U = 0$, $P = 0.100$, $r = -0.87$; note in this last comparison the small sample sizes for both species and high-effect size).

Emergence of Tactile, Visual, and Auditory Gesturing

Figure 2 shows detailed information about the age at which gestures of each sensory modality (tactile, visual, and auditory) were first observed in the 19 infants who qualified for the onset analysis. By conducting the ranking procedure, we observed that the ranks at which the tactile and visual modality appeared were similar in all species ($N = 19$; tactile: $H(3) = 0.63$, $P = 0.921$; visual: $H(3) = 1.6$, $P = 0.676$). Auditory gestures (considering only the African species) also emerged at similar positions in our ranking system ($H(2) = 3.05$, $P = 0.266$; $N = 13$).

For African apes, some gesture modalities appeared earlier than others (Friedman test: $\chi^2(2) = 14.94$, $P < 0.001$; $N = 13$). Post hoc testing revealed that auditory signals were produced

significantly later than both tactile (Wilcoxon test: $T = 0$, $P < 0.001$, $r = -0.61$) and visual signals ($T = 3$, $P = 0.006$, $r = -0.53$). The order that the tactile and visual modalities appeared was similar ($T = 21$, $P = 0.339$, $r = -0.22$). This result was confirmed when orangutans were added to the analysis ($T = 53$, $P = 0.450$, $r = -0.13$; $N = 19$).

Use of Gestures Over Time

Sensory modality

To explore the role of sensory modality in the production of gestures over time (regardless of the respective signal types), we divided the observation period of 9 months (the earliest median onset age for any species) to 20 months into two time periods: 9–14 months inclusive and 15–20 months inclusive. Here, we considered only those individuals who were observed for at least 1 month in each time block.

Because the three African species were similar in the order in which they first displayed all three sensory modalities (tactile and visual together, auditory significantly later), we compared them collectively over the two time periods. Orangutans, who did not start gesturing until a median age of 15 months, could only be considered in the latter period 15–20 months. To incorporate these developmental differences in our analyses, we only contrasted the first 6 months of gesturing in both comparative groups (i.e., African apes, 9–14 months vs. orangutans, 15–20 months). Overall, these analyses incorporated 6 orangutans and 15 African apes (6 bonobos, 7 chimpanzees, and 2 gorillas; see Table II).

Figure 3 presents the mean percentages of gestures used in each modality for African apes and orangutans over the specified time periods. In African apes, the proportion of visual signals increased significantly over the two periods ($T = 25$, $P = 0.047$, $r = -0.36$), whereas tactile gesturing significantly decreased ($T = 23$, $P = 0.035$, $r = -0.38$). For the auditory domain, we found a trend for an increase ($T = 3$, $P = 0.078$, $r = -0.34$).

Between 15 and 20 months of life, orangutans displayed a similar percentage of tactile ($U = 38.5$, $P = 0.631$, $r = -0.11$) and visual signals ($U = 42$, $P = 0.834$, $r = -0.05$) to that of African apes between 9 and 14 months (Fig. 3).

Behavioral context

We focused on the three main behavioral contexts in which infants employed their gestures: play, ingestion, and affiliation. Single cases of additional contexts, access, agonism, sexual, and locomotion, were assigned to the category “other.”

As described above, African apes were compared across the two time periods, whereas orangutans (15–20 months) were contrasted with the early performance of African apes (9–14 months).

TABLE IV. Individual Gesture Production in Observed Time Frames Over Their First 20 Months

Modality and gesture type	Bonobos (N = 6)						Chimpanzees (N = 8)								Gorillas (N = 3)					Orangutans (N = 7) ^a					
	Habari	Hongo	Huenda	Kivu	Luiza	Nayembi	Gihneau	Kara	Kofi	Lobo	Lome	Mora	Nafia	Tai	Kibara	Louma	Shaila	Dayang	Güsa	Ito	Kila	Merah	Pagai	Raja	
Tactile																									
Arm on			2		1	1	4	1	5	1	2		4		2	4			1		2	4	4		
Body beat	1	3		1			2	1	1						1	4									
Formal bite																							4		
Gentle touch																					1		3		
Hit	4	2		1	1		11		3				2		1			2			1	2	1	3	
Lip-lip touch	1			1			2																		
Nudge									1	4											2		1		
Push																							1		
Rest head																								1	
Touch with genitals																				2					
Visual																									
Arm raise	12	2	1	4		1	8	1	1					2	2									1	
Extend arm	2	3		1	1	3		1	4	2	2		3		1					1	1	4	1	1	
Hands around head					1				1																
Head shake						1	2	1																	
Lay back						1	1																		
Move object	1																							1	
Peer		6	3		1		3	1	4	3			3		3	8		1		2	1	1	4	4	
Running back															1										
Shake		3			1	5	1		2	1				2						1		1	3		
Shake object	3			2	1			2					2		2										
Somersault							2																		
Swagger							1	1	1	1															
Auditory																									
Beat object															8										
Body slap															1										
Chest beat															1										
Foot stomp		2																							
Hit object	3			2					1	1			1		2										
Total number of gestures	27	21	6	10	8	12	35	7	22	18	7	2	9	10	24	17	1	3	1	6	8	12	21	11	
Total number of gesture types	8	7	3	5	8	6	10	6	11	9	3	1	4	4	11	4	1	2	1	4	6	5	8	6	

^aOne subject excluded.

Figure 4 presents the mean percentages of signals employed in the behavioral contexts observed for African apes and orangutans.

African apes did not reveal any significant context differences over time (play: $T = 29$, $P = 0.273$, $r = -0.21$; ingestion: $T = 13$, $P = 0.160$, $r = -0.27$), although we found a clear trend for a lower percentage of affiliation-related signals in slightly older apes ($T = 11$, $P = 0.054$, $r = -0.36$). Within each time block, however, more signals were proportionally produced in certain contexts (9–14 months: $\chi^2(3) = 12.34$, $P = 0.004$; 15–20 months: $\chi^2(3) = 20.88$, $P < 0.001$). Post hoc testing revealed that infants produced a significantly greater percentage of signals in the play context than in the ingestion ($T = 5$, $P = 0.039$, $r = -0.38$) and in “other” contexts ($T = 0$, $P = 0.002$, $r = -0.52$) between 9 and 14 months. The proportion of play- and affiliation-related gestures that were shown did not differ ($T = 21.5$, $P = 0.318$, $r = -0.19$). Between 15 and 20 months of life, gestures were produced significantly more often in play than in any other context (ingestion: $T = 15$, $P = 0.016$, $r = -0.43$; affiliation: $T = 3$, $P = 0.001$, $r = -0.57$; “other”: $T = 5$, $P = 0.001$, $r = -0.57$).

Orangutans, between 15 and 20 months of age, showed a greater percentage of food-related gestures than African apes in the 9–14 month period ($U = 16$, $P = 0.018$, $r = -0.51$). No differences were detected for the play ($U = 42$, $P = 0.834$, $r = -0.05$) and affiliation context ($U = 40$, $P = 0.713$, $r = -0.09$; Fig. 4). Within 15–20 months, no significant variability was observed across the contexts in which orangutans used their gestures ($\chi^2(3) = 5.4$, $P = 0.143$).

DISCUSSION

In this study, we captured the onset of gestural communication in all four nonhuman great ape species. Orangutans did not show any auditory gestures and started gesturing at around 15 months of age, at least 4 months later than bonobos, chimpanzees, and gorillas. Although African apes made use of all three signal modalities, auditory gestures were only employed after the onset of tactile and visual. In their first 6 months of gesturing, the African species and orangutans displayed comparable proportions of tactile and visual signals. African apes, however, showed an increase of visual signals at the expense of tactile gestures with age. In terms of the behavioral contexts in which gestures were employed, orangutans showed proportionally more food-related signals than African ape infants in their first 6 months of gesturing.

Regarding the age of gestural onset in chimpanzees, our data are largely consistent with Plooijs' [1978, 1984] systematic observation of wild conspecifics. Plooijs observed the first gestures around 9 months, whereas in our sample the median age was

10 months for chimpanzees. Compared with the African species, orangutans were the slowest to start. This finding supports our prediction that Asian apes would differ in their onset ages from other species as they are the slowest among all apes to reach their ontogenetic markers [Wich et al., 2004, 2009]. Our data also provide some support for the prediction that gorillas would be the first to gesture [see Pika et al., 2003, for similar observations]. Gorillas showed a possible accelerated onset when compared with bonobos, but not to chimpanzees. This coincides with our knowledge of gorilla's expedited developmental trajectory [Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009]. Regarding the prediction that both *Pan* species would share similar developmental trajectories, bonobos and chimpanzees did not differ in their onset ages. Recent experimental research offers, however, a contrasting view. Wobber et al. [2010] have shown a developmental delay in certain sociobehavioral and cognitive abilities in bonobos when compared with chimpanzees (although it should be noted that the observed individuals were older than in this study).

Motility may play an important role in the varying gestural onset times in the species observed. Although this was not examined systematically in our study, we regularly witnessed that infants with less-advanced locomotion (hence, higher rates of close body contact with their mother) displayed a slower gestural onset. Typically, we observed this in orangutans [see also Horwich, 1989; cf., Miller & Nadler, 1981] and also in other species. For example, one female chimpanzee (Kara), who showed the latest gestural onset among her conspecifics (15 vs. 10 months species median), was the least independent from the mother (i.e., was continually in close body contact with her mother). Congruent with the proposed influence of motility on early signaling was the fact that distal (i.e., visual) gesturing increased over time at the expense of tactile signals in African apes. Tactile gestures appeared more frequently in infants when close body contact with the mother was important, but were superseded by distal gestures as infants' matured and gained independence [see van Lawick-Goodall, 1967]. Similarly, Bard et al. [2005], who studied mutual gazing in chimpanzees, proposed that this form of visual interaction becomes more important as physical distance between mother and infant increases.

As it has been suggested for human infants, the onset of locomotion has far-reaching implications on the maturation of the perceptual system and cognitive development [see Campos et al., 2000, for a review]. Moreover, the development of independent locomotion seems to be closely linked with the emerging ability for social referencing within the mother–infant dyad [Bertenthal & Campos, 1990; Rochat, 2004]. When starting to crawl, for example, infants use their mothers' emotional reaction as

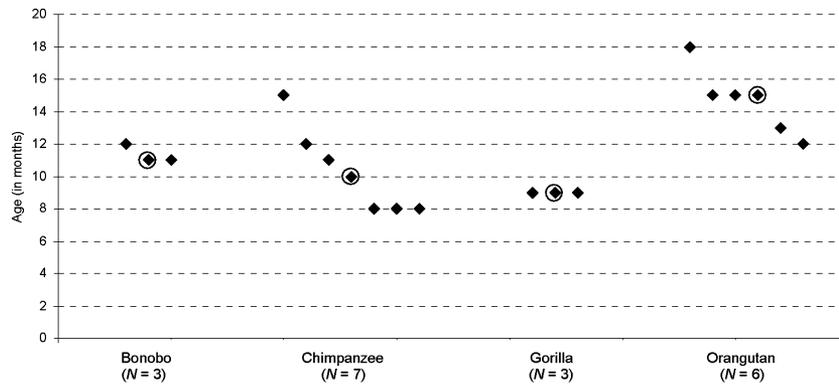


Fig. 1. Infants' gestural onset ($N = 19$); circle represents median onset age in each species.

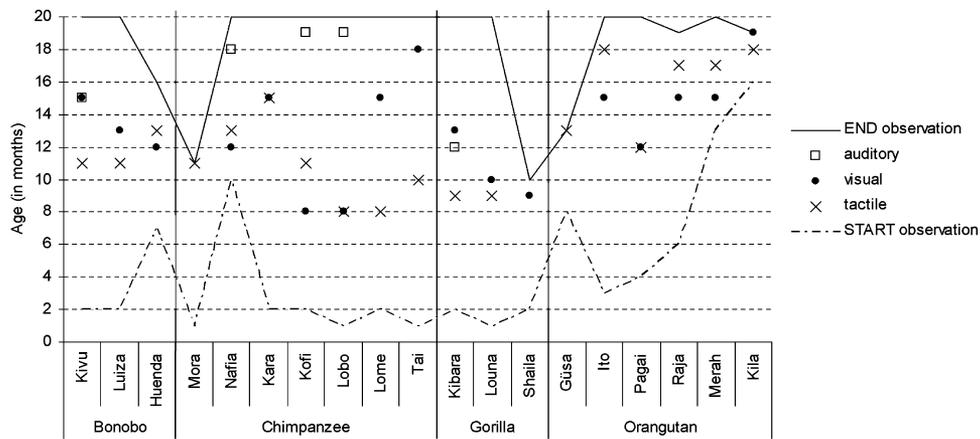


Fig. 2. First appearance of gestures in all four species broken down by the three sensory modalities ($N = 19$).

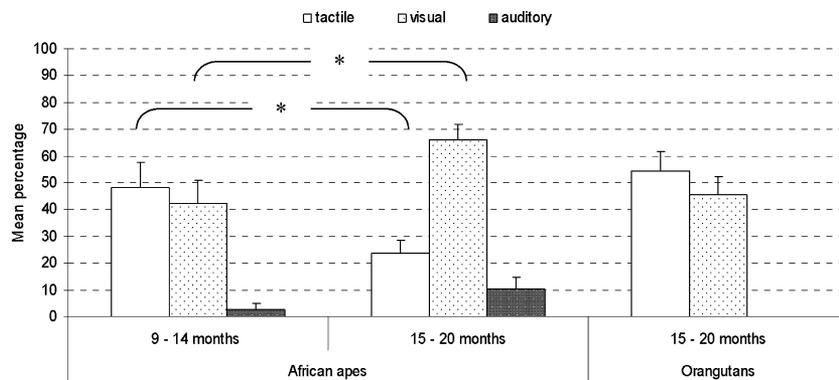


Fig. 3. Mean percentages (plus standard error bar) for the three sensory modalities utilized by African apes ($N = 15$) and orangutans ($N = 6$) in the specified time periods ($*P < 0.05$).

information source in potentially dangerous situations [Bertenthal & Campos, 1990]. Social referencing might, therefore, serve as the connection between an infant's caregiver (who provides security) and the exploration of the environment [Rochat, 2004].

Although the potential link between motility and gestural onset is an intriguing possibility that warrants further research, it needs to be treated

with caution until it is empirically verified. It should be acknowledged, for example, that nonhuman apes have generally more advanced motor skills than human infants [Gómez, 2010; Leavens & Racine, 2009]. We might, therefore, expect ape infants to gesture earlier than they did. What may be as important, in this respect, is the time frame when leaving the "security range" provided by the mother

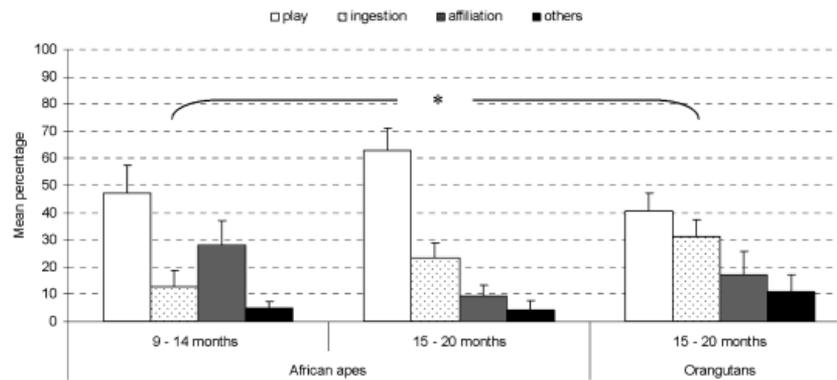


Fig. 4. Mean percentages (plus standard error bar) of the gesturing context for African apes ($N = 15$) and orangutans ($N = 6$) in the specified time periods ($*P < 0.05$).

and entering the complex social structure that surrounds them [van Lawick-Goodall, 1968]. The development of gestures may rely as much on the infant leaving the security zone and starting to communicate with other group members as on their motility skills per se.

In regard to the behavioral contexts in which gestures were employed in their first 6 months of gesturing, orangutans displayed a higher proportion of signals in food-related interactions than African apes. An explanation for this might be that African apes beg less for food as their mothers are more likely to share; although this is more likely to happen through passive than active sharing [see Maestriperi et al., 2002]. Recent studies seem to indicate that bonobos, for example, are more tolerant and cooperative than other apes when it comes to food access and distribution [Hare et al., 2007; Wobber et al., 2010; cf., Jaeggi et al., 2010].

Despite the different developmental trajectories of tactile and visual signals, both emerged close in time and were shown in similar proportions in the first 6 months of gesturing for all four species. These findings emphasize the importance of visual gesturing in the apes' early life and thereby challenge the view that tactile gestures are dominant in youngsters, as previously proposed for chimpanzees [Tomasello & Camaioni, 1997]. Differing results have been reported in monkeys. Grigor'eva and Deryagina [1987], who examined the early gestural communication in stump-tailed macaques (*Macaca arctoides*) and hamadryas baboons (*Papio hamadryas*), found that visual gestures appeared later than tactile in their ontogeny, in fact, in the early stages visual gestures were virtually nonexistent. Overall, therefore, signals of the visual domain might have gained phylogenetic importance in nonhuman great ape species but not in monkeys. In contrast, auditory gestures played a minor role in the African apes and only gained importance in the later stages of gestural development (only 5 out of 13 African apes showed auditory signals in their first 20

months; see Fig. 2). This is in accordance with previous research on African apes reporting that gestures of this modality were less often used than tactile and visual gestures [see Call & Tomasello, 2007a, for a discussion of the use of the auditory modality across species].

Although this research is the largest explorative study on ape infants' communication skills conducted to date, the data had various limitations. Most important, sample sizes were small. Time constraints and other logistical obstacles also meant that overall observation times for each species were limited and individual observation times varied (i.e., infants were observed for differing time periods during their first 20 months). As a consequence, it was only possible to incorporate subsamples in the analyses (e.g., only 19 of 25 subjects were included in onset analysis). Another important limitation is that these findings and their interpretations are based on captive individuals living in restricted and rather predictable environments. Consequently, it remains an open question whether our findings in terms of communicational and locomotion behavior can be generalized to other populations, especially wild ones. With respect to the gestural onset, however, it should be noted that Plooij [1978, 1984] reported similar onset ages for wild chimpanzees as we did for captive individuals. This indicates that the results, on this feature at least, are comparable across captive and wild populations [see also Kummer & Kurt, 1965]. Follow-up studies with larger sample sizes and more extended observation periods per individual, as well as additional comparative samples from wild environments, would therefore strengthen the generalizability of our findings.

In our exploration of apes' gestural beginnings, we found orangutans to differ markedly from African apes. Most notably, and in accordance with their proposed slow life history, orangutans were the slowest in gestural onset when compared with the African species. However, there were also similarities. Unlike monkeys, early gestures were

likely to be visual or tactile in all ape species. This may indicate the phylogenetic importance of the visual channel in early communication in nonhuman ape species. It is suggested that motility is an important ontogenetic antecedent embroiled in gestural acquisition and its development. The extent that this may be the case is one of the intriguing questions this research has raised and should be further explored.

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REFERENCES

- Altman DG. 1991. Practical statistics for medical research. London: Chapman & Hall.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Bard KA. 1988. Behavioral development in young orangutans: ontogeny of object manipulation, arboreal behavior, and food sharing. Ann Arbor: UMI.
- Bard KA. 1992. Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development* 63:1186–1197.
- Bard K, Myowa-Yamakoshi M, Tomonaga M, Tanaka M, Costal A, Matsuzawa T. 2005. Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology* 41:616–624.
- Bates E, Camaioni L, Volterra V. 1975. The acquisition of performatives prior to speech. *Merrill-Palmer Quarterly* 21:205–226.
- Bates E, Benigni L, Bretherton I, Camaioni L, Volterra V. 1979. The emergence of symbols: cognition and communication in infancy. New York: Academic Press.
- Bertenthal BI, Campos JJ. 1990. A systems approach to the organizing effects of self-produced locomotion during infancy. In: Rovee-Collier C, Lipsitt LP, editors. *Advances in infancy research* (Vol. 6). Norwood, New Jersey: Ablex. p 1–60.
- Bogin B. 1999. Evolutionary perspective on human growth. *Annual Review of Anthropology* 28:109–153.
- Bruner JS. 1981. Intention in the structure of action and interaction. In: Lipsitt L, editor. *Advances in infancy research* (Vol. 1). Norwood, New Jersey: Ablex. p 41–56.
- Call J, Tomasello M. 2007a. Comparing the gestures of apes and monkeys. In: Call J, Tomasello M, editors. *The gestural communication of apes and monkeys*. New Jersey: Lawrence Erlbaum Associates, Publishers. p 197–220.
- Call J, Tomasello M. 2007b. *The gestural communication of apes and monkeys*. New Jersey: Lawrence Erlbaum Associates, Publishers.
- Campos JJ, Anderson DI, Barbu-Roth MA, Hubbard EM, Hertenstein MJ, Witherington D. 2000. Travel broadens the mind. *Infancy* 1:149–219.
- Capone NC, McGregor KM. 2004. Gesture development: a review for clinical and research practices. *Journal of Speech, Language, and Hearing Research* 47:173–186.
- Cartmill EA, Byrne RW. 2010. Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition* 13:793–804.
- Cheney DL, Seyfarth RM. 1990. *How monkeys see the world*. Chicago: University of Chicago Press.
- Cohen J. 1988. *Statistical power analysis for the behavioural sciences* (2nd edition). New York: Academic Press.
- de Waal FBM. 1988. The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour* 106:183–251.
- Field A. 2005. *Discovering statistics using SPSS* (2nd edition). London: Sage Publications.
- Fouts RS, Hirsch AD, Fouts DH. 1982. Cultural transmission of a human language in a chimpanzee mother–infant relationship. In: Fitzgerald HE, Mullins JA, Gage P, editors. *Child nurturance—volume 3 studies of development in nonhuman primates*. New York and London: Plenum Press. p 27–61.
- Gardner RA, Gardner BT, van Cantfort TE. 1989. Teaching sign language to chimpanzees. Albany: Suny Press.
- Genty E, Byrne RW. 2010. Why do gorillas make sequences of gestures? *Animal Cognition* 13:287–301.
- Genty E, Breuer T, Hobaiter C, Byrne RW. 2009. Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Animal Cognition* 12:527–546.
- Goldin-Meadow S. 1999. The role of gesture in communication and thinking. *Trends in Cognitive Sciences* 3:419–429.
- Gómez J-C. 2010. The ontogeny of triadic cooperative interactions with humans in an infant gorilla. *Interaction Studies* 11:353–379.
- Goodall J. 1986. *The chimpanzees of Gombe—patterns of behavior*. Cambridge: The Belknap Press of Harvard University Press.
- Greenfield PM, Savage-Rumbaugh E. 1990. Grammatical combination in *Pan paniscus*: processes of learning and invention in the evolution and development of language. In: Taylor Parker S, Gibson KR, editors. "Language" and intelligence in monkeys and apes—comparative developmental perspectives. Cambridge: Cambridge University Press. p 540–578.
- Grigor'eva OM, Deryagina MA. 1987. Gestural forms of communication in primates: I. Development of gestural communication in ontogeny and phylogeny. *Biologicheskije Nauki* 1:45–50.
- Gullberg M, de Bot K, Volterra V. 2008. Gestures and some key issues in the study of language development. *Gesture* 8:149–179.
- Hare B, Melis AP, Woods V, Hastings S, Wrangham R. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology* 17:619–623.
- Hobaiter C, Byrne RW. 2011. The gestural repertoire of the wild chimpanzee. *Animal Cognition* 13:745–767.
- Horwich RH. 1989. Cyclic development of contact behavior in apes and humans. *Primates* 30:269–279.
- Jaeggi AV, Stevens JMG, van Schaik CP. 2010. Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology* 143:41–51.
- Kelley J. 1997. Paleobiological and phylogenetic significance of life history in *Miocene hominoids*. In: Begun DR, Ward CV, Rose MD, editors. *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. New York: Plenum Press. p 173–208.
- Kendon A. 1988. How gestures can become like words. In: Poyatos F, editor. *Cross-cultural perspectives in nonverbal communication*. New York: C J Hogrefe. p 131–141.

- Kimura D. 1993. Neuromotor mechanisms in human communication. Oxford: Oxford University Press.
- Kummer H, Kurtz F. 1965. A comparison of social behavior in captive and wild hamadryas baboons. In: Vagtborg H, editor. The baboon in medical research: proceedings of the first international symposium on the baboon and its use as an experimental animal. Austin: University of Texas Press. p 65–80.
- Leavens DA, Racine TP. 2009. Joint attention in apes and humans: are humans unique? *Journal of Consciousness Studies* 16:240–267.
- Liebal K. 2004. Social communication in great apes. Leipzig: Universität Leipzig.
- Liebal K, Pika S, Tomasello M. 2006. Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* 6:1–38.
- MacKinnon J. 1974. The behaviour and ecology of wild orangutans (*Pongo pygmaeus*). *Animal Behaviour* 22:3–74.
- Maestriperi D, Ross SK, Megna NL. 2002. Mother–infant interactions in Western Lowland Gorillas (*Gorilla gorilla gorilla*): spatial relationships, communication, and opportunities for social learning. *Journal of Comparative Psychology* 116:219–227.
- Marler P. 1976. Social organization, communication and graded signals: the chimpanzee and the gorilla. In: Bateson PPG, Hinde RA, editors. *Growing points in ethology*. Cambridge: Cambridge University Press. p 239–280.
- McNeill D. 1992. Hand and mind: what gestures reveal about thought. Chicago: The University of Chicago Press.
- Miles HLW. 1990. The cognitive foundation for reference in a signing orangutan. In: Taylor Parker S, Gibson KR, editors. “Language” and intelligence in monkeys and apes—comparative developmental perspectives. Cambridge: Cambridge University Press. p 511–539.
- Miller LC, Nadler RD. 1981. Mother–infant relations and infant development in captive chimpanzees and orangutans. *International Journal of Primatology* 2:247–261.
- Mundry R, Fischer J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from animal behaviour. *Animal Behaviour* 56:256–259.
- Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M. 1999. Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science* 107:141–188.
- Pika S, Liebal K, Tomasello M. 2003. Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *American Journal of Primatology* 60:95–111.
- Pika S, Liebal K, Call J, Tomasello M. 2005a. The gestural communication of apes. *Gesture* 5:39–54.
- Pika S, Liebal K, Tomasello M. 2005b. Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *American Journal of Primatology* 65:39–61.
- Plooj FX. 1978. Some basic traits of language in wild chimpanzees? In: Lock A, editor. *Action, gesture and symbol—the emergence of language*. London: Academic Press. p 111–131.
- Plooj FX. 1979. How wild chimpanzee babies trigger the onset of mother–infant play and what the mother makes of it. In: Bullowa M, editor. *Before speech: the beginning of interpersonal communication*. London: Cambridge University Press. p 223–243.
- Plooj FX. 1984. The behavioral development of free-living chimpanzee babies and infants. New Jersey: Ablex Publishing Corporation.
- Pollick AS. 2006. Gestures and multimodal signaling in bonobos and chimpanzees. Atlanta: Emory University.
- Read AF, Harvey PH. 1989. Life history differences among the eutherian radiations. *Journal of Zoology* 219:329–353.
- Rijksen HD. 1978. A field study on Sumatran orangutans (*Pongo pygmaeus abelii*, Lesson 1827): ecology, behavior and conservation. Wageningen: Mededelingen Landbouwhogeschool.
- Rochat P. 2004. *The infant’s world*. Cambridge, MA: Harvard University Press.
- Schaller GB. 1963. *The mountain gorilla, ecology and behaviour*. Chicago: The Chicago University Press.
- Schneider C, Call J, Liebal K. 2010. Do bonobos say NO by shaking their head? *Primates* 51:199–202.
- Siegel S, Castellan NJ. 1988. *Nonparametric statistics for the behavioral sciences* (2nd edition). New York: McGraw-Hill.
- Tanner JE. 2004. Gestural phrases and gestural exchanges by a pair of zoo-living lowland gorillas. *Gesture* 4:1–24.
- Tomasello M, Caramazza L. 1997. A comparison of the gestural communication of apes and human infants. *Human Development* 40:7–24.
- Tomasello M, George BL, Kruger AC, Farrar MJ, Evans A. 1985. The development of gestural communication in young chimpanzees. *Journal of Human Evolution* 14:175–186.
- 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* 35:137–154.
- 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. *Evolution of Communication* 1:223–259.
- van Hooff JARAM. 1973. A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In: von Cranach M, Vine I, editors. *Social communication and movement*. New York: Academic Press. p 75–162.
- van Lawick-Goodall J. 1967. Mother–offspring relationships in free-ranging chimpanzees. In: Morris D, editor. *Primate ethology*. London: Weidenfeld and Nicolson. p 287–346.
- van Lawick-Goodall J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1:161–311.
- van Schaik CP. 2004. *Among orangutans—red apes and the rise of human culture*. Cambridge: The Belknap Press of Harvard University Press.
- Watts DP, Pusey AE. 2002. Behavior of juvenile and adolescent great apes. In: Pereira ME, Fairbanks LA, editors. *Juvenile primates—life history, development, and behavior*. Chicago: The University of Chicago Press. p 148–167.
- Wetherby AM, Cain DH, Yonclas DG, Walker VG. 1988. Analysis of intentional communication of normal children from the prelinguistic to the multiword stage. *Journal of Speech and Hearing Research* 31:240–252.
- Wich SA, Utami-Atmoko SS, Mitra Setia T, Rijksen HD, Schürmann C, van Hooff JARAM, van Schaik CP. 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution* 47:385–398.
- Wich SA, de Vries H, Ancrenaz M, Perkins L, Shumaker RW, Suzuki A, van Schaik CP. 2009. Orangutan life history variation. In: Wich SA, Utami-Atmoko SS, Mitra Setia T, van Schaik CP, editors. *Orangutans—geographic variation in behavioral ecology and conservation*. Oxford: Oxford University Press. p 65–75.
- Wobber V, Wrangham R, Hare B. 2010. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology* 20:1–5.