Maternal behaviors that mediate skill development in Sumatran orangutans

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Abstract

Although orangutans are closely related to humans, very little is known about their ontogenetic development. In particular, there is a lack of systematic research on the maternal behaviors that mediate skill development in early infancy. To address this topic, we conducted a longitudinal study in which a Sumatran orangutan (*Pongo abelii*) mother-infant dyad was systematically observed across 28 months, starting with the infant's birth. Our data revealed several classes of maternal behavior that potentially influenced infant skill development. The timing of these behaviors was contingent upon infant competence level, as active interventions were intense during periods of skill acquisition. The same behaviors were flexibly deployed independent of whether the infant was in the process of acquiring foraging, locomotor or social skills. Our findings suggest that the maternal behaviors that mediate infant skill development in Sumatran orangutans have features reminiscent of human scaffolding, and raise questions about intentionality in such behaviors.

Keywords: orangutan ontogeny, skill acquisition, scaffolding, teaching

Introduction

Orangutans are among our closest genetic relatives, sharing 96,4% of our genetic makeup. Surprisingly, in spite of this close relatedness to humans, very little is known about their ontogenetic development. In particular, research on skill development in Sumatran orangutans (*Pongo abelii*) during early infancy is lacking. It is therefore unknown how orangutans' journey towards becoming skillful foragers and competent social individuals begins. In the most informative study to date (Chevalier-Skolnikoff, 1983), four orangutan infants were periodically assessed using behavioral parameters derived from Piaget's sensorimotor stages for human ontogenetic development (Piaget, 1952). In humans, these stages include skills that are acquired between birth and two years of age through trial and error, and range from reflexive motor activity (first stage, at one month) to insight-based problem solving (sixth stage, at 24 months). In this study, orangutans achieved the first piagetian stages earlier than humans, but lagged at reaching the later stages. Stage five behaviors, which involve exploration through relational experimentation (e.g., flailing ropes, tossing objects in the air), were first displayed at 12 months of age, while the sixth stage was completed between five-eight years of age.

Additional observations come from less systematic reports of orangutan development in early infancy, which mention first attempts at hanging, standing or back-riding (seemingly assisted by the mother), food manipulation, first contact breaking, infant genital exploration by the mother, instances of social play, and solitary play (e.g., Maple, Wilson, Zucker et al., 1978; Miller & Nadler, 1981).

A first limitation of some of these studies is that there is no distinction between orangutan species. Yet this is highly relevant, since recent research documents significant socio-cognitive differences between Bornean (*Pongo pygmaeus*) and Sumatran (*Pongo abelii*) orangutans, which seem to be related to different sociality styles (Forss, Willem, Call et al., 2016). As such, Sumatran orangutans are more gregarious and socially tolerant than their Bornean counterparts, show superior problem-solving skills (Forss et al., 2016), and have broader repertoires of culturally transmitted behaviors, which encompass both social and ecological skills (e.g., Schuppli,

Meulman, Forss et al., 2016). It is therefore imperative to study the early development of skills separately for each of the orangutan species.

Additional limitations derive from the impoverished housing conditions of the involved individuals. Rearing conditions have a major impact on the socio-emotional and cognitive development of primates (e.g., Maestripieri, 2018). Continuous contact with the mother - so that the physical and social needs of the infants are appropriately attended to - nurtures the development of social and communicative skills, and ensures optimal cognitive, social and emotional outcomes. In contrast, social deprivation has a tremendously negative impact on all these developmental outcomes. As such, only tentative conclusions can be drawn from studies on nursery-raised individuals, such as, e.g., the study on orangutan sensorimotor development by Chevalier-Skolnikoff (1983). In addition, restrictive housing conditions (as in Maple et al., 1978; Miller & Nadler, 1981) negatively impact the normal development of young primates. For example, in the study by Miller and Nadler (1981), the studied individuals were housed in 2,4 m high cages with an area of 5,76 m^2 indoors and 9,6 m^2 outdoors. This drastically limits the expression of species-specific behaviors by the mother, thus limiting the repertoire of behaviors and skills that the infant is exposed to, and has the opportunity to acquire through social learning. Restrictive housing conditions are also likely to affect maternal physical and psychological well-being, leading to increased levels of stress and depression. In turn, insufficient maternal welfare negatively impacts infant socio-emotional and socio-cognitive development (e.g., Maestripieri, 2018). More recent studies, especially if conducted in the wild, bypass these issues. However, these studies usually do not include the early stages of infancy (e.g., Bard, 1995; Schuppli et al., 2016). If young infants are included, Sumatran orangutans are not represented, or data recorded from infants is minimal (e.g., Scheider, Call & Liebal, 2012).

In this paper, we present a longitudinal study of skill development in the early infancy (0-28 months of age) of a Sumatran orangutan female, in which we focus on *maternal behaviors* that mediate the maturation of locomotor, foraging and social skills. In particular, our aims are (1) to report the findings of a systematic qualitative analysis of such behaviors, as documented in over 300 hours of observations of the mother-infant dyad, and (2) to outline the details of a method for the systematic investigation of such behaviors.

There is widespread agreement that, in all primate species, the mothers constitute the most important source of influence on infant development, and that such influence is exerted on several levels: physiological, reproductive, behavioral, emotional, cognitive and social (for recent reviews see Maestripieri, 2018; Whiten & de Waal, 2018). This is especially the case for Sumatran orangutans, who display the longest period of maternal dependency in the animal kingdom (of up to 10 years), as well as the longest interbirth interval of all mammalian species, since females with offspring do not reproduce (van Noordwijk & van Schaik, 2005). Moreover, given the semi-solitary nature of orangutans, developmental influences from other conspecifics than the mother are nearly absent during orangutan early infancy, although, starting with three years of age, immatures begin to increasingly socialize with others (Schuppli et al., 2016).

Available data suggests that, in nonhuman apes, maternal influences on skill development are passively exerted, with the offspring being primarily responsible for skill acquisition. For great apes, this relationship has been described using an apprenticeship analogy, whereby the novice's presence (the immature offspring) is tolerated by the skilled master (the mother), and the novice is motivated to acquire the skill through observation learning (Matsuzawa, 2001). By keeping close proximity to the mother, immatures are provided with learning opportunities by mere exposure to species-appropriate actions in social and non-social contexts. As such, infants will explore and eventually consume the food items consumed by their mothers, thus acquiring the species-appropriate foraging repertoire, while also learning the location of food sources (e.g., Schuppli et al., 2016). By watching their mothers interact with conspecifics, infants will acquire their social skills (e.g., Maestripieri, 2018). The cognitive mechanisms implicated in such learning processes are likely to be stimulus and local enhancement (e.g., More, 2013; Whiten & de Waal, 2018). In great apes, who frequently engage in complex forms of food processing, more advanced mechanisms such as emulation or even imitation may be also involved (as reviewed by Moore, 2013; Whiten & de Waal, 2018). To date, imitation learning in great apes is primarily documented in juveniles, although Russon and Galdikas (1995) also report a small number of occurrences in younger Bornean orangutans starting with three years of age. Note that an active maternal involvement in this learning process is not reported in any of these cases.

The literature, however, is not completely devoid of examples in which primate mothers appear to take a more active role in shaping infant skill acquisition. Such examples are reminiscent of interventions that in the human literature are regarded as **scaffolding**, whereby the expert (e.g., the mother) engages in activities that mediate skill acquisition in the pupil. An important feature of scaffolding is that skill acquisition should take place in the so-called zone of proximal development of the pupil, meaning that the expert needs to be sensitive to the knowledge level of the pupil. Another relevant feature is that such facilitation (the 'scaffold') is gradually removed by the expert, as the pupil becomes more proficient (e.g., Palincsar, 1986).

In the animal literature, such scaffolding behaviors have been described as a form of functional teaching. This notion is meant to capture the functional consequences of facilitating learning in others, as opposed to intentional teaching, which is based on an explicit intention to cause an individual to learn

(e.g., Caro & Hauser, 1992). In functional teaching, a skilled individual modifies its behavior in the presence of novices, thereby actively facilitating learning in the novices, i.e. the latter learns a skill earlier, more rapidly or efficiently than in the absence of the expert's behavior, or even bypasses the risk of not learning that skill at all (Caro & Hauser, 1992). Examples of functional teaching have been described for a number of species, including ants, birds, and a number of mammalian taxa, such as felids, meerkats, cetaceans, pinnipeds, and primates. In primates, the most prominent examples of functional teaching include maternal encouragement and discouragement, as well as tool transfer in chimpanzees (as reviewed, e.g., by Maestripieri, 2018; Moore, 2013; Whiten & de Waal, 2018).

Methods

Site and participants

Data collection was conducted at Lund University Primate Research Station Furuvik, where a mother-infant dyad (Dunja-Indah) was observed for 28 consecutive months, starting with the infant's birth, in November 2017 and ending with March 2020, when travel to the research station was restricted due to the pandemic. Dunja was 25 years old at parturition, and Indah is her firstborn. The mother-infant dyad is housed in a semi-naturalistic enclosure that consists of an indoor area and an outdoor area. The indoor enclosure has natural flooring, and is enriched with logs, platforms, hammocks, and ropes. Adjacent to it, there are three smaller rooms, which have been built for research purposes. Glass walls separate the indoor enclosure from the visitor area, which runs as a long corridor parallel to the enclosure. The outdoor area consists of two islands, which are cultivated with edible plants. On the islands, there are also wooden platforms, logs, trees and bushes. In the outdoors, the visitors can watch the orangutans from several wooden platforms that are built around the enclosure.

The mother-infant dyad shares this enclosure with the male that sired Indah (Naong), who was 26 years old at Indah's birth. Naong was separated from Dunja a few weeks prior to parturition, and joined the dyad about four weeks after Indah's birth. During this separation time, the orangutans had visual access to each other. Occasionally, they could also come in close proximity, which enabled tactile interactions through the mesh. The orangutans are fed a varied diet, composed of vegetables, fruits, seeds, nuts, vitamin-enriched pellets and various protein sources. To limit the intake of soluble sugars, fruit is primarily provided as reinforcement during husbandry training and experimental research. Several food items are provided on a daily basis as part of various enrichment routines, based on a weekly updated schedule.

Data collection

Data collection relied on continuous observation, with systematic video-recording of mother-infant activities for subsequent micro-analysis. The observations were taken primarily from the visitor areas, and occasionally from restricted areas. An all-occurrence sampling approach was used, which targeted the dyad's activities. Written notes were also taken if activity onset was sudden, or if relevant activities were in progress at the start of a session of data collection, before the filming equipment was set up. Whenever the dyad was inactive or out of sight (hidden behind a log, under a blanket, up in a hammock, etc.), data collection was complemented with five-minute scan sampling.

The observation schedule varied with the infant's age, since the level of activity and the predictability of the orangutans' activity budget varied as a function of age. Thus, the observation schedule was very intense during the first month of the infant's life, amounting to six hours daily for at least 24 hours / week. During this month, there was a high risk of missing relevant behaviors, as the orangutans' activity level was low, and the occurrence of activity periods highly unpredictable. Toward the end of the first month, however, activity periods had become predictable, and relevant behaviors re-occurred with sufficient frequency to justify a reduced observation schedule. From now on, the dyad was followed for a minimum of two hours / weekly, thus totaling 337 hours and 27 minutes of observation for the overall 28-month period of data collection.

Data analysis

Given the absence of previous systematic research on maternal behaviors that support skill development in orangutan infants, the first stage of data analysis consisted of systematic qualitative analysis. The filmed material was screened in its entirety, to extract suitable themes and categories of behavior. In order to study the kind of maternal responses (henceforth *maternal behaviors*) that influence skill development, it was important to also record the infant's activities that were likely to trigger a maternal response. To determine the immediate effects of *maternal behaviors* on the infant, we also examined the *infant's response* whenever an active *maternal behavior* was recorded.

To follow up with a quantitative treatment of target behaviors (i.e., *maternal behaviors*, *infant responses*), the filmed material is annotated using the video-annotation software ELAN. To this end, relevant tiers have been set up in ELAN, including *Indah's activity, Dunja's activity, maternal behavior, infant response.* Annotations corresponding to these categories are entered in the respective tiers whenever relevant behaviors are identified on film. *Indah's activity* is meant to capture infant actions that could elicit a maternal response, while *Dunja's activity* is meant to capture the actions carried out by the mother concomitant with the activities of the infant, and, thus, prior to a *maternal behavior*. The categories annotated as *activities* are based on commonly used ethograms and include: *Rest seated, Rest lying / sleeping, Eat seated / lying, Forage, Nursing, Travel horizontal, Travel vertical, Nesting, Solitary*

locomotor (play), Social play, Agonistic interaction (with Naong), Grooming, Object manipulation, Oral exploration, Other social interaction, Other activity.

Each annotated episode is also recorded in a spreadsheet, where we also record information about the date and duration of each behavior, and codify relevant variables, such as *proximity, gaze direction and timing of facial expressions*.

Findings

In this paper, we present the main findings of the qualitative analysis, in particular an inventory of *maternal behaviors* that have the potential to influence skill development in orangutan infants, as well as an inventory of *infant responses* triggered by active forms of *maternal behavior*. We also delineate the longitudinal progression of target behaviors, and discuss a number of examples. Finally, we also present preliminary results from the quantitative analysis of *maternal behaviors* targeting infant object-directed actions.

Maternal behaviors

Based on the qualitative data analysis carried out for the purposes of this study, *maternal behaviors* with a potential to mediate infant skill acquisition were classified in the following categories: **tolerate, interference, approach, ignore, molding, take-over, co-action, social visits**.

Tolerate comprises a class of situations in which the infant's activity is carried out within the mother's visual field, so that the mother can observe it, but the mother does nothing to respond to it, other than monitoring the infant's activity. This behavior was recorded in response to a great variety of actions performed by the infant, including locomotion, foraging, object manipulation, social interaction, etc. Developmentally, **tolerate** was often preceded by **interference**, and succeeded by **ignore**. In this category, we have also included a number of examples that in previous anecdotal observations have been presented in more active terms, as encouraging or supporting infant locomotion. For example, we observed that the infant used the mother's stretched arm as a support during her first attempts to stand, or used the mother's body as a ladder or bridge for climbing or crossing a gap. We classified these examples as **tolerate**, since it was not possible to ascertain that the mother was actively supporting the infant's actions.

Interference refers to situations in which the mother intervenes, and stops the infant's activity within the first 30 seconds of infant engagement in that activity. For example, Dunja prevents Indah to continue climbing on the mesh, by removing her from the mesh, or prevents Indah to put objects (bark, food, toys) into her mouth, by removing them from her hand or mouth. This type of intervention (also called *discouragement*) is considered to be the most common expression of active maternal influence on infant skill development (e.g., Maestripieri, 2018). Our data suggests a developmental progression with respect to **interference** targets. Initially, **interference** seemingly targeted resting, i.e. the mother actively intervened to activate her infant after a period of rest. Once the infant was able to grasp, and achieved hand-mouth coordination, **interference** was frequently observed when the infant attempted to explore objects, including food items, bark pieces, small containers, blankets, sheets, etc. **Interference** that targeted object exploration was intensively documented during a short period of time (of several weeks), after which, in these very same situations, the dominating response was **tolerate**. **Interference** targeting locomotor attempts (climbing, walking away) was manifested for a longer period of time (of several months). A final target of intensive **interference** documented in this study was social interaction, in particular attempts to socialize with the male Naong.

Approach captures situations in which the activity of the infant triggers the mother to approach from some distance, and to monitor the infant's activity, but without any further intervention. It can be argued that, in such situations, the mother's interest acts to increase the salience of the activity carried out by the infant, thereby reinforcing it.

Ignore includes situations in which the mother does not appear to monitor the infant's activity in any way. This also includes situations in which the infant's activity is carried out in a location that is not within the mother's visual field, and the mother does not make any effort to gain visual access to the activity in which the infant is engaged. **Ignore** was frequent in the second year of the infant's life, when the infant achieved good proficiency at foraging, feeding, locomoting, and manipulating certain objects. The last category of infant activity to be responded to with **ignore**, at about two years of age, was engagement in social interactions with Naong.

Molding refers to situations in which the mother places the infant in a specific position or location. **Molding** has been previously described in the literature, and anecdotal observations have been reported in chimpanzees. For example, the sign-language trained chimpanzee Washoe was observed to mold her foster infant's hand as to sign FOOD (Fouts, Fouts & van Cantfort, 1989). In our data, molding was represented by situations in which the mother actively placed the infant into a position that facilitated mutual gaze (a behavior described in chimpanzees by Bard, Myowa-Yamakoshi, Tomonaga et al., 2005), placed the infant in a nursing position, attempted to place the infant in a back-riding position, or placed the infant on the ground in the context of independence training. Mutual gaze facilitation was observed during the first month of Indah's life only, with mutual gaze being achieved by the infant within this period. The first back-riding attempt was first documented when Indah was two-month old, and then again at five, six and 16 months of age. All these attempts were unsuccessful. Independence training was serendipitously captured across two consecutive days, when Indah was nine-month old. The first occurrence was documented on an outdoor island, where Dunja was seen placing Indah on the ground, among tall

grasses, and moving away from her while keeping eye contact. Indah reached to her mother, and clung onto her. Dunja, again, placed Indah on the ground, then slowly backed away, while keeping eye contact with Indah. Shortly after she returned to Indah. On the following day, in the indoor enclosure, the dyad sat in close proximity when Dunja slowly pushed Indah away. A gap of several meters was created between the two, before Dunja returned to Indah and patted her with the back of the hand. Dunja moved away from Indah once more, but Indah no longer seemed to react to the separation.

Take-over captures situations in which the mother interrupts the infant's activity, and engages herself in that activity. Situations that prompted **take-over** were situations in which the infant manipulated, e.g., a food item, which was then removed by the mother, who consumed it. Based on current knowledge and data, it is difficult to determine if such behavior could be interpreted as a scaffolding behavior, or if the mother behaves selfishly. Either way, the behavior has stimulus enhancing effects, and is, thus, likely to contribute to skill development in the infant.

Co-action refers to situations in which the mother and the infant are simultaneously or sequentially (i.e., taking turns) engaged in the same activity or act on the same or similar material. Here, we present two examples from our data, in which, during co-action, the mother performed a more skillful version of the infant's activity, which, in turn, resulted in apparent behavior copying by the infant. The first case occurred when Indah was seven-month old, and several structures in the enclosure had been baited with porridge as part of an enrichment activity. Traveling around to lick, and dip for porridge was a novel experience for the infant. After foraging for porridge with the mouth or fingers at several stations, the mother-infant dyad stopped in the vicinity of a rock formation that was also baited. The travel was initiated from a nearby platform, where they foraged using mouth and fingers. Before initiating travel to the ground, Dunja collected an approximately 25 cm long stick from the platform. Upon arriving at the rock formation, Dunja slightly modified one end of the stick, and two larger splinters of about 8 cm each fell on her chest, within Indah's reach. Dunja glanced briefly to Indah as she picked one of the splinters with her lips and the other with her hand. Subsequently, Dunja turned her gaze to the porridge and leaned forward touching the rock with the stick she held between her lips. Indah watched her mother's action, and almost touched the rock with the splinter she carried in her hand. As her mother leaned back, Indah's attention moved to the splinter. As Dunja inserted the other end of the stick into her mouth, Indah did the same with her splinter. Dunja bit off a splinter for herself, and, as she placed the larger stick on the ground looked toward Indah who was intently looking at her own splinter and the porridge. Subsequently, Dunja leaned forward to collect porridge, causing Indah to also lean forward and attend to the foraging process. Indah too attempted to touch the rock with her own splinter, but she lost the tool. Dunja glanced briefly toward Indah then to the baited crevice, released her own splinter and foraged with the lips. Indah watched intently, then both continued foraging with the lips, yet on different, but nearby located spots. Dunja, once more, dipped her splinter into a crevice on Indah's side, while Indah watched intently. As Dunja leaned back, Indah (who was attached in ventrolateral position), leaned forward, collected her lost splinter and placed it between the lips. Dunja glanced at Indah during this time, then switched to monitoring the male (Naong), who was foraging at another station in the vicinity. Indah turned around, and looked away in the same direction as Dunja. Dunja dipped her splinter into the porridge pool once more, but Indah no longer showed interest in foraging. Within seconds, they traveled away from the baited station. Although tool use is prominent in the episode described above, it has to be noted that Dunja is typically not a tool user. She commonly approaches this type of enrichment by using her fingers or her lips to the bait (porridge, honey, peanut butter, etc.).

The second case occurred when Indah was 12-month old, and she found herself, again, in a novel situation. It was the first fall day when the outdoors temperature had fallen below the freezing point. Frost in the outdoors occasionally causes one of the windows in the enclosure to be covered with a thin sheet of ice. Dunja (carrying Indah) approached the frosty window, and collected ice, either by scraping it with her fingers or by licking it. Indah watched Dunja intently for nearly two minutes, after which, when Dunja stopped, approached the window and attempted to scrape ice using her fingers. After a while, Dunja began watching Indah's attempts, and briefly interrupted her scraping actions to lick the ice collected on Indah's nails. They left shortly after, but Indah returned alone about ten minutes later, and began foraging ice from the window. Rather than scraping the window without interruption as previously, she would now stop to lick the ice collected on her nails after a couple of scraping movements.

Social visits. Shortly after being reunited with Naong, Dunja (carrying Indah) began making short visits to wherever Naong was located at that time of the day. There was no obvious trigger to these visits, and they did not happen on a precise schedule. Once in proximity to Naong, Dunja would sit close to him for several minutes. Body contact between Naong and Indah was, however, not allowed during these visits, at least not until Indah had achieved locomotor proficiency.

Preliminary results: maternal responses to the infant's object-directed actions

A total of 336 bouts of object-directed actions were identified through systematic data coding (as described above) in the data analyzed so far, which spans the interval between birth (November 21st 2017) and December 30th 2018. Of these, 124 bouts are manual actions (reaching,

exploration) and 212 are bouts of oral exploration of objects. During this period of 12 months and 10 days, the great majority of *maternal responses* to the infant's object-directed actions took the form of **interference** (N=77) and **tolerate** (N=240). An additional number of 19 responses were **approach, co-action** or **take-over**. Of the 77 **interference** *responses*, 32 were in response to oral object exploration and 45 were in response to manual actions directed at objects. Of the 240 **tolerate** responses, 163 were in response to oral exploration and 77 were in response to manual actions.

Nearly half of the **interference** responses documented between birth and December 2018 (i.e. 49.35%) was deployed in February-April, i.e. during the period when oral and manual exploratory skills were under development (between 3-5 months of age). For comparison, only 61 (25.42%) **tolerate** responses were documented during the same period. In addition, the ratio of **interference-to-tolerate** *responses* decreased constantly from 1.1 in March to 0.5 during April, to then decline to 0.3 in May and June, then to 0.2 and 0.1 in July and August respectively. Finally, preliminary data show that the mean latency of maternal **interference** had significantly increased ($t(35)=3.359$, $p=0.002$) from March (M=7.91 seconds, SEM=1.866) to April (M=17.19 seconds, SEM=1.610), suggesting that the amount of time that the mother allowed the infant to (manually or orally) explore objects had gradually increased during this period of skill maturation.

Infant responses

The qualitative analysis revealed five categories of *infant responses* to active forms of *maternal behaviors*: (1) **compliance**: infant ceases activity, and does not engage in a new activity; (2) **compliance followed by mother-initiated activity**: infant ceases activity and engages in an activity initiated by the mother; (3) **compliance followed by self-initiated activity**: infant ceases ongoing activity and directly engages in a new one; (4) **re-start**: the infant re-engages in the same activity as previously, after a brief (up to one minute) interruption; (5) **protest**: infant does not adjust the ongoing activity, and may display protesting gestures (e.g., push, charge, bite). Since the main focus of this paper is on *maternal behaviors* that influence skill development, here we discuss only category (2) **compliance followed by mother-initiated activity**. This was observed to occur especially if maternal **interference** was unsuccessful, and the infant **re-started** the activity shortly after the **interference**. In such cases, immediately after a new **interreference** the mother engaged the infant in finger-sucking, play, foraging, or manipulating an object, as if to distract the infant from the activity that she attempted to discourage.

Conclusions

In this study we sought to examine *maternal behaviors* that potentially mediate skill development in Sumatran orangutan infants, by conducting a systematic qualitative analysis on the activities of a mother-infant dyad across 28 months, starting with the infant's birth. The findings of this study suggest several important conclusions. First, we found that orangutan mothers begin to deploy *maternal behaviors* that have a formative effect on the infant already from birth, and several such behaviors are displayed already in the first few months of life. Second, from early on, these behaviors target locomotor and foraging skills (as noted by previous anecdotal observations), but also social skills. Thirdly, the timing of these *maternal behaviors* appears contingent upon the infant's competence level in a given domain, thus exhibiting similar timing features as described for human **scaffolding**. We documented the intensive occurrence of more active forms of *maternal behaviors* (molding, interference, take-over, co-action) during periods when infant skill in the targeted domain (e.g., mutual gaze, object manipulation, locomotion, food repertoire, foraging techniques) was under development. As the infant's skills developed, such active forms were supplanted by passive ones, i.e. **tolerate**, and eventually **ignore**. This conclusion is also supported by preliminary results from a quantitative treatment of responses to infant object-directed actions, which show that active **interference** peaked during a period of skill acquisition between 3-5 months of age, being subsequently replaced by **tolerate**. By the end of the observation period, visual monitoring of the infant's activities was rare, and **ignore** was the dominating *maternal behavior* documented.

As mentioned in the Introduction, examples of functional teaching have been described for several non-primate species. In all these species, however, the behaviors described as teaching were limited to one domain and one skill only. In contrast to these species, our data show that such scaffolding behaviors exhibit context flexibility, targeting locomotor, foraging and social skills. This finding is intriguing considering that such flexibility (and generalizability) is discussed as a key feature of human intentional teaching (e.g., Caro and Hauser, 1992; Moore, 2013), thus raising the question of intentionality in the *maternal behaviors* that scaffold skill development in orangutans, and in great apes, in general. Even more so in the light of recent evidence suggesting that great apes are capable of understanding others' goals (Kano & Call, 2014) and intentions (Frölich, Wittig & Pika, 2019), are sensitive to others' knowledge states (Krupenye, Kano, Hirata et al., 2016) and competence (Kendal, Hopper, Whiten et al., 2015), and may exhibit shared intentionality, i.e. a motivation to promote shared psychological states with others (as discussed in Persson, Sauciuc & Madsen, 2018).

We hope that the method and data presented here will stimulate similar research in additional mother-infant dyads (to address the inherent limitations of cases studies, such as the one presented here), and in other primate species. Data from detailed and systematic observations will enable more systematic and bias-free comparisons with human parenting behaviors, and will further our understanding of processes and mechanisms that support skill development in Hominids.

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References

Bard, K., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Costall, A., & Matsuzawa, T. (2005). Group differences in the mutual gaze of chimpanzees (Pan troglodytes). *Developmental psychology, 41 4*, 616-24.

Bard, K. A. (1995). Sensorimotor cognition in young feral orangutans (Pongo pygmaeus). *Primates, 36*(3), 297–321.

Caro, T., & Hauser, M. (1992). Is There Teaching in Nonhuman Animals? *The Quarterly Review of Biology, 67*, 151 - 174.

Chevalier-Skolnikoff, S. (1983). Sensorimotor development in orang-utans and other primates. *Journal of Human Evolution, 12*, 545-561.

Forss, S., Willems, E., Call, J., & Schaik, C.V. (2016). Cognitive differences between orang-utan species: a test of the cultural intelligence hypothesis. *Scientific Reports, 6*, 30516.

Fröhlich, M., Wittig, R., & Pika, S. (2019). The ontogeny of intentional communication in chimpanzees in the wild. *Developmental science, 22*, e12716 .

Fouts, R. S., Fouts, D. H., & Van Cantfort, T. E. (1989). *The infant Loulis learns signs from cross-fostered chimpanzees.* In R. A. Gardner, B. T. Gardner, & T. E. Van Cantfort (Eds.), *Teaching sign language to chimpanzees*. State University of New York Press.

Kano, F., & Call, J. (2014). Great Apes Generate Goal-Based Action Predictions. *Psychological Science, 25*, 1691-1698.

Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S., Lambeth, S., Schapiro, S.J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and human behavior, 36 1*, 65-72.

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science, 354*, 110 - 114.

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology, 72*, 1-12.

Maple, T., Wilson, M.E., Zucker, E., & Wilson, S.F. (2006). Notes on the development of a mother-reared orang-utan: The first six months. *Primates, 19*, 593-602.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). *Emergence of culture in wild chimpanzees: Education by master-apprenticeship.* In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior*. Springer-Verlag Publishing.

Miller, L.C., & Nadler, R.D. (2007). Mother-infant relations and infant development in captive chimpanzees and orang-utans. *International Journal of Primatology, 2*, 247-261.

Moore, R. (2013). Social learning and teaching in chimpanzees. *Biology & Philosophy, 28*, 879-901.

Noordwijk, M., & Schaik, C. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology, 127*, 79-94.

Palincsar, A.S. (1986). The Role of Dialogue in Providing Scaffolded Instruction. *Educational Psychologist, 21*, 73-98.

Persson, T., Sauciuc, G., & Madsen, E. (2017). Spontaneous cross-species imitation in interactions between chimpanzees and zoo visitors. *Primates, 59*, 19-29.

Piaget, J. (1952). The Origins of Intelligence in Children. (Trans. M. Cook.) New York: International Universities Press.

Russon, A., & Galdikas, B.M. (1995). Constraints on great apes' imitation: model and action selectivity in rehabilitant orangutan (Pongo pygmaeus) imitation. *Journal of Comparative Psychology, 109*, 5-17.

Schneider, C., Call, J., & Liebal, K. (2012). Onset and early use of gestural communication in nonhuman great apes. *American Journal of Primatology, 74*.

Schuppli, C., Meulman, E., Forss, S., Aprilinayati, F., & Schaik, C. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour, 119*, 87-98.

Whiten, A., & Waal, E.V. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology, 72,* 80.