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Orang-utans and chimpanzees cooperate strategically based on the partner's incentives

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Chimpanzees, *Pan troglodytes*, are often regarded as a model species for the evolution of human cooperation. However, whether chimpanzees' decision-making in cooperative contexts differs from that of other, less gregarious great ape species such as orang-utans remains unclear. In this study, the performance of zoo-housed chimpanzees and Sumatran orang-utans, *Pongo abelii*, was compared in a cooperation task with individual foraging alternatives for both participants. In each trial, one individual had access to a tool that she could either use to retrieve an immediate food reward (thereby forfeiting further tool use) or pass to a partner. Then, the partner could use the tool in a cooperative apparatus, releasing food rewards for both individuals or for an individual foraging option. The quality and presence of food rewards were manipulated in individual and cooperative apparatuses. Chimpanzees and orang-utans cooperated at similar rates, with decisions primarily driven by their own immediate payoffs. However, both species were also more likely to transfer the tool when the partner had an incentive to cooperate. Chimpanzee tool givers were more responsive to recipients' attention-getting signals than orang-utans. These findings suggest that what distinguishes chimpanzees as a more gregarious species may not be their propensity to cooperate per se but rather their use of communicative strategies to facilitate cooperation.

Mutualistic cooperation has been hypothesized to play a decisive role in human evolution (Tomasello et al., 2012). According to the interdependence hypothesis, cooperative foraging activities (such as big-game hunting) provide an advantage over individual foraging. However, maintaining such collaborative foraging activities might require flexible coordination and communication abilities. Comparative studies with nonhuman great apes provide a baseline for identifying which components of these skills are shared through common ancestry and which have been shaped by socioecology.

Most experimental research has focused on cooperation in chimpanzees, *Pan troglodytes* (Völter et al., 2017), as the main model species for the evolution of human-like cooperation. Wild chimpanzees show multiple forms of cooperation, including cooperative hunting of monkeys (Boesch & Boesch, 1989; Gilby, 2006; Samuni et al., 2018), territorial boundary patrols (Watts & Mitani, 2001), coalitionary support during aggression and grooming-based maintenance of agonistic support (Kaburu & Newton-Fisher, 2015; Watts, 2002). These contexts require individuals to monitor the behaviour of partners, adjust their own behaviour accordingly and, in some cases, produce or respond to attention-directing cues (Crockford et al., 2012, 2017). Individuals that participate in a cooperative activity, such as group hunting, have also been found to receive greater payoffs than bystanders, irrespective of their begging effort (Samuni et al., 2018). This finding is consistent with experimental work reporting that zoo-housed chimpanzees deliver food rewards to a conspecific if that conspecific had previously assisted them (Schmelz et al., 2017).

Studying social decision-making in species with a different social structure (i.e. less gregarious species) can prevent drawing false conclusions (Lameira & Call, 2020) if the ecological validity of the task for the species being compared is deemed likely. One indication of this can be that the task affordances and

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contingencies are similarly intuitive for all species (e.g. control conditions can ensure similar performance when the cooperative requirements are removed, and task requirements can be trained over similar trial numbers). Among great apes, orang-utans, *Pongo* spp., have a different social structure compared with chimpanzees or bonobos, *Pan paniscus*. They have been described as semi-solitary, that is, they are often solitary but also form temporary parties occasionally, often in large fruiting trees or when travelling between food sources (Delgado & Van Schaik, 2000; Van Schaik, 1999). Cooperative exchanges such as grooming or food sharing among unrelated adults are rare (Fröhlich et al., 2020), but co-feeding in productive fruit trees tends to be tolerant. Mothers rarely actively share food with their offspring but passively allow them to take food (Jaeggi et al., 2008).

Thus, comparing chimpanzees and orang-utans in a cooperative decision-making task allows us to examine whether (1) flexible cooperation based on self- and partner payoffs is a phylogenetically old trait in great apes, predating the divergence of *Pongo* and *Pan* or (2) whether such flexibility is amplified by socioecological conditions that involve frequent cooperation among nonkin. If both species behave similarly in a cooperative decision-making task, then this capacity is likely ancestral, whereas any systematic differences, such as higher cooperation rates, greater sensitivity to others' payoffs or greater reliance on communicative cues in chimpanzees, could indicate a socio-ecological specialization. In captivity, differences in socioecology are less apparent as orang-utans and chimpanzees are usually housed in stable social groups. Nevertheless, the comparison between chimpanzees and orang-utans can help clarify to what extent chimpanzees' performance in cooperation tasks reflects specialized cognitive abilities related to their species-specific social organization irrespective of the actual housing conditions.

Experimental work can help elucidate the extent to which apes actively coordinate and communicate during cooperative foraging. In particular, the stag-hunt game (Skyrms, 2004) captures the decision-making process between individual and collaborative foraging opportunities. Just as in the case of a group hunt, the cooperative foraging opportunity (the 'stag') provides potentially higher payoffs but only if all individuals collaborate (and share the spoils afterwards, although the latter requirement is usually not part of stag-hunt experiments). Previous experimental research provided evidence that chimpanzees engage in a leader–follower strategy with very little communication to coordinate decision-making compared with human children (Bullinger et al., 2011; Duguid et al., 2014). Chimpanzees successfully coordinated on the collaborative option especially when they could see the other individual and when their nonsocial alternative (the 'hare') was of low value.

Coordination based on monitoring others' behaviour and without clear signs of communication has been found in a variety of paradigms in chimpanzees and bonobos (Duguid et al., 2014; Sánchez-Amaro et al., 2017). The likelihood of communication is mainly affected by the strength of the social bond between the participants, their proximity in space and the contextual challenges associated with the task; for example, communication is unlikely if the participants have access to the same information towards solving the task and they can monitor each other (Melis & Rossano, 2022). A recent study has examined the role of communication in chimpanzee cooperation in a task with more asymmetric information among the study participants. The main evidence for communication was that individuals approached the apparatus containing a tool set that both of them required to obtain food while sometimes also touching the apparatus, looking at the apparatus or passing the key to the partner close to the apparatus (Melis & Tomasello, 2019). In turn, the partner was more likely to open the correct apparatus (the one containing the tool set) when the subject had approached and passed the tool close to the correct apparatus. However, to what extent their positioning was an intentional communicative act remains unclear.

Collectively, these studies show that coordination can be successful even without communication when individuals monitor the behaviour of potential collaborators and follow their lead. Another way to coordinate with others is to predict other individuals' behaviour based on their expected payoffs and preferences. To what extent chimpanzees pay attention to a partner's payoffs and flexibly decide on the basis of this evidence to cooperate or defect is poorly understood. Evidence from the prosocial choice task indicates that chimpanzees prefer the option that yields food not only for themselves but also for another individual placed in a neighbouring enclosure (Bueno-Guerra et al., 2019; Horner et al., 2011), although other studies found no such evidence (Amici et al., 2014; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008; Yamamoto & Tanaka, 2010). In the ultimatum game, one of two individuals can propose how to split a reward. The other individual, the recipient, can either accept the offer or reject it, resulting in the loss of the reward for both individuals. For humans, relative payoffs (that is, own payoffs in relation to the proposer's payoffs) matter. In many (but not all) cultures, recipients reject unfair offers under a certain threshold (Oosterbeek et al., 2004). By contrast, chimpanzee recipients behave as rational maximizers, accepting all nonzero offers (Jensen et al., 2007; Kaiser et al., 2012). Inequity aversion paradigms also address whether individuals react to the payoffs of others, particularly whether they show negative reactions (e.g. the rejection of a low-value reward) when others receive better payoffs for the same action. The evidence for inequity aversion in chimpanzees is mixed (Bräuer et al., 2006, 2009; Brosnan et al., 2005, 2010; Hopper et al., 2014; Ritov et al., 2024), and a recent study and meta-analysis indicate that any effect might be explained by social disappointment in the experimenter rather than a direct comparison with the payoff of the conspecific (Engelmann et al., 2017; Ritov et al., 2024). Based on these studies, whether chimpanzees pay attention to others' payoffs especially in cooperative contexts remains unclear. Even if they did so, whether they would also make predictions concerning others' subsequent behaviour based on the latter's payoffs remains unknown.

In a pioneering study, Chalmeau et al. (1997) reported that orang-utans performed similarly to chimpanzees in a cooperative string-pulling task. More recently, orang-utan mothers were found to physically manipulate their offspring as social tools to acquire out-of-reach rewards and stick tools (Völter et al., 2015). In a different situation, to obtain food, orang-utan mothers had to hand the tool over to the offspring who could then operate an apparatus releasing food for both. The mothers spontaneously switched from coercion to cooperation by passing the tool on to their offspring (similar to chimpanzees in a comparable tool-passing paradigm; Melis & Tomasello, 2013, 2019). In other paradigms, orang-utans show neither a preference for prosocial choices (Kim et al., 2015), nor signs of inequity aversion (Brosnan et al., 2011). However, as previously mentioned, both paradigms yielded also inconsistent results with chimpanzees. Thus, the cooperative problem-solving studies with orang-utans to date do not provide evidence for substantial differences between chimpanzees and orang-utans, although clearly more research is needed.

In the current study, data from a tool-passing paradigm (Melis & Tomasello, 2013, 2019; Völter et al., 2015) with zoo-housed orang-utans and chimpanzees asking whether apes take payoffs and constraints of their partner into account were reported. In experiment 1, tool transfers in orang-utan mother–offspring dyads asking whether mothers consider physical access

constraints and the partner's payoffs when deciding whether to cooperate or not were examined. In experiment 2, orang-utans and chimpanzees were directly compared in a version of the task resembling a 'stag-hunt' game, in which individuals could choose either an individual foraging option or a cooperative option by passing the tool to the partner. In addition, the food value of the individual foraging option and whether the cooperative option on the tool recipient's side was baited or not was systematically varied (that is, whether the tool recipient had any incentive to cooperate). Whether chimpanzees and orang-utans adapted their decision-making to the payoffs of the partner, which might predict the latter's performance, was also examined. Moreover, the extent to which apes' communication and attention getters influenced their partners' decisions was compared. Based on previous research, we expected orang-utans to perform similarly to chimpanzees despite their differences in social organization.

EXPERIMENT 1

In experiment 1, whether orang-utan mothers consider physical barriers and the payoffs of their offspring when deciding whether to pass a tool to the offspring or to use it on a purely self-serving apparatus was examined. Thus, whether orang-utan mothers would consider the factors influencing whether their offspring could and would cooperate with them was investigated.

Methods

Subjects

Two orang-utan, *Pongo abelii*, mother–offspring dyads housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo (Germany) participated in this experiment (mothers: Padana: 16.3 years and Dokana: 25.2 years; juveniles: Suaq: male 4.9 years old and Tanah: female 4.8 years old). Both dyads had participated in earlier versions of this paradigm involving the same apparatuses (experiment 4 in Völter et al., 2015).

The subjects were housed in social groups of eight individuals, and they spent the day in indoor (185 m^2) or outdoor (1870 m^2) enclosures, depending on the season. All enclosures were spacious and equipped with climbing structures, natural vegetation and enrichment devices to foster extractive foraging activity. The subjects were tested in the sleeping rooms interconnected by lockable doors. They were also provided with fresh fruits, vegetables, eggs, cereals, leaves and meat (once a week) distributed in three main meals; some more food was dispensed multiple times over the day, as part of the enrichment programme. Water was available ad libitum during testing.

Ethical note

The study (experiments 1 and 2) was reviewed and approved by an ethics committee from the Max Planck Institute for Evolutionary Anthropology and the Leipzig Zoo (no approval number was licensed). The procedures used are in accordance with the Weatherall report on the use of nonhuman primates in research (Weatherall's Working Group, 2006), the European Association of Zoos and Aquaria's Standards for the Accommodation and Care of Animals in Zoos and Aquariums (EAZA, 2024), the World Association of Zoos and Aquariums' (WAZA) Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums (Sato & Tomonaga, 2010) and the ASAB/ABS's Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB Ethical Committee/ABS Animal Care Committee, 2025). IACUC approval was not necessary to conduct this research because it did not meet the criteria for animal experiments under the German Animal Welfare Act (TierSchG) and the EU Directive 2010/63/EU. Testing was always voluntary; the individuals were not deprived of food or water, and a trained animal caretaker did the handling. The subjects were allowed to return to their social group at any moment of the test and we terminated the test when signs of discomfort or distress were observed. Infants were not separated from their mothers.

Set-up

The test was conducted in the orang-utans' sleeping area, which consisted of four enclosures (labelled from left to right: enclosure 1–4) connected by hydraulic sliding doors (Fig. 1).

The set-up has been described in detail in Völter et al. (2015). The social apparatus consisted of a slanted tube (length 340 cm, diameter 5 cm, made of transparent Perspex) that was mounted to the mesh outside of two nonadjacent enclosures of the orang-utan sleeping area (lower end: enclosure 2; upper end: enclosure 4). Holes were drilled in the walls of the tube to allow the insertion of uncooked spaghetti fragments (length 8–10 cm) horizontally across the tube. Food rewards were attached to the protruding end of the spaghetti fragments outside the tube. Underneath the suspended food rewards, slanted trays (50 cm width $\times$ 48 cm depth) were mounted to the mesh of the enclosures. When the tool (made of grey PVC, 3.5 cm $\times$ 3.5 cm and 25.0 cm long) was inserted in the upper end of the tube, it slit down the tube towards enclosure 2, thereby breaking the spaghetti fragments. Consequently, the attached food fell on to the slanted trays where they rolled towards the mesh, within reach of the subjects.

The nonsocial apparatus (made of transparent Perspex; Fig. 1) consisted of a horizontal chute (length 25 cm, 4 cm height $\times$ 4 cm width) where the tool could be inserted. On the back of the chute, a hole (diameter 7 cm) was drilled so that the food placed at the end of the chute could be pushed inside the hole with the tool. The food items would fall on a ramp and roll towards the mesh, within reach of the subjects. To push the food inside this hole, the subjects had to insert the tool into the chute entirely, which made retrieval of the tool impossible.

As a high-value reward, a combination of a banana pellet and a grape attached to one end of spaghetti fragments was used. As low-value rewards, similar-sized pieces of apple or carrot were used.

Procedure and design

A 2 $\times$ 2 within-subject design was used to manipulate whether the door between enclosures 3 and 4 was open (wide enough for the juvenile, but not the mother, to pass through) or closed and whether the tube (social apparatus) was baited for the juvenile (with a high-value reward) or empty. The mothers' social apparatus was always baited with a high-value reward, whereas the nonsocial apparatus was always baited with a low-value reward. In the previous versions of this task, all individuals had repeatedly used the tool successfully, and the mothers had passed the tool to the juveniles repeatedly. In addition, in these earlier versions of the task, the door between enclosures 3 and 4 was always open, and the tube was always baited for the juvenile (experiment 4 in Völter et al., 2015).

Eight sessions with eight trials each were conducted for a total of 64 trials per dyad. In every session, every combination of conditions was administered two times. The conditions were blocked within sessions, and the order of the blocks was randomized across the sessions. Both dyads were first run with apple as the low-value reward. For one dyad, a floor effect concerning tool passing was observed, although both mothers preferred pellets over apple pieces in 100% of trials in food preference tests (Sánchez-Amaro et al., 2016). The procedure for this dyad was repeated with another low-value reward (carrot; this individual, Dokana, preferred pellet over carrot and apple over carrot in 100% of trials in a food preference test; Sánchez-Amaro et al., 2016).

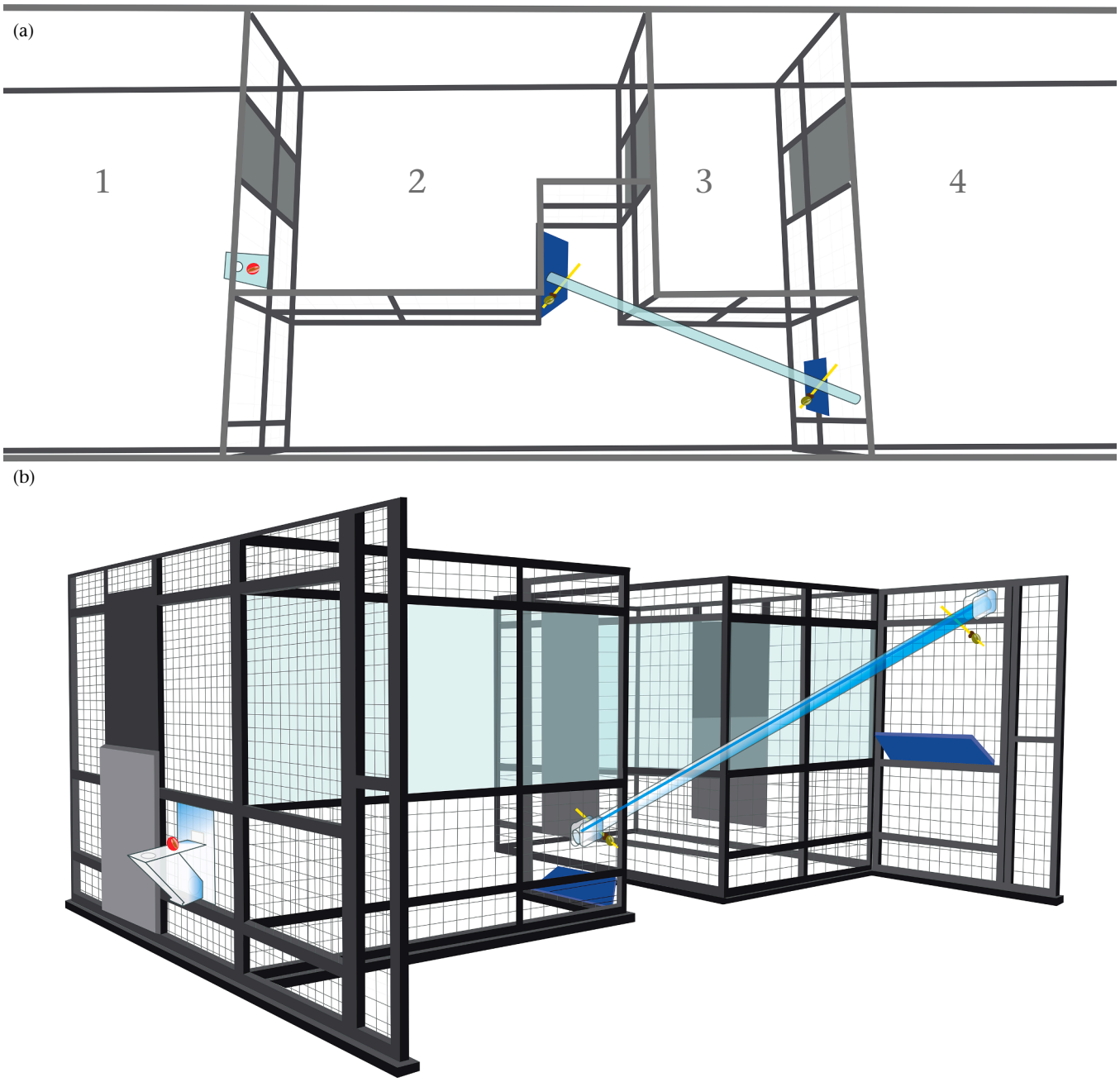

Figure 1. Set-up of experiment 1. (a) Top view and (b) side view. The mothers were placed in enclosure 2 (from the left) throughout the experiment. The state of the door between enclosure 3 and 4 was manipulated (shown as open). The door between enclosure 2 and 3 was open so that the juvenile but not the mother could move freely between enclosures 2 and 3. The nonsocial apparatus mounted at the mesh between enclosure 1 and 2 was always baited with a low-value reward (apple or carrot).

In the beginning of each trial, the experimenter (E) baited the social and nonsocial apparatus in full view of both subjects. Then, E passed the tool to the mother in enclosure 2 at a location equidistant from the nonsocial apparatus and the door to enclosure 3. A trial ended when the tool was inserted into one of the two apparatuses or dropped outside the enclosure (inaccessible to both subjects).

Scoring and analysis

All trials were recorded using four cameras (Video S1). Whether or not the mothers passed the tool on to the juvenile and in which apparatus the tool was inserted eventually was scored. The tool-transfer data for each dyad were analysed separately by running multiple generalized linear models (GLM) with a binomial error structure and logit link function (McCullagh & Nelder, 1989) using the function glm of the R package lme4 (Bates et al., 2015). A likelihood ratio test (Dobson, 2002) was used to compare the full models with respective null models comprising only the intercept (Forstmeier & Schielzeth, 2011). Collinearity was not an issue in any of the models (maximum variance inflation factor 1.0).

Results and Discussion

Orang-utan mothers considered the state of the door and passed the tool primarily when the juveniles had access to the enclosure where they could use the tool. However, no evidence that the orang-utan mothers considered the payoffs of the juveniles was found.

Tool passing was mostly an active transfer from the mother to the offspring rather than passively allowing the juvenile to take the tool (Dokana: 84% of transfers that could be categorized; Padana: 100%). Padana (full-null model comparison: $\chi^2_4 = 37.95$, $P < 0.001$) passed the tool on to her son more often when the door was open ($\chi^2_1 = 36.52$, $P < 0.001$) but irrespective of her son's payoff ($\chi^2_1 = 1.15$, $P = 0.283$; Fig. S1, Table S1). By contrast, Dokana used the tool in most trials to obtain a piece of apple from the nonsocial apparatus, and the predictor variables did not significantly affect her tool passing (full-null model comparison: $\chi^2_4 = 0.96$, $P = 0.915$). When the apple as a low-value reward was replaced with a piece of carrot, Dokana (full-null model comparison: $\chi^2_4 = 40.66$, $P < 0.001$) showed the same tool-transfer pattern as Padana. Dokana passed the tool more frequently when the door was open ($\chi^2_1 = 35.0$, $P < 0.001$) irrespective of her daughter's payoffs ($\chi^2_1 = 0.48$, $P = 0.491$). In addition, the tool-passing rates of Dokana increased across trials ($\chi^2_1 = 4.73$, $P = 0.030$) and sessions ($\chi^2_1 = 5.44$, $P = 0.020$).

When the juveniles received the tool (and the door was open), they were significantly more likely to insert the tool in the social apparatus when it was baited than when it was empty. Suaq inserted the tool 11 times out of 12 when the social apparatus was baited for him but only three out of 10 times when it was empty (Fisher's exact test $P = 0.006$). Tanah (with carrot as reward for the mother's nonsocial option) inserted the tool 12 times when the social apparatus was baited for her but only five out of 13 times when it was empty (Fisher's exact test $P = 0.002$). When the juveniles did not insert the tool in the tube, they usually brought it back to the mothers who then usually inserted it in the nonsocial apparatus (Dokana–Tanah: six out of eight times when Tanah refused to insert the tool in the tube; Padana–Suaq: seven out of eight times).

These results indicate that orang-utan mothers consider physical constraints and their own payoffs when cooperating with their offspring. Their performance does not provide evidence that they also paid attention to the payoffs of a partner. However, the baiting status of the juveniles' end of the tube might have been difficult to see from the mothers' location (although we tried to capture their attention by calling their names when baiting the upper end of the tube). In addition, we did not offer the offspring an alternative use for the tool. Consequently, in most cases, the juveniles brought the tool back to the mother's enclosure when they did not insert it into the tube. Therefore, passing the tool on to the offspring was not very costly for the mothers. In experiment 2, the set-up was modified to resolve these issues and to answer the question whether orang-utans and chimpanzees consider their partner's payoffs when deciding to hand over the tool.

EXPERIMENT 2

In experiment 2, chimpanzee and orang-utan dyads were compared in a similar task but with nonsocial alternatives for both individuals. The payoffs that the apes could obtain from cooperation and from defection were varied. The partners were also moved closer together to increase the visibility of the payoffs. We hypothesized that the apes that acted as the tool giver would not only consider their own payoffs but also the recipients' payoffs when deciding whether to pass the tool on or not.

Methods

Subjects

Five orang-utans, *Pongo abelii*, aged 5–26 years (one male, four females) and 10 chimpanzees, *Pan troglodytes*, aged 6–39 years (six males, four females) were trained with the cooperative problem-solving apparatus. All five orang-utans and six chimpanzees (four males and two females) passed the training and advanced to the test phase (the training criteria are discussed below). The subjects were paired with multiple individuals in their group, except for two orang-utan juveniles who could only be tested with their mothers. A total of 21 dyads were tested. Of the 10 orang-utan dyads, six were mother–offspring dyads (in two of these dyads, the offspring was an adult female); two of the 11 chimpanzee dyads were mother–offspring dyads. All subjects were housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo (Germany). All subjects were experienced in tool-use tasks and pretests established that they could successfully use the tools in the current apparatuses to retrieve the food (see below).

The subjects were housed in social groups of 6–22 individuals, and they spent the day in indoor (175–430 m^2) or outdoor (1400–4000 m^2) enclosures, depending on the season. All enclosures were spacious, and they were equipped with climbing structures, natural vegetation and enrichment devices to foster extractive foraging activity. The subjects were tested in the sleeping rooms interconnected by lockable doors. They were provided with fresh fruits, vegetables, eggs, cereals, leaves and meat (once a week) distributed in three main meals; some more food was dispensed multiple times over the day, as part of the enrichment programme. Water was available ad libitum during testing.

Set-up

The same apparatuses as in experiment 1 were used with some modifications (Fig. 2). The two individuals were placed in enclosures 3 and 4, and all connecting doors were closed. The tool was always given to the individual in enclosure 3, who could pass it on actively to the individual in enclosure 4 through the mesh. The social tube apparatus could be baited for enclosure 3 and 4: food rewards were suspended from the tube in front of these two enclosures (and trays capturing the food rewards were mounted underneath these two locations). In addition, two nonsocial apparatuses mounted at the same height were used, one in front of enclosure 3 and one in front of enclosure 4 (below the tray underneath the upper end of the social apparatus).

As high-value rewards, a banana pellet and a grape pinned on a spaghetti fragment were used again. When placed in the nonsocial apparatus, the spaghetti–pellet–grape fragment was shortened to allow its passing through the hole. Carrots were used as low-value rewards for most individuals. Two orang-utans (Padana and Suaq) and one chimpanzee (Bangolo) did not eat the carrot pieces during the first training or pretest sessions. To ensure that these subjects would eat both food types presented, similar-sized pieces of apple were used as the low-value option for these subjects.

Design

A $2 \times 2 \times 2$ within-subject design was used to manipulate the food quality of the nonsocial alternative for the tool giver (low versus high), the food quality of the nonsocial alternative for the tool recipient (low versus high) and whether the social alternative of the tool recipient was baited (with a high-value reward) or empty. This design resulted in eight different trial types. In all trials, the social option of the tool giver was baited with the high-value reward. Within a session, each trial type was presented once, resulting in eight trials per session. A total of 12 sessions were run for a total of 12 trials per trial type and dyad.

Procedure

Individual training. To ensure that the apes understood the mechanism of the social tube apparatus, they first underwent an

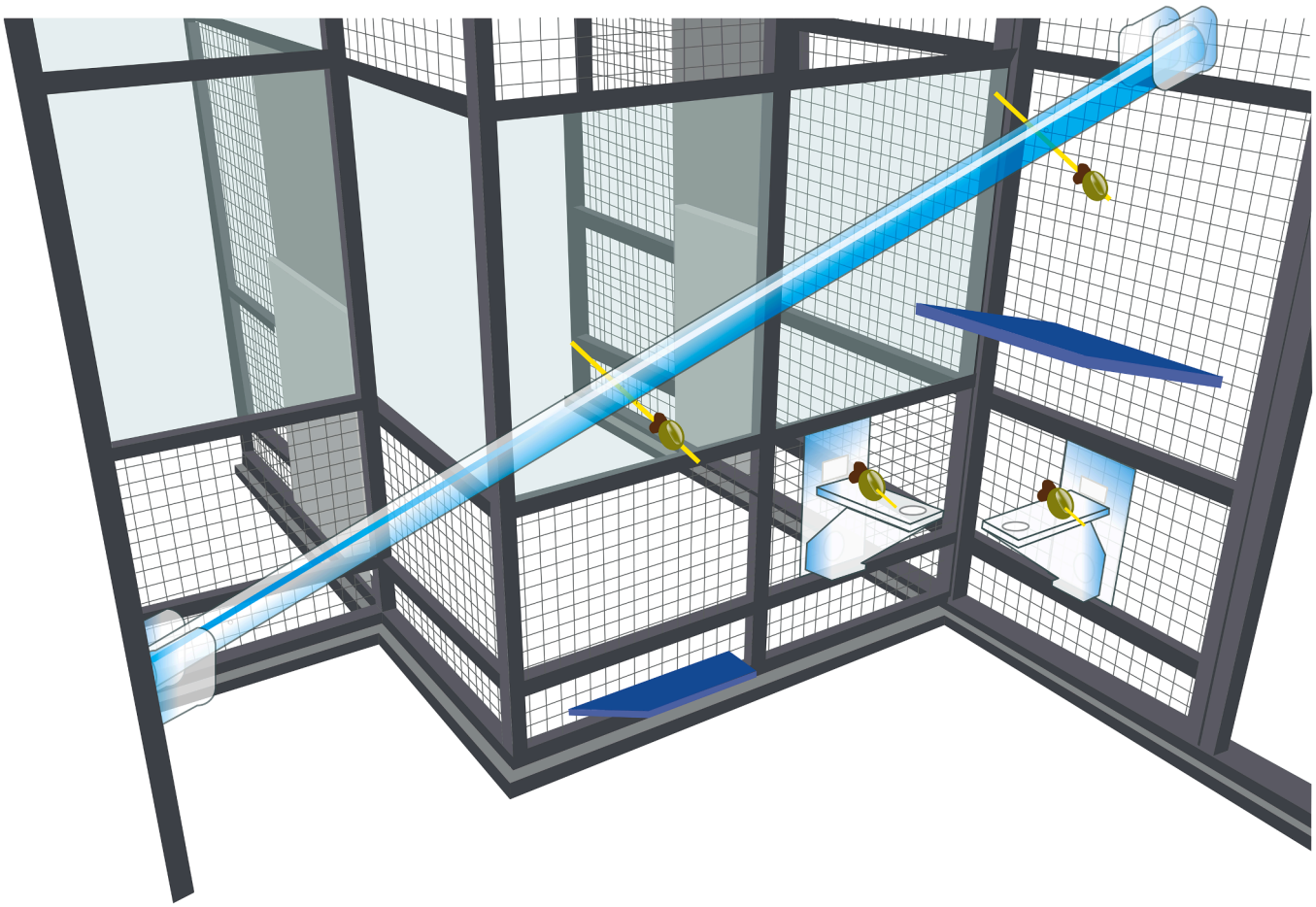

Figure 2. Set-up of experiment 2. The tool giver was placed in enclosure 3 (middle), whereas the tool recipient was placed in enclosure 4 (right). The illustration depicts the configuration in which the social and nonsocial apparatuses for both individuals were baited with high-value rewards.

individual training. The subjects were tested individually in their sleeping enclosures (2–4). The interconnecting doors were kept open so that the subjects could move freely between the three enclosures. The apparatus consisted only of the tube and reward collection trays, but no nonsocial apparatus was set up. The tube was either baited near the end in front of enclosure 2 or near the top of the tube in front of enclosure 4. Initially, only one grape was attached to a spaghetti fragment. If subjects refused to participate, then a pellet was added to increase motivation. After the tube was baited in full view of the subject, the experimenter (E) passed the tool to the subject through the mesh at enclosure 2. In each session, apes received six trials in which the tube was always baited at the same position, which alternated between sessions. If the tool was not inserted in the tube within 3 min, then E requested the tool back, and the next trial started. The subjects passed the individual training stage if they successfully retrieved the reward 12 times in each location, which corresponds to a minimum of four sessions.

Dyadic training. Orang-utans had participated in different versions of the tool-transfer task prior to this study, including the version in which dyadic (Völter et al., 2015; experiment 1) or triadic cooperation (Völter et al., 2017) was necessary to obtain food. However, they had not encountered a situation in which the recipient had an alternative tool-use option.

The chimpanzees received a dyadic training phase to ensure that they would also pass the tool to a conspecific if they had no alternative tool-use option. The chimpanzees were assigned to dyads and placed in enclosures 3 and 4 with closed interconnecting doors. Except for the absence of nonsocial apparatuses, the set-up was the same as that in the test phase. The tube was always baited in full view of the subjects with spaghetti–grape–pellet rewards in front of enclosures 3 and 4. Subsequently, the tool was given to the subject in enclosure 3. The subjects passed the training when the tool giver passed the tool on, and the recipient subsequently used the tool to obtain the reward in four trials. If they did not pass the tool in the first four trials, then the subjects moved on to the intermediate training phase. If they started tool passing within the first four trials, then they were given a maximum of seven trials to pass the criterion of four successful trials. After the subject in enclosure 3 had completed 4–7 trials (depending on success), the apes swapped positions, and the dyadic training for the second individual of the dyad began. A trial was considered unsuccessful when no tool passing occurred within 3 min.

Intermediate dyadic training (optional, chimpanzees only). If the subjects did not pass the dyadic training session ($N = 3$), then other training variants were carried out. In the 'seen' version of the dyadic training, four trials per session were conducted. The first and third trials resembled the dyadic training. By contrast, in the second and fourth trial, the experimenter passed the tool directly to the subject in room 4. This manipulation showed the subject in

room 3 that the conspecific in room 4 was competent to use the tool and, thus, able to release the rewards for both of them.

A maximum of six seen sessions were conducted if subjects did not meet four successful passing trials earlier. When both apes in a dyad were still in the training phase, the roles were reversed after one subject completed a session. If the subjects did not reach the criterion during the six seen sessions, then they moved on to the 'door open' training. This training encompassed a maximum of two sessions with the same structure as in the dyadic training. The only difference was that the door connecting rooms 3 and 4 was opened approximately 20 cm so that subjects could poke their arm through but were not able to enter the other room. This set-up facilitated tool passing physically and enlarged the range of begging gestures. All subjects that remained unsuccessful during the door open training were reshuffled with new partners that had passed the tool before. These reshuffled dyads underwent up to six sessions in the pattern of the seen training. The prior successful giver was always the first to be in room 3. After four trials, both apes switched rooms and the prior unsuccessful subject was given the chance to pass the tool. If the subjects did not pass this training step, then they were excluded and did not participate in the actual test. When a subject did not pass the tool after 3 min or pushed it repeatedly out of the cage in any of these training steps, the trial was counted as unsuccessful, and the subject moved on to the next trial.

Individual pretest. Finally, the apes were presented with an individual pretest (with an open door between enclosures 3 and 4) in which we ensured that they used the tool to obtain the highest quality reward available from the nonsocial and social apparatuses. The subjects were presented with the four different reward combinations of the tube (high value/nothing) and the nonsocial apparatus (high/low value). Individually, the subjects were placed in the connected enclosures (3 and 4). E passed the tool to enclosure 3, but the tube and nonsocial apparatus were only baited in enclosure 4. The pretest consisted of eight trials in which every possible reward combination was presented two times in a randomized order. The subjects passed the pretest and moved on to the test phase if they chose the high-value over the low-value reward and any reward over nothing in every trial with a reward imbalance between the options. If the subjects failed to show the expected behaviour, then the pretest was repeated in the next session until they successfully achieved five out of six trials (only considering trials with a reward imbalance). A maximum of two pretest sessions were conducted. Two chimpanzees did not receive the pretest (experimenter mistake). These two subjects passed the tool every time to the recipient when they had a low-value reward in their nonsocial alternative in their first test session, indicating that they paid attention to the nonsocial alternative.

Test. During the test, the tool giver was placed in enclosure 3, and the tool recipient was placed in enclosure 4 with closed interconnecting doors. Before the trial, E baited the tube and both nonsocial apparatuses in full view of the subjects. E baited the apparatuses for enclosure 3 or enclosure 4 in an alternating order across sessions. E held the rewards up and, if necessary, called the subjects' names when baiting the apparatuses to ensure that they watched the baiting process. The trial started when E gave the tool to the tool giver in enclosure 3. The trial ended when the tool was fully inserted into one of the apparatuses (Videos S2 and S3). If the tool was not inserted or passed on after 3 min or repeatedly pushed back into the experimenter's area, then the trial was terminated.

Scoring

All test sessions were videotaped by using two cameras: one camera with a wide-angle lens to record the entire set-up and another camera focusing on the mesh between enclosures 3 and 4 (where individuals could pass the tool on to the partner). Whether the tool givers passed the tool on to the partner (tool transfers were coded when the tool was completely passed through the mesh to the neighbouring enclosure and the tool giver gave up control over it) and in which apparatus the tool giver or recipient inserted the tool were scored (insertions were coded when the food was released and the apes could not extract the tool any more). Whether the tool recipient was present at the mesh next to the tool giver's enclosure when the giver received the tool was also scored (close to the location where the apparatuses were mounted or where they would typically receive the tool). In addition, whether the giver passed the tool to the recipient in a high position was scored (that is, closer to the upper end of social tube apparatus; Video S4). A high pass was coded if one of two conditions was met: if the tool givers made an effort to transfer the tool above a horizontal metal bar in the mesh between enclosures 3 and 4 (height from the floor 119 cm; width 10 cm) or if the tool givers passed the tool through the mesh at an unusual location above their heads. Finally, whether or not the recipient produced behaviours aimed at getting their partners' attention or requesting an action (henceforth attention getters) in the period between the start of the trial and the decision by the tool giver was scored. These attention getters included begging gestures (sticking fingers or lips through the mesh towards the partner or holding a hand with the palm facing upwards close to the mesh; Video S5) and other potential attention-grabbing behaviours. The additional attention-grabbing behaviours included waving, clapping or shaking a limb, spitting through mesh at the partner, rocking/swinging (moving the body back and forth or left to right in an exaggerated pendulum movement), stomping on the ground, hitting the mesh in an audible manner with a limb, grunting and scratching in an exaggerated manner. These behaviours have been identified as candidates for intentional communication in captive orang-utans and chimpanzees in previous research in a context in which they requested food from a human or a conspecific (Cartmill & Byrne, 2007; Hostetter et al., 2001; Leavens et al., 2005; Rossano & Liebal, 2014). A second coder naive to the experimental hypotheses scored 350 trials (17.4% of all trials) to assess interobserver reliability, which was acceptable for all variables (Table 1).

Only trials in which subjects inserted the tool into one of the apparatuses within 3 min after E had passed the tool to the tool giver were analysed. In three trials, tool givers did not choose one of the options within 3 min (remaining trials: 2013). In 110 of the 2013 trials, attention getters by the recipient could not be scored

Table 1
Interobserver reliability of the scored variables

	Agreement (in %)	Kappa	*N*	*P*
Tool transfer	100	1.00	350	<0.001
Tool in tube[1]	100	1.00	61	<0.001
High passing[1]	95.08	0.90	61	<0.001
Presence[2]	92.55	0.78	349	<0.001
Attention getter (with NAs?)[3]	86.29	0.69	350	<0.001
Attention getter (without NAs)[4]	94.39	0.84	303	<0.001

[1] Based on a subset of trials in which the tool was transferred to the recipient.
[2] One reliability trial was missing because of camera failure.
[3] Attention-getter coding based on three categories (present/absent/not fully visible).
[4] Attention-getter coding without the trials scored as not visible or unclear. These trials were not included in tool transfer analysis (generalized linear mixed model 01).

because the recipient was not visible during the critical period. Therefore, analyses involving attention getters as predictor variables were performed on the basis of the remaining 1903 trials generalized linear mixed models (GLMM) 01 (Table S2). In GLMM S01, this analysis was repeated without attention getters as predictor variable and including all observations in which attention getters could not be scored ($N = 2013$; Table S3).

GLMM (Baayen, 2008) with a binomial error structure and logit link function (McCullagh & Nelder, 1989) were fitted to analyse the choices of tool givers ('tool transfer') and tool recipients ('tool inserted in tube'). In all models, tool giver ID, recipient ID and dyad ID were included as random effects as well as all possible random slope components (Barr et al., 2013) except for the correlation parameters among random intercepts and random slopes terms (see Supplementary Material for more details on the analyses).

In GLMM01, the extent to which the following predictor variables explained variance in the tool transfer response was analysed: available nonsocial reward quality of the tool giver (high-value versus low-value food), the social (baited with high-quality food versus empty) and nonsocial (high versus low) payoffs of the recipient as well as the interaction between these two factors. Moreover, the presence of the recipient at the beginning of the trial (present/absent), the recipients' attention getters (present/absent; representing begging gestures and other potential attention-grabbing behaviours), species (orang-utan and chimpanzee) and the interaction between species and attention getters were included. The interaction between species and attention getters was also included because of potential species differences concerning the effect of gestural communication on apes' willingness to cooperate (Pelé et al., 2009). Finally, the control predictors session and trial number (within session) were also included. The sample of GLMM 01 consisted of 1903 observations of 11 tool givers and recipients and 21 dyad combinations. In GLMM S01 (Supplementary material), this analysis was repeated without attention getters as predictor variable and including all observations in which attention getters could not be scored ($N = 2013$).

In GLMM02, the extent to which the following predictor variables explained variance in the tool recipient's choices of the social tube apparatus over the nonsocial alternative was analysed (only based on tool-transfer trials): the social (baited with high-quality food versus empty) and nonsocial (high versus low) payoffs of the recipient as well as the interaction between these two factors. Moreover, the high-tool-passing response of the tool giver and species (orang-utan and chimpanzee) as well as the control predictors session and trial number (within session) were included.

As an overall test of the effect of the predictor variables for both GLMMs, the respective full model was compared with a null model that lacked the test predictors but comprising the same control predictors and random effect structure as the full model (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson, 2002). *P* values for the individual effects were based on likelihood ratio tests comparing the full model with respective reduced models (Barr et al., 2013) using R function drop1 with argument 'test' set to 'Chisq'. The model was implemented in R (version 3.5.2; R Development Core Team, 2018) using the function glmer of the R package lme4 (Bates et al., 2016). CIs were derived using the function bootMer of the R package lme4, using 1000 parametric bootstraps and bootstrapping over the random effects.

Prior to model fitting, all covariates were *z*-transformed (to a mean of zero and SD of one). The variance inflation factors (Field, 2005) for standard linear models excluding the random effects were determined using the R package car (Fox & Weisberg, 2011). Collinearity was no issue (maximum variance inflation factor: GLMM 01: 1.14; GLMM 02: 1.34; GLMM S01: 1.1; GLMM S02: 1.21; GLMM S03: 1.0).

Results and Discussion

Tool giver

GLMM01 examined the variables that predicted the tool transfer. The full model fitted the data significantly better than a null model that lacked the test predictor variables and comprised the same control predictors (session and trial number) and random effect structure (likelihood ratio test $\chi^2_8 = 45.10$, $P < 0.001$). A significant interaction was found between species and attention getters ($\chi^2_1 = 3.93$, $P = 0.047$). The interaction between the social and nonsocial payoff options of the recipient was not significant ($\chi^2_1 = 1.14$, $P = 0.287$). The latter interaction was removed, and the model was refitted (see Table S2 for the model results). The tool giver transferred the tool mostly to the partner when the tool giver's own nonsocial payoff was a low-value reward ($\chi^2_1 = 21.69$, $P < 0.001$; Fig. 3a). In addition, they passed the tool to the recipient significantly more often when the social option for the recipient was baited, that is, when the recipient had an incentive to cooperate ($\chi^2_1 = 3.86$, $P = 0.049$; Fig. 3b). By contrast, no significant evidence that the tool givers considered the food quality in the tool recipient's nonsocial apparatus was found ($\chi^2_1 = 1.78$, $P = 0.182$). Thus, the decision of the apes to cooperate partially incorporated the recipients' payoffs. In addition, the tool givers passed the tool on with a higher probability when the recipient was present at the mesh in the beginning of the trial ($\chi^2_1 = 10.56$, $P = 0.001$; Fig. 3c). Finally, in the case of chimpanzees, the tool recipients were more likely to receive the tool when they produced a begging gesture or another type of attention-grabbing behaviour ($z = 2.79$, $P = 0.005$; Fig. 4). By contrast, the tool transfer rates of orang-utan tool givers were not significantly influenced by such behaviours on the part of the recipients ($z = -0.50$, $P = 0.616$).

In addition, the apes sometimes passed the tool high above their head in a quite unusual manner (Video S4). Compared with chimpanzees, orang-utans were significantly more likely to pass the tool high to the recipient ($\chi^2_1 = 8.12$, $P = 0.004$; GLMM S02; Table S4; Fig. S2a). Tool givers were more likely to pass the tool high to the recipient if the recipient's nonsocial payoff was low ($\chi^2_1 = 4.55$, $P = 0.033$; Fig. S2b) and if the recipient had inserted the tool into the social tube apparatus the last time the tool giver had passed the tool to the recipient ($\chi^2_1 = 4.18$, $P = 0.041$; Fig. S2c). The social payoff of the tool recipient did not significantly predict the high-passing response ($\chi^2_1 = 0.47$, $P = 0.492$).

Tool recipient

The tool recipient's probability to produce an attention-getter did not differ between the two species ($\chi^2_1 = 0.77$, $P = 0.380$; GLMM S03; Table S5), but apes were more likely to show attention getters when there was a high-value reward either in their social or nonsocial apparatus (interaction between the social and nonsocial payoffs of the tool recipient: $\chi^2_1 = 6.47$, $P = 0.011$; Fig. S3).

GLMM02 examined the variables that predicted whether the tool recipient inserted the tool in the social tube apparatus or the nonsocial alternative option. The full model fitted the data significantly better than a respective null model ($\chi^2_5 = 46.29$, $P < 0.001$). However, the interaction between the social and nonsocial payoff options of the recipient was not significant ($\chi^2_1 = 3.44$, $P = 0.064$). The interaction was removed, and the model was refitted (see Table S6 for the model results). Tool recipients were more likely to cooperate by inserting the tool in the social tube apparatus if the tube was baited for them ($\chi^2_1 = 18.22$, $P < 0.001$) and if their nonsocial alternative contained a low-value reward than when it was baited with a high-value food ($\chi^2_1 = 23.46$, $P < 0.001$). When the social and nonsocial apparatus

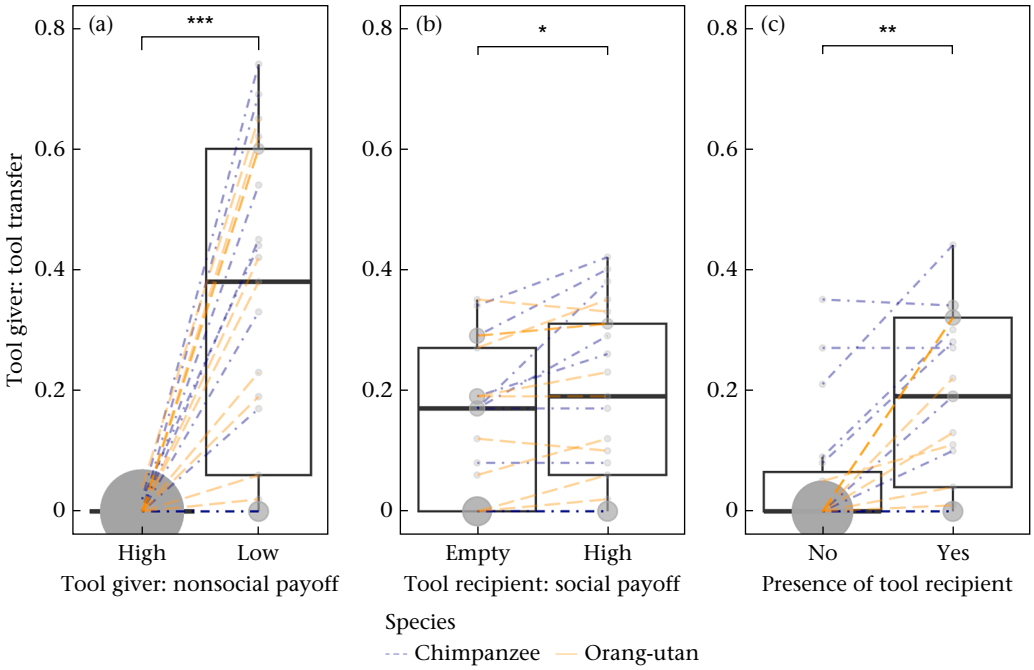

Figure 3. Box plots showing the tool transfer rates. Tool transfer is shown as a function of (a) the tool giver's payoffs, (b) the tool recipient's social payoff and (c) the presence of the tool recipient at the mesh. The grey dots represent the dyads. The area of the dots is proportional to the number of dyads with a given value. The blue, dash-dotted line connects chimpanzee dyads with the same values, whereas the orange, dashed line connects orang-utan dyads. The boxes indicate the quartiles; the black horizontal lines inside the boxes indicate the median values, and the whiskers extend to 1.5 times the IQR from the upper and lower ends of the boxes. Generalized linear mixed model 01: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

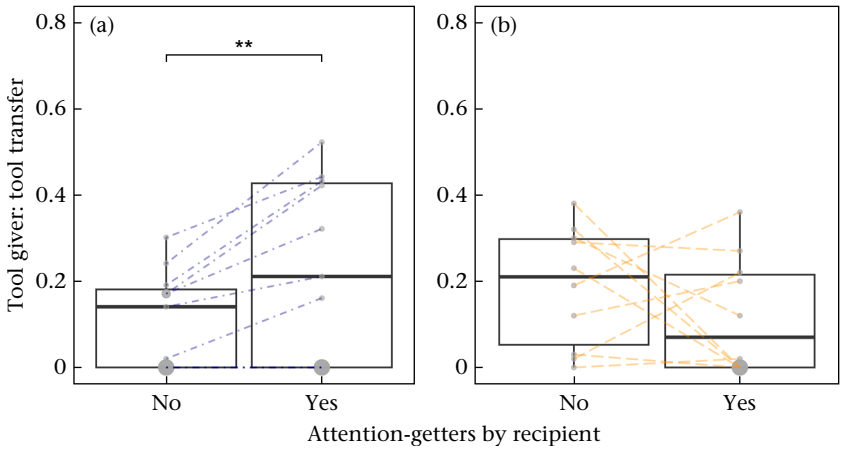

Figure 4. Box plot showing the tool transfer as a function of attention getters by the tool recipient. (a) Chimpanzees and (b) orang-utans. The grey dots represent the dyads. The area of the dots is proportional to the number of dyads with a given value. The blue, dash-dotted line connects chimpanzee dyads with the same values, whereas the orange, dashed line connects orang-utan dyads. The boxes indicate the quartiles; the black horizontal lines inside the boxes indicate the median values, and the whiskers extend to 1.5 times the IQR from the upper and lower ends of the boxes. Generalized linear mixed model 01: $**P < 0.01$.

were baited with a high-value reward, apes cooperated on average in 18.8% of all trials (95% CI 1.9%–32.7%; Fig. 5a), which was less than when only the tube was baited with a high-value reward (mean 93.8%; 95% CI 93.6%–100%) but more than when the tube was not baited but the nonsocial apparatus was baited with a high-value reward (mean 1.0%; 95% CI 0%–0.1%; Fig. 5b). Whether or not the tool giver passed the tool high did not have a significant effect on the tool recipient's choices ($\chi^2_1 = 1.69$, $P = 0.193$). Species, session or trial number had no significant effect either (Table S6).

The apes in both roles decided flexibly to cooperate primarily based on their own payoffs. Tool givers also partially took into consideration the incentives of their partner to cooperate. However, they failed to fully consider their partner's potential payoffs. If their partner had a better payoff in the nonsocial option, then their tool passing was often not rewarded. Tool recipients also primarily considered their own payoffs. However, although choosing the social option was more effortful as it required the recipient to climb up, the apes sometimes cooperated if the social and nonsocial options provided the same high-value reward (mean 18.8% of trials; Fig. 5a) and sometimes if the social option was not baited for them at all (nonsocial apparatus baited with a low-value reward and tube not baited: mean 12.5%; Fig. 5b). Thus,

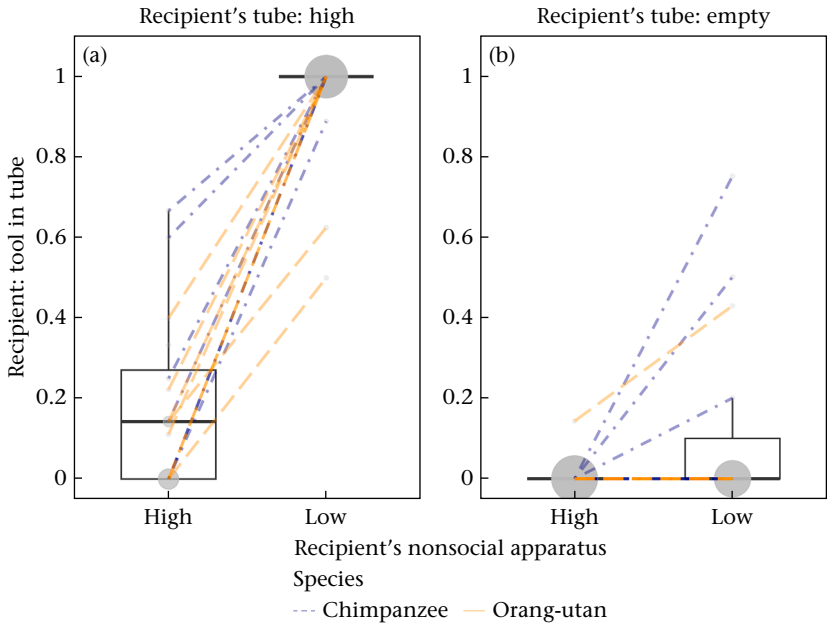

Figure 5. Box plot showing the tool recipient's cooperative choices. The recipient's cooperative choices (tool inserted in the tube apparatus) are plotted as a function of the tool recipient's payoffs in the social tube apparatus and the nonsocial apparatus. (a) Tool apparatus baited with a value reward and (b) unbaited tool apparatus. The grey dots represent the dyads. The area of the dots is proportional to the number of dyads with a given value. The blue, dash-dotted line connects chimpanzee dyads with the same values, whereas the orange, dashed line connects orang-utan dyads. The boxes indicate the quartiles; the black horizontal lines inside the boxes indicate the median values, and the whiskers extend to 1.5 times the IQR from the upper and lower ends of the boxes.

chimpanzees (overall tool transfer rate 15.4%; cooperation rate by the recipient 39.2% of trials) and orang-utans (overall tool transfer rate 19.1%; cooperation rate by the recipient 36.6%) cooperated if the food-related costs for themselves were not too high, and they were sometimes willing to give up low-value rewards for their partner to receive a high-value reward (see Tables S7 and S8 for more details on the cooperation rates per species).

Attention getters by the tool recipient had an effect on chimpanzee tool givers but not on orang-utans, although the frequency of these behaviours did not vary significantly across species and orang-utans did not show lower rates of begging gestures than chimpanzees (Table S5, Fig. S4). No overall difference in tool-passing rates was found across species. The differences in pre-experience with the problem-solving situation do not plausibly explain why the species reacted differently to attention getters by the tool recipients.

GENERAL DISCUSSION

Chimpanzees and orang-utans flexibly decided between individual foraging and cooperation with a conspecific mainly with regard to their own payoffs and the availability of the recipient. However, some evidence, albeit much weaker, showed that they took the payoffs of the other individual into consideration. They were more likely to pass on the tool when the partner's cooperative option was baited (compared with when it was empty) without considering the payoffs in the partner's individual foraging alternative. Overall, no species differences in tool-passing rates were found. However, unlike orang-utans, chimpanzees passed the tool more often in response to the attention getters produced by the recipient. Apes sometimes cooperated even when that meant to forgo a low-value food reward. In addition, experiment 1 provided evidence that orang-utan mothers were also sensitive to physical constraints that prevented their offspring from inserting the tool.

From an evolutionary perspective, the similar overall response profiles we observed suggested that the basic mechanisms for cooperative decision-making in a foraging task based on own and others' payoffs may be ancestral in great apes. This interpretation is consistent with prior reports of comparable performance of orang-utans and chimpanzees in another cooperative foraging paradigm (Chalmeau et al., 1997). When the cooperative activity does not allow for resource monopolization, chimpanzees, as a species with a highly gregarious lifestyle, do not seem to perform significantly different than the less gregarious orang-utans. However, when there is no physical separation and a resource can be monopolized, which is arguably the more naturalistic situation, the species differences among great apes seem to be more apparent (Hare et al., 2007; Liebal & Rossano, 2017). For example, bonobos will share food with group members and conspecific strangers (Hare & Kwetuenda, 2010; Tan & Hare, 2013)in contrast to chimpanzees in comparable situations. Their tolerance allowed them to succeed in a loose-string cooperation task in which the reward can be monopolized (Hare et al., 2007) and in which chimpanzees had failed (Melis et al., 2006). The highly tolerant bonobos do not pass on tools to conspecifics, although they do pass on food (Krupenye et al., 2018), whereas an inverse pattern has been found for chimpanzees (Melis & Tomasello, 2013, 2019; Yamamoto et al., 2009, 2012).

Our findings also highlight differences between chimpanzees and orang-utans, which might be attributed to their different socioecology. In the current task, chimpanzees showed greater responsiveness to attention getters by their partners than orang-utans. Evidence from the wild indicates that chimpanzees produce warning signals depending on the composition and knowledge states of the audience possibly to inform them about a potential source of danger (Crockford et al., 2012, 2017). A socioecology in which attention to others' signals can provide such benefits might favour individuals that pay attention to conspecific signals and respond to their signals. By contrast, species such as

orang-utans, whose natural social life primarily consists of tolerant but infrequent associations, might not favour such responsiveness (Delgado Jr & Van Schaik, 2000; Van Schaik, 1999).

One might argue that our coding system might have better captured communication in chimpanzees than orang-utans. However, previous research reported that the coded behaviours are produced in situations in which both chimpanzees and orang-utans request a food resource, and they met the criteria of intentional communication in both species, such as elaboration on the part of the signaller when the desired outcome is not achieved (Cartmill & Byrne, 2007; Hostetter et al., 2001; Leavens et al., 2005; Rossano & Liebal, 2014). In the current study, the frequency of attention getters did not vary significantly across species; both species only rarely produced begging gestures, and there is no reason to assume that we have missed orang-utan attention getters particularly in trials with tool transfers (which could explain the species differences in responsiveness to attention getters).

This responsiveness to social/communicative signals in chimpanzees is also supported by previous experimental studies with mutualistic cooperation (Bullinger et al., 2011; Duguid et al., 2014) and helping tasks (Melis et al., 2010; Yamamoto et al., 2012). In a recent study using a touchscreen-based coordination task, chimpanzees produced more attention getters when the task was rigged such that it appeared that the other individual did not cooperate any more (Voinov et al., 2020). Together with these previous findings, our results show that although chimpanzees do not communicate a lot in coordination games, communication can still help them to sustain cooperation (see also Melis & Rossano, 2022). By contrast, orang-utans did not show the same reactivity to communicative signals in our study. One explanation for this could be that orang-utans have a lower sensitivity to begging than chimpanzees. Consistent with this interpretation, when provided with an easily monopolizable food resource (the same group of), captive orang-utans resisted requests (involving begging gestures) and attempts to take the food more often than chimpanzees (Liebal & Rossano, 2017). However, this does not mean that orang-utans ignore begging gestures and other apparent requests all the time. In the same experimental paradigm, involving the provision of monopolizable food to captive orang-utans, begging gestures resulted in a successful food transfer in approximately 50% of the instances (Rossano & Liebal, 2014). In another study, an adult, male orang-utan received more tokens (that could be exchanged for food) by females after he produced pointing gestures (Pelé et al., 2009). It is therefore possible that the receptivity of orang-utans for communicative signals depends on the relationship quality between the participants.

Moreover, unlike chimpanzees, orang-utans often passed the tool high above their heads particularly when the recipient had previously cooperated and when the recipient's nonsocial payoff was low. The high-passing response may indicate that the orang-utans tried to manipulate the recipient's behaviour, albeit unsuccessfully. This is consistent with the idea that cooperation in orang-utans can be described as a form of social tool use (Völter et al., 2017). Accordingly, they may use a similar form of means-end reasoning when they cooperate with others compared with when they use physical tools. In previous research, the same orang-utan mothers manipulated their offspring physically like a tool to get access to a desired food item or a stick tool (Völter et al., 2015). That study further showed that the orang-utans seamlessly switched from taking the tool away from their offspring to passing it on to them depending on what was required to retrieve a food reward. They sometimes even combined coercion with cooperation by restraining the offspring until the latter grabbed the stick tool that was offered by the mother. Our results in experiment 1 add another layer of complexity: orang-utan mothers also considered the physical constraints of their offspring when deciding whether to transfer the tool or not.

The conclusions that can be drawn from our experiments are limited in several ways: first, only a small sample of zoo-housed apes was tested. Whether the results would generalize to other ape populations remains unclear especially given that the housing conditions of the zoo-housed orang-utans do not closely match the socioecology of wild populations. Behavioural differences between wild and zoo-housed orang-utans have been documented in the literature (Forss et al., 2015; Fröhlich et al., 2024; Laumer et al., 2025; Van Schaik et al., 2016), for example indicating that the nonvocal communicative repertoire of orang-utan immatures directed at conspecifics other than their mothers is larger in zoo settings than in the wild (Fröhlich et al., 2024) and that zoo-housed orang-utans are more exploratory and innovative than wild ones (Van Schaik et al., 2016). Second, the effect of relationship quality and kinship (e.g. mother–offspring dyads and bonding partners) or sex could not be tested because of the limited sample size. However, differences across pairs were accounted for by adding dyad as a random effect. Our orang-utan sample only included one (juvenile) male. Previous experimental research with zoo-housed orang-utans showed that juvenile male orang-utans can successfully cooperate with each other in problem-solving tasks (Chalmeau et al., 1997). In our study, the male juvenile orang-utan passed the tool more often to his mother (19% of trials) than the female juvenile orang-utan to her mother (2% of trials) when there was an incentive to do so. However, we cannot generalize from these individual performances. Regarding kinship, the mother–offspring dyads did not stand out, and they were well within the range of nonkin dyads with regard to tool-passing rates in chimpanzees and orang-utans. Finally, the prior experience of orang-utans and chimpanzees with the cooperative problem-solving apparatus differed to some extent. The dyadic training that the chimpanzees underwent in experiment 2 served to ensure that they were competent in transferring the tool at least when they did not have an individual foraging alternative prior to the test phase similar to orang-utans. Crucially, neither of the groups had experience with a version of this paradigm in which the partner could use the tool for an individual foraging alternative.

Orang-utans and chimpanzees cooperated with conspecifics at similar rates. Both species maximized their outcomes by taking their own and partly others' incentives into consideration. Previous studies reported that bonobos and chimpanzees performed similarly in certain cooperative problem-solving and coordination tasks (Kaiser et al., 2012; Sánchez-Amaro et al., 2017), at least when the spoils could not be monopolized (Hare et al., 2007). Thus, tasks involving physical separation or rewards that cannot be easily monopolized (both features of the current tool-passing task) might not be ideal to examine cooperative decision-making that is specific to highly gregarious species. Cofeeding tolerance (Hare et al., 2007) and sensitivity to others' communication may be more distinctive features of gregarious species than their strategic decision-making based on their own and others' payoffs. However, the observed similarities in performance may result partly also from similar social housing conditions in captivity. Future research should examine whether different housing conditions (e.g. in sanctuaries) affect the cooperation strategies in orang-utans and chimpanzees. Finally, potential species differences were also identified in this study: while chimpanzees were more susceptible to communicative signals, orang-utans attempted more often to manipulate others by passing the tool high above their heads. Therefore, communication might play a more important role to elicit cooperation in chimpanzees than in orang-utans.

Author Contributions

Christoph J. Völter: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elisa Felsche:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Josep Call:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Federico Rossano:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Data Availability

The data sets supporting this article have been uploaded as part of the supplementary material.

Declaration of Interest

All authors declare that they have no conflicts of interest to disclose.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123512.

References

Amici, F., Visalberghi, E., & Call, J. (2014). Lack of prosociality in great apes, capuchin monkeys and spider monkeys: Convergent evidence from two different food distribution tasks. *Proceedings of the Royal Society B: Biological Sciences, 281*(1793), Article 20141699. https://doi.org/10.1098/rspb.2014.1699

ASAB Ethical Committee/ABS Animal Care Committee. (2025). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Animal Behaviour, 219*, Article 123065. https://doi.org/10.1016/S0003-3472(24)00376-2

Baayen, R. H. (2008). Analyzing linguistic data: A practical introduction to statistics using R. In *Analyzing linguistic data: A practical introduction to statistics using R*. https://doi.org/10.1017/CBO9780511801686

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., & Eigen, C. (2016). Package 'lme4'. In *Comprehensive R archive network (CRAN)*.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology, 78*(4), 547–573. https://doi.org/10.1002/ajpa.1330780410

Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proceedings of the Royal Society B: Biological Sciences, 273*(1605), 3123–3128.

Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 71*(2), 175–181. https://doi.org/10.1002/ajp.20639

Brosnan, S. F., Flemming, T., Talbot, C. F., Mayo, L., & Stoinski, T. (2011). Orangutans (*Pongo pygmaeus*) do not form expectations based on their partner's outcomes. *Folia Primatologica, 82*(1), 56–70. https://doi.org/10.1159/000328142

Brosnan, S. F., Schiff, H. C., & De Waal, F. B. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 272*(1560), 253–258.

Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010). Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal Behaviour, 79*(6), 1229–1237.

Bueno-Guerra, N., Völter, C. J., de las Heras, Á., Colell, M., & Call, J. (2019). Bargaining in chimpanzees (*Pan troglodytes*): The effect of cost, amount of gift, reciprocity, and communication. *Journal of Comparative Psychology, 133*(4), 542–550.

Bullinger, A. F., Wyman, E., Melis, A. P., & Tomasello, M. (2011). Coordination of chimpanzees (*Pan troglodytes*) in a stag hunt game. *International Journal of Primatology, 32*(6), 1296–1310. https://doi.org/10.1007/s10764-011-9546-3

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology, 17*(15), 1345–1348. https://doi.org/10.1016/j.cub.2007.06.069

Chalmeau, R., Lardeux, K., Brandibas, P., & Gallo, A. (1997). Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 18*(1), 23–32. https://doi.org/10.1023/a:1026337006136

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C., Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances, 3*(11), Article e1701742. https://doi.org/10.1126/sciadv.1701742

Delgado Jr, R. A., & Van Schaik, C. P. (2000). The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 9*(5), 201–218. https://doi.org/10.1002/1520-6505(2000)9:5<201::aid-evan2>3.3.co;2-p

Dobson, A. (2002). *An introduction to generalized linear models* (2nd ed.). Boca Raton: Chapman & Hall/CRC Press. https://doi.org/10.1201/9781420057683

Duguid, S., Wyman, E., Bullinger, A. F., Herfurth-Majstorovic, K., & Tomasello, M. (2014). Coordination strategies of chimpanzees and human children in a stag hunt game. *Proceedings of the Royal Society B: Biological Sciences, 281*(1796). https://doi.org/10.1098/rspb.2014.1973

Engelmann, J. M., Clift, J. B., Herrmann, E., & Tomasello, M. (2017). Social disappointment explains chimpanzees' behaviour in the inequity aversion task. *Proceedings of the Royal Society B: Biological Sciences, 284*(1861), Article 20171502. https://doi.org/10.1098/rspb.2017.1502

European Association of Zoos and Aquaria. (2024). *EAZA Standards for Welfare, Accommodation and Management of Animals in Zoos and Aquariums*.

Field, A. (2005). Discovering statistics using SPSS (2nd ed.). *Journal of Advanced Nursing*. https://doi.org/10.1111/j.1365-2648.2007.04270_1.x

Forss, S. I. F., Schuppli, C., Haiden, D., Zweifel, N., & Van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology, 77*(10), 1109–1121. https://doi.org/10.1002/ajp.22445

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*, 47–55. https://doi.org/10.1007/s00265-010-1038-5

Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* (2nd ed.). Thousand Oaks CA: Sage (Sage).

Fröhlich, M., Kunz, J., Fryns, C., Falkner, S., Rukmana, E., Schuppli, M., Knief, U., Utami Atmoko, S. S., Schuppli, C., & Van Noordwijk, M. A. (2020). Social interactions and interaction partners in infant orang-utans of two wild populations. *Animal Behaviour, 166*, 183–191. https://doi.org/10.1016/j.anbehav.2020.06.008

Fröhlich, M., Van Noordwijk, M. A., Mitra Setia, T., Van Schaik, C. P., & Knief, U. (2024). Wild and captive immature orangutans differ in their non-vocal communication with others, but not with their mothers. *Behavioral Ecology and Sociobiology, 78*(1), 12. https://doi.org/10.1007/s00265-023-03426-3

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour, 71*(4), 953–963. https://doi.org/10.1016/j.anbehav.2005.09.009

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology, 20*(5), R230–R231. https://doi.org/10.1016/j.cub.2009.12.038

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619–623. https://doi.org/10.1016/j.cub.2007.02.040

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2014). Social comparison mediates chimpanzees' responses to loss, not frustration. *Animal Cognition, 17*(6), 1303–1311.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences, 108*(33), 13847–13851. https://doi.org/10.1073/pnas.1111088108

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology, 115*(4), 337–343. https://doi.org/10.1037/0735-7036.115.4.337

Jaeggi, A. V., Van Noordwijk, M. A., & Van Schaik, C. P. (2008). Begging for information: Mother–offspring food sharing among wild Bornean orangutans. *American Journal of Primatology, 70*(6), 533–541. https://doi.org/10.1002/ajp.20525

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science, 318*(5847), 107–109. https://doi.org/10.1126/science.1145850

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 273*(1589), 1013–1021. https://doi.org/10.1098/rspb.2005.3417

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour, 99*, 61–71. https://doi.org/10.1016/j.anbehav.2014.10.018

Kaiser, I., Jensen, K., Call, J., & Tomasello, M. (2012). Theft in an ultimatum game: Chimpanzees and bonobos are insensitive to unfairness. *Biology Letters, 8*(6), 942–945. https://doi.org/10.1098/rsbl.2012.0519

Kim, Y., Martinez, L., Choe, J. C., Lee, D.-J., & Tomonaga, M. (2015). Orangutans (*Pongo* spp.) do not spontaneously share benefits with familiar conspecifics in a choice paradigm. *Primates, 56*(2), 193–200. https://doi.org/10.1007/s10329-015-0460-8

Krupenye, C., Tan, J., & Hare, B. (2018). Bonobos voluntarily hand food to others but not toys or tools. *Proceedings of the Royal Society B: Biological Sciences, 285*(1886), Article 20181536. https://doi.org/10.1098/rspb.2018.1536

Lameira, A. R., & Call, J. (2020). Understanding language evolution: Beyond *pan*-centrism. *BioEssays, 42*(3), Article 1900102. https://doi.org/10.1002/bies.201900102

Laumer, I. B., Kansal, S., Van Cauwenberghe, A., Rahmaeti, T., Setia, T. M., Mundry, R., Haun, D., & Schuppli, C. (2025). Wild and zoo-housed orangutans differ in how they explore objects. *Scientific Reports, 15*(1), Article 14853. https://doi.org/10.1038/s41598-025-97926-z

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development, 76*(1), 291–306. https://doi.org/10.1111/j.1467-8624.2005.00845.x

Liebal, K., & Rossano, F. (2017). The give and take of food sharing in Sumatran orangutans, Pongo abelii, and chimpanzees, Pan troglodytes. *Animal Behaviour, 133*, 91–100. https://doi.org/10.1016/j.anbehav.2017.09.006

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd ed.). Chapman & Hall.

Melis, A. P., Hare, B., & Tomasello, M. (2006). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2005.09.018

Melis, A. P., & Rossano, F. (2022). When and how do non-human great apes communicate to support cooperation? *Philosophical Transactions of the Royal Society B: Biological Sciences, 377*(1859), Article 20210109. https://doi.org/10.1098/rstb.2021.0109

Melis, A. P., & Tomasello, M. (2013). Chimpanzees' (*Pan troglodytes*) strategic helping in a collaborative task. *Biology Letters, 9*(2), Article 20130009. https://doi.org/10.1098/rsbl.2013.0009

Melis, A. P., & Tomasello, M. (2019). Chimpanzees (*Pan troglodytes*) coordinate by communicating in a collaborative problem-solving task. *Proceedings of the Royal Society B, 286*(1901), Article 20190408. https://doi.org/10.1098/rspb.2019.0408

Melis, A. P., Warneken, F., Jensen, K., Schneider, A.-C., Call, J., & Tomasello, M. (2010). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences, 278*(1710), 1405–1413. https://doi.org/10.1098/rspb.2010.1735

Oosterbeek, H., Sloof, R., & Van De Kuilen, G. (2004). Cultural differences in ultimatum game experiments: Evidence from a meta-analysis. *Experimental Economics, 7*(2), 171–188. https://doi.org/10.1023/b:exec.0000026978.14316.74

Pelé, M., Dufour, V., Thierry, B., & Call, J. (2009). Token transfers among great apes (*Gorilla gorilla, Pongo pygmaeus, Pan paniscus*, and *Pan troglodytes*): Species differences, gestural requests, and reciprocal exchange. *Journal of Comparative Psychology, 123*(4), 375–384. https://doi.org/10.1037/a0017253

R Development Core Team. (2018). *R: A language and environment for statistical computing*. R foundation for statistical computing. https://doi.org/10.1017/CBO9781107415324.004

Ritov, O., Völter, C. J., Raihani, N. J., & Engelmann, J. M. (2024). No evidence for inequity aversion in non-human animals: A meta-analysis of accept/reject paradigms. *Proceedings of the Royal Society B: Biological Sciences, 291*(2035), Article 20241452. https://doi.org/10.1098/rspb.2024.1452

Rossano, F., & Liebal, K. (2014). "Requests" and "offers" in orangutans and human infants. In *Requesting in social interaction* (pp. 335–364). John Benjamins Publishing Company. https://doi.org/10.1075/slsi.26.13ros.

Sánchez-Amaro, A., Duguid, S., Call, J., & Tomasello, M. (2017). Chimpanzees, bonobos and children successfully coordinate in conflict situations. *Proceedings of the Royal Society B: Biological Sciences, 284*(1856), Article 20170259. https://doi.org/10.1098/rspb.2017.0259

Sánchez-Amaro, A., Peretó, M., & Call, J. (2016). Differences in between-reinforcer value modulate the selective-value effect in great apes (*Pan troglodytes, P. Paniscus, Gorilla gorilla, Pongo abelii*). *Journal of Comparative Psychology, 130*(1), 1–12. https://doi.org/10.1037/com0000014

Samuni, L., Preis, A., Deschner, T., Crockford, C., & Wittig, R. M. (2018). Reward of labor coordination and hunting success in wild chimpanzees. *Communications Biology, 1*(1), 138. https://doi.org/10.1038/s42003-018-0142-3

Sato, Y., & Tomonaga, M. (2010). WAZA (World Association of Zoos and Aquariums) Ethical Guidelines for the conduct of research on animals by zoos and aquariums. *Japanese Journal of Animal Psychology, 60*(2), 139–146. https://doi.org/10.2502/janip.60.2.4

Schmelz, M., Grueneisen, S., Kabalak, A., Jost, J., & Tomasello, M. (2017). Chimpanzees return favors at a personal cost. *Proceedings of the National Academy of Sciences, 114*(28), 7462–7467. https://doi.org/10.1073/pnas.1700351114

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaro, J., & Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature, 437*(7063), 1357–1359. https://doi.org/10.1038/nature04243

Skyrms, B. (2004). *The stag hunt and the evolution of social structure*. Cambridge University Press.

Tan, J., & Hare, B. (2013). Bonobos share with strangers. *PLoS One, 8*(1), Article e51922. https://doi.org/10.1371/journal.pone.0051922

Tomasello, M., Melis, A. P., Tennie, C., Wyman, E., & Herrmann, E. (2012). Two key steps in the evolution of human cooperation: The interdependence hypothesis. *Current Anthropology, 53*(6), 673–692. https://doi.org/10.1086/668207

Völter, C. J., Rossano, F., & Call, J. (2015). From exploitation to cooperation: Social tool use in orang-utan mother-offspring dyads. *Animal Behaviour, 100*, 126–134. https://doi.org/10.1016/j.anbehav.2014.11.025

Völter, C. J., Rossano, F., & Call, J. (2017). Social manipulation in nonhuman primates: Cognitive and motivational determinants. *Neuroscience & Biobehavioral Reviews, 82*, 76–94. https://doi.org/10.1016/j.neubiorev.2016.09.008

Van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in Orangutans. *Primates, 40*(1), 69–86. https://doi.org/10.1007/BF02557703

Van Schaik, C. P., Burkart, J., Damerius, L., Forss, S. I. F., Koops, K., Van Noordwijk, M. A., & Schuppli, C. (2016). The reluctant innovator: Orangutans and the phylogeny of creativity. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1690), Article 20150183. https://doi.org/10.1098/rstb.2015.0183

Voinov, P. V., Call, J., Knoblich, G., Oshkina, M., & Allritz, M. (2020). Chimpanzee coordination and potential communication in a two-touchscreen turn-taking game. *Scientific Reports, 10*(1), 3400. https://doi.org/10.1038/s41598-020-60307-9

Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., Schapiro, S. J., & Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour, 75*(5), 1757–1770. https://doi.org/10.1016/j.anbehav.2007.09.036

Watts, D. P. (2002). Reciprocity and Interchange in the social relationships of wild male chimpanzees. *Behaviour, 139*(2/3), 343–370. https://doi.org/10.1163/156853902760102708. JSTOR.

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour, 138*(3), 299–327. https://doi.org/10.1163/15685390152032488

Weatherall's Working Group. (2006). *The use of non-human primates in research. A working group report chaired by Sir David Weatherall FRS FMedSci*. London: Sir David Weatherall's Working Group, 2006.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *PLoS One*. https://doi.org/10.1371/journal.pone.0007416

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences, 109*(9), 3588–3592. https://doi.org/10.1073/pnas.1108517109

Yamamoto, S., & Tanaka, M. (2010). The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Animal Behaviour, 79*(3), 595–602. https://doi.org/10.1016/j.anbehav.2009.11.034