**From exploitation to cooperation: Social tool-use in**

**orang-utan mother-offspring dyads**

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27     Social manipulation represents an important aspect of human social interactions, including

28     cooperative ones. Yet, little is known about social manipulation of conspecifics in nonhuman

29     great apes. We investigated how orang-utan (*Pongo abelii*) mothers used their offspring as a

30     means to access food in competitive and cooperative test situations. In the competitive

31     situations, only the offspring could retrieve high-value food rewards. Here, orang-utan

32     mothers often stole the food from their offspring and even coerced them into retrieving it to

33     begin with, by moving the offspring to the test site, guiding their arms and bodies towards the

34     food, and even re-orienting their hands so that they would grab the food. However, modifying

35     the task constraints so that mothers were now required to cooperate with their offspring to

36     obtain the food changed the mothers' behaviour completely. Suddenly, mothers cooperated

37     with their offspring by handing them tools that only their offspring could use to activate a

38     mechanism delivering food for both of them. We conclude that orang-utans, like humans, are

39     able to flexibly use conspecifics as a social tool and that this kind of social tool-use supports

40     their ability to cooperate.

41

44   In recent years, the psychological processes underlying cooperation have received

45   considerable research attention from a comparative perspective. Experimental studies have

46   shown that several group-living primate species including chimpanzees, *Pan troglodytes*

47   (Chalmeau, 1994; Crawford, 1937; Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006a,

48   2006b; Melis & Tomasello, 2013), bonobos, *Pan paniscus* (Hare, Melis, Woods, Hastings, &

49   Wrangham, 2007), capuchin monkeys, *Sapajus apella* (Brosnan, Freeman, & De Waal, 2006;

50   Chalmeau, Visalberghi, & Gallo, 1997; de Waal & Berger, 2000; de Waal & Davis, 2003;

51   Hattori, Kuroshima, & Fujita, 2005; Mendres & de Waal, 2000; Visalberghi, Quarantotti, &

52   Tranchida, 2000), and cottontop tamarins, *Saguinus oedipus* (Cronin, Kurian, & Snowdon,

53   2005; Cronin & Snowdon, 2008) are able to coordinate their actions flexibly in cooperative

54   problem-solving tasks. For instance, chimpanzees can coordinate with their partners by either

55   carrying out identical (Chalmeau, 1994; Crawford, 1937; Hirata & Fuwa, 2007; Melis et al.,

56   2006a, 2006b) or complementary actions (Melis & Tomasello, 2013) to achieve their

57   objectives.

58   Temporal coordination is often crucial and chimpanzees can wait until their partners are

59   ready to jointly engage in the task (Hirata & Fuwa, 2007). Furthermore, chimpanzees know

60   who the best cooperators are and actively select them to work together (Melis et al., 2006a).

61   However, given a choice between working with others and working alone, chimpanzees

62   prefer the latter (Bullinger, Burkart, Melis, & Tomasello, 2013; Bullinger, Melis, &

63   Tomasello, 2011; Melis et al., 2006b; Rekers, Haun, & Tomasello, 2011). Also, although

64   some studies found that chimpanzees may help others even if they do not directly benefit

65   (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto, Humle,

66   & Tanaka, 2009, 2012), other studies did not find such prosocial tendencies (Jensen, Hare,

67   Call, & Tomasello, 2006), and most studies reporting sustained cooperation elicited it in

68   situations in which both individuals would benefit (mutual cooperation). It has therefore been

69 suggested that chimpanzees conceive their cooperators as social tools and that they are - in

70 contrast to humans - not intrinsically motivated to cooperate (Bullinger et al., 2011;

71 Warneken, Gräfenhain, & Tomasello, 2012).

72 The considerable research effort devoted to investigate the motivational basis of cooperation

73 contrasts with how little is known about how individuals manipulate others as tools. We

74 define social tool-use as the physical and psychological manipulations of animate beings

75 towards some goal. Social tool-use has an instrumental and a motivational dimension. The

76 motivational dimension involves the motives (self- or other-regarding) underlying those

77 manipulations whereas the instrumental dimension involves the actual means-end

78 manipulations of animate beings. We can subdivide the instrumental dimension of social

79 tool-use into four levels depending on the degree of direct physical influence that the tool-

80 user exerts over the social tool. Level 1 represents the highest degree of physical influence

81 since it involves the physical manipulation of others' bodies analogous to the manipulation of

82 inanimate objects. Here, the social tool is treated as an object (not an agent) and the tool-user

83 completely controls it (e.g. pulling the arm of a conspecific to access the food that she is

84 holding in her hand). Level 2 combines the physical control of the social tool with the

85 opportunistic exploitation of self-initiated and -controlled actions by the social tool that are

86 not under direct control of the tool-user (e.g., guiding the arm of the conspecific toward a

87 target object and pulling it back but only after the social tool has grabbed the target object).

88 Level 3 relies entirely on the social tool's self-initiated and -controlled actions and involves

89 no direct physical control by the tool-user. Here, the tool-user treats the social tool as a self-

90 propelled agent (e.g. passing a tool over to the social-tool who will then act independently of

91 the tool-user but in line with the goals of the latter). This level of tool-use depends on the

92 social tool's willingness to cooperate (either because of their aligned goals or her prosocial

93 tendencies). In the cooperation literature, social tool-use is commonly used in this latter sense

94    (level 3). Finally, level 4 represents the lowest level of direct physical influence on the social

95    tool and involves communication and the psychological effects derived from it (manipulating

96    the social tool by communicating with it without any direct physical interaction; e.g. Bard,

97    1990). In the current study, we will focus on level 1 and 2 (coercive) and level 3

98    (cooperative) instances of social tool-use.

99    Clear-cut cases of social tool-use involve physical manipulations of the tool (i.e., level 1 and

100    2). For this type of social tool-use to occur (especially when it only results in food for the

101    tool-user), there has to be a power differential between partners. However, power differential

102    is often associated with low social tolerance, which has been identified as a major factor

103    limiting cooperation in chimpanzees (Melis et al., 2006b), macaques (Petit, Desportes, &

104    Thierry, 1992), and capuchin monkeys (Brosnan et al., 2006; Chalmeau, Visalberghi, et al.,

105    1997; de Waal & Davis, 2003). It is therefore not surprising that direct evidence for goal-

106    directed and selective manipulations of others as if they were tools has been rarely

107    documented in cooperative problem-solving tasks. If the power differential between partners

108    is large, social tolerance is low and conversely, if tolerance is high, the power differential

109    may not be large enough to create the conditions for social tool-use to appear. There are some

110    exceptions, however. In an instrumental cooperation task with keas, *Nestor notabilis,* in

111    which one kea needed to operate a lever so that another conspecific could retrieve food from

112    a box, three dominant individuals aggressively approached their subordinate co-operators

113    until the subordinates would push down the lever (Tebbich, Taborsky, & Winkler, 1996).

114    Thus, dominant individuals were enforcing cooperation by means of social manipulations.

115    There is some evidence for social tool-use in primates. In a tool-use task that required

116    throwing stones into a pipe to retrieve a food reward, one Japanese macaque, *Macaca*

117    *fuscata,* repeatedly used her infants to retrieve the food by actively pushing them into the pipe

118    and pulling them back as soon as they had grabbed the food (Tokida, Tanaka, Takefushi, &

5

Hagiwara, 1994). When this kind of social tool-use was unsuccessful, the female macaque

used a stick or a stone as tool instead, suggesting that she considered her infants as a tool in

this problem-solving situation. In another cooperation study, a pair of subadult male orang-

utans, *P. pygmaeus,* simultaneously pulled a handle to retrieve food (Chalmeau, Lardeux,

Brandibas, & Gallo, 1997). Interestingly, in some instances one of the two individuals pushed

the other orang-utan towards one of the handles, thereby, soliciting cooperation – something

suggestive of social tool use. Moreover, two adult orang-utans, *P. abelii,* have been found to

exchange tokens reciprocally when each individual possessed only tokens that were useless

for themselves but that the other individual could exchange for food (Dufour, Pelé, Neumann,

Thierry, & Call, 2009). In fact, orang-utans were much more likely to donate tokens to

conspecifics, which the recipient could exchange for food with the experimenter, than

chimpanzees, gorillas, and bonobos (Pelé, Dufour, Thierry, & Call, 2009).

Thus, orang-utans seem to be a promising species to explore various levels of social tool-use.

Mother-offspring dyads in particular might offer the ideal scenario (as suggested by Tokida et

al. 1994) because they combine a marked power differential with high levels of tolerance

between partners. Mothers' physical strength allows them to steal food resources from their

offspring at very low direct costs as they do not have to fear aggressive retribution (which

might be the case amongst adults). Moreover, mothers show high levels of tolerance towards

their offspring, whose survival (including obtaining food) depend on their mothers for an

extended period of time (van Noordwijk & van Schaik, 2005). On the other hand, the balance

of power between mother and offspring may be shifted by changing the experimental setup.

In particular, creating a situation in which mothers have no direct physical control over their

offspring (level 3 social tool-use) may transform the mother's social tool-use from an

exploitative to a cooperative activity.

143 The aim of the current study was to investigate whether and how three Sumatran orang-utan

144 mothers, *P. abelii,* manipulated their dependent offspring as social tools to achieve their

145 goals. We varied the extent to which mothers could physically control their offspring's

146 actions across different experimental situations. We were interested in how flexibly mothers

147 would adjust their manipulations to changing test situations and task constraints. Therefore,

148 we provided the offspring with privileged access to high-value food (competitive situations)

149 or with the exclusive opportunity to activate a mechanism delivering food either to both

150 mother and offspring or only to the offspring (cooperative situation). We examined mothers'

151 response towards their offspring across these situations. In experiment 1, we investigated

152 whether mothers stole high-quality food from their offspring when only the offspring was

153 able to reach it. Crucially, we investigated whether they would manipulate their offspring

154 before the offspring had retrieved the food, to accelerate this process (level 1 and 2 social

155 tool-use). In experiment 2 and 3, we examined whether mothers would also manipulate their

156 offspring to obtain an out-of-reach stick tool that mothers, in turn, could use to retrieve a

157 high-value reward. Finally, in experiment 4, we presented a cooperative situation in which

158 mothers had initial control over the stick tool but this time only infants could use it to operate

159 the apparatus and obtain the food rewards. Thus, mothers could only retrieve the food by

160 giving the tool to their offspring so that the offspring could use it (level 3 social tool-use).

161 EXPERIMENT 1

162 *Methods*

163 *Subjects*

164 Three orang-utan mother-offspring dyads, *P. abelii,* participated in this study. All orang-utans

165 were mother-reared. Two of the juveniles were males. The age of the juveniles ranged

166 between 3 years, 7 months and 4 years. The orang-utans were housed at the Wolfgang Köhler

167    Research Centre, Leipzig Zoo (Leipzig, Germany). The study complied with the European

168    and World Associations of Zoos and Aquariums (EAZA and WAZA) Ethical Guidelines and

169    was approved by the joint ethical committee of the MPI-EVA and Leipzig Zoo.

170    *Procedure and design*

171    We presented the orang-utan mother-offspring dyads with two different situations, in which

172    juveniles got privileged access to the food. In the first situation, we used a sliding platform

173    that was fixed perpendicularly to a metal frame of a transparent Plexiglas glass panel

174    separating the apes and the experimenter (E). This panel contained three horizontally aligned,

175    circular holes (diameter 6.0 cm) whose small size allowed only juveniles to reach through.

176    We attached a tray on the platform outside of the Plexiglas panel and baited the tray with six

177    grapes (platform situation, see Fig. 1*a*). The tray was out of reach of the mothers but not of

178    the juveniles as the juveniles could pass their arms through the holes in the panel. If

179    necessary, we adjusted the distance between the tray holding the grapes and the Plexiglas

180    panel according to the arm length of the juveniles. After the juveniles had retrieved all six

181    grapes the tray was re-baited for a total of twelve grapes per session. The juveniles retrieved

182    the grapes one by one, i.e. the retrieval of each grape corresponded to one arm insertion.

183    Therefore, each retrieved reward was treated as a separate event. Each mother-offspring dyad

184    received four sessions for a total of 48 events per mother-offspring dyad.

185    In the second test situation, E placed a food reward (a monkey chow pellet) in the testing

186    compartment adjacent to the one where the mother-offspring dyad was located. The two

187    cages were connected by a sliding door that was closed during baiting. The food pellet was

188    placed 120 cm away from the sliding door so that the mother's arm was not long enough to

189    reach the food when the sliding door was opened. Then the sliding door connecting the two

190    compartments was partly opened (approximately 20-30 cm wide) so that only the juvenile

191  (but not the mother) could slip through (door situation, see Fig. 1*c*). Each dyad received two

192  trials per session and 4 sessions in total. Because for one mother-offspring dyad (Pini and

193  Batak) the juvenile repeatedly resisted his mother's attempts to move him to the room with

194  the food reward (even though Pini moved Batak to the half-opened door in all 4 sessions and

195  tried to push him toward the food in 3 of 4 sessions) we excluded the data of this dyad in the

196  door situation. A human observer was present at all times, to ensure that no harm could be

197  inflicted on the juveniles.

198  *Scoring and analysis*

199  We videotaped all sessions and scored who retrieved the food/tool (first contact with the

200  food/tool), who inserted the tool, who ate the food, and whether the mother manipulated the

201  offspring's actions toward the reward before she could gain access to the food (see Table 1

202  for the behaviours that we coded as social tool-use). A second coder scored 20 % of all trials

203  to assess inter-observer reliability which was excellent (Cohen's kappa: reward eaten by

204  mother or juvenile: $K = 0.84$, $N = 39$, $P<0.001$; social tool-use: $K = 0.90$, $N = 41$, $P<0.001$).

205  *Results and Discussion*

206  We found that orang-utan mothers ate more than half of the rewards retrieved by their

207  juveniles (Mean ± SE: platform: $64.2 \pm 10.2$ %; door: $56.3 \pm 6.3$ %). In every event/trial

208  (100%) in which the mothers ate the reward, the mothers stole the reward from their

209  offspring. Sometimes this involved also removal of food from the juvenile's mouth, who

210  never voluntarily shared the food with their mothers. In $46.0 \pm 22.8$ % (platform, see Fig. 2*a*)

211  and $91.1 \pm 5.9$ % (door, see Fig. 2*b*) of events/trials in which the orang-utan mothers got the

212  reward, they manipulated their offspring's actions before their juveniles had obtained the out-

213  of-reach reward. In the platform situation, these social tool-use actions included recruiting the

214  juveniles (i.e. moving the juvenile actively to the platform, mostly by pulling from their arms

and legs), pushing their arms toward the food (i.e. pushing the hand of the juvenile through

the hole in the Plexiglas panel, sometimes involving squeezing the fingers to facilitate

pushing the hand through the hole and turning the arm of the juvenile so that the juvenile's

fingers touched the reward, see Fig. 1*b* and Supplementary Movie 1) or pulling the juvenile's

arm as soon as she grabbed the food. In the door situation, these actions involved recruiting

the juveniles (i.e. bringing the juvenile to the door), pushing them through the half-opened

door, holding the juveniles by their arm or leg while the juveniles reached for the food and

pulling them back as soon as they grabbed it (see Fig. 1*d* and Supplementary Movie 2). These

actions were usually combined in a sequence. In the remaining events/trials in which orang-

utan mothers ate the reward (platform: $54.0 \pm 22.8$ %; door: $10.0 \pm 10.0$ %), they waited until

the juvenile had retrieved it and then stole it.

In $91.1 \pm 5.9$ % (platform) and $73.3 \pm 6.7$ % (door) of the events/trials in which we observed

social tool-use, the orang-utan mothers ate the reward in the end. In the remaining

events/trials, the social tool-use was unsuccessful and the juveniles retrieved the food after

their mothers had left the platform or they retrieved and ate the reward in the adjacent cage

away from their mothers.

EXPERIMENT 2: SEQUENTIAL SOCIAL TOOL-USE

Having established in experiment 1 that the orang-utan mothers used their offspring as tools

to retrieve an out-of-reach reward, we next examined whether they would also use their

juveniles to retrieve an out-of-reach tool that, in turn, mothers could use to retrieve food.

Thus, the question was whether the orang-utan mothers would be able to sequentially use a

social tool to retrieve a physical (stick) tool. We presented the same orang-utan mother-

offspring dyads from experiment 1 with situations identical to what they experienced in

experiment 1 except that this time juveniles could retrieve a stick instead of grapes.

*Methods*

240 *Procedure and design*

241 At the beginning of the session, we fixed a tool-use apparatus (see Fig. 3) made of transparent

242 Plexiglas at the mesh of the cage. The apparatus consisted of a horizontal chute (length 25

243 cm, height x width 4 x 4 cm). At the end of this chute (out of reach of mother and juvenile)

244 there was a hole (diameter 7 cm) in the Plexiglas. Anything that fell into this hole would fall

245 on a ramp and roll toward the mesh. A food reward (e.g. grapes) was placed at the end of the

246 horizontal chute close to the hole. By inserting a stick tool (made of grey PVC, length x

247 height x width 25.0 x 3.5 x 3.5 cm), in this chute, the apes could push the reward into the hole

248 and thus bring the reward via the ramp within reach. The mothers had prior experience with a

249 similar apparatus that required the same type of tool-use.

250 In the beginning of each trial, E baited the apparatus with a grape (platform situation) / a

251 monkey chow pellet (door situation) in full view of the mother-offspring dyads. The tool was

252 then placed on the platform (platform situation) or in the adjacent room (door situation) out

253 of reach of the mother. The procedure was identical to experiment 1 in every other respect. In

254 the platform situation, the mother-offspring dyads received eight sessions with six trials each;

255 in the door situation, they received four sessions with two trials each.

256 *Results and Discussion*

257 The number of trials in which dyads retrieved the tools varied considerably across dyads,

258 possibly due to the juveniles differing interest in the tool (see Table 2). In particular, Suaq

259 rarely grabbed the tool even when his mother forced him to touch it with his fingers. In every

260 trial (100%) in which the mothers could get access to the tool, they used it right away to

261 obtain and eat the food reward from the apparatus. In all trials in which the juvenile retrieved

262    the tool, the mothers stole the tool from their offspring (i.e. there was no instance of the

263    juvenile giving the tool spontaneously to the mother). In $23.3 \pm 19.3$ % (platform) and 100%

264    $\pm 0$% (door) of these trials the mothers took action before the juvenile had retrieved the tool

265    in an identical manner to that observed in experiment 1, which included actions like

266    recruiting the juvenile and guiding the juveniles' arm toward the tool (platform situation) or

267    pushing the juvenile through the half-opened door, holding the juvenile by one limb, and

268    pulling the juveniles back as soon as they grabbed the tool (door situation). We observed

269    these actions usually in sequence and in this order. In the remaining trials of the platform

270    situation ($75.7 \pm 19.3$ %), the mothers waited until the juveniles had retrieved the tool on

271    their own and did not physically manipulate their offspring beforehand.

272    In $81.3 \pm 18.8$ % (platform) and $87.5 \pm 12.5$ % (door) of the trials, respectively, in which we

273    observed social tool-use, the orang-utan mothers obtained the tool (and ate the reward). In the

274    remaining trials, the social tool-use was unsuccessful and the juvenile did not retrieve the

275    tool.

276    These results indicate that in the platform situation, mothers preferred to wait until the

277    juvenile had retrieved the tool and took it away from her only then (except for Padana whose

278    offspring only rarely retrieved the tool voluntarily). In the door situation, mothers lost control

279    over their juvenile if they had not taken action before the juvenile entered the adjacent room.

280    For this reason, social tool-use was more important in the door situation than in the platform

281    situation. This might explain why we observed social tool-use more frequently in the door

282    situation as compared to the platform situation. Together, the results demonstrate that the

283    orang-utan mothers sequentially used their juveniles as tools to retrieve a stick tool, which

284    they in turn used to access the food reward.

285

286 EXPERIMENT 3: GOAL-DIRECTEDNESS OF SOCIAL TOOL-USE

287 Previous experiments established that the orang-utan mothers used their juveniles as tools to

288 retrieve out-of-reach rewards (experiment 1) and tools (experiment 2). Next, we examined the

289 goal-directedness of this behaviour by presenting the same three orang-utan mother-juvenile

290 dyads with a choice between a grape and the tool, a grape and a distractor, or the tool and a

291 distractor. The tool, in turn, could be used to retrieve a higher value reward (a dry food

292 pellet). The distractor had no food-related value. For the juveniles, only the reward had a

293 food-related value, for the mother, the tool had a higher value as they consistently preferred

294 pellets to grapes. We examined whether the mothers directed the juvenile's actions toward

295 the tool contrary to the juveniles' preference to reach directly for the grape.

296 *Methods*

297 *Procedure and design*

298 In the beginning of each trial, E baited the tool-use apparatus (see Fig. 3) with a monkey

299 chow pellet in full view of the mother-offspring dyads. Again, we used the two previously

300 established test settings.

301 In the platform situation, E placed two objects simultaneously on the platform outside the

302 enclosure (i.e. only accessible to the juvenile). E placed the objects in front of the right and

303 left hole of the Plexiglas panel, respectively. In the door situation, one item was placed in the

304 compartment to the left of the mother-juvenile dyad; the other one was placed in the

305 compartment to the right. Subsequently, both doors were opened simultaneously so that the

306 juvenile (but not the mother) could slip through it. The object pairs were either a distractor (a

307 wooden block, length x height x width 6 x 3 x 3 cm) and a grape, the distractor and the tool,

308  or a grape and the tool. The location of each object was counterbalanced across trials.

309  Preference tests confirmed that all three mothers preferred pellets over grapes.

310  In the platform situation, the mother-offspring dyads received eight sessions with six trials

311  each (each trial type was presented twice per session); in the door situation, there were eight

312  sessions with three trials each (each trial type was presented once per session). An important

313  difference between the two tasks was that in the platform situation the juveniles could

314  retrieve both objects in sequence, whereas in the door situation they could only access one of

315  the items since we closed the other door as soon as the juvenile had left the middle

316  compartment (where the mother was located).

317  *Analysis*

318  We used binomial tests and the Freeman–Halton extension of Fisher's exact test for 2 x 3

319  contingency tables (Freeman & Halton, 1951). All p-values reported here are exact and two-

320  tailed.

321  *Results and Discussion*

322  *Platform situation*

323  When food was on the platform, the juveniles retrieved the food first in most trials (food vs.

324  tool trials: 100%; food vs. distractor trials: $95.8 \pm 4.2$ %; see Table 3). When the juveniles

325  could choose between the distractor object and the tool, two of three juveniles had a

326  preference for the distractor ($79.2 \pm 8.3$ %). When the juveniles retrieved the food, the

327  mothers ate the reward in most of the trials $63.5 \pm 12.7$%. In every trial (100%) in which the

328  juveniles retrieved the tool, the mothers took the tool away from the juveniles and used it to

329  obtain and eat the food pellet from the apparatus.

Of the trials in which the mother obtained the food / tool at the end of the trial (mean number of trials ± SE: 40 ± 3), the mothers used their juveniles in 44.0 ± 21.3 % of trials as a social tool. In the remaining trials (66.0 ± 21.3 %), the mothers waited until the juvenile had retrieved the food / tool and took it away from the juvenile thereafter. Following social tool-use, the mothers obtained the food reward in 92.5 ± 2.5% of trials with food on the platform whereas they obtained the tool only in 27.3 ± 5.1% of trials with the tool on the platform. Mothers obtained the tool more often when the other object on the platform was the distractor (46.3 ± 1.9%) as compared to the food reward (8.3 ± 8.3%).

*Door situation*

When presented with the choice between the distractor and the tool / food, juveniles retrieved the food / tool more often than the distractor (see Table 4). When they retrieved the food, their mothers ate the reward only in one instance (5.6 ± 5.6 %). In contrast, in every trial (100%) in which the juveniles retrieved the tool the mothers took the tool away and used it to obtain the food pellets from the apparatus. The mothers ate the reward that they obtained from the apparatus in every trial (100%).

In every trial (100%) in which the mother ate the reward or obtained the tool, the mother manipulated the juvenile beforehand (Dokana-Tanah: 13 trials; Padana-Suaq: 6 trials). Crucially, we found a significant effect of social tool-use on their juveniles' first decision: juveniles only entered the room with the tool when they were forced by their mothers but went for the food without pressure from their mothers (Fisher's exact test: Dokana-Tanah: $P<0.01$; Padana-Suaq: $P<0.01$). Considering only trials in which mothers tried to manipulate their juveniles (Dokana-Tanah: 14 trials; Padana-Suaq: 9 trials), we found that the mothers obtained the tool in 93.8 ± 6.3% of trials with the tool.

353 The results of experiment 3 indicate that when forced to decide for one of two options (door

354 situation) the orang-utan mothers influenced the decision of their juvenile by pulling the

355 juvenile toward the room with the tool. When both objects could be retrieved within a given

356 trial (platform situation), for the most part the orang-utan mothers did not influence the first

357 decision of the juvenile (except for Padana whose offspring only rarely retrieved one of the

358 objects voluntarily). Together, these results suggest that the orang-utan mothers' social tool-

359 use was goal-directed and depended on their juveniles' willingness to obtain the food reward

360 or stick tool.

361 EXPERIMENT 4: SOCIAL TOOL-USE IN A COOPERATIVE SITUATION

362 In experiment 1-3, orang-utan mothers physically manipulated their offspring like a tool to

363 retrieve out-of-reach food rewards or stick tools. In experiment 4, we investigated whether

364 orang-utan's social-tool use would also extend to situations in which the mothers had no

365 direct physical control over their offspring (level 3 social tool-use). Thus, the question was

366 whether orang-utan mothers would also cooperate with their offspring as circumstances

367 demanded. More specifically, we examined whether orang-utan mothers would pass the stick

368 tool on to their offspring if this was required to retrieve the food.

369 *Methods*

370 *Procedure and design*

371 We mounted a slanted tube (length: 340 cm, diameter: 5cm) to the mesh outside the orang-

372 utan enclosure which connected two non-adjacent rooms of the enclosure (room 2 and 4 of

373 the enclosure, see Fig. 1*e*). We baited the tube by inserting uncooked, dried spaghetti

374 fragments (length 10-12cm) into the tube through drilled holes in the tube at two different

375 locations (in front of room 2 and 4). We put a grape and a monkey chow pellet on these

spaghetti fragments outside of the tube. When the tool was inserted in the tube in room 4, the

tool slid toward room 2 breaking the spaghetti fragments that, in turn, fell down together with

the attached grape and pellet. Underneath the tube, we mounted slanted trays (width x depth:

50 x 48 cm) to ensure that the falling rewards would roll toward the mesh of the enclosure.

These trays functioned to capture the fallen reward. Due to the inclination of these trays, the

reward then rolled towards the mesh of the enclosure. At that point the food reward would

become accessible to the apes. We manipulated whether mothers could move to room 4

(where the tool could be inserted, training phase) or whether only the offspring could go there

(experiment 4a: test phase) by adjusting the width of the opening between the rooms. In every

trial, mothers received the tool in room 2.

As initial training for the mothers, we baited either room 2 or room 4 with a grape and a

pellet and opened the doors between room 2 and 4 so that mothers could move between these

rooms. After the baiting of the apparatus, mothers received the tool in room 2. All three

mothers completed 4-5 sessions for a total of 24 trials (12 trials with room 2 baited and with

room 4 baited, respectively).

Like in the previous experiments, Batak did not enter another room without his mother; the

data of this mother-offspring dyad was therefore excluded from data analysis. In the test

phase, mother-offspring dyads were in room 2 and we baited the apparatus in front of room 2

and 4. We opened all sliding doors (between room 1 and 4) minimally (20 – 30 cm) so that

only the juveniles could freely move between rooms. Then mothers received the tool in room

2. We ran 12 trials per dyad.

After Suaq's initial failure to use the tool in the test phase, we presented him with three

training sessions in which he was in room 4 and his mother was in room 3. We baited the

tube for room 3 and room 4. Suaq received the tool next to the tube in room 4. After Suaq's

400    initial failure we allowed his mother to enter room 4 and to insert the tool (6 trials).

401    Thereafter, Suaq started to insert the tool in the apparatus. We ran another 12 trials to ensure

402    that Suaq would reliably insert the tool in the tube. After this additional training, we

403    presented Suaq and Padana again with the test phase.

404    Six months after this experiment, we presented the two dyads with a follow-up experiment

405    (experiment 4b) in which again only the juveniles could enter room 4 and we manipulated

406    whether both mother and juveniles were rewarded (as before, room 2 and 4 were baited) or

407    whether only the juveniles would receive a reward when they inserted the tool (room 4 baited

408    only). Again the tool was passed to the mother in room 2. We ran four sessions of six trials

409    each. In session 1 and 3 both rooms were baited; in session 2 and 4 only room 4 was baited.

410    *Scoring and analysis*

411    We scored the same variables as in experiment 1. Additionally, we coded the type of tool-

412    transfer between mother and offspring either as 'active' or 'passive'. We coded an active

413    transfer when mothers held the tool out towards the juvenile and allowed the juvenile to grab

414    it or when mothers slid the tool under the fencing across the floor of room 3 in the direction

415    of the juvenile. We coded a passive transfer when the tool was abandoned by the mother

416    (which happened only twice in the follow-up experiment when only room 4 was baited) or

417    when it was in the mother's possession and the juvenile took it out of her hands, feet, or lap

418    without resistance of the mother and without the mother holding the tool out toward the

419    juvenile. A second coder scored 100% of all trials of experiment 4a to assess inter-observer

420    reliability which was excellent (type of tool transfer: $K = 1.0$, $N = 24$, $P<0.001$; social tool-

421    use: $K = 0.90$, $N = 24$, $P<0.001$).

422    *Results and Discussion*

423    First, we established that mothers were able to operate the apparatus by themselves. All three

424    mothers quickly learnt to solve the task (Padana and Pini in session 1, Dokana in session 2)

425    by inserting the tool on their own and successfully completed 24 trials (12 trials with room 2

426    baited and room 4 baited, respectively). The juveniles could observe their mothers operating

427    the apparatus during this training phase and in some instances even retrieved some of the

428    food rewards after their mothers had inserted the tool (when room 2 was baited and mothers

429    needed some time to get back from room 4 to room 2).

430    For the test sessions (experiment 4a), we reduced the opening of the sliding doors so that only

431    the offspring but not their mothers could move between rooms 1 to 4. Then E passed the tool

432    to the mother. In the first trial of the first test session (room 2 and 4 baited), Padana pushed

433    her son Suaq to room 3 and also offered him the tool in room 3. However, Suaq never took

434    the tool to room 4 to insert it into the tube. Dokana did not actively pass the tool on to Tanah

435    in the first trial but she allowed Tanah to take it from her. After having obtained the tool,

436    Tanah went straight to room 4 and inserted the tool which released the food for both mother

437    and daughter. From this first trial onwards, Dokana actively passed the tool on to Tanah by

438    holding the tool out towards Tanah in room 3 or even sliding the tool across the floor of room

439    3 towards Tanah who was in room 4 (see Supplementary Movie 3).

440    Because Suaq did not use the tool after his mother had passed the tool on to him, we

441    conducted two additional training sessions with Suaq. After Suaq had learnt to insert the tool

442    reliably (12 trials in two sessions while Padana could watch her son inserting the tool into the

443    tube), we presented Padana and Suaq again with the initial test phase in which the mother

444    received the tool but only the juvenile could insert it in the tube. Suaq and Padana now

445    successfully completed 12 trials and in every trial with Padana actively passing the tool on to

446    Suaq (see Fig. 1*f*, Table 5, and Supplementary Movie 4).

447    In the test phase, we also observed in total 7 trials with social tool-use including mothers

448    moving their offspring to the door to room 3 and pushing them through the half opened door.

449    In every trial in which the juvenile was within mother's reach when E gave her the tool, she

450    actively moved the juvenile toward the door before passing it on to the juvenile. In two

451    instances, Padana pushed her son through the door and held his leg while she was offering the

452    tool. In one of those instances, Padana only released him after Suaq would take the tool (see

453    Supplementary Movie 5).

454    In the follow-up experiment (experiment 4b), we manipulated across the test sessions

455    whether only the juveniles were rewarded (room 4 baited) or both mothers and juveniles

456    (room 2 and 4 baited). When room 2 and 4 were baited mothers always transferred the tool

457    actively to their offspring and in some cases mothers manipulated their offspring by moving

458    them towards the door and pushing them through the opening towards room 4 (see Table 6).

459    When only the juveniles could receive a reward, mothers still passed the tool on to the

460    juvenile in the majority of trials. However, the frequency of active and passive tool transfers

461    differed significantly between the two baiting conditions at least for one of the two dyads

462    (Fisher's exact test: Dokana-Tanah: $P<0.05$; Padana-Suaq: $P=0.09$): when only the juvenile

463    was rewarded, mothers were more passive and often would simply allow their offspring to

464    grab the tool after some time. In one trial, Padana did not allow her son to take the tool at all

465    but passed the tool back to the experimenter. Social tool-use was also more frequent for one

466    of the two dyads in the room 2 and 4 baited condition (Fisher's exact test: Dokana - Tanah:

467    $P<0.05$). For the most part (except for three trials), Padana did not even have the opportunity

468    to manipulate her son physically as he stayed in room 3 or 4 (thus beyond his mother's reach)

469    when both got rewarded.

470

GENERAL DISCUSSION

In the current series of experiments, we systematically documented how orang-utan mothers manipulated their juvenile offspring as a social tool in a flexible and goal-directed manner to obtain a desired object and to activate a mechanism that would eventually deliver food to both of them. In experiments 2 and 3, mothers even used their offspring to retrieve an object that mothers (but not the offspring) preferred. Finally, we showed in experiment 4 that mothers spontaneously cooperated with their offspring by handing them a tool that the latter needed to activate a device that delivered food rewards for both mother and offspring. When only the offspring benefited from the insertion of the tool, mothers' motivation for cooperation declined even though mothers for the most part still continued to hand the tool over to the offspring (or at least allowed them to grab it).

Taken together, these findings show that orang-utans are able to manipulate conspecifics flexibly in order to achieve their goals. This ability can be assumed to support their (and possibly other primates') ability to cooperate. Although chimpanzees prefer to work alone rather than together in problem-solving tasks, they will choose to cooperate when the payoff of cooperative tasks exceeds that of individual tasks (Bullinger et al., 2013; Bullinger et al., 2011; Melis et al., 2006a; Rekers et al., 2011). However, cooperation collapses when the food reward is monopolizable by one individual (de Waal & Davis, 2003; Hare et al., 2007; Melis et al., 2006b) or requires individuals to reciprocate their partners actions over multiple trials (Yamamoto & Tanaka, 2009). Likewise, in the present study we found that orang-utan mothers shifted their strategy from stealing food and tools to donating tools to their offspring to maintain cooperation, presumably based on a self-regarding motivation.

Our results also document the limits of social tool-use and coercion. While the orang-utan mothers manipulated their offspring's actions, they could not coerce them into grabbing the

495     tool (experiment 2 and 3) or inserting the tool into the tube (experiment 4). And in fact,

496     mothers were less successful in retrieving the tool (preferred by mothers but not by the

497     offspring) as compared to the grapes when they manipulated their offspring. The offspring's

498     willingness to cooperate was therefore critical for mothers' success. It is quite likely that the

499     offspring's willingness to cooperate was driven by her own selfish interest in retrieving

500     rewards. However, mothers often passed the tool to their offspring even without obtaining a

501     direct benefit (experiment 4b). This result suggests that orang-utans, at least when there are

502     no costs to themselves, help their offspring in an instrumental task – a finding that has also

503     been reported in chimpanzees (Melis et al., 2011; Warneken et al., 2007; Yamamoto et al.,

504     2009, 2012). However, mothers' reinforcement history of passing the tool on to their

505     offspring (experiment 4a) might have increased their willingness to cooperate in the current

506     study even when there was no direct benefit for them. It is an open question whether orang-

507     utans would maintain cooperation solely based on other-regarding preferences or by

508     motivating their offspring with some delayed reciprocation (e.g., food sharing). Our results

509     show that orang-utan cooperation is supported by (and possibly grounded in) social

510     manipulative abilities but this does not preclude the existence of prosocial tendencies. The

511     extent to which orang-utans exhibit prosocial motivations to help others is not clear yet and

512     should be further explored by future research.

513     The cognitive processes underlying physical tool-use might form the basis of social tool use

514     (Byrne & Whiten, 1988). Orang-utan mothers in the current study physically manipulated

515     their offspring in a manner analogous to using a stick (corresponding to level 1 social tool-

516     use). Namely, we detected several important features characterizing physical tool-use in the

517     social realm including sequential tool-use (experiment 2 and 3), goal-directedness

518     (experiment 3), and a dissociation between a tool and its functions (i.e. using a tool for

519     multiple purposes, cf. experiment 1-3 vs. 4). However, the social tool-use observed in the

520   current study went beyond physical tool-use (and level 1 social tool-use) because mothers

521   treated their offspring as self-propelled agents. They expected them to execute certain actions

522   spontaneously (e.g., grabbing the food) that combined with their own manipulations (e.g.,

523   guiding their offspring arm) could potentially bring the food within their reach (level 2 social

524   tool-use). More importantly, they expected their offspring to complete a series of actions

525   (without any physical guidance, level 3 social tool-use) that included bringing the tool to the

526   correct location (beyond the mothers' immediate reach) and executing the required action to

527   release the reward.

528   It is worth noting that Padana started passing the tool on to Suaq already in the very first trial,

529   whereas Dokana started passing the tool on to her daughter after she saw Tanah solving the

530   task once (and continued to do so from the second trial onwards). While Dokana's

531   performance might be explained by one-trial reinforcement learning, Padana's spontaneous

532   performance cannot be reduced to reinforcement learning. Thus, social tool-use as

533   documented in the present study might originate from physical tool-use but it cannot merely

534   be reduced to a variant of physical tool-use. Key features that make social tool-use different

535   from its physical counterpart are the actions of the social tool that are not under direct control

536   of the tool user but that are nevertheless taken into account and even anticipated by the tool-

537   user. To what extent orang-utans and other great apes understand causal agency and use this

538   knowledge to manipulate others might be explored by future studies. An interesting question,

539   for example, would be whether orang-utan mothers take their offsprings' needs and

540   knowledge states into account when they pass on tools. There is already some evidence that

541   chimpanzees take the needs of others into account in a helping task by selectively passing on

542   tools that a conspecific needs to access food (Yamamoto et al., 2012).

543   In summary, the current series of behavioural experiments showed how orang-utan mothers

544   manipulated their offspring mostly according to selfish motives to obtain high-quality food.

545 They applied their social tool-use flexibly to achieve their goals. Depending on the

546 constraints of the task they switched from exploitation to cooperation to achieve their goals.

547 This type of social tool-use might form the evolutionary basis for more complex forms of

548 human cooperation possibly forged by the intervention of some forms of other-regarding

549 motives (Tomasello & Vaish, 2013). Future studies should be aimed at investigating whether

550 cooperation can also appear and be maintained in orang-utans based on other-regarding

551 motives or even some form of self-regarding motives satisfied by delayed reciprocation.

552

557

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653    Table 1

654    Definitions of social tool-use actions.

| Type | Level | Description |
|---|---|---|
| Pulling | 1 | Pulling the juvenile's limb as soon as she grabs the target object to bring it within the tool-user's reach. |
| Recruiting | 1 | Moving the juvenile to the apparatus by dragging, pushing, or carrying her after the reward had been made accessible to the juvenile. |
| Pushing | 1 | Pushing the juvenile through the half opened door towards the target object. |
| Holding | 2 | Holding the juvenile (located in the adjacent room) by one limb (to prevent her from escaping) until the juvenile grabs the target object. |
| Guiding | 2 | Moving the juvenile's hand and arm through the hole in the panel toward the food reward. |
| Active transfer | 3 | Passing the tool on to the juvenile by handing it out or by sliding it over the floor of room 3 towards the juvenile located in room 4. |

655    The level refers to the degree of direct physical control that the tool-user exerted over the

656    social tool (1: full control; 2: partial control; 3: no control).

657

658 Table 2

659 Individual performance in experiment 1 and 2.

| | Experiment 1 | | | | Experiment 2 | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Platform | | Door | | Platform | | Door | |
| | ME | ST | ME | ST | ME | ST | ME | ST |
| **Dokana - Tanah** | 21 / 48 | 2 / 48 | 5 / 8 | 5 / 8 | 48 / 48 | 4 / 48 | 8 / 8 | 8 / 8 |
| **Padana - Suaq** | 31 / 42 | 30 / 42 | 4 / 8 | 6 / 8 | 8 / 8 | 5 / 8 | 6 / 8 | 8 / 8 |
| **Pini - Batak** | 36 / 48 | 15 / 48 | - | - | 48 / 48 | 0 / 48 | - | - |

660 ME (mother eating): number of rewards eaten by the mothers and the total number of rewards

661 that were retrieved by the juveniles; ST (social tool-use): number of cases of social tool-use.

662 Padana and Suaq received fewer trials but the same number of sessions compared to the other

663 dyads in the platform situation of both experiments because Suaq stopped participating in

664 some sessions.

665

666     Table 3

667     Experiment 3: First choice of the orang-utan juveniles in the platform situation as function of

668     condition.

| Trial type | Distractor-Tool | | Food-Tool | | Food-Distractor | |
|---|---|---|---|---|---|---|
| Dyads (Mother – Juvenile) | Distractor | Tool | Food | Tool | Food | Distractor |
| Dokana - Tanah | 14** | 2 | 16*** | 0 | 16*** | 0 |
| Padana - Suaq | 5 | 3 | 15*** | 0 | 15*** | 0 |
| Pini - Batak | 14** | 2 | 16*** | 0 | 14** | 2 |

669     Binomial tests: **$P<0.01$; ***$P<0.001$

670

671    Table 4

672    Experiment 3: First choice of the orang-utan juveniles in the door situation as function of

673    condition.

| Trial type | Distractor-Tool | | Food-Tool | | Food-Distractor | |
|---|---|---|---|---|---|---|
| Dyads (Mother – Juvenile) | Distractor | Tool | Food | Tool | Food | Distractor |
| Dokana - Tanah | 1 | 7 | 3 | 5 | 6 | 2 |
| Padana - Suaq | 3 | 5 | 6 | 2 | 6 | 2 |

674

675    Table 5

676    Experiment 4a: Performance of the orang-utan mother-offspring dyads in cooperation task.

| Dyads (Mother - Juvenile) | Completed Trials | Active / Passive Tool Transfer | Social Tool-Use |
|---|---|---|---|
| Dokana - Tanah | 12 | 11 / 1 | 3 |
| Padana - Suaq | 12 | 12 / 0 | 4 |

677    Note: Suaq received two additional training sessions with the apparatus.

678

679    Table 6

680    Experiment 4b: Performance of the orang-utan mother-offspring dyads in the cooperation

681    task as a function of the reward distribution.

| Dyads (Mother - Juvenile) | Mother and juvenile rewarded | | Only juvenile rewarded | |
|---|---|---|---|---|
| | Active / Passive / No Tool Transfer | Social Tool-Use | Active / Passive / No Tool Transfer | Social Tool-Use |
| Dokana - Tanah | 12 / 0 / 0 | 5 | 7 / 5 /0 | 0 |
| Padana - Suaq | 12 / 0 / 0 | 1 | 8 / 3 / 1 | 0 |

682

683

684 <div align="center">Figure legends</div>

685 *Figure 1*. Illustrations and examples of the experimental set-ups used in this study. *a)*

686 illustration of the Platform situation (experiment 1), *b)* example of an orang-utan mother

687 guiding her juvenile's arm to obtain an out-of-reach reward, *c)* illustration of the Door

688 situation (experiment 1), *d)* example of orang-utan mother holding her juvenile's leg to pull it

689 back as soon as the juvenile grabbed the reward, *e)* illustration of the Tube situation

690 (experiment 4, room 2, 3, and 4 of the enclosure are depicted), and *f)* example of an orang-

691 utan mother giving the tool to her offspring in middle room (room 3) of the Tube situation.

692 *Figure 2*. Experiment 1: Percentage of events/trials in which the mother manipulated the

693 juvenile physically in a way reminiscent of tool-use before the juvenile had retrieved the

694 reward. *a)* Platform situation, *b)* Door situation.

695 *Figure 3*. Illustration of the tool-use apparatus used in experiment 2 and 3. The orang-utans

696 could access the apparatus from behind the mesh. In this illustration the tool is already

697 inserted in the horizontal chute. By pushing the tool further, the apes could move the reward

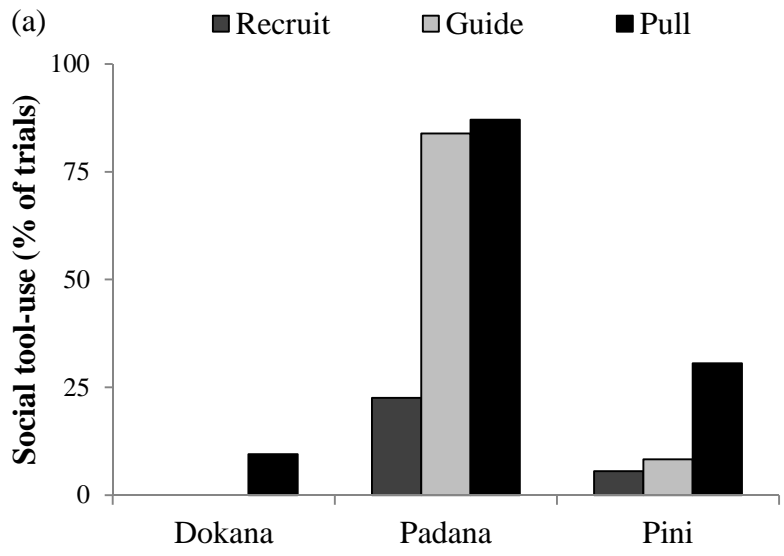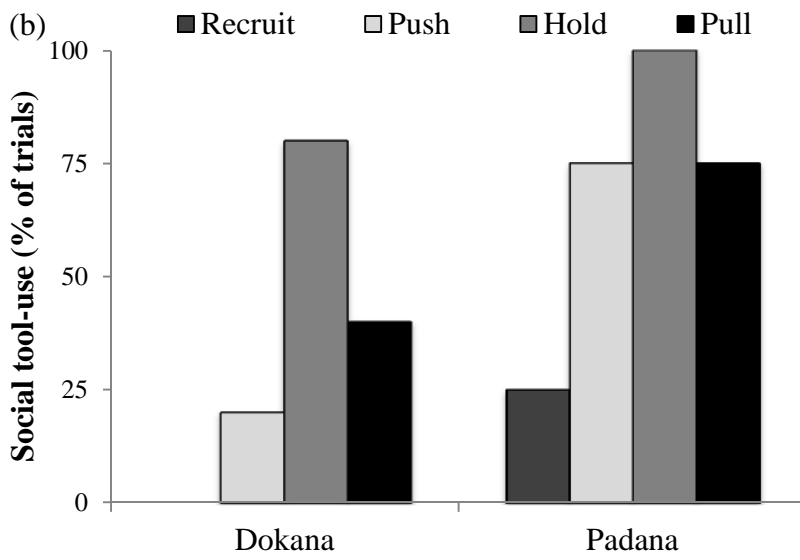698 into the hole and thus bring the reward via the ramp within reach.
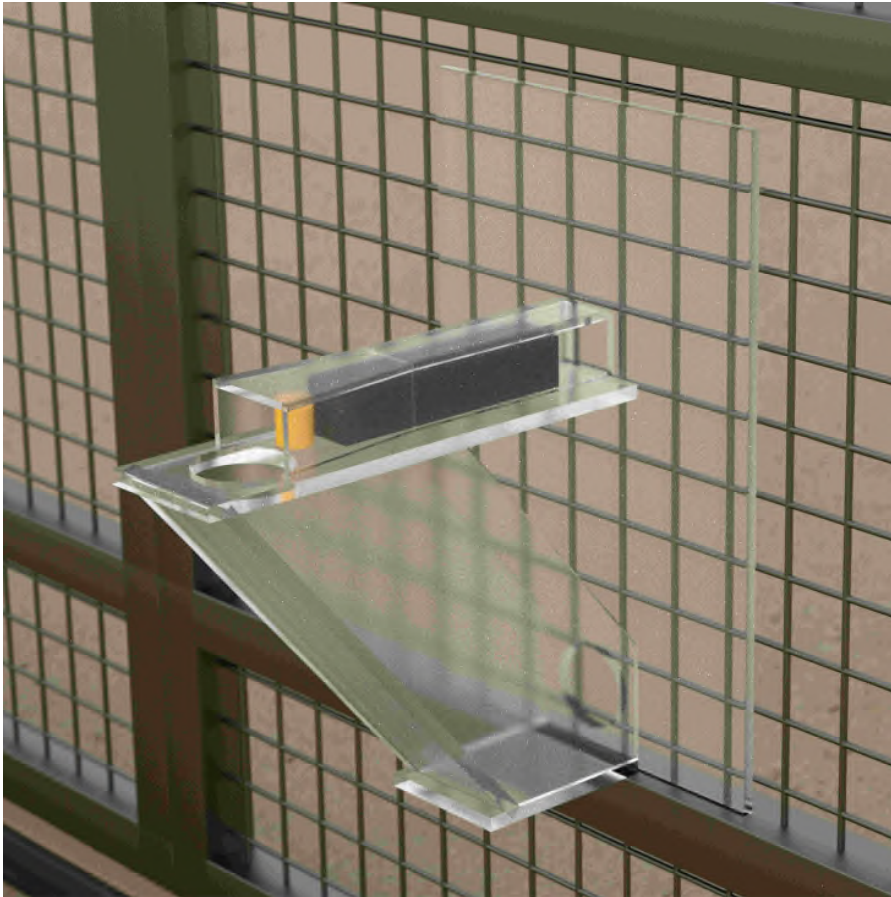
699

700 Figure 1

703    Figure 2

(a)



704

(b)



705

706     Figure 3



707