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**Bonobos voluntarily hand food to others but not toys or tools**

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24 **ABSTRACT**

25 A key feature of human prosociality is *direct transfers*, the most active form of sharing in  
26 which donors voluntarily hand over resources *in their possession*. Direct transfers buffer  
27 hunter-gatherers against foraging shortfalls. The emergence and elaboration of this  
28 behavior thus likely played a key role in human evolution, by promoting cooperative  
29 interdependence and ensuring that humans' growing energetic needs (e.g., for increasing  
30 brain size) were more reliably met. According to the *strong prosociality hypothesis*,  
31 among great apes only humans exhibit sufficiently strong prosocial motivations to  
32 directly transfer food. The *versatile prosociality hypothesis* suggests instead that while  
33 other apes may make transfers in constrained settings, only humans share flexibly across  
34 food and non-food contexts. In controlled experiments, chimpanzees typically transfer  
35 objects but not food, supporting both hypotheses. Here we show in two experiments that  
36 bonobos directly transfer food but not non-food items. These findings show that, in some  
37 contexts, bonobos exhibit a human-like motivation for direct food transfer. However,  
38 humans share across a far wider range of contexts, lending support to the versatile  
39 prosociality hypothesis. Our species' unusual prosocial flexibility is likely built on a  
40 prosocial foundation we share through common descent with the other apes.

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42 **KEYWORDS:** bonobo, chimpanzee, prosociality, cooperation, sharing, human evolution

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47 **MAIN TEXT**

48           Prosocial behavior is any positive social act—whether unselfish or selfish, costly  
49 or cost-free—that benefits another [1]. Of particular importance in considering the  
50 evolution of human prosociality is the phylogenetic origin of intentional direct transfer of  
51 food or objects, the most proactive form of sharing in which donors voluntarily hand over  
52 resources *in their possession*. Direct transfer of both objects and food emerges early in  
53 human ontogeny and likely played a key role in human evolution [2-4]. Direct transfers,  
54 including from nonkin, buffer modern hunter-gatherers against foraging shortfalls and,  
55 throughout our evolutionary history, likely helped ensure that humans more reliably met  
56 their increasing energetic needs [5, 6].

57           Many have suggested that humans are derived or unique in exhibiting strong  
58 prosocial motivations—what we collectively refer to as the *strong prosociality*  
59 *hypothesis*—and, specifically, that among great apes only humans exhibit sufficiently  
60 strong prosocial motivations to directly transfer food in their physical possession [7-13].  
61 The *versatile prosociality hypothesis* suggests instead that while other apes may make  
62 transfers in constrained contexts, only humans share flexibly across food and non-food  
63 contexts [14, 15]. Based on both observations and experiments it appears that  
64 chimpanzees (*Pan troglodytes*) directly transfer objects but not food, supporting both  
65 hypotheses. Although chimpanzees sometimes share food and tools in the wild [16, 17]  
66 and will help a conspecific access food or non-food that the actor cannot access herself  
67 [18] [but see 12], experiments show that chimpanzees typically only transfer food in their  
68 possession when they cannot escape a begging recipient. When physically separated from  
69 the potential recipient and able to avoid harassment, they do not directly transfer easily

70 monopolizable food [9, 19, 20]. However, in similar circumstances (i.e., when physically  
71 separated from the recipient), they reliably transfer tools and other objects in their  
72 possession [2, 21-23].

73         Bonobos (*Pan paniscus*) exhibit a different prosociality profile than chimpanzees.  
74 In controlled dyadic contexts, they are more socially tolerant than chimpanzees, and often  
75 choose to co-feed in close proximity [24-27, but see 28, 29]. In the wild, females have  
76 even been observed sharing food from their mouths with other non-kin females even  
77 though more fruit of the same type is readily available to both – often within reaching  
78 distance of the recipient [42]. Their high levels of dyadic tolerance allow them to  
79 spontaneously outperform chimpanzees in instrumental cooperative tasks that require  
80 sharing monopolizable food [24]. In experiments, when given the choice of eating alone  
81 or releasing a conspecific to eat together, bonobos even share their food voluntarily [30,  
82 31]. Bonobos will also help groupmates or non-groupmates in obtaining out-of-reach  
83 food that they themselves cannot obtain, even without the potential for physical  
84 interaction or active solicitation by the recipient [14, 31]. However, they do not share  
85 high-value food when they are unable to physically interact with the recipient or to  
86 control how much of their food the recipient receives [31].

87         Despite differences between chimpanzee and bonobo prosociality, the strong  
88 prosociality and versatile prosociality hypotheses were largely framed based on  
89 comparative data from chimpanzees and humans alone. A critical test of these hypotheses  
90 thus requires investigation of bonobos' tendency to directly transfer food and non-food  
91 items [14, also see related work in more distant relatives of humans: e.g., 32, 33].  
92 According to the *strong prosociality hypothesis*, bonobos—like chimpanzees—will not

93 exhibit any form of direct transfer of food. According to the *versatile prosociality*  
94 *hypothesis*, bonobos may show direct transfers but only in constrained contexts. For  
95 example, bonobos will not transfer both food and non-food items or they will only  
96 transfer low-value but not high-value food. We performed two experiments to test these  
97 competing predictions.

## 98 **Experiment 1**

### 99 *Methods*

100 In Experiment 1, we tested whether bonobos ( $N=18$ ; 6M:12F, ages 3-15; Table  
101 S1; Movie S1) would retrieve and transfer an out-of-reach object to help a human  
102 experimenter, using a method in which both human infants and chimpanzees readily do  
103 so [2]. Chimpanzees with extensive human socialization exhibit similar motivation to  
104 help both conspecifics and humans retrieve out-of-reach objects. This frequently has been  
105 interpreted to mean that motivations toward humans can reveal how chimpanzees are  
106 motivated to interact with each other [2, 3, 21-23]. We pursued this experiment first  
107 because it facilitated a direct comparison between bonobos and chimpanzees under the  
108 maximally controlled settings that are only possible with human experimenters. Bonobos  
109 were situated in a mesh-walled room and witnessed E2, in a demonstration area, steal a  
110 stick from E1 (Figure 1A). E2 then carried the stick into the hallway adjacent to the  
111 subject room and closed the door behind him. E1 grabbed the door, whimpering, and  
112 watched as E2 placed a small piece of banana under the mesh between the subject room  
113 and the hallway to position the subject at the starting location, and then placed the stick  
114 partially through the mesh about one meter from the banana. E2 then walked further  
115 down the hallway out of the testing area.

116 Each trial began when the subject ate the piece of banana. In the first 30 seconds,  
117 E1 leaned against the door, looked, and vocalized toward the stick. If, after 30 seconds  
118 the subject had not transferred the stick to E1, E1 became more communicative by calling  
119 the subject's name, banging the door and alternating his gaze between the subject and the  
120 stick. To determine whether an ostensive cue of desire can help elicit transfer, in the  
121 reaching condition ( $N=9$ ), E1 reached with effort toward the stick throughout the duration  
122 of the trial. In the no-reaching condition ( $N=9$ ), this additional cue was absent: E1 kept  
123 his arms at his side or on the door. Each trial ended when the subject transferred the stick,  
124 or after one minute. Each subject participated in a 12-trial session with ten test trials as  
125 just described and two baseline trials—one at the beginning and one at the end. Baseline  
126 trials were identical to test trials except that E1 was never present. Subjects were never  
127 rewarded for transfers to ensure that any transfer behavior was spontaneous and did not  
128 occur in response to rewarding.

### 129 ***Results and Discussion***

130 Bonobos did not transfer the stick. Although subjects often retrieved the stick  
131 (33.33% of reaching trials and 43.33% of no-reaching trials), they did not transfer it.  
132 Whereas chimpanzees and human infants in the same paradigm delivered the objects to  
133 the experimenter in approximately half of reaching trials – even when unrewarded at the  
134 time of testing [2], bonobos did so in only 1.1% of these trials and 0% of no-reaching  
135 trials (Figure 1B) [see also 34]. Examining their behavior qualitatively, subjects  
136 sometimes responded with what appeared to be teasing instead of helping (i.e., gesturing  
137 toward E1 with stick in hand, often moving the stick close and then pulling it back, and  
138 ultimately refusing to transfer the stick). Four subjects “teased” the experimenter on a

139 total of 11 trials in the reaching condition and two subjects “teased” the experimenter on  
140 a total of two trials in the no-reaching condition. This behavior, and previous work on  
141 bonobos’ understanding of others’ reaching goals [35-38], suggests that bonobos lack of  
142 direct transfers is unlikely to be explained by a failure to understand E1’s goal. The  
143 behavior of bonobos here provides additional evidence against the idea that the direct  
144 transfer of objects by chimpanzees is simply the product of previous rewarding, unless  
145 there exists a species difference in susceptibility to reward history between chimpanzees  
146 and bonobos [2, 3, 12]. Sanctuary bonobos have highly similar rearing histories to  
147 sanctuary chimpanzees and caretakers are equally motivated to reward both species for  
148 returning objects, yet here bonobos have not developed a chimpanzee-like pattern of  
149 object transfer.

150

## 151 **Experiment 2**

152 While wild bonobos use a range of tools, they have not been observed using tools  
153 in extractive foraging. In contrast, captive bonobos exhibit tool-use in a range of food  
154 acquisition contexts that mirror chimpanzees [39-41]. Bonobos at Lola ya Bonobo  
155 sanctuary often use rocks to crack palm nuts. Although they can crack these nuts with  
156 their teeth, they prefer to crack them with rock hammers and can crack and consume nuts  
157 at a median rate of 2.8 nuts per minute [40, 41]. In natural interactions at the sanctuary,  
158 bonobos have been observed to both passively and actively share nuts after cracking them  
159 (Hare, personal observation). Bonobos appear to assign nuts intermediate value between  
160 high-value fruit and low-value foliage [42]—likely, in part, because they require greater  
161 effort to open with teeth or to find a proper tool. Taking advantage of this natural context,

162 as a second test of object and food transfer, we examined whether bonobos would  
163 directly transfer either a tool (i.e., a rock) or nuts to a conspecific when each only had  
164 access to one or the other resource (Movie S2).

## 165 **Methods**

166 In Experiment 2, two bonobos (10 pairs comprised of 12 new subjects, 2M:10F;  
167 aged 5-15 years; Table S2) were situated in adjacent rooms and could physically interact  
168 only through a 1m<sup>2</sup> mesh window with a 20 x 20cm hole in the center. Subjects could  
169 thus *choose* to transfer items or interact socially (e.g. grooming, “teasing”), or to avoid  
170 sharing or interacting. In each trial of the experimental condition, one individual (i.e., the  
171 rock-owner) was provisioned with two rocks that could be used to crack palm nuts and a  
172 second (i.e., the nut-owner) was provisioned with five nuts (Figure 2A). In the rock-  
173 owner’s room, each rock was ~20 x 15 x 5cm in size (i.e., maximum length/width/height  
174 diameters) and ~2kg in weight. Both rocks were tethered to the wall of the rock-owner’s  
175 room, approximately 2m away from the hole, so that they could reliably be returned to  
176 the rock owner’s room between trials. One rock was tethered with a short rope of ~1m,  
177 and the other with a long rope of ~5m. This setup positioned both rocks out of the nut-  
178 owner’s reach, but the rock with the long rope could be transferred through the hole into  
179 the nut-owner’s room. In the nut-owner’s room, the five nuts were provisioned ~4m away  
180 from the hole, well out of the rock-owner’s reach. As a result, either subject had complete  
181 control over her items because the items were provisioned in a corner of the testing room  
182 far beyond the reach of her partner, but she could help her partner by transferring them.  
183 In the control condition, transfer was not needed as each subject received one rock and  
184 five nuts, thus controlling for baseline rates of transfer and ensuring that transfer in the



185 test could not be explained by a lack of motivation by the donor to crack and eat nuts  
186 (Figure 2B). In both conditions, between trials, any transferred rocks were returned to the  
187 rock-owner's room via the rope but untransferred or uneaten nuts could not be recovered  
188 and remained in the nut-owner's room. Each pair participated in two five-trial sessions  
189 per condition (half of dyads received the conditions in ABBA order and half in BAAB  
190 order), for a total of 10 experimental and 10 control trials. A minimum of one day, but  
191 not more than six, elapsed between sessions. To control for currency-specific reciprocity  
192 across trials, within each dyad, roles were never reversed. Trials lasted five minutes. Note  
193 that for analyses the nut-owner and rock-owner maintained their designations across  
194 conditions, even though subjects received both resources in the control condition.

195         Before qualifying for the test phase, to demonstrate their knowledge of the task  
196 and motivation to consume nuts, each subject completed a self-regard pretest in which in  
197 two five-minute trials they received three nuts and one rock [43]. To be included in the  
198 experiment, subjects had to crack at least two of six nuts ( $N=12$  passed, 6 others excluded  
199 for not meeting this criterion); however, those that met this criterion tended to crack all or  
200 nearly all six ( $M=4.83$ ; Table S2), demonstrating both skill and high motivation to  
201 consume the nuts. To ensure their understanding that both the rock and nut were relevant  
202 for nut-cracking, in a subsequent tool-use mastery pretest, subjects had to transport nuts  
203 to a rock on the other side of the room and crack at least one nut within five minutes.  
204 Subjects who did not meet this criterion after two trials were not included in the test  
205 phase ( $N=0$  excluded). To assess the role of dominance on transfer behavior, each pair  
206 additionally participated in seven trials of a standard food dominance test [based on 26]  
207 in which they were fed on opposite sides of a testing room and then allowed to compete

208 over a monopolizable piece of food located directly between them. The individual who  
209 acquired the food in a majority of trials was scored as dominant (in all dyads the food-  
210 dominant individual acquired at least 6 of 7 pieces of food, and reliability coding  
211 produced 100% agreement; Table S2).

212         During the test phase, we recorded whether or not in a trial the following  
213 behaviors occurred (i.e., as a binary measure) as well as the number of items transferred  
214 in each way [definitions largely followed 44]: (1) *direct transfer*, in which the possessor  
215 transferred an item through the test window into the adjacent room, (2) *tolerated theft*, in  
216 which the recipient acquired an item from the possessor's side of the window (including  
217 on the floor and in the hands of the possessor) without resistance (or aggression) from the  
218 possessor, and (3) *forced claim*, in which the recipient acquired an item from the  
219 possessor's side of the window while the possessor resisted by pulling back the  
220 recipient's hand, pulling back the item, or racing to grab the item off the floor. To assess  
221 whether sharing occurred proactively or in response to request, we also recorded  
222 *gesturing* (potential request behavior) whenever an individual reached through the  
223 window empty handed, as long as her hand remained empty when she retracted it  
224 (reliability on all measures was excellent, Kappa > 0.85; see Supplemental materials for  
225 details). Much work suggests that chimpanzees tend to share and help reactively, whereas  
226 increasingly it appears that bonobos may be proactively prosocial [2, 18, 21, 22, 31].

## 227 ***Results and Discussion***

228         Bonobos exhibited tolerated thefts and direct transfers but not forced claims (rates  
229 presented in Figure 2C and D and Table S3). Bonobos shared nuts on significantly more  
230 trials in the experimental condition than in the control both by tolerated theft and by

231 direct transfer (tolerated theft:  $M=2.1 \pm \text{s.e.}=0.745$  trials in experiment,  $M=0.1 \pm 0.105$   
 232 trials in control,  $z = -2.207$ ,  $N = 10$ ,  $T+ = 6$ , ties = 4,  $p = 0.027$ ; direct transfer:  $M=1.8 \pm$   
 233  $0.858$  trials in experiment,  $M=0.1 \pm 0.105$  trials in control,  $z = -1.980$ ,  $N = 10$ ,  $T+ = 6$ ,  
 234 ties = 3,  $p = 0.048$ , two-tailed related samples Wilcoxon signed rank tests). However,  
 235 frequency of rock sharing by tolerated theft or by direct transfer did not differ between  
 236 conditions (tolerated theft:  $M=0.7 \pm 0.446$  trials in experiment,  $M=0 \pm 0$  trials in control,  
 237  $z = -1.604$ ,  $N = 10$ ,  $T+ = 3$ , ties = 7,  $p=0.109$ ; direct transfer:  $M=0.2 \pm 0.211$  trials in  
 238 experiment,  $M=0.1 \pm 0.105$  trials in control,  $z = -1$ ,  $N = 10$ ,  $T+ = 1$ , ties = 9,  $p = 0.317$ ,  
 239 two-tailed related samples Wilcoxon signed rank tests).

240         There was no difference in the number of trials involving sharing of nuts versus  
 241 rocks in the control condition (tolerated theft:  $z = -1.000$ ,  $N = 10$ ,  $T+ = 1$ , ties = 9,  $p =$   
 242  $0.317$ ; direct transfer:  $z = 0$ ,  $N = 10$ ,  $T+ = 1$ , ties = 8,  $p = \text{NS}$ , two-tailed related samples  
 243 Wilcoxon signed rank tests). However, in the experimental condition subjects shared nuts  
 244 on significantly more trials than rocks both by tolerated theft and by direct transfer  
 245 (tolerated theft:  $z = -2.401$ ,  $N = 10$ ,  $T+ = 7$ , ties = 3,  $p = 0.016$ ; direct transfer:  $z = -2.226$ ,  
 246  $N = 10$ ,  $T+ = 6$ , ties = 4,  $p = 0.026$ , two-tailed related samples Wilcoxon signed rank  
 247 tests). Of the 495 shareable nuts in the experimental condition (one dyad received only 9  
 248 experimental trials), nut-owners directly transferred 40 nuts (8.08%) and shared an  
 249 additional 41 nuts (8.28%) via tolerated theft, producing an overall sharing rate of  
 250 16.36% (Table S3). Three dyads never shared, meaning that the sharing rate for those that  
 251 did was 23.14% (of 350 shareable nuts). We did not observe any form of aggression  
 252 throughout and only witnessed instances of potential teasing with the rock on 2.22% of  
 253 experimental trials and 4% of control trials (see Supplemental materials for coding

254 definitions). Together, these results reveal that bonobos both passively and actively  
255 shared nuts in their possession, in the absence of aggression or resistance. Most  
256 strikingly, in direct contrast to other primates, in which direct food transfers either never  
257 or almost never occur [45], bonobos' direct food transfers were not an occasional act;  
258 they occurred frequently (18.18% of experimental trials) and at comparable rates to  
259 tolerated thefts (21.21% of experimental trials). However, consistent with Experiment 1,  
260 bonobos almost never shared non-food items – tools in this case.

261       To further explore bonobos' food sharing behavior, we investigated the predictors  
262 of tolerated theft and direct transfer of nuts on a trial-by-trial basis in separate GLMMs  
263 using the *glmer* function in *lme4* in R. Both models included the same random effects and  
264 predictor variables, but differed in the dependent measure: tolerated theft or direct  
265 transfer of nuts. Both measures were binary (i.e., 0/1: whether or not, within the trial, the  
266 nut owner transferred at least one nut by the given means). To account for multiple  
267 observations, we included the subject pair as a random intercept. Our models also  
268 included several fixed effects: condition (to account for differences in transfer between  
269 the experimental and control conditions), gesture by the rock owner (to determine  
270 whether help was provided proactively, or in response to request; [18, 21]), rock transfer  
271 in the same trial (combined tolerated theft and active transfer; to assess the influence of  
272 within-trial interchange), food-dominance (to determine whether transfers were directed  
273 up or down the hierarchy), and trial number (to account for change over time). It is  
274 possible that bonobos might have exchanged nuts for grooming or “teased” their partner  
275 to reduce proximity; however, both behaviors occurred infrequently (grooming: 6.5% of  
276 trials; “teasing”: 3.0% of trials) and neither co-occurred with tolerated theft or direct

277 transfer on more than a single trial. Therefore, we did not include either factor. We first  
278 compared our full models with null models that included only the random effects (and no  
279 fixed effects) using likelihood ratio tests. Both comparisons were significant (tolerated  
280 theft =  $\chi^2=31.428$ ,  $df=5$ ,  $p < 0.001$ ; direct transfer:  $\chi^2=25.212$ ,  $df=5$ ,  $p < 0.001$ ),  
281 permitting interpretation of the full models. P-values for fixed effects were generated  
282 using likelihood ratio tests comparing the full models with models in which individual  
283 fixed effects were removed.

284 Consistent with our previous analyses, both models showed that bonobos shared  
285 nuts significantly more in the experimental condition than in the control ( $p < 0.001$  for  
286 both models; see Tables S4-5). However, there was no effect of trial number in either  
287 model, indicating that learning or changes in motivation did not influence nut sharing of  
288 either type. We also found no effect of dominance, indicating that sharing did not simply  
289 occur up or down the hierarchy. Although gesturing by the rock-owner occurred on  
290 26.5% of trials, there was no relationship between gesturing and nut sharing of either  
291 type, consistent with sharing being unsolicited. This finding is in line with evidence that  
292 bonobos perform prosocial behaviors proactively [14, 31], which contrasts with the  
293 reactive nature of chimpanzee helping [2, 18, 21, 22, but see 46].

294 We found that tolerated theft of nuts (but not direct transfer of nuts) was predicted  
295 by sharing of rocks in the same trial ( $p = 0.040$ ). This apparent reciprocal pattern might  
296 result from intentional interchange of resources or, more parsimoniously, from the  
297 physical proximity shared by tolerant partners. The majority of rock transfers (7 of 10)  
298 were also tolerated thefts [i.e., symmetry-based reciprocity; 47, 48]. Interestingly, we  
299 only documented two trials in which a nut owner acquired any pieces of cracked nuts

300 from the rock owner after transferring uncracked nuts to her. Recovery of pieces of  
301 cracked nuts occurred in a single pair (nut owner: Waka, rock owner: Masisi) and only  
302 via tolerated theft. Finally, since some subjects participated in two dyads (once as the nut  
303 owner and once as the rock owner), in a separate model we confirmed that generalized  
304 reciprocity did not impact direct transfer of nuts (see supplementary materials and Table  
305 S6).

306 Bonobos frequently shared food but not tools even though they had passed a self-  
307 regard pretest and a tool mastery pretest, demonstrating their motivation to crack and eat  
308 nuts and their understanding of the functionality of the tool. Although there was no cost  
309 to transferring the rock in the experimental condition, since subjects had a second rock  
310 and the rocks could be easily picked up with one hand (Figure S1), they did not exhibit  
311 transfers of this kind. Instead, subjects chose to transfer nuts on many trials. Because  
312 food was given to the subject ~4 meters from the window between the subject and  
313 recipient, all food transfers required the subject to first bring food within reach of the  
314 recipient and then actively or passively transfer it. It is possible that subjects did not  
315 transfer large stones because they did not receive a pre-test in which they experienced  
316 transferring stones for their own use. The ability of subjects to spontaneously transfer  
317 nuts without a similar pre-test argues against this possibility. This account is also unlikely  
318 to explain differences in food versus non-food transfer for at least three additional  
319 reasons. First, bonobos were not motivated to transfer even much lighter non-food items  
320 in Experiment 1. Second, they are very familiar with large stones and often carry them  
321 around the sanctuary (see Figure S1 of an infant carrying a similarly-sized rock). Finally,

322 four pairs did transfer stones (via theft or direct transfer) through the window on at least  
323 one occasion, demonstrating that they were capable of doing so.

#### 324 **GENERAL DISCUSSION**

325         These experiments support the versatile prosociality hypothesis by providing  
326 evidence that while bonobos will proactively transfer a type of food to non-relatives, they  
327 do not transfer toys or tools as chimpanzees do. Although neither bonobos nor  
328 chimpanzees demonstrate the range of prosocial behaviors observed in human infants and  
329 adults, each species exhibits forms of prosociality that have been hypothesized to be  
330 unique to our species. The current work suggests instead that it is the diversity and  
331 degree of prosociality that is derived in the human lineage [14].

332         In direct conflict with the predictions of the strong prosociality hypothesis, we  
333 provide the first experimental evidence that bonobos spontaneously hand conspecifics  
334 pieces of easily monopolizable food. Transfers required that a subject carry nuts several  
335 meters and within reach of the window separating the subject from the potential recipient.  
336 While bonobos did not transfer nuts or tools on the majority of trials, they did transfer  
337 nuts both passively and actively at relatively high rates. Importantly, both tolerated theft  
338 and direct transfer of nuts occurred more often in the experimental condition than in the  
339 control, and at higher rates than theft or direct transfer of rocks. We also never observed  
340 the bonobos discarding nuts by passing them out of the room except through the sharing  
341 window. This pattern is consistent with intentional sharing: subjects collected uncracked  
342 nuts, carried them within reach of the recipient, and either tolerated taking or actively  
343 handed them through the window for their partner to crack. The bonobos never attempted  
344 to prevent their partner from retrieving the food they had shared (i.e., no forced claims)

345 and gesturing by the recipient was unrelated to nut transfers within each trial, suggesting  
346 that direct transfers were proactive. Subjects rarely transferred nuts in the control when  
347 both the subject and recipient possessed both nuts and stones. This pattern makes it  
348 difficult to characterize the observed sharing as an accidental by-product of stimulus  
349 enhancement or social facilitation [e.g., 12, 43]. Even if some tolerated thefts occurred  
350 because tolerant nut-owners were attracted to the window by the rock in the adjacent  
351 room and brought the nuts with them, such behavior cannot explain nuts that were  
352 actively shared via direct transfer. Subjects were also not sharing under pressure since  
353 neither subject could harass the other given their physical separation and size of the large  
354 testing rooms. Instead, the bonobos' food sharing behavior appears to be intentional [13,  
355 49].

356         There is little evidence that social or nonsocial rewards motivated the bonobos'  
357 direct food transfers. Since pairs of subjects never swapped roles in the experimental  
358 condition, rock-owners could not directly reciprocate by passing whole nuts to nut-  
359 owners, and we almost never observed subjects obtain cracked nuts after sharing them  
360 with recipients. There also was no interchange or generalized reciprocity associated with  
361 direct nut transfers. The direct transfer of uncracked nuts and stone tools between nut-  
362 owners and rock-owners did not correspond within trials, and the tendency for a subject  
363 to directly transfer nuts in a session was not related to whether or not she had recently  
364 received nuts when participating as a rock owner. We found no effect of trial number on  
365 bonobos' direct transfer behavior, suggesting that motivation to share was stable despite a  
366 lack of immediate rewards. The dominance relationship between the nut-owner and rock-



367 owner was also unrelated to transfers, making it difficult to argue that sharing was  
368 motivated by status-striving [50].

369 Nut-owners incurred a moderate cost by directly transferring food. They had to  
370 carry the nuts across the room, within reach of the rock-owner, and transfer them.  
371 Although they prefer to use stone tools to open nuts, they are capable of cracking this  
372 type of nut with their teeth after some effort. They also could have brought the uncracked  
373 nuts into the outdoor enclosure, following the test session, and cracked them with  
374 naturally available rocks. By transferring nuts they were thus forfeiting edible food.  
375 Nonetheless, we rarely saw subjects use their teeth to crack nuts in this experimental  
376 setting. This may suggest that without a tool available, uncracked palm nuts are a  
377 relatively low value food that only increases in value once cracked. It may therefore be  
378 that nut transfer was relatively low cost for the nut-owner but highly beneficial to the  
379 rock-owner. Despite the fact that nuts only have intermediate value as a food, the  
380 bonobos were highly motivated to eat them if they had a stone tool available to process  
381 them.

382 Although quantitative comparisons cannot be made between species due to  
383 differences in methodology, qualitative comparisons suggest that this instance of bonobo  
384 food sharing is unlike that seen in chimpanzees and highly unusual among nonhuman  
385 primates. Although different empirical approaches have produced some differing results  
386 about food tolerance and sharing between species [see 14 for important discussion of this  
387 point] [24-26, 28, 29], controlled dyadic experiments can clarify rates of sharing when  
388 alternative motivations like harassment and group dynamics are controlled for. When  
389 chimpanzees are separated from a potential recipient, proactive and direct transfers are

390 almost non-existent [9, 19, 51]. In contrast, bonobos exhibited direct transfers of nuts  
391 nearly as frequently as they did tolerated thefts (in 18.18% and 21.21% of experimental  
392 trials respectively). In fact, 49.38% of nuts shared in the experimental condition were  
393 directly transferred and 50.62% were shared via tolerated theft. Even in capuchin  
394 monkeys (*Sapajus apella*), who have been described as tolerant food-sharers, direct  
395 transfers only account for 0.3% of sharing events [44]. Bonobos' rates of direct transfer  
396 are higher even than those reported for cooperative-breeding  
397 callitrichid adults sharing with other adults ( $M=0\% \pm SD=0\%$  of sharing events) and with  
398 infants ( $16.44\% \pm 17.88\%$  of sharing events) [8, 45]. While we note that there are  
399 important differences between studies (e.g., in the specific types of food being shared and  
400 their potential values, the absolute amount of sharing, and the experimental setups), only  
401 bonobos have been observed to directly transfer food at such high rates without kinship,  
402 harassment, or mating opportunities as proximate motivators. Future work can use this  
403 paradigm to directly compare bonobos with chimpanzees and other species, and with  
404 bonobos from other groups and of other ages, that have experience with nut-cracking.  
405 Given that wild adult bonobos show the highest rates of sharing, it may be that bonobos'  
406 delayed development of social intolerance relative to chimpanzees contributed important  
407 preconditions for the emergence of proactive food sharing [25, 50].

408         It is equally interesting to consider what behaviors we did not observe from the  
409 bonobos. In Experiment 1, bonobos did not return an object they had seen forcefully  
410 taken from an experimenter [34]. While subjects often retrieved the experimenter's toy  
411 for themselves, they never responded to the experimenter's request to return it with  
412 anything but playful "teasing" behaviors. These cases appeared to be an attempt to

413 initiate a social interaction but it was not the helpful response displayed by chimpanzees  
414 in a nearly identical experimental context [i.e., 2]. The pattern seen in the current dyadic  
415 interaction is also consistent with the previous finding that bonobos even prefer  
416 individuals that hinder rather than help a third party trying to retrieve an object [52]. In  
417 Experiment 2, we also documented a striking absence of stone tool sharing. Rock owners  
418 had a surplus of rocks, yet rarely passed one of them through the sharing window. This is  
419 again unlike the response of chimpanzees who readily share tools that will help others  
420 obtain food [22].

421         Several explanations can be ruled out for the failure of bonobos to share objects in  
422 both experiments. Bonobos have as complex gestural repertoires and understand human  
423 gestures as well as or even better than chimpanzees [53-55]. Bonobos from this same  
424 sanctuary also successfully discriminate between helpful and unhelpful experimenters in  
425 a similar context [52]. It is unlikely that bonobos did not understand the experimenter's  
426 requests or the nut-owner's need for a stone tool [35, 38]. A host of experimental and  
427 observational studies also show that bonobos are not more attracted to or possessive of  
428 novel objects or tools than chimpanzees [56-58]. However, in their everyday  
429 interactions, sanctuary bonobos have been observed to refuse to share nut-cracking stones  
430 and even carry them around for several consecutive days [41, Krupenye, personal  
431 observation] (Movie S2, Figure S1). Future research can test whether in some contexts  
432 bonobos perceive objects as having unusually high value. For example, bonobos may  
433 especially value stone tools or toys that make them more attractive to other bonobos and  
434 increase opportunities for play, sex, and food sharing. Until then, the lack of object  
435 sharing in bonobos remains enigmatic.

436 Any form of bi-directional direct transfer was also completely absent during  
437 Experiment 2. After cracking nuts that nut-owners had passed through the window, rock-  
438 owners rarely, if ever, passed any food back to the nut-owner. Rock-owners could have  
439 easily shared a small proportion of the nuts they cracked or at least provided a stone to  
440 help the nut-owner crack their remaining nuts. Communication was also limited and did  
441 not appear to influence sharing. Regardless of the role they were playing, bonobos could  
442 have persistently or more overtly gestured for help to initiate turn-taking and reciprocity.  
443 Future research can further explore if alternating the roles of the nut- and rock-owners  
444 can facilitate bi-directional sharing across trials, and continue to investigate any role of  
445 communication in mediating sharing levels. Work in the wild and in captivity suggests  
446 that sharing is goal-directed and has a social function [50, 59]. However, it would also be  
447 interesting to specifically examine bonobos' sensitivity to others' needs of nuts and  
448 stones (or others' capacity to profit from sharing) by investigating whether nut-owners  
449 selectively transfer nuts to partners in possession of rocks.

450 Experiments have now demonstrated that both bonobos and chimpanzees are  
451 capable of the most active form of sharing—direct transfers—but the context in which  
452 each species does so is different. Here we show that bonobos exhibit this behavior with at  
453 least one type of food. Given the xenophilic preferences previously observed in bonobos  
454 and their willingness to aid strangers attempting to obtain out of reach food, it's possible  
455 that bonobos would even transfer nuts to conspecifics with which they have never had a  
456 social interaction [14, 31, 59]. The findings from the present studies (and other recent  
457 work with bonobos) suggest that the motivation driving human hunter-gatherers to  
458 proactively share may have evolved through a quantitative shift from their common

459 ancestor with the other apes, rather than the radical qualitative shift that has previously  
460 been suggested [60, 61]. This seems increasingly likely considering food sharing in  
461 human hunter-gatherers, such as Hadza men, actually occurs after donors have already  
462 met their daily caloric needs [62], and across human populations highly costly altruism  
463 toward strangers is exceptionally rare [63, 64]. While the quantity of food shared and its  
464 role in buffering group members against caloric shortfalls is unparalleled in humans [6],  
465 it is less difficult to explain provisioning with surplus food that is of high value to the  
466 recipient and of relatively low value to the possessor. This is analogous to the cost-  
467 benefit payoff seen in Experiment 2 for the bonobos sharing uncracked palm nuts. The  
468 challenge may not be in explaining how humans became extreme in our prosociality but  
469 instead understanding how our lineage evolved so much versatility in recognizing when  
470 low cost helping is of greatest benefit to others [65, 66].

471

## 472 ETHICS

473 These noninvasive behavioral studies were approved by Duke University (IACUC  
474 #A078-08-03) and adhered to the legal requirements of the Ministry of Research and the  
475 Ministry of Environment in D.R. Congo (permit MIN.RS/SG/004/2009). Animal  
476 husbandry and care practices complied with the policies of Lola ya Bonobo, as well as  
477 the Pan-African Sanctuary Alliance Primate Veterinary Healthcare Manual.

478

## 479 DATA, CODE, AND MATERIALS

480 Data are tabulated in tables S1-3. Trial-by-trial data for the GLMMs in Experiment 2 will  
481 be deposited in Dryad.

482

483

484 COMPETING INTERESTS

485 We have no competing interests.

486

487 AUTHOR CONTRIBUTIONS

488 CK and JT conducted the experiments; CK, JT, and BH designed the experiments,

489 analysed the data, and wrote the paper.

490

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504

505 **REFERENCES**

506 \*Note that there are a couple minor citation errors that were fixed during the proof stages

507 and are correct in the published manuscript

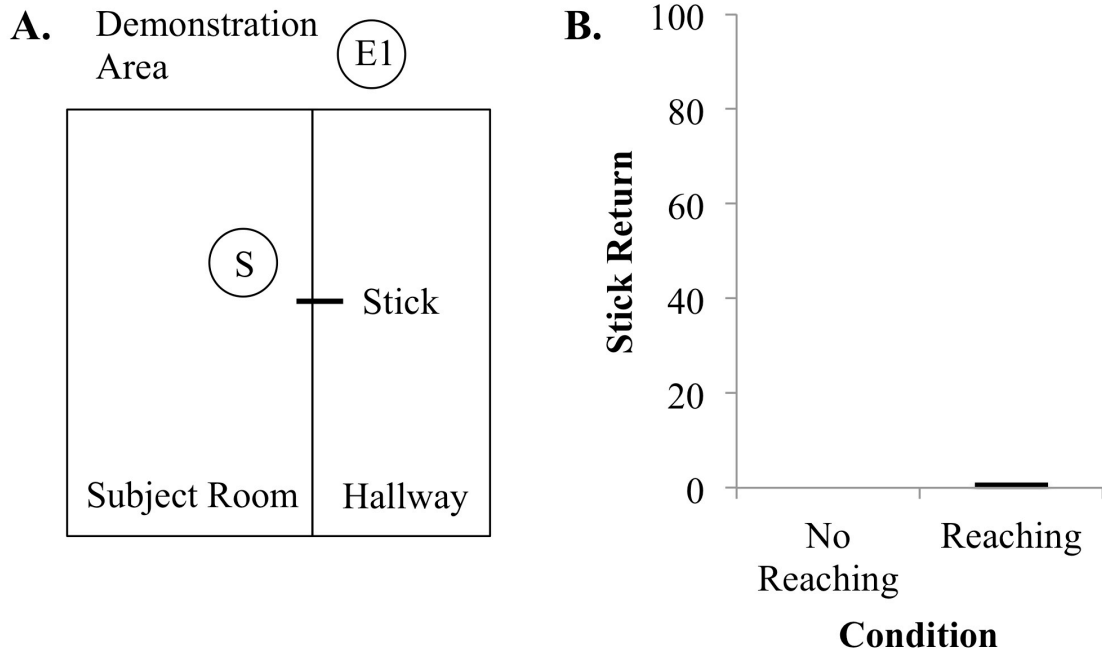
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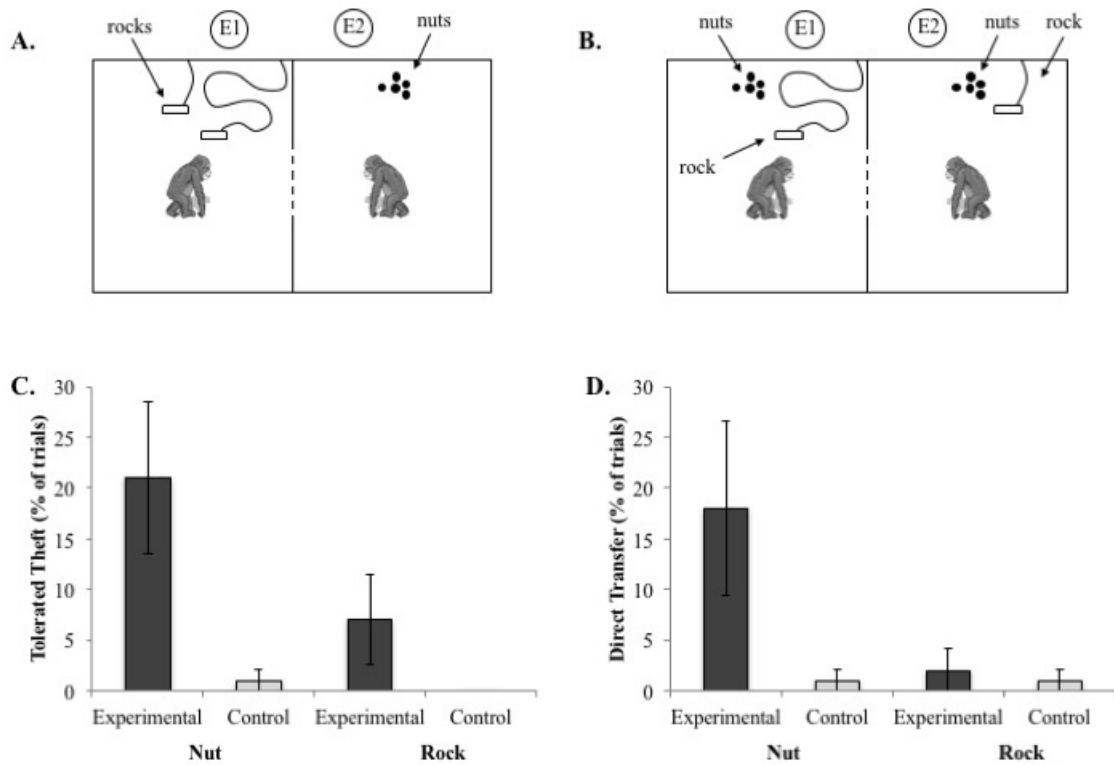
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- 679



680

681 **Fig. 1. Testing setup (A) and results (B) of Experiment 1.**

682



683

684 **Fig. 2. Testing setup and results of Experiment 2.** A. Experimental condition. B.

685 Control condition. Located in adjacent rooms, subjects could interact through a single  
 686 window (dashed line). Round dots represent nuts provided to subjects in each trial while  
 687 rectangles attached to rounded lines depict rocks and their tethers. Nuts and rocks were  
 688 provisioned far beyond the reach of the bonobo in the adjacent room. E1 and E2 served

689 as experimenters and camera-people. C. Percent of trials in which subjects exhibited

690 tolerated theft of rocks and nuts in the experimental and control conditions. D. Percent of

691 trials in which subjects exhibited direct transfer of rocks and nuts in the experimental and

692 control conditions. Error bars denote standard error.

693

694