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Manipulative repertoire of bonobos (*Pan paniscus*) in spontaneous feeding situation

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Indicate which taxonomic group was the subject of your study (select all that apply or type another option)::	Apes (non-human)
Keywords:	<i>Pan paniscus</i> , Food manipulation, Grasping postures, Tool use

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Research highlights

- Our study provides a description of a large manipulative repertoire, from precision to power grips, including 22 grasping postures, while individuals fed on foods of different shapes and sizes and on different substrates.
- Our results show an enrichment of the manipulative repertoire from juveniles to adult individuals.
- We described a spontaneous use of tools with a female-bias and a use of specific grasping postures for this context.

For Peer Review

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3 **1 Manipulative repertoire of bonobos (*Pan paniscus*) in spontaneous feeding situation**
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8 **3 Short title: Repertoire of food manipulation in zoo-housed bonobos**
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Abstract

Comparative behavioral studies of hand use amongst primate species, including humans, have been central in research on evolutionary mechanisms. In particular, the manipulative abilities of our closest relatives, the chimpanzee (*Pan troglodytes*), have been widely described in various contexts, showing a high level of dexterity both in zoo and in natural conditions. In contrast, the study of bonobos' manipulative abilities has almost exclusively been carried out in experimental contexts related to tool use. The objective of the present study is to describe the richness of the manipulative repertoire of zoo-housed bonobos, in a spontaneous feeding context including various physical substrates to gain a larger insight into our evolutionary past. Our study describes a great variety of grasping postures and grip associations in bonobos, close to the range of manipulative repertoire in chimpanzees, confirming that the two species are not markedly different in terms of cognitive and morphological constraints associated with food manipulation. We also observed differences in manipulative behaviors between juveniles and adults, indicating a greater diversity in ~~manual postures~~ grip associations and grasping postures used in isolation with age, and a sex-biased use of tools ~~since~~with females ~~used~~using tools more often than males. These results are consistent with the previous results in the *Pan* genus and reinforce the hypothesis that the evolutionary mechanisms underlying the flexibility of manipulative behaviors are shared by both species and that these ecological strategies would have already evolved in their common ancestor.

Keywords: *Pan paniscus*, food manipulation, grasping posture, tool-use

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4
56 50 **Introduction**

7
8 51 Grasping ability is defined as “movements in which an object is seized and held securely
9
10 52 partly or wholly within the hand [or the foot]” (Napier, 1956, p.902) and more broadly manual
11
12 53 dexterity implies “the ability to make coordinated hand and finger movements to grasp and
13
14 54 manipulate objects” (Makofske, 2011, p.1522). Manipulative abilities in hominids (i.e., great
15
16 55 apes and humans and their extinct relatives (Wood et al., 2011)) has been an important
17
18 56 subject of interest in evolutionary studies. The human hand is traditionally considered as
19
20 57 having a uniquely high degree of dexterity compared to other primates (Key et al., 2018;
21
22 58 Marzke, 2013; Marzke et al., 1992), such as forceful precision grips between the pad of the
23
24 59 thumb and the pads of the fingers and complex intra-manual precision manipulative
25
26 60 movements (Kivell, 2015; Marzke, 1997, 2013; Marzke et al., 2015; Napier, 1960; Pouydebat
27
28 61 et al., 2011). Morphological evidence from fossils shows that, in early hominin (i.e., modern
29
30 62 humans, and their extinct relatives) hands were characterized by a combination of ape-like
31
32 63 and human-like features (e.g., Almécija et al., 2010; Feix et al., 2015; Kivell, 2015; Kivell et al.,
33
34 64 2011; Richmond et al., 2016; Tocheri et al., 2008). Comparative behavioral studies of hand use
35
36 65 in our closest living relatives, in zoo and free-ranging conditions, can improve our
37
38 66 understanding of the functional morphology in early hominins as well as fossil apes (Bardo et
39
40 67 al., 2017; Feix et al., 2015; Pouydebat et al., 2008, 2011; Susman, 1998). Since the pioneering
41
42 68 work conducted by Napier (1956, 1960), who distinguished only two categories (i.e., power
43
44 69 and precision grips) when describing manual grips in primates, many advances have been
45
46 70 made. More diverse types of grasping postures and in-hand movements have been described
47
48 71 in apes and humans (but see also in capuchins, *Sapajus spp*: G. Byrne & Suomi, 1996; Truppa
49
50 72 et al., 2019; and macaques, *Macaca spp* : Macfarlane & Graziano, 2009; Pal et al., 2018),
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1
2
3 73 including a wider range of manipulative behaviors compared to other mammals, both in zoo
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5 74 and in natural conditions (e.g., Bardo et al., 2017; Byrne et al., 2001; Christel, 1993; Christel et
6
7
8 75 al., 1998; Crast et al., 2009; Jones-Engel & Bard, 1996; Marzke & Wullstein, 1996; Neufuss et
9
10 76 al., 2018; Pouydebat et al., 2011).

11
12
13 77 Tool use in particular is thought to have been a crucial adaptation during human
14
15 78 evolution and the potential of tool use behavior in great apes has been central in functional
16
17
18 79 studies of grasping (e.g., Bardo et al., 2017; Bardo et al., 2018; Osuna-Mascaró et al., 2020).
19
20 80 The definition of tool use has been revisited many times (see Bentley-Condit & Smith, 2010
21
22 81 for a review) but an inclusive one could be “ [. . .] the external employment of an unattached
23
24 82 environmental object to alter more efficiently the form, position, or condition of another
25
26
27 83 object, another organism, or the user itself when the user holds or carries the tool during or
28
29 84 just prior to use and is responsible for the proper and effective orientation of the tool” (Beck,
30
31 85 1980, p.10). Among great apes, chimpanzees (e.g., Boesch & Boesch, 1983, 1990; Goodall,
32
33 86 1964; Inoue-Nakamura & Matsuzawa, 1997; McGrew, 2010; Sanz & Morgan, 2013), gorillas
34
35 87 (*Gorilla gorilla sp.*) (Breuer et al., 2005; Grueter et al., 2013; Kinani & Zimmerman, 2015;
36
37 88 Wittiger & Sunderland-Groves, 2007) and orangutans (*Pongo sp.*) (Fox et al., 1999; Meulman
38
39 89 & van Schaik, 2013; van Schaik et al., 1996) use tools in natural conditions, for social, feeding
40
41
42 90 or hygienic (cleaning and protection) purposes. In free-ranging bonobos (*Pan paniscus*), it has
43
44
45 91 only been observed in social (communication and play) and hygienic contexts (Furuichi et al.,
46
47 92 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982; Nishida et al., 1999; Samuni et
48
49 93 al., 2021). However, studies in zoos and laboratories (Bardo et al., 2015, 2016; Boose et al.,
50
51 94 2013; Takeshita & Walraven, 1996; Toth et al., 1993; Visalberghi et al., 1995) or semi free-
52
53
54 95 ranging conditions (i.e, sanctuary) (Gruber et al., 2010; Neufuss et al., 2017) have shown their
55
56
57 96 functional, behavioral and cognitive abilities to modify and use objects as tools to enhance
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1
2
3 97 food accessibility. Furthermore, these studies have shown a differential tool use behavior
4
5 98 between males and females. Females in bonobos use more diverse kinds of tools, especially
6
7
8 99 in play and feeding contexts (e.g., sticks to dig in the mud) and they use them more frequently
9
10
11 100 than males (Boose et al., 2013; Gruber et al., 2010). Similar sex differences were also observed
12
13 101 in chimpanzees (i.e., W. McGrew, 1979; Pruetz & Bertolani, 2007). In ~~the Pan~~
14
15 102 ~~genus~~ chimpanzees and bonobos, juveniles and novice individuals (regardless of their age)
16
17
18 103 learn tool-use behaviors through both individual and social learning, and it has been shown
19
20 104 that females acquire these behaviors more quickly than males (Biro et al., 2003; Boose et al.,
21
22
23 105 2013; Lonsdorf, 2005; Matsuzawa, 2011; and see the review of Moore, 2013).

24
25 106 Studies about tool use have brought many clarifications on the ability of monkeys and
26
27
28 107 great apes to use precision grips similar to those used by humans, bringing into question ~~the~~
29
30 108 ~~idea that~~ what aspects of the human hand ~~would be~~ unique. But one limitation is that
31
32 109 ~~they~~ these studies often involve standardized objects of small size or of uniform shape, which
33
34
35 110 enables cross-species or cross-study comparisons but offers only a partial description of the
36
37
38 111 full manipulative repertoire of the species. Moreover, ~~if~~ although the effect of gender and age
39
40 112 has been well studied for tool-use ~~is~~ ~~the~~ ~~in~~ Pan-genus, few studies have explored the
41
42
43 113 importance of these individual factors on the detailed manipulative repertoire. In the few
44
45 114 studies in chimpanzees, no difference has been found between males' and females'
46
47 115 manipulative repertoires without tool-use (i.e., Jones-Engel & Bard, 1996; Tonooka &
48
49
50 116 Matsuzawa, 1995) but age has been shown to be an important factor by influencing the use
51
52 117 of grasping postures, with young chimpanzees performing a lower frequency of precision grips
53
54
55 118 than adults (Butterworth & Itakura, 1998; Pouydebat et al., 2011). Such studies are not
56
57 119 available in bonobos leading to a lack of knowledge on the influence of these two factors in
58
59 120 this species' manipulative repertoire.
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1
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3 121 More generally, tool use is not the only interest of non-human primate manual abilities
4
5
6 122 as the hand serves to explore and interact with the environment as a whole. Manual, but also
7
8 123 pedal, skills in primates can be observed during more diverse grasping and manipulative
9
10 124 behaviors, such as locomotion, feeding behavior and social interactions. ~~Even if it is now~~
11
12 ~~known as insufficient and non-exclusive, one of the historical hypotheses on the origins of~~
13 125
14 ~~grasping abilities in primates has focused on the selective pressures linked with food~~
15 126
16 ~~properties and the arboreal environment.~~ Bonobos express arboreal and terrestrial feeding
17 127
18 128 behaviors and although this environmental context has been well-studied in chimpanzees
19
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21
22 129 since 1960s (e.g., Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996;
23
24
25 130 Pouydebat et al., 2011), few studies have investigated the foraging strategies, food processing
26
27
28 131 skills and manipulation abilities in bonobos. Furthermore, previous studies with bonobos have
29
30 132 focused on precise experimental procedures with selected kinds and sizes of foods (Christel,
31
32 133 1993; Christel et al., 1998) which may have constrained the range of manipulative behavior
33
34
35 134 observed. For a better understanding of the evolution of feeding strategies in primates,
36
37 135 further research on manipulation in various feeding contexts (i.e., with and without tools, with
38
39 136 diverse manipulated food and in both terrestrial and arboreal environments) is needed,
40
41
42 137 particularly for this lesser-known species.

43
44 138 The aim of this study was to describe and quantify the manipulative repertoire in
45
46 139 spontaneous feeding situations, with and without tools, in zoo-housed bonobos, with a variety
47
48
49 140 of food they could encounter in different ecological contexts, both terrestrial and on
50
51
52 141 structures inducing suspended positional activities. Our hypothesis was that bonobos could
53
54 142 use a much wider range of manipulative behaviors than those described previously in a tool-
55
56
57 143 use context because of a greater variety of shapes and sizes found in consumed food than in
58
59 144 experimental settings. We also expected to describe a similar variety of manual postures to
60

1
2
3 145 that documented in chimpanzees given their ~~closely~~ similar hand anatomy. Based on the
4
5
6 146 literature in chimpanzees, we did not expect to observe a sex difference in this repertoire but,
7
8 147 based on previous studies about tool use in bonobos (Boose et al., 2013; Gruber et al., 2010)
9
10 148 we expected to observe a more frequent use of tools in females. We also considered the range
11
12 149 of these manipulative behaviors in juveniles, subadults and adults. We expected to observe a
13
14 150 more limited repertoire in juveniles, expanding with growing age and social or individual
15
16 151 learning, as described in tool-use situations in young chimpanzees.
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22

23 153 **Methods**

24
25 154 This research adhered to the legal requirements of France and all the experiments were
26
27 155 carried out following the principles of laboratory animal care in accordance with the CNRS
28
29 156 guidelines. It complies with the American Society of Primatologists (ASP) Principles for the
30
31 157 Ethical Treatment of Non-Human Primates and conforms to Directive 2010/63/EU of the
32
33 158 European Parliament and of the Council of 22 September 2010 on the protection of animals
34
35 159 used for scientific purposes.
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42 161 **1. Subjects and housing**

43
44 162 The study was conducted from January 27, 2020 to January 31, 2020 at the zoological
45
46 163 park "la Vallée des singes" (France). This park houses a group of seventeen bonobos composed
47
48 164 of nine adults (six females from 16- to 52-year_s old and three males from 15- to 23-year_s old),
49
50 165 two subadults (one female and one male, both 10-year_s old) and six juveniles (four females
51
52 166 from 3- to 7-year_s old and two males of 5- and 7-year_s old). We used the Pontzer & Wrangham
53
54 167 (2006) method for the determination of age categories ~~see~~. In total, ~~this group~~
55
56 168 includes observations were made on N=11 females and N=6 males.
57
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1
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3 169 The bonobos were observed during the day in an indoor building where two large
4
5
6 170 cages, connected to each other (98m² and 8 m height each), were visible. They also had access
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8 171 to five smaller cages (from 16 to 24 m²) and to a naturally vegetated outdoor island (0.7 ha)
9
10 172 that was accessible to the group according to the weather. Many climbing structures, made
11
12
13 173 of platforms, ladders and ropes, were available in the cages.

14
15 174 At least two water taps were available *ad libitum* and the group was fed four times a
16
17
18 175 day. Their food ration included mainly vegetables and one fruit (i.e., apple). It was
19
20 176 complemented by commercial pellets, seeds, eggs, chicken necks and a homemade mix
21
22
23 177 containing cereals, vitamins and vegetal oils. The food was distributed on the top of the cages
24
25 178 (i.e, ceiling grid) or inside the cages, on the floor and the platforms (Figure 1). Daily enrichment
26
27
28 179 was provided with tree branches (i.e, hazel or willow tree) and cooked rice placed inside tubes
29
30 180 or wooden logs.

31
32 181

33 34 35 182 **2. Data collection**

36 37 183 **2.1. Video recording**

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39
40 184 One or several individuals were followed throughout a feeding session, balancing the
41
42 185 distribution of records for each individual between observation days and periods of the day.
43
44
45 186 The selection of focal subjects was made according to a daily list (based on the cumulative
46
47 187 previous observation days) and visibility of individuals to the observer. One handheld camera
48
49
50 188 (PANASONIC® HC-V380) was used to record the simultaneous movements of the hands, feet
51
52 189 and mouth. At the end of the feeding sessions and between the meals, the foraging behavior
53
54
55 190 and the feeding on enrichments were video recorded using the same balance of distribution
56
57 191 between focal individuals. The recordings were performed at 50 frames/sec.

58
59 192
60

193 2.2. Video scoring

194 2.2.1. Manipulative sequences

195 Video recordings were analyzed frame by frame with VLC Media Player (VideoLan,
196 2020), using the individual focal sampling method (Altmann, 1974). Videos were divided
197 according to our definition of a “manipulative sequence”, including contact, grasping and
198 manipulation of the food items. It began with the first contact between an individual and an
199 item (direct or through the use of a tool) and ended when the food was consumed in its
200 entirety (whole fruit/vegetable, bunch, branch previously sectioned, bark, buds, etc.) or
201 abandoned before total consumption (partially or not consumed). A total of 3h30 of recorded
202 sequences (N=792) were analyzed. The parameters recorded during the sequence were the
203 individual, the food item (details of food items are available in Appendix 1), the manual/pedal
204 grip adopted, the hand(s)/foot used and the duration of each behavior. We recorded data
205 with the frequencies technique, in which every sequence was considered and not only the first
206 of a series of similar actions (i.e., bout technique) (e.g., Bardo et al., 2016; Hopkins, 1995).

207

208 2.2.2. Grasping postures

209 Every encountered grasping posture involving the hands or the feet was described and
210 linked to the existing literature on humans and apes (Bardo et al., 2016, 2017; Jones-Engel &
211 Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier, 1956; Parry, 1966;
212 Pouydebat et al., 2011). To name the grasping postures, we used Marzke’s grasping typology
213 (Marzke et al., 2015; Marzke & Wullstein, 1996) and we divided manual postures into six grip
214 categories (Table 2):

- 215 • Precision grips (PCG): contact between distal phalanges of the thumb and the index
216 finger. This category corresponds to the category also called “precision grip” in

- 1
2
3 217 Jones-Engels and Bard (1996), “Thumb-index grips” in Pouydebat et al. (2011) and
4
5
6 218 “Category 1” in Bardo et al. (2016).
7
8 219 • Thumb lateral (TL): contact between the distal phalanx of the thumb, the lateral
9
10 220 side of the middle, proximal phalanxes of the index finger and the item. This
11
12
13 221 category includes the grasping postures also called “thumb lateral” in Pouydebat
14
15 222 et al. (2011) and “Category 2” in Bardo et al. (2016).
16
17
18 223 • Without thumb: contact between one or several fingers, except the thumb, and
19
20 224 the item, also called “without thumb” in Pouydebat et al. (2011) and “Category 3”
21
22
23 225 in Bardo et al. (2016). We distinguished ~~in this category~~ two variants of the “scissor
24
25 226 hold”: the “dorsal scissor hold” ~~from~~ and the “palmar scissor hold” as the hand is
26
27
28 227 respectively systematically ~~placed in supination~~ oriented dorsally and palmar
29
30 228 relative to the item, and fingers 2 and 3 are always flexed in the dorsal grip and not
31
32
33 229 in the palmar grip.
34
35 230 • Palm grips (PMG): contact involving the palm, the thumb and one or several part
36
37 231 of other fingers and the item, involving the power grasping posture (Napier, 1956;
38
39 232 Jones-Engels & Bard, 1996), and also called “palm grips” in Pouydebat et al. (2011)
40
41
42 233 and “Category 4” in Bardo et al. (2016).
43
44
45 234 • Other grips (OG): contact types which fell outside the above categories, called
46
47 235 “other grips” in Jones-Engels and Bard (1996) and “Category 5” in Bardo et al.
48
49
50 236 (2016). In our study, it only involves one grasping posture.
51
52 237 • Manipulative finger movements (MFM): contact types without real grasping (i.e.,
53
54 238 contact for moving or stabilizing the item and probe for sticking food to the finger)
55
56
57 239 and involving the fingers (including the thumb) only. This category includes the
58
59
60

1
2
3 240 “Manipulative finger movement” in Marzke et al. (2015) and these contacts are
4
5
6 241 called “non-prehensile movements” in Jones & Lederman (2006).
7

8 242 During the same sequence, the passage from one grip to another, without a change of
9
10 243 hand, involved in-hand movements but this part of the sequence was not described and
11
12
13 244 quantified in our study.
14

15 245

18 246 **2.2.3. Grip associations and compound grips**

20 247 The grip associations included the cases of bimanual manipulation where the grasping
21
22 248 posture of each hand was recorded and compiled. In the case of asymmetric coordinated
23
24 249 bimanual movements, individuals held or maintained the food or the enrichment with one
25
26
27 250 hand and extracted or picked up the food with the other hand.
28

30 251 We also included the compound grips (e.g., Jones & Fragaszy, 2020; Neufuss et al.,
31
32 252 2018) in which several pieces of the same item were held in one hand. Compound grips could
33
34
35 253 be used when the item broke during the course of manipulation.
36

37 254

40 255 **3. Data analyses**

42 256 **3.1. Dataset evaluation**

44
45 257 To assess the extent to which our observations ~~maximized the number of possible~~
46
47 258 ~~grasping postures~~ included the whole manipulative repertoire, we plotted two accumulation
48
49 259 curves (Colwell et al., 2004) of the number of grip associations and ~~grasping~~ le postures used
50
51
52 260 in isolation (i.e., only one grasping posture used during unimanual manipulation) as a function
53
54 261 of the number of sequences and as a function of the number of food items.
55

56
57 262

59 263 **3.2. Age and sex effects**

1
2
3 264 All the means were calculated with the standard error of the mean (SEM). The
4
5
6 265 distribution of sequences and the number of distinct grip associations and graspingle postures
7
8 266 used in isolation in the manipulative repertoire were compared between the three age
9
10 267 categories and between males and females using a Pearson's Chi-squared test or a Fisher's
11
12 268 exact test (if the expected test values were less than 5). The different number of individuals in
13
14 269 categories (fewer juveniles and subadults than adults and fewer males than females) could
15
16 270 have induced an important bias. So, in every contingency table, we weighted the distribution
17
18 271 by the proportion of individuals in the sample: males (N=6/17), females (N=11/17), adults
19
20 272 (N=9/17), subadults (N=2/17) or juveniles (N=6/17) according to the test.

25 273 Multiple comparisons of the mean number of grips associations and graspingle
26
27 274 postures used in isolation ~~used-observed~~ per individual between age categories were
28
29 275 performed using the Kruskal-Wallis test and we used the Wilcoxon rank sum test for the
30
31 276 comparisons between males and females.

35 277 All statistics were computed using the R 3.6.3 statistical environment (R Core Team
36
37 278 2020).

40 279

42 280 **Results**

45 281 **1. Dataset evaluation**

47 282 The two accumulation curves plateaued (Figure 2), which meant that there was little
48
49 283 benefit in carrying out additional sampling to extend our evaluation of the manipulative
50
51 284 repertoire (Colwell et al., 2004).

54 285

57 286 **2. Grasping postures**

1
2
3 287 Manual manipulations appeared in 83.5% of all sequences recorded (N=661/792; Table
4
5
6 288 1), and the remaining 16.5% are for the use of the mouth only (N=131/792; Table 1). Every
7
8 289 individual (N=17) was represented in the sequences (mean \pm SEM=47 \pm 5 sequences per
9
10 290 individual, including mean \pm SEM=39 \pm 6 sequences with manual manipulation per individual).
11
12
13 291 We found 22 distinct grasping postures (Table 2): the most frequent was the “lateral thumb-
14
15 292 index grip” (N=325/792 or 41% of the sequences) and the second most frequent were the
16
17
18 293 power grips (with thumb (N=158/792 or 20% of the sequences) and without thumb (N=49/792
19
20 294 or 6% of the sequences). ~~This repertoire also included one new variant, never described for
21
22
23 295 bonobos in the literature. The dorsal scissor hold (in the “without thumb” category) is a variant
24
25 296 of the palmar scissor hold, with the hand in supination and the fingers flexed.~~

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27
28 297 Every age category was represented in the sample with N=416/792 (or 53%) sequences
29
30 298 involving adults, N=135/792 (or 17%) with subadults and N=241/792 (or 30%) sequences with
31
32 299 juveniles (Table 3). Manual manipulation occurred in 80.0% (N=333/416) of the sequences in
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34
35 300 adults, 78.5% (N=106/135) in subadults and 92.1% (N=222/241) in juveniles, and the
36
37 301 remaining 20.0% for adults, 21.5% for subadults and 7.9% for juveniles ~~were~~ are for the use
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39
40 302 of the mouth only (respectively N=83/416, N=29/135 and N=19/241; Table 3). Both males and
41
42 303 females s were also represented in the sample with N=530/792 (or 67%) sequences involving
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44
45 304 females and N=262/792 (or 33%) sequences with males.

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47 305 We detected a very limited use of the feet, always with an alternating use of the hands,
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49
50 306 in 1.1% of the sequences (N=9/792), involving only one foot at a time and with only two
51
52 307 different postures (Table 4). These foot grips were used for storage only, not to grasp the item
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54
55 308 or carry it to the mouth and occurred in both adults and juveniles (Tables 3 and 4). There was
56
57 309 no significant difference between the two age categories in the sequence distribution
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3 310 involving the feet (Fisher's exact test, $p>0.05$) nor between males and females (Fisher's exact
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5 311 test, $p>0.05$).

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9 10 313 **3. Grip associations and compound grips**

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12
13 314 The whole repertoire of the group included 28 distinct grip associations (bimanual
14
15 315 manipulation or compound grips) and 21 graspingle postures used in isolation (Table 5). One
16
17 316 of the grasping postures was never used in isolation (i.e, the “fifth finger probe” is always used
18
19 317 in association with “power grips”) and only 28 grip associations out of the 484 possible ones
20
21 318 ($N=22^2$) were actually observed. The number of distinct grip associations and graspingle
22
23 319 postures used in isolation per sequence ranged from 1 to 8 (mean \pm SEM= 1.46 ± 0.04) and
24
25 320 each individual used between 3 and 19 distinct grip associations and graspingle postures used
26
27 321 in isolation (mean \pm SEM= 11 ± 1 or $23.3 \pm 2.4\%$ of the recorded grip associations and graspingle
28
29 322 postures used in isolation).

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34 323 The bimanual manipulations represented the large majority of the grip associations
35
36 324 while only two cases of compound grips were observed. The first one was the “Palmar scissor
37
38 325 hold + Power grip with thumb” that occurred in one sequence involving an adult female during
39
40 326 the prehension of an item that broke into two pieces. The second one was the “Power grip
41
42 327 with thumb + Lateral thumb-index grip” in one sequence involving a subadult female in the
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44 328 same context (i.e., prehension of one item broken into two pieces).

45
46
47 329 The manipulative repertoire was significantly larger in adults with 43 grips associations
48
49 330 and graspingle postures used in isolation ~~used against~~ compared with 24 in juveniles (Pearson's
50
51 331 Chi-squared test, $p<0.05$). We also detected 21 grips associations and graspingle postures
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53 332 used in isolation in the two subadult individuals. But the number of distinct grip associations
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55 333 and graspingle postures used in isolation ~~used-observed~~ per individual was not significantly
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3 334 different between the three age categories (mean_{adults} ± SEM=13 ± 1; mean_{subadults} ± SEM=14
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5 335 ± 6; mean_{juveniles} ± SEM=9 ± 2;) (Kruskal-Wallis test: khi2= 2.8006, df=2, p > 0.05). The most
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7
8 336 frequent grip associations or grasping postures used in isolation were the same in the three
9
10 337 age categories: “lateral thumb-index grip” (N=145/416 or 35% of the sequences in adults,
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12 338 N=58/135 or 43% of the sequences in subadults and N=122/241 or 51% of the sequences in
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14 339 juveniles; Table 5) and “power grip with thumb” (N=62/416 or 16% of the sequences in adults,
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16 340 N=25/135 or 19% of the sequences in subadults and N=48/241 or 20% of the sequences in
17
18 341 juveniles; Table 5). The major differences between adults and juveniles was the use of the fifth
19
20 342 finger for probing in adults and the middle finger in juveniles. Unlike the adults, the juveniles
21
22 343 did not use the “cup hold” grip and the “lateral thumb index” in grip associations.
23
24 344 Furthermore, juvenile individuals only used the “palmar scissor hold” grip and never used the
25
26 345 other variant (i.e., “dorsal scissor hold” grip). They also did not use the “finger tips support”
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28 346 to maintain the food item.

29
30 347 The number of distinct grip associations and graspingle postures used in isolation per
31
32 348 individual was not significantly different between males (N=6/17 individuals; mean ± SEM=12
33
34 349 ± 1) and females (N=11/17 individuals; mean ± SEM=11 ± 2) (Wilcoxon test, W=31, p > 0.05).
35
36 350 The manipulative repertoire was slightly larger in females with 42 grips associations and
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38 351 graspingle postures used in isolation used against compared with 35 in males but this
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40 352 difference was not significant when weighted by the number of individuals (Fisher's Exact Test,
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42 353 p>0.05).

43 354

4. Tool use

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45 356 Branches were used as tools to reach food in about 10% of the sequences (N=81/792;
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47 357 Table 1). Sequences with tool use included 27 grip associations and graspingle postures used

358 in isolation (i.e., 55.1% of the whole repertoire) of which 8 (i.e., 16.5% of the repertoire) are
359 not found in sequences without tools (Table 5).

360 We observed tool use in the three age categories (4/9 individuals in adults, 1/2 in
361 subadults and 1/6 in juveniles) and there was no significant difference in frequencies between
362 these categories (Fisher's exact test, $p > 0.05$) (Table 3).

363 The use of tools occurred significantly more frequently in female (N=77/530 or 15% of
364 the sequences in 11 individuals) than in males (N=4/262 or 2% of the sequences in 6
365 individuals) (Pearson's chi-squared test, $p < 0.05$).

367 Discussion

368 Despite the long-recognized importance of hand functionality in hominid evolution
369 (Almécija et al., 2015; Harrison & Rein, 2016; Kivell, 2015; Pouydebat et al., 2008), little is
370 known about the manipulative repertoire of bonobos, either in natural conditions or in zoos.
371 Our study provides the first description of the manipulative repertoire spontaneously used by
372 zoo-housed bonobos in a feeding context and is the first to include diverse foods and physical
373 environments. Our analyses show a large manipulative repertoire, including precision and
374 power grips, ~~as well as one new grasping posture, labeled "dorsal scissor hold"~~. This study
375 also shows the enrichment of this manipulative repertoire from juveniles to adult individuals.
376 The following discussion details the implications of our findings with regard to the evolution
377 of manual abilities in hominids.

379 1. A large manipulative repertoire and preferred grasping postures

380 The aim of our study was to provide a first description of the spontaneous repertoire
381 used by bonobos in a feeding context, under zoo conditions. Our hypothesis was that bonobos

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3 382 could use a much wider range of manipulative behaviors than those described previously in a
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6 383 tool-use context because of a greater variety of consumed food and environments than in
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8 384 experimental settings. We also expected to ~~describe~~observe a similar variety of manual
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10 385 postures to that documented in chimpanzees given their ~~closely~~ similar hand anatomy. Our
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12
13 386 results confirm these predictions with a wide variety of grip categories, from precision to
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15 387 power grips. This species has proportionally longer fingers and shorter thumb than humans,
16
17 388 and lacks a true flexor pollicis longus muscle (FPL) (Marzke & Wullstein, 1996; Susman, 1998;
18
19 389 van Leeuwen et al., 2018), all of which constrain the use of powerful opposition of the thumb
20
21
22 390 to the other digits in comparison to human hands. The use of precision grips, close to those
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24 391 used by humans, confirms the results of previous studies in bonobos for both tool use (Bardo
25
26 392 et al., 2016) and for grasping small items (Christel, 1993; Christel et al., 1998). Our study
27
28 393 supports the general capacities of great apes to manipulate items with a great variety of
29
30 394 grasping postures since we have identified 22 distinct grasping postures used in 49 grip
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32 395 associations and graspingle postures. ~~Twenty-one used in isolation. All the~~ grasping postures
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35 396 of the repertoire were already described in the literature on apes and humans (Bardo et al.,
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37 397 2016, 2017; Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier,
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39 398 1956; Parry, 1966; Pouydebat et al., 2011), ~~and we described one new variant (i.e., the "dorsal~~
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41
42 399 ~~scissor hold") never observed in other species, including chimpanzees. These but these new~~
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45 400 data enrich our knowledge on grasping postures and grip associations variety in bonobos.
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49 401 In our study a focus has been made on the compound grips as there is a lack of their
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51 402 description in bonobos and more broadly, few studies have taken them into account in non-
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53 403 human primates (e.g., "digit role differentiation" and "compound grips" in gorillas (*Gorilla*
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55 404 *gorilla beringei*) in respectively Byrne et al., 2001 and Neufuss et al., 2018; "unimanual
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57 405 multitasking" in chimpanzees in Corp & Byrne, 2002; "compound grips" in macaques (*Macaca*
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3 406 *mulatta*) in Macfarlane & Graziano, 2009 and in capuchins in Jones and Fragaszy, 2020) (and
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5
6 407 see the review of Fragaszy & Crast (2016)). Only two cases were recorded in our study because
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8 408 of our consideration of one item in a time according to our definition of a manipulative
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10 409 sequence. These two cases correspond to one item broken into two pieces but we suspect
11
12 410 that the study of storage behavior, especially in a competitive environment like in zoo,
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14 411 including the manipulation of several items ~~in~~ at the same time, would have led to many
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16
17 412 more observations of compound grips. As described in the literature (and named “the one-
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19 413 handed storage grip” in Macfarlane & Graziano, 2009), the two compound grips were an
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21 414 association between a power grip (“power grip with thumb”) used to store the first piece
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23 415 against the palm and a more precise grip (respectively “lateral thumb index grip” and “palmar
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25 416 scissor hold”) involving two digits. These compound grips involve a high level of coordination
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27 417 with independent digit movements. So, despite the low frequency of these behaviors in our
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29 418 study, our results confirm this ability in bonobos, as previously shown in chimpanzees.
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31 419 Furthermore, although present, the in-hand movements have not been considered in this
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33 420 study. But, the passage from one grip to another, without a change of hand, are “transfer
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35 421 movements” (Fragaszy & Crast ,2016). These would be interesting to describe in the
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37 422 manipulative behavior as a dynamic process in further studies (Bardo et al., 2016).
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44 423 The existence of preferred grasping postures in bonobos is consistent with previous
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46 424 results in human and other great apes (e.g., Christel, 1993; Pouydebat et al., 2011; Bardo et
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48 425 al., 2016). In our study, the most frequent grasping posture is the “lateral thumb index grip”,
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50 426 as also reported in the literature, whether it involves tools (Bardo et al., 2016) or to grasp
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52 427 small objects (Christel et al., 1998). The second preferred grasping postures used by the
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54 428 bonobos were the power grips involving the thumb and without the thumb. This strong
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56 429 preference for powerful postures has been described in stone hammer tasks in sanctuary
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3 430 (Neufuss et al., 2017) but these postures were not as frequent in previous studies focusing on
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6 431 tool use (Bardo et al., 2016) or small object manipulation (Christel et al., 1998). Thus, this is
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8 432 the first report showing a high prevalence of the powerful postures used by bonobos coping
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10 433 with a wide range of food items (in size, shape and hardness) not exclusively in a tool use
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12 434 context. This result is also consistent with the manipulation of large objects in chimpanzees,
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14 435 in which the preferred grasping postures are the “power grips” (Pouydebat et al., 2011). Our
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16 436 results highlight the importance of considering the size and shape of manipulated objects in
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18 437 studies addressing manipulation of food/objects/tools, in non-human primates as well as
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20 438 humans, to better understand the evolution of these behaviors (e.g., Key et al., 2018;
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22 439 Pouydebat et al., 2009).

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27 440 Despite their marked differences in whether or not to use tools in natural conditions
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29 441 (but see Hohmann & Fruth, 2003), chimpanzees and bonobos are very similar not only in their
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31 442 hand morphology (Diogo et al., 2017; Druelle et al., 2018; van Leeuwen et al., 2018), but also
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33 443 in their manipulative abilities. However, some differences appear when comparing our
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35 444 findings to the literature on apes, specifically the preference for the “palmar thumb index”
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37 445 grip in human and chimpanzees with small object manipulation (including both “tip-to-tip”
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39 446 and “pad-to-pad” grips) (Christel, 1993; Pouydebat et al., 2011). Nevertheless, our findings
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41 447 confirm the ability of bonobos to execute this grip. Our observations suggest that bonobos are
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43 448 not markedly different from chimpanzees in terms of morphological constraints associated
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45 449 with food manipulation. This supports the hypothesis that the functional mechanisms
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47 450 underlying flexible manipulation are shared by both species and would have already been
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49 451 present in their common ancestor.

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2. Sex and age influence on the manipulative repertoire

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3 454 Based on the literature in chimpanzees, our predictions were a more limited
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6 455 manipulative repertoire in juveniles and no significant differences between sexes. These are
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8 456 confirmed by our results showing that juveniles used less diverse grip associations and
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10 457 grasping postures used in isolation than adults, and that males and females used the same
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12
13 458 diversity of grip associations and grasping postures used in isolation.

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15 459 ~~Nevertheless, while~~While sharing the same preference for the “lateral thumb index
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18 460 grip” in adults and juveniles, juvenile individuals also used the precision grips as the “palmar
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20 461 thumb-index grip” and the “dynamic tripod grip”, showing the same ability as the adults to
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23 462 use precision in their manipulative behavior. These results are consistent with the previous
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25 463 studies in young chimpanzees where they used the two categories (i.e., precise and unprecise
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27 464 grips) but more often “the unprecise grip category” (Pouydebat et al., 2011) including the use
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29
30 465 of the lateral side of the index finger. But the third precision grip of our study, the “middle-
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32 466 thumb grip”, has not been observed in juveniles. This result suggests that this grip could be an
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35 467 additional manipulative strategy developed by individuals later in ontogeny. A study focusing
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37 468 on mother-juvenile pairs would be useful to evaluate the resemblance between mother and
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40 469 juvenile manipulative repertoire and to better understand the developmental processes of
41
42 470 the manipulative behaviors in bonobos, especially the influence of individual and social
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45 471 learning (Hayashi et al., 2006). Indeed, young chimpanzees are particularly observant of their
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47 472 mother’s behavior while they use tools (Biro et al., 2003; Lonsdorf, 2005).

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49 473 Besides sex and age, additional individual parameters also could be important in the
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51
52 474 range of the manipulative repertoire and the preference for grasping postures, as suggested
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54 475 by the inter-individual differences found in previous manipulative studies in zoo and sanctuary
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56
57 476 bonobos (Bardo et al., 2016; Neufuss et al., 2017) and chimpanzees (Pouydebat et al., 2011).
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59 477 Social status could be particularly important (Garber et al., 2009) in bonobos since dominant
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3 478 females are less impacted by intra-group feeding competition and can spend more time
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5 479 manipulating food compared to males. So, it is needed, especially in complex social structures
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8 480 such as bonobo communities, to incorporate not only the ecological context but also the
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10 481 individual and social parameters in a further study.
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15 483 **3. Tool-use**

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18 484 Our prediction about tool-use was that this context offers only a partial description of
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20 485 the full manipulative repertoire. Based on previous studies about tool-use in bonobos (Boose
21
22 486 et al., 2013; Gruber et al., 2010), our second hypothesis was a more frequent use of tools in
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24
25 487 females. First, we observed a spontaneous use of tools (i.e., branches) to enhance the access
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28 488 to food, confirming the morphological and cognitive abilities of this species to use tools, as
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30 489 shown previously in zoo and semi-free ranging conditions (Bardo et al., 2015, 2016; Boose et
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32 490 al., 2013; Takeshita & Walraven, 1996; Visalberghi et al., 1995). ~~Bonobos developed eight grip~~
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35 491 ~~associations and single postures observed only when individuals used tools but they~~ During
36
37 492 tool-use, bonobos used only the half of the whole manipulative repertoire described in this
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39
40 493 study. Eight grip associations and grasping postures used in isolation of the repertoire were
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42 494 specific to this context of tool-use and never observed in sequences without tool. This result
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45 495 confirms our hypothesis that the description of the manipulative repertoire in a tool-use
46
47 496 context is not representative of the full manipulative abilities but it also highlights the need
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49
50 497 not to exclude it: to avoid missing grasping postures. Nevertheless, some grips observed in
51
52 498 previous studies on tool use in bonobos (e.g., Bardo et al., 2016; Neufuss et al., 2017) were
53
54 499 not observed. This may be due to the differences in the size and shape of the tools (e.g., stone
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56
57 500 hammer in Neufuss et al., 2017) or in the tasks (labyrinths in Bardo et al., 2016). The difference
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59 501 between males and females in the frequency of using tools, observed in our study is consistent
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3 502 with the results of previous studies. Females used tools significantly more frequently than
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5 503 males although this result needs to be confirmed with a larger number of individuals of both
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7
8 504 sexes. In the previous studies, female bonobos were quicker to learn, attempt and be
9
10 505 successful at using tools (Boose et al., 2013) and used tools in a larger range of contexts than
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12 506 males (Gruber et al., 2010). These results are similar to those described in chimpanzees (e.g.,
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14 507 Lonsdorf, 2005; W. McGrew, 1979) suggesting that this sex-biased behavior was already
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16 508 present in the *Pan* common ancestor, around 1 million years ago (Won & Hey, 2005). From an
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18 509 evolutionary perspective, the socio-ecological models suggest that the “key strategy” for
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20 510 females is the feeding strategy in contrast to males who are more limited by their access to
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23 511 reproduction (Wrangham, 1980). Thus, this greater tool-use propensity in females could have
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25
26 512 evolved to enhance the access to their limiting factor: feeding resources (Gruber et al., 2010).
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32 514 Finally, in an evolutionary context, research on tool use behavior of nonhuman
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34 515 primates has contributed to development of theories of evolution of human language, brain
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36 516 and tool-using (Greenfield, 1991; Parker & Gibson, 1979; Washburn, 1960) but all kind of
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38 517 manipulative skills are instructive. An extensive knowledge about manipulation in different
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40 518 ecological contexts is needed to improve our understanding of evolution of foraging behaviors
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43 519 and ecological strategies.
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48 49 521 **Conclusion**

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51 522 Manipulating food is part of the foraging strategies. In this context, knowing the
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53 523 differences and/or similitudes between humans and our closest living relatives, especially
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55 524 chimpanzees and bonobos, is of critical importance for our understanding of the evolutionary
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57 525 origins of hominid patterns of foraging strategies. In our study, we revealed a range of
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3 526 manipulative abilities in bonobos similar to that previously described in chimpanzees, from
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6 527 precision to power grips. The comparison of our results with data on free-ranging bonobos in
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8 528 further studies is now essential to have an insight into the flexibility of manipulative behaviors
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10 529 in bonobo. More broadly, the investigation of manipulative behavior as a more complete
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13 530 dynamic process and including a consideration of the socio-ecological context is needed to go
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15 531 further into our understanding of the mechanisms underlying bonobos manipulative
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17
18 532 strategies.

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41
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43
44
45 543 the experiments: CG. Analyzed the data: CG. Wrote the manuscript: CG, AB, VN, BS.

46
47 544 The data that support the findings of this study are available from the corresponding author
48
49
50 545 upon reasonable request. All authors have no conflict of interest (any potential sources of
51
52 546 conflict of interest that could inappropriately influence their work and objectivity) to declare.

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Tables:**Table 1.** Distribution and characteristics of the sample of manipulative sequences.

	N sequences	Proportion of the sample (%)	ID
Total	792	100	17
With manual manipulation	661	83.46	17
With unimanual manipulation	615	77.65	17
With bimanual manipulation	115	14.52	12
With pedal manipulation	9	1.14	4
With the mouth <u>only</u>	131	16.54	10
Without tool	711	89.77	17
With tool	81	10.23	6
Complete	769	97.10	17
Incomplete	23	2.90	NA






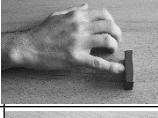

Table 2. Variability of grasping postures involving the hands: occurrence in isolation or in grip associations (number of sequences) and individuals using them in isolation or in grip associations.




Grip category	Name in the literature	Reference(s)	Name	Description	Occurrence in N sequences (/792)			Used by N individuals (/17)			Illustration
					Total	In isolation	In grip associations	Total	In isolation	In grip associations	
Precision grips (PCG)	Two-jaw chuck pad-to-pad/Two-jaw chuck tip-to-tip/Two-jaw chuck pad-to-pad side	Marzke and Wullstein 1996; Bardo et al. 2017	Palmar thumb-index grip	Item held between the distal phalanges of the thumb and the index finger.	60	59	1	11	11	1	
	Thumb tip/pad to any part of distal phalanx of middle finger	Jones-Engel 1996	Thumb-middle grip	Item held between the distal phalanges of the thumb and the middle finger.	18	18	0	3	3	0	
	Dynamic tripod grip	Wynn-Parry 1966	Dynamic tripod grip	Item held between radial side of third finger and thumb pulp, with index pulp on top of the item.	10	9	9	3	3	3	

1 2 3 4 5 6 7 8	Thumb lateral (TL)	Two-jaw chuck tip-to-side/Two-jaw chuck pad-to-side	Marzke and Wullstein 1996; Bardo et al. 2017	Lateral thumb-index grip	Item held between the thumb and side of the pad of the index finger.	375	325	54	17	17	7	
9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46	Without thumb (WT)	Scissor held	Marzke et al. 2015	Palmar scissor or hold (palmar)	Item held between the index and middle fingers, <u>and grasped</u> with the hand in <u>pronation</u> oriented <u>palmary relative to the item</u> . The <u>index and middle fingers can be lightly flexed or not</u> .	72	71	4	15	15	4	
Dorsal scissor or hold (dorsal)				Item held between the flexed index and middle fingers, <u>and grasped</u> with the hand in <u>supination</u> , oriented <u>dorsally relative to the item</u> . The <u>index and middle fingers are flexed</u> .	10	10	0	5	5	0		
Fingers hook				Marzke and Wullstein 1996	Fingers hook	Item enclosed by 2 or 3 flexed fingers.	20	15	6	12	11	5

	Index finger hook		Index finger hook	Item enclosed by the flexed index.	7	4	3	5	3	2	
Palm grips (PMG)	Cup held	Marzke and Wullstein 1996	Cup hold	Item held with the palm of the supinated hand and the lightly flexed joined 4 fingers, except the thumb.	6	4	2	3	2	2	
			Cup hold with thumb	Item held with the palm of the supinated hand and the lightly flexed joined 4 fingers and with a pressure applied by the opposed thumb.	2	2	0	2	2	0	
	Brush grasp	Bardo et al. 2017	Brush grasp	The 5 fingers are gathered along the item with the object end against the palm.	9	9	0	8	8	0	
	Power grip	Bardo et al. 2017	Power grip	Item held in opposition between the palm and flexed fingers, except the thumb.	49	32	18	9	9	2	

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			Power grip with thumb	Item held in opposition between the palm and flexed fingers with a pressure applied by the opposed thumb.	158	138	69	16	16	12	
Other grips (OG)	V pocket	Marzke et al. 2015	V pocket	Item held in web between full thumb and index finger, other fingers are flexed but not in contact with the item.	34	28	7	11	10	3	
Manipulative finger movements (MFM)	Finger probe	Marzke and Wullstein 1996	Index finger probe	Item probed by the extended index finger.	38	13	26	8	2	7	
			Thumb probe	Item probed by the extended thumb.	12	2	10	5	1	4	
			Middle finger probe	Item probed by the extended middle finger.	3	3	0	1	1	0	
			Fifth finger probe	Item probed by the extended fifth finger.	20	0	20	1	0	1	
			Fingers contact	Item moved by the distal phalanges of 2 or 3 fingers.	12	11	1	7	6	1	

			Index finger contact	Item moved by the distal phalange of the index finger.	43	41	8	8	8	4	
			Middle finger contact	Item moved by the distal phalange of the middle finger.	3	3	0	3	3	0	
	Finger tips support	Bardo et al. 2017	Finger tips support	Item maintained by the tips of 4 or 5 fingers, but not held.	34	1	34	2	1	2	

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Table 3. Distribution and characteristics of the sample of manipulative sequences in every age category (adults, subadults and juveniles).

Age category	Adults	Subadults	Juveniles
N total sequences (/792)	416	135	241
N sequences with manual manipulation	333	106	222
N sequences with the mouth only	83	29	19
N sequences with pedal manipulation	3	0	6
N sequences with tool use	55	3	23

Table 4. Variability of grasping postures involving the feet: occurrence (number of sequences) and number of individuals using them in the whole sample (total) and in every age category (adults, subadults and juveniles).

Name	Description	Occurrence in N sequences				Used by N individuals			
		Adults (/416)	Subadults (/135)	Juveniles (/241)	Total (/792)	Adults (/9)	Subadults (/2)	Juveniles (/6)	Total (/17)
Power grip with first toe	Item held in opposition between the sole and flexed toes with a pressure applied by the first toe.	3	0	6	9	2	0	2	4
Foot V pocket	Item held in web between full first and second toes, other toes are not in contact with the item.	0	0	1	1	0	0	1	1

Table 5. Variability of grip associations (in bimanual manipulation or compound grips) and grasping postures ~~used alone~~ used in isolation: occurrence (number of sequences) with and without tool and number of individuals using them in the whole sample (total) and in every age category (adults, subadults and juveniles).

Grip associations and grasping postures <u>in isolation</u>	Occurrence in N sequences				N sequences with tool (/81)	N sequences without tool (/580)	Used by N individuals			
	Adults (/333)	Subadults (/106)	Juveniles (/222)	Total (/631)			Adults (/9)	Subadults (/2)	Juveniles (/6)	Total (/17)
Brush grasp	5		4	9	1	8	5		3	8
Cup hold	1		3	4		4	1		1	2
Cup hold + Power grip with thumb	2			2		2	2			2
Cup hold with thumb	2			2		2	2			2
Dorsal scissor hold	8	2		10	1	9	4	1		5
Dynamic tripod grip	1	7	1	9	1	8	1	1	1	3
Dynamic tripod grip + Dynamic tripod grip	1			1	1		1			1
Dynamic tripod grip + V pocket			1	1		1			1	1
Fifth finger probe + Power grip	17			17		17	1			1
Fifth finger probe + Power grip with thumb	20			20		20	1			1
Finger tips support	1			1	1		1			1

Finger tips support + Lateral thumb-index grip	33			33	33		1			1
Finger tips support + Power grip with thumb	1			1		1	1			1
Finger tips support + V pocket	1			1	1		1			1
Fingers contact	6	2	3	11	2	9	2	1	3	6
Fingers contact + Index finger contact	1			1		1	1			1
Fingers hook	8	1	6	15	2	13	7	1	3	11
Fingers hook + Palmar thumb- index grip	1			1	1		1			1
Fingers hook + Power grip with thumb	2		3	5	1	4	2		2	4
Index finger contact	31	6	4	41	1	40	6	1	1	8
Index finger contact + Index finger contact	6	1		7		7	3	1		4
Index finger hook	3	1		4		4	2	1		3
Index finger hook + Index finger probe			2	2		2			1	1
Index finger hook + Power grip with thumb	1		2	3		3	1		1	2
Index finger probe	1		12	13		13	1		1	2
Index finger probe + Dynamic tripod grip	1	3		4	1	3	1	1		2
Index finger probe + Lateral thumb-index grip	1			1		1	1			1

Index finger probe + Power grip with thumb		14	4	18	1	17		2	2	4
Index finger probe + V pocket	2			2	2		1			1
Lateral thumb-index grip	145	58	122	325	9	316	9	2	6	17
Lateral thumb-index grip + Lateral thumb-index grip	2			2	1	1	2			2
Lateral thumb-index grip + Thumb probe	1			1		1	1			1
Middle finger contact	3			3	1	2	3			3
Middle finger probe			3	3		3			1	1
Palmar scissor hold	48	9	14	71		71	9	2	4	15
Palmar scissor hold + Power grip with thumb	4			4		4	4			4
Palmar thumb-index grip	42	1	16	59	2	57	6	1	4	11
Power grip	6	1	25	32	20	12	4	1	4	10
Power grip + Power grip with thumb	1			1	1		1			1
Power grip with thumb	62	25	48	135	15	120	8	2	1	16
Power grip with thumb + Dynamic tripod grip	2			2	2		1			1
Power grip with thumb + Lateral thumb-index grip	15	4	1	20	16	4	4	2	1	6
Power grip with thumb + Power grip with thumb	4	1		5	3	2	2	1		3

Power grip with thumb + Thumb probe	2	3	1	6		6	1	1	1	3
Power grip with thumb + V pocket	1	1	2	4	1	3	1	1	1	3
Thumb probe			2	2		2			1	1
Thumb probe + Dynamic tripod grip		3	1	4		4		1	1	2
Thumb-middle grip	14	4		18		18	2	1		3
V pocket	11	5	12	28	8	20	5	2	3	10

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Figures:



Figure 1. The three substrates of food manipulation in the bonobos' indoor enclosure in La Vallée des Singes (France): a. the ceiling grid, b. the platforms, c. the ground. (©C. Gérard)

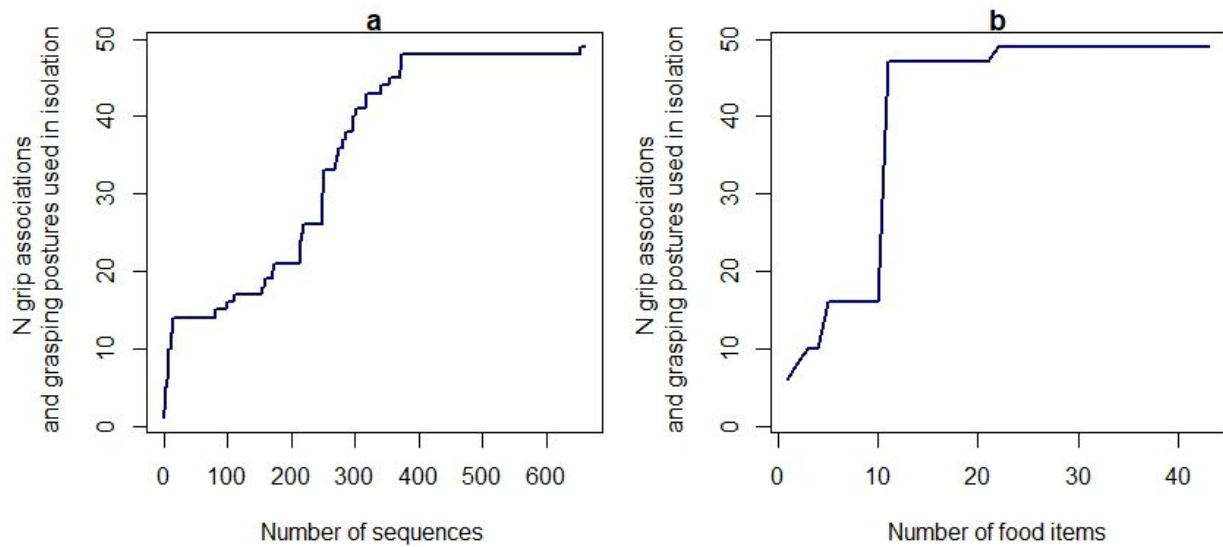


Figure 2. Accumulation curves representing the cumulative number of grip associations and grasping postures used in isolation observed as a function of the number of sequences (a) and number of food items (b). The 17 individuals of the group are represented in this sample (mean \pm SEM = 47 ± 5 sequences per individual; min = 19; max = 89).

Supporting information

Appendix 1. List of the 43 food items handled by the bonobos of the group in the scored videos. Vegetables were distributed in their whole or cut by the zookeepers before being distributed, with different cutting sizes (N) (from the whole vegetable to a small stick).

Food	N cutting sizes
Black radish	1
Broccoli	3
Cake	1
Carrot	4
Cauliflower	6
Celery	4
Cucumber	2
Endive	2
Green cabbage	5
Hazel bark	1
Hazel catkins	1
Leek	4
Lettuce	2
Oak leaf	1
Onion	2
Pepper	2
Seeds	1
Zucchini	1