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Manipulative repertoire of bonobos (*Pan paniscus*) in spontaneous feeding situation: the influence of food properties and context highlighted by new methodological approaches

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3 1 **Manipulative repertoire of bonobos (*Pan paniscus*) in spontaneous feeding situation: the**
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5 2 **influence of food properties and context highlighted by new methodological approaches**
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10 4 **Short title: Repertoire of food manipulation in zoo bonobos**
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Abstract

In contrast to chimpanzees, the study of bonobos' manipulative abilities has been carried out in experimental contexts ~~essentially~~ related to tool use. The objective of the present study is to describe the richness of the manipulative repertoire of ~~zoo~~ bonobos, in a spontaneous feeding context including various physical substrates to gain a larger insight into our evolutionary past. In order to characterize the manipulative strategies spontaneously employed by bonobos, we performed a sequential analysis of manual postures during a complete feeding sequence. We analyzed the performance with an effectiveness score defined as the food intake (i.e, in number of mouthfuls) related to the manipulative effort (i.e, diversity and changes of manual postures) during the sequence. Our study describe a great variety of grasping postures and different strategies, used differently depending on the environmental context and the morphometric properties of food. Our results also show that the manipulative effort is higher for large foods and on substrates with less ~~stability~~. But the effectiveness is not significantly lower for these items since the effort seems to be compensated by a greater number of mouthfuls. It appears that the strategy employed ~~involve~~ a trade-off between the complexity of the manipulation and the food intake obtained and would be linked to the cost-benefit balance. This study is the first to provide a broad description of the bonobo manipulative repertoire and allowed us to test and validate innovative analysis methods that are applicable to a large number of ethological studies.

Keywords: *Pan paniscus*, food manipulation, grasping posture, food properties, sequential analysis

49 Introduction

50 Grasping ability (i.e., “movements in which an object is seized and held securely partly
51 or wholly within the hand” (Napier, 1956, p.902) or the foot) and more broadly manual
52 dexterity (i.e., “the ability to make coordinated hand and finger movements to grasp and
53 manipulate objects” (Makofske, 2011, p.1522)) in hominids has been an important subject of
54 interest in evolutionary studies. Human hand is traditionally considered as having a unique
55 high degree of dexterity compared to other primates (Key et al., 2018; Marzke, 2013; Marzke
56 et al., 1992), such as forceful precision grips between the pad of the thumb and the pads of
57 the fingers and complex intra-manual precision manipulative movements (Kivell, 2015;
58 Marzke, 1997, 2013; Marzke et al., 2015; Napier, 1960; Pouydebat et al., 2011). Morphological
59 evidence on fossils shows that, in early hominids, the hand seems to have evolved a
60 combination of ape-like features and human-like features (Feix et al., 2015; Kivell et al., 2011).
61 Comparative behavioral studies of hand use in our closest living relatives, in zoo and free-
62 ranging conditions, can then improve our understanding of the functional morphology of the
63 earliest hominids (Bardo et al., 2017; Feix et al., 2015; Pouydebat et al., 2008, 2011; Susman,
64 1998). The first description of manual grips in primates were made in human and chimpanzees
65 (*Pan troglodytes*), by Napier (1956, 1960), who distinguished two categories, power and
66 precision grips. Since the pioneering work conducted by Napier, more diverse types of
67 grasping postures and in-hand movements have been described in apes and humans (but see
68 also in monkeys: e.g., capuchins (G. Byrne & Suomi, 1996; Truppa et al., 2019) and macaques
69 (Macfarlane & Graziano, 2009; Pal et al., 2018)), including a wider range of manipulative
70 behaviors compared to other mammals, both in zoo and in natural conditions (e.g., Bardo et
71 al., 2017; Byrne et al., 2001; Christel, 1993; Christel et al., 1998; Crast et al., 2009; Jones-Engel
72 & Bard, 1996; Marzke & Wullstein, 1996; Neufuss et al., 2018; Pouydebat et al., 2011).

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2
3 73 Tool use in particular is thought to have been a crucial adaptation during human
4
5
6 74 evolution and the potential of tool use behavior in hominids has been central in functional
7
8 75 studies of grasping (e.g., Bardo et al., 2017; Bardo et al., 2018; Osuna-Mascaró et al., 2020).
9
10 76 Among great apes, chimpanzees (e.g., Boesch & Boesch, 1983, 1990; Goodall, 1964; Inoue-
11
12 77 Nakamura & Matsuzawa, 1997; McGrew, 2010; Sanz & Morgan, 2013), gorillas (*Gorilla gorilla*
13
14 78 *sp.*) (Breuer et al., 2005; Grueter et al., 2013; Kinani & Zimmerman, 2015; Wittiger &
15
16 79 Sunderland-Groves, 2007) and orangutans (*Pongo sp.*) (Fox et al., 1999; Meulman & van
17
18 80 Schaik, 2013; van Schaik et al., 1996) use tools in natural conditions, for social, feeding or
19
20 81 hygienic (cleaning and protection) purposes. In free-ranging bonobos (*Pan paniscus*), it has
21
22 82 only been observed in social (communication and play) and hygienic contexts (Furuichi et al.,
23
24 83 2015; Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982; Nishida et al., 1999) but studies
25
26 84 in zoos (Bardo et al., 2015, 2016; Boose et al., 2013; Takeshita & Walraven, 1996; Toth et al.,
27
28 85 1993; Visalberghi et al., 1995) or semi free-ranging conditions (i.e, sanctuary) (Gruber et al.,
29
30 86 2010; Neufuss et al., 2017) have shown their functional, behavioral and cognitive abilities to
31
32 87 modify and use different kinds of tools to enhance food accessibility.
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40 88 Studies about tool use have brought many clarifications on the ability of great apes to
41
42 89 use precision grips close to those used by humans and have then questioned the idea that the
43
44 90 human hand would be unique. But one limitation is that they often involve standardized
45
46 91 objects of small size or of uniform shape, enabling cross-species or ~~studies~~ comparisons,
47
48 92 therefore ~~giving a partial description of the whole species~~ manipulative repertoire.
49
50
51 93 Furthermore, tool use is not the only interest of non-human primate manual abilities as the
52
53 94 hand serves to explore and interact with the environment in its whole. Hand (and feet) skills
54
55 95 in primates can be observed during more diverse grasping and manipulative behaviors, such
56
57 96 as locomotion, feeding behavior and social interactions. Even if it is now known as insufficient
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1
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3 97 and **unexclusive** (as reviewed by Sussman, ~~Tab~~-Rasmussen, & Raven, 2013), one of the
4
5
6 98 historical hypotheses on the origins of grasping abilities in primates focused on the selective
7
8 99 pressures linked with food properties and the arboreal environment (Cartmill, 1974; Jones,
9
10
11 100 1916). Many studies showed the effect of food properties and arboreal substrate on grasping
12
13 101 strategies, showing how much food difficult to extract (e.g., preys) and complex arboreal
14
15 102 substrates (orientation, sizes) increase the use of the hand (MacKenzie & Iberall, 1994; Patel
16
17 103 et al., 2015; Reghem et al., 2012; Toussaint et al., 2015). The link between the shape and/or
18
19 104 the size of the object and the grasping postures used to manipulate it has already been
20
21 105 considered in some studies in human and non-human primates, especially showing that
22
23 106 precision grasping is preferentially chosen to manipulate small objects in all studied primates
24
25 107 (e.g., Key et al., 2018; Pouydebat et al., 2009). Bonobos express arboreal and terrestrial
26
27 108 feeding behaviors ~~but if~~ this environmental context has been well-studied in chimpanzees
28
29 109 since 1960s (e.g., Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996;
30
31 110 Pouydebat et al., 2011), few studies have investigated the foraging strategies, food processing
32
33 111 skills and manipulation abilities in bonobos. Furthermore, they focused on precise
34
35 112 experimental procedures with selected kind and size of food (Christel, 1993; Christel et al.,
36
37 113 1998) which may have constrained the range of manipulative behavior observed. For a better
38
39 114 understanding of the evolution of feeding strategies in primates, further research on
40
41 115 manipulation in various feeding ~~context~~, with and without tools, is needed as the ecological
42
43 116 context could have a non-negligible influence on the manipulative strategies, particularly for
44
45 117 this lesser known species.

54 118 The first aim of this study was to describe, ~~document~~ and quantify the manipulative
55
56 119 repertoire in spontaneous feeding situations, with and without tools, in zoo bonobos, with ~~all~~
57
58 120 ~~kind of food~~ they could encounter in different feeding context, both terrestrial and kind of
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3 121 arboreal structures. Our hypothesis is that bonobos can use a much wider range of
4
5 122 manipulative behaviors than the one described in a tool-use context because of a greater
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7
8 123 variety of shapes and sizes found in the consumed food than in experimental settings.
9

10 124 Secondly, we considered the manipulative sequence in its whole and the continuity of
11
12
13 125 movement between the grasping postures by using a sequence analysis method, derived from
14
15 126 molecular biology. By looking for the first time at the similarities/dissimilarities between the
16
17
18 127 sequences, we expected to distinguish several manipulative patterns, characterized by a
19
20 128 different prevalence of the grip categories between the patterns. We also expected the use of
21
22
23 129 these patterns to vary according to the morphometric properties of the manipulated food as
24
25 130 well as the physical substrate on which the individual manipulated an object (i.e, ~~terrestrial-~~
26
27 ~~like context like floor, and arboreal context such as the above ground artificial structure and~~
28 131 ~~ceiling grid).~~
29
30 132

31
32 133 The third aim of this study was to evaluate the performance of manipulation according
33
34
35 134 to the item and the substrate. We built an “effectiveness score”, defined as the food intake
36
37 135 related to the manipulative effort. Through this innovative methodological approach, we
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39
40 136 calculated this score from two manipulative parameters usually studied in the literature
41
42 137 (Bardo et al., 2016, 2017): the number of distinct grasping postures used during a sequence
43
44
45 138 and the number of posture changes during that sequence. We expected to observe an
46
47 139 influence of both the morphometric parameters of manipulated objects (i.e, morphometric
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49
50 140 measures and hardness) and the substrate on the manipulative effort and effectiveness, as
51
52 141 well as on the choice of manipulative strategies.
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54 142

57 143 **Methods**

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1
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3 144 This research adhered to the legal requirements of France and all the experiments were
4
5
6 145 carried out following the principles of laboratory animal care in accordance with the CNRS
7
8 146 guidelines. It complies with the American Society of Primatologists (ASP) Principles for the
9
10 147 Ethical Treatment of Non-Human Primates and followed the American Society of
11
12
13 148 Primatologists Code of Best Practices for Field Primatology.
14

15 149

18 150 **1. Subjects and housing**

20 151 The study was conducted from January 27, 2020 to January 31, 2020 at the zoological
21
22
23 152 park “la Vallée des singes” (France). This park houses a group of seventeen bonobos (i.e,
24
25 153 **Continuous Full Contact** (group)) composed of nine adults (six females from 16- to 52-year old
26
27 154 and three males from 15- to 23-year old), two subadults (one female and one male, both 10-
28
29 155 year old) and six juveniles (four females from 3- to 7-year old and two males of 5- and 7-year
30
31
32 156 old).
33

35 157 The bonobos were observed during the day in an indoor building where only two large
36
37 158 cages, connected to each other (98m² each), were visible. They also have access~~ed~~ to five
38
39 159 smaller cages (from 16 to 24 m²) and to a naturally vegetated outdoor island (0.7 ha) that was
40
41
42 160 accessible to the group according to the weather. Many climbing structures, made of
43
44
45 161 platforms, ladders and ropes, were ~~settled~~ in the cages.
46

47 162 At least two water taps were available *ad libitum* and the group was fed four times a
48
49 163 day. Their food ration included mainly vegetables and one fruit (i.e, apple). It was completed
50
51
52 164 by pellets, seeds, eggs, chicken necks and a homemade mix containing cereals, vitamins and
53
54 165 vegetal oils. The food was distributed on the top of the cages (i.e, ~~grid ceiling~~) or inside the
55
56
57 166 cages, on the floor and the platforms. Daily enrichment was provided with tree branches (i.e,
58
59 167 hazel or willow tree) and cooked rice placed inside tubes or wooden logs.
60

168 2. Data collection

169 2.1. Food morphometric properties

170 In order to evaluate the influence of food morphometric characteristics on the
171 manipulative behavior, morphometric measurements ~~have been~~ taken on every kind of food
172 manipulated by the bonobos of the group (Appendix 1). Vegetables were measured as
173 distributed, in their whole or cut by the zookeepers before being distributed, so every
174 category of shape and size has been measured and weighted separately. The aim of these
175 measurements was to classify food items depending on their morphometric parameters.
176 Every food item (mean \pm SD = 4 ± 2 per category) was characterized by six quantitative values,
177 except cooked rice contained in enrichments that is a particular case (not measurable in the
178 same way) and treated separately in the analysis: length (cm), width (cm), height (cm), volume
179 (cm^3), mass (gr) and hardness (N). We collected hardness data using a portable analog
180 durometer (Force Dial™ FDN 50, Wagner Instruments). The durometer plunger was applied
181 at several positions of each sample (mean \pm SD = 2.0 ± 1.5 per sample) allowing us to calculate
182 the average value (McGraw et al., 2014).

183

184 2.2. Video recording

185 One or several individuals were followed throughout a feeding session, balancing the
186 distribution of records for each individual between observation days and periods of the day.
187 The selection of focal subjects was made according to a daily list (based on the cumulative
188 previous observation days) and visibility of individuals to the observer. One handheld camera
189 (PANASONIC® HC-V380) was used to record the simultaneous movements of the ~~hand~~, feet
190 and mouth. At the end of the feeding sessions and between the meals, the foraging behavior
191 of additional individuals was recorded. The bonobos could also feed on enrichments, provided

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2
3 192 between the meals, and were recorded using the all-occurrence sampling method (Altmann,
4
5 193 1974). The recordings were performed at 50 frames/sec.
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8 194
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10 195 **2.3. Video scoring**

11 196 **2.3.1. Manipulative sequences**

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14
15 197 Video recordings were analyzed frame by frame with VLC Media Player (VideoLan,
16
17 198 2020), using the individual focal sampling method (Altmann, 1974). Videos were divided
18
19 199 according to our definition of a “manipulative sequence”, including contact, grasping and
20
21 200 manipulation of the food items. It began with the first contact between an individual and an
22
23 201 item (direct or through the use of a tool) and ended when the food was consumed in its whole
24
25 202 (whole fruit/vegetable, bunch, branch previously sectioned (small fruit, bark, buds, etc.)) or
26
27 203 abandoned before total consumption (partially or not consumed). A total of 3h30 of recorded
28
29 204 sequences were analyzed. The parameters recorded during the sequence were the individual,
30
31 205 the food consumed (categorized by species and by size, characterizing a “food item”), the
32
33 206 substrate (ground, platform or grid), the manual/foot grip adopted, the hand(s)/foot used and
34
35 207 the duration of each behavior. We recorded data with the frequencies technique (e.g.,
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37 208 Hopkins, 1995).
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47 210 **2.3.2. Grasping postures**

48
49 211 Every encountered grasping posture involving the hands or the feet was described and
50
51 212 linked to the existing literature on human and apes (Bardo et al., 2016, 2017; Jones-Engel &
52
53 213 Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier, 1956; Parry, 1966;
54
55 214 Pouydebat et al., 2011). To name the grasping postures, we used the Marzke’s ~~typology of~~
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1
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3 215 grasp and we divided them into five grip categories: Precision grips, Thumb lateral, Without
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6 216 thumb, Palm, and Other grips (see Tableau 2 for details).
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218 2.3.3. Grip associations and compound grips

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13 219 The grip associations included the cases of bimanual manipulation where the grasping
14
15 220 posture of each hand was recorded and compiled. In the case of asymmetric coordinated
16
17 221 bimanual hand movements, individuals had to hold or maintain the food or the enrichment
18
19 222 with one hand and extract or pick up the food with the other hand. The hand used to extract
20
21 223 the food was considered as dominant in some further analysis, based on previous studies
22
23 224 about coordinated bimanual action (Bardo et al., 2015; Hopkins, 1995; Meguerditchian et al.,
24
25 225 2013).
26
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30 226 We also included the compound grips (e.g., Jones & Fragaszy, 2020; Neufuss et al.,
31
32 227 2018) with which several pieces of the same item were held. It could be used when the item
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34 228 broke during the manipulation and when two grips were used in the same time with only one
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36 229 hand.
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41 230

42 231 3. Data analyses

43 44 232 3.1. Manipulative repertoire

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46
47 233 In order to describe the manipulative repertoire of this captive group of bonobos, the
48
49 234 maximum of grasping postures was observed. To assess the extent to which our observations
50
51 235 maximized the number of possible postures, we plotted two accumulation curves of the
52
53 236 number of grip associations as a function of the number of sequences or food items (Appendix
54
55 237 2a and b). Both curves plateaued, which meant that there was little benefit in carrying out
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3 238 additional sampling to extend our evaluation of the manipulative repertoire (Colwell et al.,
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5 239 2004).

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10 241 **3.2. Food items classification**

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13 242 We observed 44 food items from 19 different plants or edible species (Appendix 1)
14
15 243 during the video scoring. To classify them according to their morphometric characteristics (i.e.,
16
17 244 classification of 43 items, except for cooked rice) and simplify the analyses by decreasing the
18
19 245 variability of food items properties, a Principal Component Analysis (PCA) and a Hierarchical
20
21 246 Cluster Analysis (HCA) with Ward's method (*agnes* function of *Cluster* package; Maechler,
22
23 247 2013) were performed on the six morphometric variables (i.e, hardness, height, mass, volume,
24
25 248 length and width). A pairwise comparison (see below for statistical details) was then carried
26
27 249 out to investigate which variables were characterizing each cluster. The HCA analysis revealed
28
29 250 two clusters describing item morphometric characteristics (Appendix 3). The six
30
31 251 morphometric variables used for cluster discrimination differed significantly between the two
32
33 252 clusters (Appendix 4). The first cluster (Cluster 1) corresponds to small, light and soft items
34
35 253 and the second cluster (Cluster 2) corresponds to large, heavy and hard items. For further
36
37 254 analyses, we assigned cooked rice to a third cluster (Cluster 0) as this item was uncountable
38
39 255 and not measurable.
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49 257 **3.3. Sequences analysis and manipulative patterns**

50 51 258 **3.3.1. Optimal matching analysis**

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53
54 259 We also analyzed the sequences of manipulative behaviors by considering grip
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56 260 associations through their succession within a sequence. First of all, we calculated the pairwise
57
58 261 dissimilarities between the sequences thanks to the optimal matching analysis (i.e, calculation
59
60

1
2
3 262 of the minimal number of modifications - substitutions, deletions, insertions - that one of the
4
5
6 263 sequences must undergo to obtain another one) with the *seq.dist* function of the *TraMineR*
7
8 264 package (Gabadinho et al., 2011). Derived from molecular biology, this method is usually used
9
10 265 in social sciences to analyze time-ordered sequences of socio-economic states that individuals
11
12 266 have experienced. It is particularly adapted to analyze categorical sequence data and
13
14
15 267 retemporalize action by analyzing it as a process. To our knowledge, this method has only
16
17
18 268 been used in our field by Borel et al., 2017, in which they described and quantified the
19
20 269 sequential dynamic strategies of tool grip and manipulation of five human subjects during a
21
22 270 tool-task. Here, we considered all the modifications of the sequences (i.e, substitutions,
23
24
25 271 deletions and insertions) equally important. From the distances calculated between each pair
26
27
28 272 of sequences, we performed a Hierarchical Cluster Analysis (HCA) with Ward's method, with
29
30 273 the *agnes* function of the *Cluster* package (Maechler, 2013), in order to distinguish several
31
32 274 manipulative patterns. We created an additional cluster containing the sequences without any
33
34
35 275 manipulation (named "Manipulative pattern 0") (i.e, the item was grasped with the mouth
36
37 276 and consumed directly), corresponding to a specific foraging strategy.
38
39
40 277

41 42 278 **3.3.2. Grip categories proportions and manipulative patterns**

43
44 279 The proportion of our five grip categories in a sequence was calculated as the number
45
46
47 280 of grasping postures of the considered category divided by the number of distinct grasping
48
49
50 281 postures used in the sequence. In bimanual manipulation, we only considered the action of
51
52 282 the dominant hand (i.e, the hand extracting food) in this analyze. We performed multiple and
53
54
55 283 pairwise comparisons to figure out if the manipulative patterns (obtained with the Optimal
56
57 284 matching analysis) were characterized by some grip categories.
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3 285 **3.3.3. Manipulative patterns use according to the food item and the**
4
5
6 286 **substrate**

7
8 287 The aim was to determine the influence of the morphometric properties of the
9
10 288 manipulated food items and the physical substrates on the manipulative patterns used by the
11
12
13 289 individuals. After performing a multiple correspondence analysis (MCA) for visual evaluation
14
15 290 of the link between the three variables (i.e, food item clusters, substrates and manipulative
16
17
18 291 patterns), we considered all the possible modalities of the interaction between item clusters
19
20 292 and substrates (see above). Because of the small or null samples in some modalities, we
21
22
23 293 performed exact multinomial and binomial had hoc tests on the distribution between the
24
25 294 manipulative patterns for every item-substrate modality, by comparing them to an
26
27
28 295 homogeneous distribution (*multinom.test* and *binom.test* functions of *rstatix* package
29
30 296 (Kassambara, 2020)). We then applied a Bonferroni correction on the p-values.

31
32 297

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34
35 298 **3.4. Handling score and manipulative effectiveness**

36
37 299 In the literature, the manipulative performance during one task is evaluated using the
38
39
40 300 number of manual posture changes (C), the number of distinct grasping postures used during
41
42 301 a sequence (P) and the time needed to perform a task (Bardo et al., 2016, 2017; Neufuss et
43
44
45 302 al., 2017). Unfortunately, the first variable (C) does not distinguish the sequences without
46
47 303 manipulation (i.e, only using the mouth) from the ones involving only one grasping posture.
48
49 304 The second variable (P) did not fit with our analysis as it did not include the repetitions of
50
51
52 305 grasping postures in one manipulative sequence. We therefore created a handling score
53
54 306 associating those two first parameters:

55
56
57 307
$$\textit{Handling score (HS)} = P + C$$

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59
60

1
2
3 308 The additive rather than multiplicative term is justified by the need to allow for the distinction
4
5
6 309 of different sequences described above.

7
8 310 To evaluate the manipulative effectiveness (E), we created a second score, by
9
10 311 comparing the handling score with the number of mouthfuls counted during the sequence.
11
12 312 Effectiveness is here defined as the ratio of ingestion to the manipulative effort required for
13
14 313 processing that food, but in no way has energetic implications:

15
16
17
18 314
$$\text{Effectiveness } (E) = \frac{N \text{ mouthful}(s)}{P + C + 1}$$

19
20
21 315 For a mathematical purpose, we added the value of one to the handling score which was
22
23 316 sometimes equal to zero.

24
25
26 317 We performed multiple and pairwise comparisons on the handling score on the one
27
28 318 hand and effectiveness on the other hand, between the different item-substrate modalities
29
30 319 (N=9).

31 320 32 33 34 35 36 321 **3.5. Statistical analyses**

37
38 322 All the multiple comparisons were performed using the Kruskal-Wallis test and for
39
40 323 pairwise comparisons, we used the Wilcoxon rank sum test with Bonferroni continuity
41
42 324 correction. All statistics were computed using the R 3.6.3 statistical environment (R Core Team
43
44 325 2020).

45 46 47 48 326 49 50 327 **Results**

51 52 328 **1. Manipulative repertoire**

53 54 329 **1.1. Grasping postures**

1
2
3 330 Manual or foot manipulations accounted for 83.5% of all sequences recorded (N=792;
4
5
6 331 Table 1), and the remaining 16.5% are for the use of the mouth only. We found 22 distinct
7
8 332 grasping postures including two new variants, never described for bonobos in the literature
9
10 333 (Table 2). The thumb-middle grip (in the “precision grips” category) is a variant of the palmar
11
12 334 thumb-index grip but involving the middle finger instead of the index. The dorsal scissor hold
13
14 335 (in the “without thumb” category) is a variant of the palmar scissor hold, with the hand in
15
16 336 supination and the fingers flexed. We detected a very restraint use of the feet (N=9/792) and
17
18 337 with only two grasping postures (Table 3).

19
20
21
22 338 The most frequent grasping posture was the “lateral thumb-index grip” (N=325/792)
23
24 339 and the second most frequent were the power grips (with thumb (N=158/792) and without
25
26 340 thumb (N=49/792)). The use of branches as tools was observed in N=81/792 sequences.
27
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31 32 342 **1.2. Grip associations and compound grips**

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34
35 343 The whole repertoire included 28 distinct grip associations (bimanual manipulation or
36
37 344 compound grips) and 21 single postures (Table 4). One of the grasping postures was never
38
39 345 used alone (i.e, the “fifth finger probe” is always used in association with “power grips”) and
40
41 346 only 28 grip associations out of the 484 possible ones (N=22²) were actually observed.
42
43

44
45 347 The number of distinct grip associations per sequence ranged from 1 to 8 (mean \pm
46
47 348 SEM=1.46 \pm 0.04) and each individual used between 3 and 19 distinct associations throughout
48
49 349 ~~this study~~ (mean \pm SEM=11.4 \pm 1.16 or 23.3 \pm 2.37% of the recorded grip associations).
50
51
52 350 Branches were used as tools to reach food in about 10% of the sequences (Table 1). Sequences
53
54 351 with tool use included 27 grip associations of which 8 (i.e, 16.5% of the recorded grip
55
56 352 associations) are not found in sequences without tools.
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59 353
60

2. Manipulative patterns

3.1. Sequences classification

From the overall non-interrupted sequences recorded (N=638, including N=48/49 grip associations), 120 distinct sequences varying from 1 to 17 successive grip associations were found. We extracted six patterns of sequences from the HCA analysis, of which only four were considered in our subsequent analyses (Appendix 5). The last two indeed contained only one or two sequences and were therefore too rare and particular to be considered as general patterns. The sequences in the four patterns we considered varied from 1 to 11 successive grip associations.

3.2. Grip categories proportions and manipulative patterns

Each pattern was distinguished by one or two dominant grip categories (Figure 1). Pattern 1 was associated with precision grips (PCG) (Kruskal-Wallis test: $\chi^2=169.88$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$), pattern 2 with grips without the thumb (WT) (Kruskal-Wallis test: $\chi^2=418.78$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$), pattern 3 with lateral thumb grips (TL) (Kruskal-Wallis test: $\chi^2=401.52$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$), and finally pattern 4 was distinguished by two grip categories: palm grips (PMG) (Kruskal-Wallis test: $\chi^2=254.25$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$) and grips not included in the previous categories (OG) (Kruskal-Wallis test: $\chi^2=125.74$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$).

4. Manipulative patterns and effectiveness for various food items and substrates

4.1. Manipulative pattern use according to the food item and the substrate

1
2
3 377 We compared the prevalence of every manipulative pattern within each modality of
4
5
6 378 the interaction between the food item clusters (N=3) and the substrates (N=3) (Table 5, see
7
8 379 also Appendix 6). Significant differences were found between the manipulative patterns used
9
10 380 for all the items at the grid and on the platform (Exact multinomial tests, $p < 0.05$ except for all
11
12
13 381 the items on the ground)).

14
15 382 Pattern 0 (mouth manipulation) was significantly associated with small items on the
16
17 383 platform (Binomial had hoc test, $p < 0.001$) while pattern 1 (associated with PCG) was
18
19 384 significantly associated with cooked rice (on the grid and the platform) (Binomial had hoc
20
21 385 tests, $p < 0.001$). Pattern 2 (associated with WT) was the least frequently used (N=64/766). It
22
23 386 seemed to be prevalent for small items on all substrates (especially ground) but the difference
24
25 387 is not significant. Pattern 3 (associated with TL) was predominant especially for small items
26
27 388 (Binomial had hoc tests, $p < 0.001$), except on the ground where it was well represented but
28
29 389 the difference was not significant, and for large items on the grid (Binomial had hoc test,
30
31 390 $p < 0.001$) and the platform (Binomial had hoc test, $p < 0.05$). Lastly, pattern 4 (associated with
32
33 391 PMG and OG) was significantly associated with cooked rice on the platform (Binomial had hoc
34
35 392 test, $p < 0.001$). Grid manipulations (all items) were also well represented in this pattern 4 but
36
37 393 the difference was not significant. Finally, cooked rice was more frequently manipulated using
38
39 394 pattern 1 (at the grid) and 4 (at the grid and on platform), large items more frequently with
40
41 395 pattern 3 (at the grid and on platform) and small items with pattern 0 (on platform) and
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43 396 pattern 3 (on all substrates).

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54 398 **4.2. Handling score and manipulative effectiveness according to the food items**
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57 399 **and the substrate**

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59 400 **4.2.1. Handling score**
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1
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3 401 Figure 2a shows how the handling score varies between item-substrate modalities
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5
6 402 (Kruskal-Wallis test: $\chi^2=328.15$, $df=8$, $p<0.001$). The large items manipulated at the grid
7
8 403 required more manipulations than other items: the difference was significant when compared
9
10 404 to the cooked rice at the grid (Wilcoxon test, $p<0.05$) and to the small items on the platform
11
12 405 (Wilcoxon test, $p<0.001$) and on the ground (Wilcoxon test, $p<0.001$). Large items were more
13
14 406 rarely manipulated on the ground ($N=4$ sequences) and on the platforms ($N=8$ sequences). On
15
16 407 these substrates, the handling score differences between the large items and the others were
17
18 408 not significant (i.e, no difference or too small class size), except for the large items on the
19
20 409 platform that were significantly higher than the small items on the ground (Wilcoxon test,
21
22 410 $p<0.001$).

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24
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26
27 411 Cooked rice, whatever the substrate, was the second item that involved more
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29 412 manipulations, especially compared to the small items on the platform (Wilcoxon test,
30
31 413 $p<0.001$ for the three substrates) and on the ground (Wilcoxon test, $p<0.001$ for the three
32
33 414 substrates). The handling score appeared higher at the grid than on the platform (Wilcoxon
34
35 415 test, $p<0.05$) for this item.

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37
38
39 416 Finally, the small items required less manipulations than the other items, except at the
40
41 417 grid where the difference was not significant. The substrate had an important effect on the
42
43 418 manipulation of these items as the handling score is higher at the grid compared to the ground
44
45 419 (Wilcoxon test, $p<0.001$) and the platform (Wilcoxon test, $p<0.001$), and it is also higher on
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47 420 the ground compared to the platform (Wilcoxon test, $p<0.001$).

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53 54 422 **4.2.2. Effectiveness**

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56
57 423 The effectiveness was significantly different between some item-substrate modalities
58
59 424 (Kruskal-Wallis test: $\chi^2=254.94$, $df=8$, $p<0.001$) (Figure 2b). The effectiveness was lower for
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1
2
3 425 cooked rice whatever the substrate compared to the small items on the platform (Wilcoxon
4
5
6 426 test, $p < 0.001$ for the three substrates) and on the ground (Wilcoxon test, $p < 0.001$, for the
7
8 427 three substrates). A lower effectiveness was also observed on the platform compared to the
9
10 428 grid (Wilcoxon test, $p < 0.05$).

11
12
13 429 Manipulation of large items at the grid was less effective than the manipulation of the
14
15 430 small items on the platform (Wilcoxon test, $p < 0.05$) but there was no significant difference
16
17
18 431 between the different substrates for the large items.

19
20 432 Finally, the manipulation of small items appeared significantly more effective than the
21
22 433 one of cooked rice (except at the grid where the difference is not significant) and the one of
23
24 434 large items on the grid (except at the grid and on the ground where the differences are not
25
26 435 significant; Figure 2b). We also observed a difference in the manipulation of small items, being
27
28 436 less effective at the grid versus platform (Wilcoxon test, $p < 0.001$) and ground (Wilcoxon test,
29
30 437 $p < 0.001$), while effectiveness was lower on the ground than on the platform (Wilcoxon test,
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32 438 $p < 0.001$).

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40 440 **Discussion**

41
42 441 Our study provides the first description of the manipulative repertoire spontaneously
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44 442 used by zoo bonobos in a feeding context and by taking into account the diversity of
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46 443 manipulated food and physical environment. In addition, the use of two innovative
47
48 444 methodologies (i.e, the sequential analysis by optimal matching and the effectiveness score)
49
50 445 allowed us to study food manipulation as a dynamic process. Our main results validate our
51
52 446 hypotheses by showing a large manipulative repertoire, including two newly described
53
54 447 variants of grasping postures, and the existence of different manipulative strategies whose
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56 448 choice and effectiveness are dependent on the physical environmental context and the
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3 449 morphometric characteristics of food items. The following discussion details the implications
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6 450 of our findings with regard to the evolution of manual abilities in hominoids and the behavioral
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8 451 flexibility, depending on the decision-making context, allowed by these manipulative abilities.
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10 452

13 453 **1. Manipulative repertoire**

15 454 Despite the long-recognized importance of hand functionality in hominoid evolution
16
17 455 (Almécija et al., 2015; Harrison & Rein, 2016; Kivell, 2015; Pouydebat et al., 2008), little is
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19
20 456 known of the manipulative repertoire of our closest relative, bonobos, both in natural
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22
23 457 conditions and in zoos. The aim of our study was therefore to provide a first description of the
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25 458 spontaneous repertoire used by bonobos in a feeding context, under zoo conditions. It
26
27
28 459 includes a wide variety of grip categories, from precision to power grips, even if this species
29
30 460 show morphological constraints of their hands, such as long fingers and short thumb, and the
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32
33 461 lack of a true flexor *policis longus* muscle (FPL) (Marzke & Wullstein, 1996; Susman, 1998; van
34
35 462 Leeuwen et al., 2018). The ability of using precision grips, close to those used by humans,
36
37 463 confirms the results of previous studies in bonobos for both tool use (Bardo et al., 2016) and
38
39
40 464 grasping items (Christel, 1993; Christel et al., 1998). Our study supports the general capacities
41
42 465 of great apes to manipulate items with a great variety of grasping postures since we have
43
44
45 466 identified 22 distinct grasping postures as well as 49 grip associations and compound grips.
46
47 467 Twenty grasping postures of the repertoire were already described in the literature on apes
48
49
50 468 and humans (Bardo et al., 2016, 2017; Jones-Engel & Bard, 1996; Marzke et al., 2015; Marzke
51
52 469 & Wullstein, 1996; Napier, 1956; Parry, 1966; Pouydebat et al., 2011), and we described two
53
54 470 new variants (i.e, the “dorsal scissor hold” and the “thumb-middle grip”). We also observed a
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56
57 471 spontaneous use of tools (i.e, branches) to enhance the access to food, confirming the
58
59 472 morphological and cognitive abilities of this species to use tools, as shown previously in zoo
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1
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3 473 and semi-free ranging conditions (Bardo et al., 2015, 2016; Boose et al., 2013; Takeshita &
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5
6 474 Walraven, 1996; Visalberghi et al., 1995). The existence of preferred grasping postures in
7
8 475 bonobos is consistent with previous results in human and other great apes (e.g., Christel,
9
10 476 1993; Pouydebat et al., 2011; Bardo et al., 2016). In our study, the most frequent grasping
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12
13 477 posture is the “lateral thumb index grip”, as also reported in the literature, whether it involves
14
15 478 tools (Bardo et al., 2016) or to grasp small objects (Christel et al., 1998). The second preferred
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18 479 grasping postures used by the bonobos were the power grips involving the thumb and without
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20 480 the thumb. Therefore, this is the first report showing a high prevalence of the powerful
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22
23 481 postures used by bonobos coping with a wide range of food items (in size, shape and
24
25 482 hardness), while powerful postures were not as frequent in previous studies focusing on tool
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27
28 483 use (Bardo et al., 2016) or small object manipulation (Christel et al., 1998). This result is also
29
30 484 consistent with the manipulation of large objects in chimpanzees, in which the preferred
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32
33 485 grasping postures are the “power grips” (Pouydebat et al., 2011). This result highlights the
34
35 486 importance of considering more the size and shape of handled objects in studies working on
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37
38 487 manipulation of food/objects/tools, in non-human primates as well as humans, to better
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40 488 understand the evolution of these behaviors (e.g., (Key et al., 2018; Pouydebat et al., 2009).

41
42 489 Finally, despite their marked differences in whether or not to use tools in natural
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44
45 490 conditions, chimpanzees and bonobos are very similar not only in their hand morphology
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47 491 (Diogo et al., 2017; Druelle et al., 2018), but also in their manipulative abilities. However, some
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49
50 492 differences appear when comparing our findings to the literature on apes, specifically the
51
52 493 preference of human and chimpanzees for the “palmar thumb index” grip (including both “tip-
53
54 494 to-tip” and “pad-to-pad”) (Christel, 1993; Pouydebat et al., 2011). Nevertheless, the presence
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56
57 495 of this grip in the bonobo manipulative repertoire, as confirmed in our study, demonstrates
58
59 496 the ability of bonobos to execute this opposable fingers grip. These observations suggest that
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3 497 bonobos are not markedly different from chimpanzees in terms of cognitive and
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6 498 morphological constraints associated with food manipulation. This supports the hypothesis
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8 499 that the cognitive mechanisms underlying this flexibility of manipulative behaviors are shared
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10 500 by both species and would have already been present in their common ancestor, around 1
11
12 501 million years ago (Won & Hey, 2005). In an evolutionary context, research on tool use behavior
13
14 502 of nonhuman primates has established crucial knowledge for theories of human evolution of
15
16 503 language, brain and tool-using lifestyle (Greenfield, 1991; Parker & Gibson, 1979; Washburn,
17
18 504 1960) but all kind of manipulative skills are instructive. An extensive knowledge about
19
20 505 manipulation in different ecological contexts is needed to improve our understanding of the
21
22 506 development of foraging behaviors and ecological strategies through the evolution.
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508 **2. Manipulative strategies**

509 Our results show that bonobos can use different manipulative ways to gain access to
510 food. Our hypothesis was the existence of preferred manipulative strategies adapted to the
511 morphometric properties of the food and the environmental context (i.e, substrate). This
512 prediction was confirmed since some manipulative patterns were significantly more
513 frequently used for one or several kinds of food, according to the substrate used for stabilizing
514 the body during feeding. Together with the dominant grip categories assigned to each pattern,
515 the results show a trend to manipulate cooked rice preferentially using "Palm grips" or "Other
516 grips" (pattern 4) alone, or in association with "Precision grips" (pattern 1) when the substrate
517 is more complex (i.e, at the grid). This can be explained by the fact that the individuals can
518 reach the cooked rice contained in the enrichments by hitting the tube on the ground or on
519 the platform ("Palm grips" category), by probing with their fingers ("Other grips" category) or
520 by using a tool ("Precision grips" category and "V pocket grip" for storage (i.e, keeping a tool

1
2
3 521 in the hand or foot without using it)). The two last cases are bimanual manipulation as it
4
5 522 requires to stabilize the enrichment with the other hand (“Palm grips” or “Other grips”
6
7
8 523 categories).

9
10 524 The “Without-thumb grips” (pattern 2) and “Thumb-lateral grip” (pattern 3) are less
11
12
13 525 specific to one kind of food or substrate. In contrast, manipulation with only the mouth
14
15 526 (pattern 0) occurs almost exclusively with small items on the platform. This can be explained
16
17
18 527 by the absence of dirt and sand on this substrate, allowing an easier grasping of the small
19
20 528 items without foraging as suggested in the study of Christel et al. (1998) while grasping small
21
22
23 529 objects on a cleaner floor required less time than on grassy/sandy ground.

24
25 530 Our result show that the chosen manipulative strategy can differ between the
26
27
28 531 substrates for a same kind of item (i.e, cluster), depending on the substrate and confirming
29
30 532 the necessity to consider the interaction between the two parameters. Furthermore, while
31
32
33 533 some patterns are strongly associated with some modalities of item and substrate, we
34
35 534 observed different manipulative strategies for a same item-substrate modality. The choice of
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37
38 535 one specific strategy by bonobos is supposed to enhance the access to the targeted food.
39
40 536 When we looked at the manipulative effort (i.e, the complexity of manipulation) and the
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43 537 effectiveness (i.e, the food intake related to the manipulative effort) of the chosen strategy
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45 538 for every item-substrate modalities, we observed an association: the greater the manipulative
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47
48 539 effort, the lower the effectiveness. This rule was not strictly generalizable however, as the
49
50 540 great number of manipulations for large items seemed to be compensated by a large number
51
52 541 of mouthfuls ingested. This result suggests the existence of a trade-off between the
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54
55 542 manipulation effort and the food intake. It may be as efficient to process many small items
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57 543 (i.e, multiple lower effort) with many low intake ratios as few large items (i.e, higher effort)
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59 544 with a high intake ratio.
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3 545 Furthermore, we did not observe any difference of effectiveness between the different
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6 546 substrates for the large items: this can be explained by the fact that the largest items do not
7
8 547 pass through the bars of the grid without manipulation. During our observations, the large
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10 548 items were more rarely manipulated on the ground and on the platforms. In contrast, we
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12
13 549 observed a difference of effectiveness for small items where manipulation at the grid appears
14
15 550 significantly less effective than on the platform and ground. Contrary to the large items, the
16
17
18 551 complexity of manipulation imposed by the grid would not be compensated by the low
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20 552 number of mouthfuls. A lower effectiveness is also observed on the ground compared to the
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22
23 553 platform. This can be explained by the presence of dirt and sand inducing a greater number
24
25 554 of manipulations to isolate the item. Finally, even if the grid makes manipulation more
26
27
28 555 complex, it has a significant advantage related to the presence of the majority of the largest
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30 556 foods (79%). This link between the substrate choice and the position of the food has already
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32
33 557 been shown in other primates (*Microcebus murinus*, Toussaint et al., 2015). However, it
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35 558 remains significantly less effective than the manipulation of small items on the platform.
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37 559 Although it contains a majority of small items (75%), the platform has the advantage to
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39
40 560 present a support making manipulation simpler (stability and rarity of dirt and sand).

41
42 561 Our results highlight differences in manipulative strategies, and suggest the existence
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44 562 of a trade-off between manipulative complexity and quantity of food ingested. Furthermore,
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46
47 563 the variability observed in the choice of the manipulative pattern for each item and substrate,
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49
50 564 and the effectiveness of the chosen strategy could be linked to the individual decision-making
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52 565 process in bonobos. Indeed, primate foragers face daily challenges for which they have to
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54 566 regulate the balance between the costs and benefits for accessing the food (Garcia et al.,
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56
57 567 2021). As shown in research about primate decision-making, foraging decisions require the
58
59 568 integration of multiple information, both ecological (food type and quantity, travelling
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3 569 distance, temporal information, eventuality of predation) and social (presence and identity of
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5 570 congeners, including kinship and social status) (Garber et al., 2009; Rosati & Hare, 2012).
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7
8 571 Depending on the set of conditions, the foraging decisions can then differ for a same kind and
9
10 572 amount of food, leading to divergent behavioral tactics and, in our study, to variable
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12 573 manipulative strategies. From the few studies available about decision-making process in
13
14 574 bonobos, we know that compared to chimpanzees, they have a lower tolerance for risk in
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16 575 choices about food (Heilbronner et al., 2008), hypothetically linked to a less competitive and
17
18 576 variable environment (Doran et al., 2002; Furuichi et al., 2015; Hohmann & Fruth, 2003) (but
19
20 577 see also Koops, et al., 2015). But in the context of zoo, where the intragroup competition is
21
22 578 high and the food is not *ad libitum* but regularly distributed, the interest of risky choices (i.e,
23
24 579 carrying out a more complex manipulation is not always compensated by the quantity of
25
26 580 ingested food and induces a higher risk of theft by congeners) could be enhanced. The
27
28 581 individual parameters also are of critical importance in this decision process, as suggested by
29
30 582 the inter-individual differences found in previous manipulative studies in zoo bonobos (Bardo
31
32 583 et al., 2016) and chimpanzees (Pouydebat et al., 2011). Besides the physiological state of the
33
34 584 individual such as its satiation level and energy status (see the risk-prone strategy in
35
36 585 chimpanzees during periods of high diet quality; Gilby & Wrangham, 2007), age, sex and/or
37
38 586 social status could induce different manipulative strategies for a same food item. Indeed, the
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40 587 manipulative behavior, as part of the whole foraging behavior, could be reinforced by social
41
42 588 learning and/or operant conditioning and become more precise with growing age (Bouton,
43
44 589 2007). Sex and social status could also be important (Garber et al., 2009) while dominant
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46 590 females are less impacted by intra-group feeding competition and can spend more time
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48 591 manipulating food. This highlight the need, especially in complex social structures such as
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3 592 bonobo communities, to incorporate not only the ecological context but also the individual
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5 593 and social parameters in a further study.
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8 594

9
10 595 **Conclusion**

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13 596 Food manipulative process is part of the foraging strategies adopted to enhance the
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15 597 access to food resources. In this context, knowing the differences and/or similitudes between
16
17 598 humans and our closest living relatives, especially chimpanzees and bonobos, are of critical
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19 599 importance for our understanding of the evolutionary origins of hominid patterns of foraging
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21 600 strategies. In our study, we revealed a range of manipulative abilities in bonobos similar to
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23 601 that previously described in chimpanzees, from precision to power grips. Furthermore, we
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25 602 distinguished several manipulative strategies depending on the targeted food and the
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27 603 environmental context. But these two factors were not sufficient to explain the whole choice
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29 604 variability. This could be explained by the multifactorial aspect of individual making-decision
30
31 605 process, relying on both ecological and social parameters and highlighting the need to frame
32
33 606 these strategies within the whole ecological and social context. The comparison of our results
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35 607 with data on free-ranging bonobos in further studies would be of great value to improve our
36
37 608 understanding of the mechanisms underlying bonobos manipulative strategies. Finally, the
38
39 609 innovative methodologies used in this study, and applicable to any sequential behavioral data,
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41 610 enabled us to broaden our approach on the bonobo manipulative capacities to investigate a
42
43 611 more complete dynamic process.
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56
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60

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9
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12
13 620 Author Contribution: Conceived and designed the experiments: CG, VN, BS, AB, EP. Performed
14
15 621 the experiments: CG. Analyzed the data: CG. Wrote the manuscript: CG, AB, VN, BS.

17
18 622 The data that support the findings of this study are available from the corresponding author
19
20 623 upon reasonable request. All authors have no conflict of interest (any potential sources of
21
22 624 conflict of interest that could inappropriately influence their work and objectivity) to declare.
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899 **Tables:**

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





	N sequences	Proportion of the sample (%)	ID
Total	792	100	17
With manual/foot manipulation	661	83.46	17
With unimanual manipulation	615	77.65	17
With bimanual manipulation	115	14.52	12
With foot 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





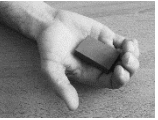

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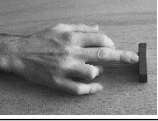
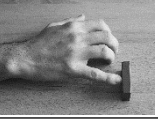
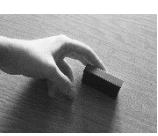



Table 2. Variability of grasping postures involving the hands: occurrence alone or in grip associations (number of sequences) and individuals using them alone or in grip associations.

Grip category†	Name in the literature	Reference(s)	Name	Description	Occurrence in N sequences (/792)			Used by N individuals (/17)			Illustration
					Total	In unimanual manipulation	In grip associations	Total	In unimanual manipulation	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	
	None	None	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	
Thumb lateral (TL)	Two-jaw chuck tip-to-side/Two-jaw chuck pad-to-side	Marzke and Wullstein 1996;	Lateral thumb-index grip	Item held between the thumb and side of the pad of the index finger.	375	325	54	17	17	7	

		Bardo et al. 2017									
Without thumb (WT)	Scissor held	Marzke et al. 2015	Palmar scissor hold	Item held between the index and middle fingers, with the hand in pronation.	72	71	4	15	15	4	
	None	None	Dorsal scissor hold	Item held between the flexed index and middle fingers, with the hand in supination,	10	10	0	5	5	0	
	Fingers hook	Marzke and	Fingers hook	Item enclosed by 2 or 3 flexed fingers.	20	15	6	12	11	5	
	Index finger hook	Wullstein 1996	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	2	2	0	2	2	0	

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				pressure applied by the opposed thumb.							
	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	
			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	

			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	
	Finger probe	Marzke and Wullstein 1996	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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3 Footnote: † PCG: contact between distal phalanges of the thumb and the index finger, also called “precision grip” in Jones-Engels and Bard (1996),
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5 “Thumb-index grips” in Pouydebat et al. (2011) and “Category 1” in Bardo et al. (2016). This category also includes one grip that wasn’t previously
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7 described and called “Thumb-middle grip”. It is described in the same way as the “Two-jaw chuck pad-to-pad side” (Bardo et al., 2016) but
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9 involves the middle finger instead of the index.
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13 TL: contact between the distal phalange of the thumb, the lateral side of the middle, proximal phalanges of the index finger and the item, also
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15 called “thumb lateral” in Pouydebat et al. (2011) and “Category 2” in Bardo et al. (2016).
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18 WT: contact between one or several fingers, except the thumb, and the item, also called “without thumb” in Pouydebat et al. (2011) and
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20 “Category 3” in Bardo et al. (2016). We distinguished in this category the “dorsal scissor hold” from the “scissor hold” as the hand is systematically
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22 placed in supination and fingers 2 and 3 are always flexed, which is not the case in the dorsal scissor hold grip.
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25 PMG: contact involving palm, the thumb and one or several part of other fingers and the item, involving the power grasping posture (Napier,
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27 1956; Jones-Engels & Bard, 1996), and also called “palm grips” in Pouydebat et al. (2011) and “Category 4” in Bardo et al. (2016).
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30 OG: contact types which fell outside the above categories, called “other grips” in Jones-Engels and Bard (1996) and “Category 5” in Bardo et al.
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32 (2016). In our study, it mostly involves non-prehensile postures (i.e., “Finger probe” and “Finger tips substrate”) (Napier, 1956).
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Table 3. Variability of grasping postures involving the feet (F): occurrence alone or in grip associations (number of sequences) and individuals using them alone or in grip associations.

Grip category	Name	Description	Occurrence in N sequences (/792)			Used by N individuals (/17)		
			Total	Used alone	In grip associations	Total	Used alone	In grip associations
Palm grips (PMG)	Power grip with thumb (F)	Item held in opposition between the palm and flexed fingers with a pressure applied by the opposed thumb.	9	9	0	4	4	0
Other grips (OG)	V pocket (F)	Item held in web between full thumb and index finger, other fingers are flexed but not in contact with the item.	1	1	0	1	1	0

Table 4. Variability of grip associations involving the grasping postures used alone and the associations in bimanual manipulation or compound grips: occurrence (number of sequences) and individuals using them.

Grip association	Occurrence in N sequences (/792)	Used by N individuals (/17)
Brush grasp	9	8
Cup hold	4	2
Cup hold + Power grip with thumb	2	2
Cup hold with thumb	2	2
Dorsal scissor hold	10	5
Dynamic tripod grip	9	3
Dynamic tripod grip + Dynamic tripod grip	1	1
Dynamic tripod grip + V pocket	1	1
Fifth finger probe + Power grip	17	1
Fifth finger probe + Power grip with thumb	20	1
Finger tips support	1	1
Finger tips support + Lateral thumb-index grip	33	1
Finger tips support + Power grip with thumb	1	1
Finger tips support + V pocket	1	1
Fingers contact	11	6
Fingers contact + Index finger contact	1	1
Fingers hook	15	11
Fingers hook + pi	1	1
Fingers hook + Power grip with thumb	5	4
Index finger contact	41	8
Index finger contact + Index finger contact	7	4
Index finger hook	4	3
Index finger hook + ind	2	1
Index finger hook + Power grip with thumb	3	2
Index finger probe	13	2
Index finger probe + Dynamic tripod grip	4	2
Index finger probe + Lateral thumb-index grip	1	1
Index finger probe + Power grip with thumb	18	4
Index finger probe + V pocket	2	1
Lateral thumb-index grip	325	17
Lateral thumb-index grip + Lateral thumb-index grip	2	2
Lateral thumb-index grip + Thumb probe	1	1
Middle finger contact	3	3
Middle finger probe	3	1
Palmar scissor hold	71	15
Palmar scissor hold + Power grip with thumb	4	4

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Palmar thumb-index grip	59	11
Power grip	32	10
Power grip + Power grip with thumb	1	1
Power grip with thumb	138	16
Power grip with thumb + Dynamic tripod grip	2	1
Power grip with thumb + Lateral thumb-index grip	20	6
Power grip with thumb + Power grip with thumb	5	3
Power grip with thumb + Thumb probe	6	3
Power grip with thumb + V pocket	4	3
Thumb probe	2	1
Thumb probe + Dynamic tripod grip	4	2
Thumb-middle grip	18	3
V pocket	28	10

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Table 5. Detailed pattern distribution in each item-substrate modality (Exact multinomial and binomial had hoc tests: number in red are significantly higher than a homogeneous distribution, number in blue are significantly lower, $p < 0.05$)

Item-support modality	Multinomial test	Pattern 0	Pattern 1	Pattern 2	Pattern 3	Pattern 4	Total
0-grille	$p < 0,001$	1	48	0	7	12	68
0-plateforme	$p < 0,001$	0	44	2	3	38	87
0-sol	ns	0	3	2	1	1	7
1-grille	$p < 0,001$	0	13	13	40	10	76
1-plateforme	$p < 0,001$	128	14	12	140	1	295
1-sol	ns	1	56	29	89	1	176
2-grille	$p < 0,001$	1	4	5	21	14	45
2-plateforme	$p < 0,05$	0	0	1	5	2	8
2-sol	ns	0	1	0	3	0	4
Total		131	183	64	309	79	766

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3 **Figure legends:**
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8 **Figure 1.** Barplots presenting the means of every grip category proportions in the sequences
9 of each manipulative pattern. (Wilcoxon rank sum test with Bonferroni continuity correction,
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13 ***: $p < 0.001$, ****: $p < 0.0001$. Error bars represent standard error of the mean (SEM))
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15 (Npattern1=183 sequences, Npattern2=64 sequences, Npattern3=309 sequences,
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18 Npattern4=79 sequences)
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22 **Figure 2.** Boxplot representing the handling score (a) and the effectiveness (b) of the
23 sequences in each of the item-substrate modalities (Wilcoxon rank sum test with Bonferroni
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significantly, on average, from each other: $p < 0.05$). Bold horizontal bars represent median
values.

Research highlights

- Our study provides the first description of the large manipulative repertoire spontaneously used by zoo bonobos in a feeding context.
- It also shows the existence of different manipulative strategies whose choice and effectiveness are dependent on the physical environmental context and the morphometric characteristics of food items.
- The application of these innovative methodologies on data from free-ranging bonobos in further studies would be of great value to improve our understanding of the mechanisms underlying bonobos manipulative strategies.

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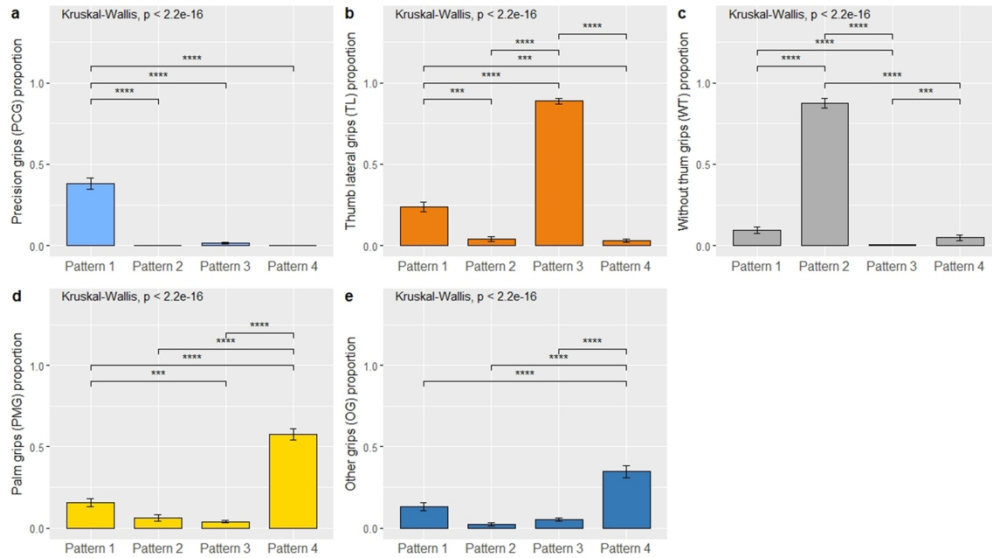


Figure 1. Barplots presenting the means of every grip category proportions in the sequences of each manipulative pattern. (Wilcoxon rank sum test with Bonferroni continuity correction, ***: $p < 0.001$, ****: $p < 0.0001$. Error bars represent standard error of the mean (SEM)) (Npattern1=183 sequences, Npattern2=64 sequences, Npattern3=309 sequences, Npattern4=79 sequences)

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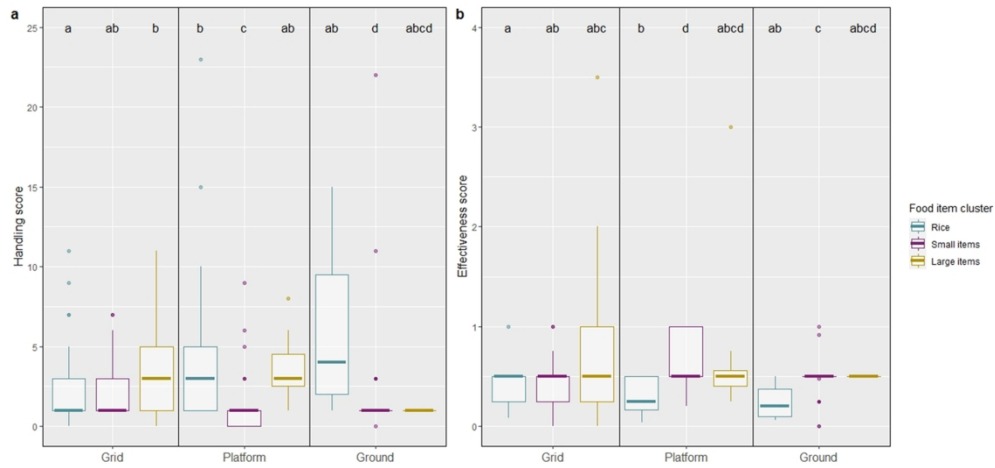


Figure 2. Boxplot representing the handling score (a) and the effectiveness (b) of the sequences in each of the item-substrate modalities (Wilcoxon rank sum test with Bonferroni continuity; modalities that share a letter within and between substrate types do not differ significantly, on average, from each other: $p < 0.05$). Bold horizontal bars represent median values.

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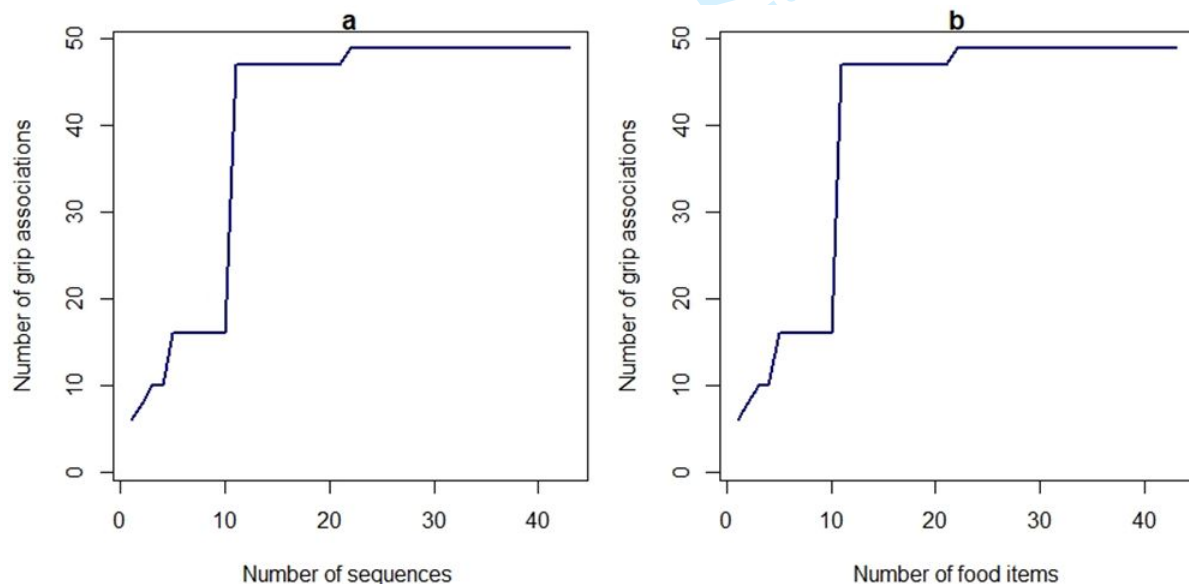
Supporting information

Appendix 1. Morphometric measurements (6 variables) of the 43 food items handled by the bonobos of the group in the scored videos. The categories (from cat 1 to cat 6) correspond to the decreasing cutting sizes of food distributed by the zookeepers.

Item	N samples	Mass (gr)		Hardness (N)		Length (cm)		Width (cm)		Height (cm)		Volume (cm ³)	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Black radish Cat2	3	27,0	3,6	10,5	0,8	6,0	0,0	5,5	0,0	1,0	0,0	33,0	0,0
Broccoli Cat1	3	42,0	6,1	23,5	0,6	14,5	0,3	6,0	0,0	5,0	0,3	435,0	30,9
Broccoli Cat2	3	18,0	2,5	20,5	0,5	6,0	0,3	6,0	0,0	5,0	0,0	180,0	8,7
Broccoli Cat3	6	3,0	0,6	0,0	0,0	2,5	0,3	2,0	0,4	1,5	0,0	7,5	2,6
Cake	3	110,0	3,0	0,0	0,0	15,0	0,0	4,0	0,0	4,0	0,0	240,0	0,0
Carrot Cat2	5	53,0	12,7	37,5	0,9	10,5	0,6	4,0	0,5	3,5	0,4	147,0	33,3
Carrot Cat3	2	41,0	1,0	31,0	1,2	17,5	2,0	3,5	0,0	2,0	0,0	122,5	14,0
Carrot Cat4	3	22,0	2,5	31,0	1,2	14,0	0,0	2,0	0,4	2,0	0,0	56,0	8,1
Carrot Cat5	2	11,0	5,0	31,0	1,2	6,0	0,0	2,5	0,7	2,5	0,0	37,5	7,5
Cauliflower Cat1	3	122,0	5,3	14,0	0,4	13,0	1,5	8,0	0,7	4,0	0,5	416,0	54,6
Cauliflower Cat2	3	78,0	4,0	26,0	0,6	17,0	1,2	8,5	1,1	2,0	0,3	289,0	54,6
Cauliflower Cat3	4	50,0	9,5	14,0	0,4	7,0	0,4	6,0	0,6	3,0	0,4	126,0	36,4
Cauliflower Cat4	3	17,0	4,0	8,5	0,5	6,0	0,3	3,0	0,7	1,5	0,0	27,0	6,2
Cauliflower Cat5	2	10,0	1,0	26,0	0,6	4,0	0,0	3,0	0,0	1,0	0,0	12,0	0,0
Cauliflower Cat6	9	2,0	0,6	0,0	0,0	2,0	0,3	2,0	0,3	1,0	0,1	4,0	1,8
Celery Cat1	2	63,0	12,0	14,5	1,0	14,0	0,0	6,0	0,0	6,0	0,5	504,0	42,0
Celery Cat2	7	19,0	2,6	14,5	1,0	21,5	1,7	6,5	1,4	1,0	0,0	139,8	35,1
Celery Cat3	3	9,0	1,5	14,5	1,0	7,0	0,0	1,5	0,0	1,5	0,0	15,8	0,0
Celery Cat4	5	2,0	0,0	0,0	0,0	13,5	0,7	6,0	0,8	0,5	0,0	40,5	7,2
Cucumber Cat1	3	32,0	1,0	11,5	0,4	11,0	0,0	3,0	0,4	2,0	0,0	66,0	6,4
Cucumber Cat3	4	21,0	3,0	11,5	0,4	7,0	1,1	3,0	0,5	2,0	0,2	42,0	14,1
Endive Cat3	1	11,0	NA	8,7	0,4	13,0	NA	5,5	NA	0,5	NA	35,8	NA
Endive Cat4	2	3,0	0,0	8,7	0,4	9,5	0,5	5,0	0,0	0,5	0,0	23,8	1,3
Green cabbage Cat1	3	167,0	11,5	34,5	0,4	19,5	0,0	9,5	1,3	6,0	0,9	1111,5	308,3
Green cabbage Cat2	5	34,0	2,9	26,0	0,9	24,0	0,9	19,0	0,7	0,5	0,0	228,0	16,3
Green cabbage Cat3	1	37,0	NA	34,5	0,4	7,5	NA	6,5	NA	6,0	NA	292,5	NA
Green cabbage Cat4	3	7,0	1,7	0,0	0,0	13,5	0,9	7,5	0,5	0,2	0,0	20,3	2,5

Green cabbage Cat5	5	1,0	0,0	0,0	0,0	6,0	0,5	3,5	0,4	0,2	0,0	4,2	0,6
Hazel bark	3	1,0	0,0	16,0	0,9	8,5	0,5	1,0	0,0	0,1	0,0	0,9	0,1
Hazel catkins	10	0,2	0,0	0,0	0,0	3,0	0,2	0,5	0,0	0,5	0,0	0,8	0,0
Leek Cat1	3	52,0	5,9	17,5	0,6	19,5	0,8	3,0	0,4	3,0	0,3	175,5	36,5
Leek Cat2	2	10,0	2,0	8,0	0,3	3,5	0,5	2,0	0,0	2,0	0,0	14,0	2,0
Leek Cat3	3	15,0	3,1	0,0	0,0	30,0	1,2	3,0	0,9	0,2	0,0	18,0	5,4
Leek Cat4	5	2,0	0,5	0,0	0,0	14,0	0,2	1,0	0,0	0,1	0,0	1,4	0,3
Lettuce Cat2	4	10,0	0,6	0,0	0,0	10,5	0,7	10,0	1,6	1,0	0,0	105,0	10,9
Lettuce Cat3	4	3,0	0,6	0,0	0,0	9,0	0,6	7,0	0,8	0,5	0,0	31,5	5,1
Oak leaf Cat4	7	1,5	0,1	0,0	0,0	7,0	0,7	5,0	1,0	0,1	0,0	3,5	0,8
Onion Cat2	2	20,0	1,0	15,0	0,0	8,0	0,0	3,5	0,7	2,0	1,0	56,0	36,0
Onion Cat3	3	4,0	1,2	5,5	0,0	6,0	0,0	2,0	0,0	0,5	0,0	6,0	0,0
Pepper Cat3	3	36,0	7,6	8,5	0,8	10,5	0,3	4,5	0,0	1,5	0,3	70,9	13,1
Pepper Cat4	4	14,0	1,6	8,5	0,8	8,5	1,2	4,0	0,7	1,0	0,2	34,0	9,1
Seeds	10	0,2	0,0	39,0	0,4	0,8	0,1	0,5	0,1	0,2	0,0	0,1	0,0
Zucchini Cat2	3	18,0	4,5	7,5	0,5	4,4	0,2	4,5	0,4	1,0	0,0	19,8	1,9

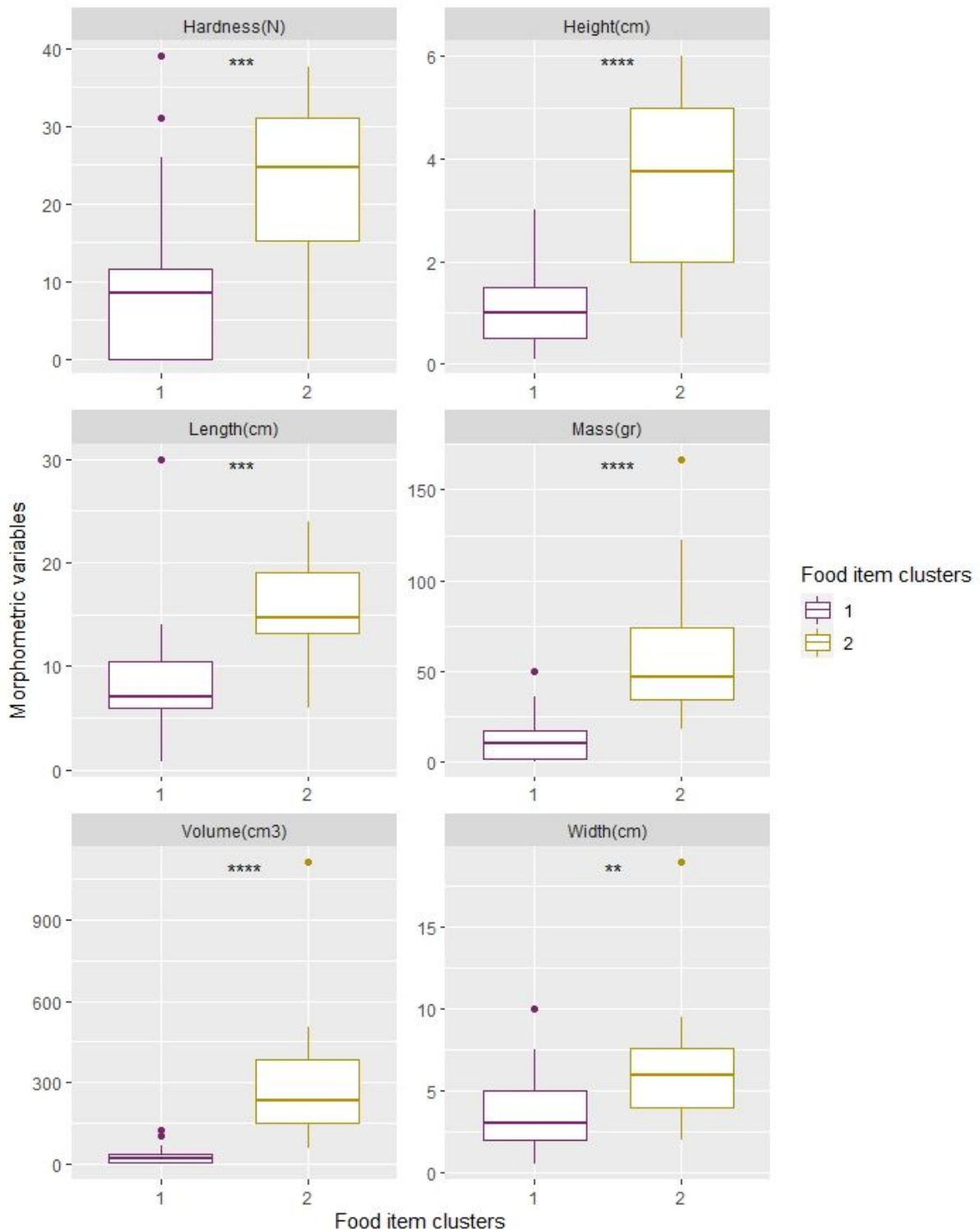
Appendix 2. Accumulation curves representing the cumulative number of grip associations observed as a function of the number of sequences (a) and number of food items (b). The 17 individuals of the group are represented in this sample (mean \pm SEM=47 \pm 5 sequences per individual; min=19; max=89).



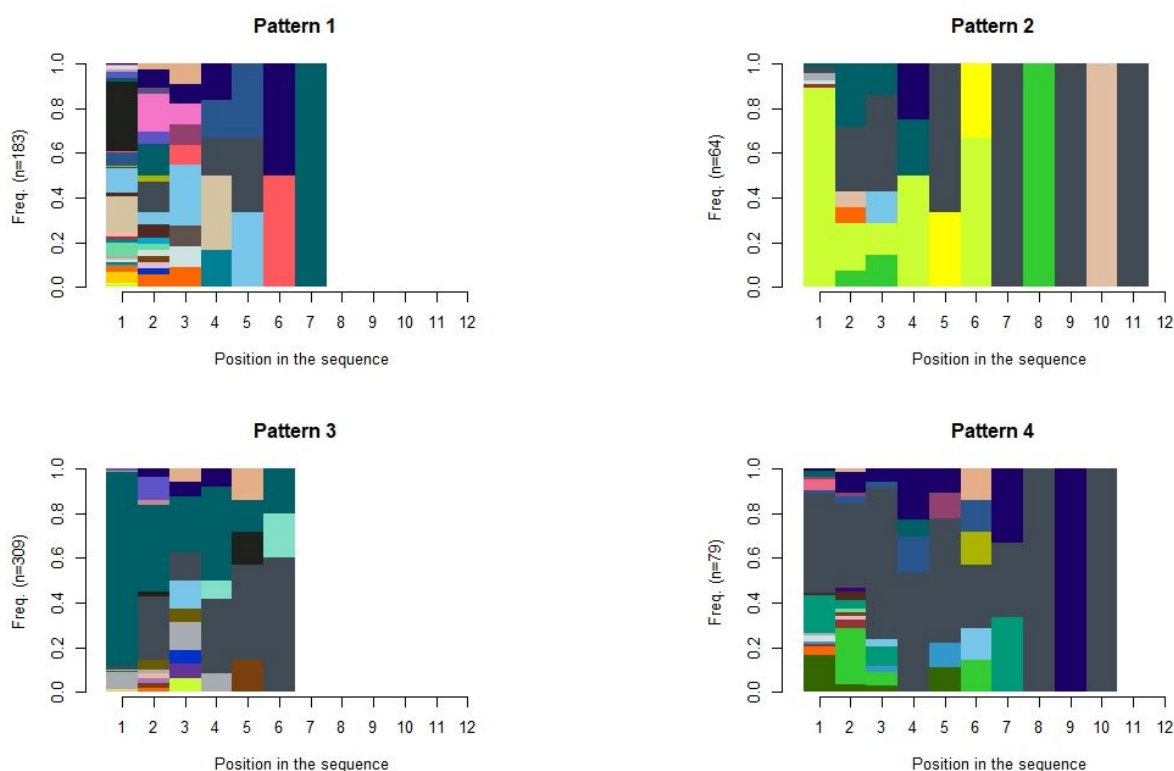
Appendix 3. Food item classification according to Hierarchical Cluster Analysis (HCA) and Ward's method. Three clusters are distinguished: Clusters 1 and 2 and Cluster 0, added for the special case of cooked rice.

Food item cluster	Cluster 0	Cluster 1	Cluster 2
Hardness (N) (mean ± SEM)	NA	8.7 ± 1.8	23.2 ± 2.8
Height (cm) (mean ± SEM)	NA	1.0 ± 0.2	3.6 ± 0.5
Length (cm) (mean ± SEM)	NA	8.2 ± 1.0	15.3 ± 1.4
Mass (gr) (mean ± SEM)	NA	11.8 ± 2.3	61.3 ± 11.7
Width (cm) (mean ± SEM)	NA	3.7 ± 0.4	6.6 ± 1.1
Volume (cm³) (mean ± SEM)	NA	29.6 ± 5.7	309.8 ± 70.7
Food items	Cooked rice	Broccoli Cat3 Black radish Cat2 Carrot Cat5 Cauliflower Cat3 Cauliflower Cat4 Cauliflower Cat5 Cauliflower Cat6 Celery stalk Cat3 Celery stalk Cat4 Cucumber Cat1 Cucumber Cat3 Endive Cat3 Endive Cat4 Green cabbage Cat4 Green cabbage Cat5 Hazel bark Hazel catkins Leek Cat2 Leek Cat3 Leek Cat4 Lettuce salad Cat2 Lettuce salad Cat3 Oak leaf lettuce Cat4 Onion Cat2 Onion Cat3 Sweet pepper Cat3 Sweet pepper Cat4 Seeds Zucchini Cat2	Broccoli Cat1 Broccoli Cat2 Cake Carrot Cat2 Carrot Cat3 Carrot Cat4 Cauliflower Cat1 Cauliflower Cat2 Celery stalk Cat1 Celery stalk Cat2 Green cabbage Cat1 Green cabbage Cat2 Green cabbage Cat3 Leek Cat1

Appendix 4. Box-plots presenting the 6 morphometric variables of the items in each of the clusters 1 (N=29) and 2 (N=14) obtained by Hierarchical Cluster Analysis (HCA) (Wilcoxon rank sum test with Bonferroni continuity correction, **: $p < 0.05$, ***: $p < 0.001$, ****: $p < 0.0001$).



Appendix 5. Graphic presenting the frequencies of the different grip associations for each position in the sequences of the four manipulative patterns. The number of sequences in each pattern is indicated, in the y labels, by (n=x). Each color corresponds to a distinct grip association and is ranked, from bottom to top, in alphabetic order. For example, in the pattern 2, the grip association represented in light green in the first position of the sequences is the palmar scissor hold used alone and represents 90% of the first position in this pattern. The color distributions indicate different sequence structures between the patterns.



Appendix 6. Results of the two first axes of an MCA performed on three qualitative variables (i.e. the manipulative patterns, the food item clusters and the substrates) of 766 sequences. The first axis (horizontal) explained 62% and the second axis (vertical) explained (48%) of the total variance. The factorial plan is the same for the three projections and enables to visually notice some overlaps between the manipulative patterns and certain item clusters and substrates.

