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Influence of food physical properties and environmental context on manipulative behaviors highlighted by new methodological approaches in zoo-housed bonobos (*Pan paniscus*)

Caroline Gérard, Ameline Bardo, Jean Pascal Guéry, Emmanuelle Pouydebat, Victor Narat, Bruno Simmen

► To cite this version:

Caroline Gérard, Ameline Bardo, Jean Pascal Guéry, Emmanuelle Pouydebat, Victor Narat, et al.. Influence of food physical properties and environmental context on manipulative behaviors highlighted by new methodological approaches in zoo-housed bonobos (*Pan paniscus*). American Journal of Primatology, inPress, 10.1002/ajp.23624 . hal-04527109

HAL Id: hal-04527109

<https://hal.science/hal-04527109>

Submitted on 29 Mar 2024

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25 *Tel. +33650037743*

26 **Abstract**

27 Research on manipulative abilities in non-human primates, in the context of hominid
28 evolution, has mostly focused on manual/pedal postures considered as static behaviors. While
29 these behavioral repertoires highlighted the range of manipulative abilities in many species,
30 manipulation is a dynamic process that mostly involves successive types of grips before
31 reaching its goal. The present study aims to investigate the use of manual/pedal postures in
32 zoo-housed bonobos in diverse dynamic food processing by using an innovative approach: the
33 optimal matching analysis that compares sequences (i.e., succession of grasping postures)
34 with each other. To characterize the manipulative techniques spontaneously employed by
35 bonobos, we performed this sequential analysis of manual/pedal postures during 766
36 complete feeding sequences of 17 individuals. We analyzed the effectiveness with a score
37 defined by a partial proxy of food intake (i.e., the number of mouthfuls) linked to a handling
38 score measuring both the diversity and changes of manual postures during each sequence.
39 We identified four techniques, used differently depending on the physical substrate on which
40 the individual performed food manipulation and the food physical properties. Our results
41 showed that manipulative techniques were more complex (i.e., higher handling score) for
42 large foods and on substrates with lower stability. But the effectiveness score was not
43 significantly lower for these items since manipulative complexity seemed to be compensated
44 by a greater number of mouthfuls. It appeared that the techniques employed involved a trade-
45 off between manipulative complexity and the amount of food ingested. This study allowed us
46 to test and validate innovative analysis methods that are applicable to diverse ethological
47 studies involving sequential events. Our results bring new data for a better understanding of
48 the evolution of manual abilities in primates in association with different ecological contexts

49 and both terrestrial and arboreal substrates and suggest that social and individual influences
50 need to be explored further.

51

52 **Keywords:** food manipulation, grasping posture, sequential analysis, manipulative technique

53

54 **List of abbreviations**

55 PCG: Precision Grips

56 TL: Thumb lateral

57 WT: Without Thumb

58 PMG: Palm Grips

59 MFM: Manipulative Finger Movements

60 OG: Other grips

61 SEM: Standard Error of the Mean

62 PCA: Principal Component Analysis

63 HCA: Hierarchical Cluster Analysis

64 MCA: Multiple Correspondence Analysis

65

66 **Introduction**

67 Food processing may require multiple and various abilities, ranging from powerful
68 action to more precise manipulations. If human hand presents the highest level of dexterity
69 compared with other primates (Key et al., 2018; Marzke, 2013; Marzke et al., 1992), with
70 forceful precision grips between the pad of the thumb and the pads of the fingers and complex
71 intra-manual precision manipulative movements (Kivell, 2015; Marzke, 1997, 2013; Marzke et
72 al., 2015; Napier, 1960; Pouydebat et al., 2011), other species have shown their ability to

73 process food in complex ways, using tools or not (e.g., Byrne et al., 2001). Comparative
74 behavioral studies of hand use in our closest living relatives, in zoo and free-ranging
75 conditions, can improve our understanding of the functional morphology in early hominins
76 (i.e., *Homo sapiens* and their extinct relatives) as well as fossil apes (Bardo et al., 2017; Feix et
77 al., 2015; Kivell et al., 2022; Pouydebat et al., 2008, 2011; Susman, 1998; Tonooka &
78 Matsuzawa, 1995). These studies continuously contribute to a better understanding of the
79 evolution of manipulative behaviors that led to this extremely large manipulative flexibility in
80 humans.

81 Complexity of food processing not only involves a large range of manual/pedal
82 postures but also requires synchronization, stabilization and ability to efficiently move the
83 food without dropping it. Although dynamic hand movements have been described in human
84 (e.g., Bullock & Dollar, 2011; Elliott & Connolly, 1984; Santello et al., 1998), only few studies
85 have explored this ability in non-human primates (e.g., in chimpanzees: Crast et al., 2009;
86 Marzke et al., 2015) but they did not consider the use and succession of manual/pedal
87 postures. To our knowledge, the consideration of this detailed sequential use of manual/pedal
88 grips has only been made in a context of tool-use (Bardo et al., 2016, 2017; Borel et al., 2017).
89 Tool-use can be defined as “[. . .] the external employment of an unattached environmental
90 object to alter more efficiently the form, position, or condition of another object, another
91 organism, or the user itself when the user holds or carries the tool during or just prior to use
92 and is responsible for the proper and effective orientation of the tool” (Beck, 1980, p.10). In
93 this context, the *Pan* genus is of particular interest because the two species (chimpanzees and
94 bonobos) present marked differences in whether or not to use tools in natural conditions (but
95 see Hohmann & Fruth, 2003) despite the fact that chimpanzees and bonobos are very similar
96 not only in their hand morphology (Diogo et al., 2017; Druelle et al., 2018; van Leeuwen et al.,

97 2018) but also in their manipulative abilities. In bonobos, tool-use in a feeding context has
98 only been observed in captive individuals (i.e., in sanctuaries, zoos and laboratories) (Bardo et
99 al., 2015, 2016; Boose et al., 2013; Gruber et al., 2010; Neufuss et al., 2017; Takeshita &
100 Walraven, 1996; Toth et al., 1993; Visalberghi et al., 1995), while it has been described for
101 hygienic and social purposes in free-ranging conditions (Furuichi et al., 2015; Hohmann &
102 Fruth, 2003; Ingmanson, 1996; Kano, 1982; Nishida et al., 1999; Samuni et al., 2021). Yet,
103 documentation about the dynamic techniques involving sequences of manual or pedal
104 postures during food processing without tool in bonobos is lacking and necessary to complete
105 our knowledge of bonobos manipulative abilities and to improve our understanding of the
106 evolution of feeding strategies in primates. Furthermore, many studies have shown the effect
107 of food properties and arboreal substrates on grasping techniques, demonstrating how much
108 a food that is difficult to extract (e.g., preys or encapsulated foods) and a complex arboreal
109 substrate (orientation and size of supporting branch) increase the complexity and diversity of
110 the hand use (MacKenzie & Iberall, 1994; Patel et al., 2015; Reghem et al., 2012; Toussaint et
111 al., 2015). The link between the shape and/or the size of the object and the grasping postures
112 used to manipulate it has already been considered in some studies in human and non-human
113 primates (e.g., Key et al., 2018; Pouydebat et al., 2009) and are of critical importance to
114 discriminate the causes of the origin of feeding manipulative behaviors in primates
115 (Pouydebat & Bardo, 2019). The effect of the environmental context (arboreal *versus*
116 terrestrial) has also been well-studied in chimpanzees since 1960s (e.g., Jones-Engel & Bard,
117 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Pouydebat et al., 2011), but it has poorly
118 been explored in the other *Pan* species, the bonobo.

119 Our previous study (Gérard et al., 2022) described for the first time the manipulative
120 repertoire of a group of zoo-housed bonobos in a feeding context. To go further and

121 considering any food manipulation as a dynamic and sequential process, the first objective of
122 this new study was to identify and characterize the different manipulative techniques used by
123 a group of zoo-housed bonobos in order to better understand the determinants and benefits
124 of accessing food resources. We measured the similarities and differences between the
125 manipulative sequences using an innovative method, the optimal matching analysis. Derived
126 from molecular biology (Abbott & Tsay, 2000), this method is usually used in social sciences
127 to analyze time-ordered sequences of socio-economic states that individuals have
128 experienced. It is particularly adapted to analyze categorical sequence data and retemporalize
129 action by analyzing it as a process. To our knowledge, this method has only been used in our
130 field by Borel et al. (2017), in which they described and quantified the sequential dynamic
131 techniques of tool grip and manipulation of five human subjects during a tool-task. With this
132 method, we expected to distinguish several manipulative techniques with a preferential use
133 of specific categories of manual postures (as identified in Gérard et al., 2022) in each of them.
134 These different techniques are expected to be associated with the physical characteristics of
135 the food (i.e., size, weight and hardness) as well as the type of substrate (i.e., ceiling grid,
136 ground or platforms), as described for the preference of some grasping postures for small
137 items (precision grips) and others for large items (palm grips) in *Pan* genus (Christel et al.,
138 1998; Pouydebat et al., 2011).

139 The second objective was to evaluate the effectiveness of the food process according
140 to the manipulated food and the substrate. To tackle this issue, we developed an innovative
141 methodological approach in which we first calculated handling score using two parameters
142 typically described in the literature to assess manual complexity (Bardo et al., 2016, 2017): the
143 number of distinct manual postures used and the number of manual posture changes during
144 a feeding sequence. Then we defined manipulative effectiveness as the number of mouthfuls

145 per sequence related to this handling score. Based on previous studies in primates showing
146 that a food difficult to extract and a complex substrate (i.e., thin or suspended) increase the
147 complexity and diversity of the hand use (MacKenzie & Iberall, 1994; Patel et al., 2015;
148 Reghem et al., 2012; Toussaint et al., 2015), we expected to observe an influence of the
149 physical parameters of the manipulated food and the substrate on the effectiveness, as well
150 as on the choice of the manipulative technique used.

151

152 **Methods**

153 This research adhered to the legal requirements of France and all the experiments were
154 carried out following the principles of laboratory animal care in accordance with the CNRS
155 guidelines. It complies with the American Society of Primatologists (ASP) Principles for the
156 Ethical Treatment of Non-Human Primates and conforms to Directive 2010/63/EU of the
157 European Parliament and of the Council of September 22, 2010 on the protection of animals
158 used for scientific purposes.

159

160 **1. Subjects and housing**

161 The data were collected between January 27, 2020 and January 31, 2020 at the
162 zoological park “la Vallée des singes” (France). The group was composed of seventeen
163 bonobos (i.e, Continuous Full Contact (group)) with nine adults (six females from 16- to 52-
164 year old and three males from 15- to 23-year old), two subadults (one female and one male,
165 both 10-year old) and six juveniles (four females from 3- to 7-year old and two males of 5- and
166 7-year old).

167 The bonobos were visible to the observer during the day in an indoor building with two
168 large connected cages (98m² each) containing climbing structures, made of platforms, ladders

169 and ropes (see Gérard et al., 2022 for more details). The ground was normal building floor
170 with wood shavings and connected to outdoor areas, access to which was usually closed at
171 this time of year because the temperature was too low.

172 The food ration was distributed four times a day on the top of the cages (i.e., ceiling
173 grid) or inside the cages, either on the ground and the platforms, and included vegetables,
174 apples, pellets, seeds, eggs, chicken necks and a homemade mix containing cereals, vitamins
175 and vegetal oils. All food items were provided in a same way on the top of the cages, on the
176 platforms or on the ground. Daily enrichment was composed of tree branches and tubes filled
177 with cooked rice (Figure 1). Like food ration, they were distributed at different locations and
178 they were free to be displaced by the individuals.

179

180 **2. Data collection**

181 **2.1. Food physical properties**

182 In order to evaluate the influence of food physical characteristics on manipulative
183 behaviors, physical measurements (i.e., size, weight and hardness) were taken on every kind
184 of food manipulated by the bonobos of the group (Appendix 1). All the means were calculated
185 with the standard error of the mean (SEM). Vegetables were measured just before being
186 distributed, as whole items or cut pieces prepared by the zookeepers. One food item was
187 defined as one cutting size of one food species (Appendix 1). The aim of these measurements
188 was to classify food items depending on their physical parameters. Every food item (mean \pm
189 SEM = 4 ± 0 samples per cutting size of each food species) was characterized by six quantitative
190 values: length (cm), width (cm), height (cm), volume (cm³) (i.e. length*width*height), mass (gr)
191 and hardness (N) (Appendix 1). We collected hardness data using a portable analog durometer
192 (Force Dial™ FDN 50, Wagner Instruments). The durometer plunger was applied at several

193 positions of each sample (mean \pm SEM = 2.0 \pm 0.3 measures per sample) allowing us to
194 calculate the average value (McGraw et al., 2014). The measures were not applicable to
195 cooked rice contained in enrichment devices (Figure 1) and we treated this food item
196 separately in the analyses.

197

198 **2.2. Video recording and scoring**

199 We used the same videos for the description of the manipulative repertoire in Gérard
200 et al., 2022 (see the article for more details). One or several individuals were followed
201 throughout a feeding session with one handheld camera (PANASONIC® HC-V380) to record
202 the movements of the hands, feet and mouth. The recordings were performed at 50
203 frames/sec.

204 Video recordings were analyzed frame by frame with VLC Media Player (VideoLan,
205 2020), using the individual focal sampling method (Altmann, 1974). Videos were divided
206 according to our definition of a “manipulative sequence” which began with the first contact
207 between an individual and a food item and ended when the food was consumed in its entirety
208 or abandoned before total consumption. A total of 3h30 of recorded sequences were analyzed
209 (N=792 sequences). The parameters recorded during the sequence were the individual, the
210 food consumed (categorized by species and by size, characterizing a “food item”), the
211 substrate supporting the individual during manipulation (ground, platform or ceiling grid), the
212 manual/pedal grasping posture adopted, the hand(s)/feet used and the duration of each
213 behavior.

214

215 **1.3. Grasping postures**

216 Every encountered grasping posture involving the hands or the feet was described and
217 linked to the existing literature on human and apes (Bardo et al., 2016, 2017; Jones-Engel &
218 Bard, 1996; Marzke et al., 2015; Marzke & Wullstein, 1996; Napier, 1956; Parry, 1966;
219 Pouydebat et al., 2011). To name the grasping postures, we used the Marzke's grasping
220 typology (Marzke et al., 2015; Marzke & Wullstein, 1996) and we divided them into six grip
221 categories (see Gérard et al., 2022 for details):

- 222 • *Precision Grips* (PCG): contact between distal phalanges of the thumb and the index
223 finger.
- 224 • *Thumb lateral* (TL): contact between the distal phalanx of the thumb, the lateral side
225 of the middle, proximal phalanxes of the index finger and the item.
- 226 • *Without Thumb* (WT): contact between one or several fingers, except the thumb, and
227 the item.
- 228 • *Palm Grips* (PMG): contact involving the palm, the thumb and one or several part of
229 other fingers and the item.
- 230 • *Manipulative Finger Movements* (MFM): contact types without real grasping (i.e.,
231 contact for moving or stabilizing the item and probe for sticking food to the finger) and
232 involving the fingers (including the thumb) only.
- 233 • *Other grips* (OG): contact types which fell outside the above categories.

234

235 The grip associations included the cases of bimanual manipulation where the grasping
236 posture of each hand was recorded and compiled. In the case of asymmetric coordinated
237 bimanual movements, individuals held or maintained the food or the enrichment device with
238 one hand and extracted or picked up the food with the other hand. The hand used to extract
239 the food was considered as dominant, based on previous studies about coordinated bimanual

240 actions (Bardo et al., 2015; Hopkins, 1995; Meguerditchian et al., 2013) but both hands were
241 considered later in the sequential analyses (see the optimal matching analysis below).

242

243 **3. Data analyses**

244 **3.1. Food items classification**

245 We observed 44 food items from 19 different plants or edible species (Appendix 1)
246 during the video scoring. To classify them according to their physical characteristics (i.e.,
247 classification of 43 items, the cooked rice being excluded) and simplify the analyses by
248 decreasing the variability of food items properties, a Principal Component Analysis (PCA) and
249 a Hierarchical Cluster Analysis (HCA) with Ward's method (*agnes* function of the R package
250 *Cluster*; Maechler, 2013) were performed on the six physical variables (i.e., hardness, height,
251 mass, volume, length and width). A pairwise comparison (see below for statistical details) was
252 then carried out to investigate which variables were characterizing each cluster. The HCA
253 analysis revealed two clusters describing item physical characteristics (Appendix 2). Each six
254 physical variables used for cluster discrimination differed significantly between the two
255 clusters (Appendix 3). The first cluster (Cluster 1) corresponded to small, light and soft items
256 and the second cluster (Cluster 2) corresponded to large, heavy and hard items. For further
257 analyses, we assigned cooked rice to a third cluster (Cluster 0) as this item was uncountable
258 and not measurable.

259

260 **3.2. Sequential analysis and manipulative techniques**

261 **3.2.1. Optimal matching analysis**

262 We analyzed the sequences of manipulative behaviors by considering grasping
263 postures used alone (unimanual or pedal manipulation) and grip associations (bimanual,

264 annotated “left hand posture + right hand posture”) through their succession within a
265 sequence. Finally, the sequences could be composed of a succession of grasping postures used
266 alone (manual or pedal) or a succession of several grip associations if the manipulation was
267 only bimanual. It could also be composed of an alternance of grasping postures used alone
268 and grip associations if the manipulation was alternatively uni and bimanual. A number was
269 attributed to every grasping posture and grip association, so every manipulative sequence was
270 a succession of numbers before analysis. First of all, we calculated the pairwise dissimilarities
271 between the sequences using optimal matching analysis (i.e., calculation of the minimal
272 number of modifications - substitutions, deletions, insertions - that one of the sequences must
273 undergo to obtain another one) with the *seq.dist* function of the R package *TraMineR*
274 (Gabadinho et al., 2011). From the distances calculated between each pair of sequences, we
275 performed a HCA with Ward’s method, with the *agnes* function of the R package *Cluster*
276 (Maechler, 2013), in order to distinguish several manipulative techniques . We added a
277 supplementary technique containing the sequences without any manipulation (named
278 “Manipulative technique 0”) (i.e., the item was grasped with the mouth and consumed
279 directly), corresponding to a specific foraging technique. Because it would require a larger
280 amount of data and could be the topic of an entire study, we performed the analyses in this
281 study at the group level and not at the individual level.

282

283 **3.2.2. Grip category proportions and manipulative techniques**

284 The proportion of the six grip categories in a sequence was calculated as the number
285 of grasping postures of the considered category divided by the number of distinct grasping
286 postures used in the sequence. Because of their rare occurrence in the sequences (Gérard et
287 al., 2022), the manipulative finger movements (MFM) and the other grips (OG) were

288 considered as a unique category in the analyses. In bimanual manipulation, we only
289 considered the action of the dominant hand (i.e., the hand extracting food) in this analysis.
290 We compared the proportion of each grip category between the manipulative techniques to
291 determine if these techniques (obtained with the Optimal matching analysis) were
292 characterized by particular grip categories.

293

294 **3.2.3. Use of manipulative techniques according to the food item and the** 295 **substrate**

296 To determine the influence of the physical properties of the manipulated food items
297 and the physical substrates on the manipulative techniques used by the individuals, we
298 considered all the possible modalities of the interaction between item clusters and substrates
299 (see above). We assessed the link between manipulative techniques and item-substrate
300 modalities by comparing the distribution of the manipulative techniques between the item-
301 substrate modalities (N = 9 modalities, 3 item clusters and 3 substrates) to a homogeneous
302 distribution (see statistical method below).

303

304 **3.3. Handling score and manipulative effectiveness**

305 In the literature, the manipulative effectiveness during one task is evaluated using the
306 number of manual posture changes (C), the number of distinct grasping postures used during
307 a sequence (P) and the time needed to perform a task (Bardo et al., 2016, 2017; Neufuss et
308 al., 2017). Unfortunately, the first variable (C) does not distinguish the sequences without
309 manipulation (i.e., only using the mouth) from the ones involving only one grasping posture.
310 Variable (C) in isolation also failed to distinguish sequences with the same length but
311 containing only distinct postures or including a repetition of the same posture. The second

312 variable (P) did not fit with our analysis as it did not include the repetitions of grasping
313 postures in one manipulative sequence and thus attributed an equal value to sequences of
314 different length. We therefore created a new score representing the manipulative complexity
315 and more representative of the variability of the sequences by combining the two variables:

$$316 \quad \textit{Handling score} = P + C$$

317 Effectiveness is here defined as the ratio of ingestion to the manipulative score
318 required for processing that food. For instance, if a food is handled with many changes of
319 posture and several different postures but only provides one mouthful to the individual, this
320 process will be less effective than the same number of manipulations on a food giving several
321 mouthfuls. Effectiveness score has no direct energetic implications since it does not account
322 for the nutrient composition of food:

$$323 \quad \textit{Effectiveness} = \frac{N \textit{ mouthful}(s)}{P + C + 1}$$

324 For a mathematical purpose, we added the value of one to the denominator because the
325 handling score (i.e., P + C) was sometimes equal to zero (for sequences involving the mouth
326 only).

327 We compared the handling score and the effectiveness score between the different
328 item-substrate modalities (N=9) to determine whether the food access techniques were
329 equally complex and effective according to the manipulated food and the environmental
330 context.

331

332 **3.4. Statistical analyses**

333 For the comparisons of every grip category proportions, handling score and
334 effectiveness score, we performed multiple comparisons using the Kruskal-Wallis test and

335 pairwise comparisons using the Wilcoxon rank sum test. Because of the small or null samples
336 in some item-substrate modalities, we performed exact multinomial and binomial *ad hoc* tests
337 on the distribution between the manipulative techniques for every item-substrate modality,
338 by comparing them to an homogeneous distribution (*multinom.test* and *binom.test* functions
339 of the R package *rstatix*, Kassambara, 2020). We then applied a Bonferroni correction on the
340 p-values. All statistics were computed using the R 3.6.3 statistical environment (R Core Team
341 2020).

342

343 **Results**

344 **1. Classification of manipulative sequences**

345 After a selection of the complete (i.e., non-interrupted) sequences (N=769), all the
346 individuals of the group were represented in the dataset (mean \pm SEM = 45 ± 5 sequences per
347 individual). From the sequences involving the hand(s) (N=638 including N=115 sequences with
348 bimanual manipulation) and/or the foot (N=9), 120 distinct sequences varying from 1 to 17
349 successive grip associations (i.e., bimanual) or grasping postures used alone (unimanual or
350 pedal) were found. The result of the optimal matching analysis associated with the HCA have
351 enabled us to identify six clusters of sequences, of which only four were considered in our
352 subsequent analyses. The last two indeed contained only one or two sequences and were
353 therefore too rare to be considered as general techniques. The sequences in the four
354 techniques we considered varied from 1 to 11 successive grip associations (i.e., bimanual) or
355 grasping postures used alone (unimanual). For instance, one sequence could eventually
356 include only one manual or pedal grasping posture (for instance the lateral-thumb posture,
357 only one grasping posture used alone) before the food was consumed, or be followed by other
358 manipulations: a bimanual manipulation (grip association) like *power grip with thumb +*

359 *lateral-thumb* or any other manual/pedal grasping postures or grip associations. The
360 sequences included until eleven grasping postures or grip associations.

361

362 **2. Grip category proportions and manipulative techniques**

363 Each technique was distinguished by one or two dominant grip categories (Figure 2).
364 Technique 1 was associated with *precision grips* (PCG) (Kruskal-Wallis test: $\chi^2=169.88$, $df=3$,
365 $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$), technique 2 with *grips without the thumb* (WT)
366 (Kruskal-Wallis test: $\chi^2=418.78$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$), technique
367 3 with *thumb lateral grips* (TL) (Kruskal-Wallis test: $\chi^2=401.52$, $df=3$, $p<0.001$; Pairwise
368 Wilcoxon tests, $p<0.001$), and finally technique 4 was distinguished by three grip categories:
369 *palm grips* (PMG) (Kruskal-Wallis test: $\chi^2=254.25$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests,
370 $p<0.001$), *manipulative finger movements* (MFM) and *other grips* (OG) (Kruskal-Wallis test:
371 $\chi^2= 125.74$, $df=3$, $p<0.001$; Pairwise Wilcoxon tests, $p<0.001$).

372

373 **3. Manipulative techniques and effectiveness for various food items and substrates**

374 **3.1. Manipulative techniques use according to the food item and the substrate**

375 We compared the prevalence of every manipulative technique within each modality of
376 the interaction between the food item clusters ($N=3$) and the substrates ($N=3$) (Table 1).
377 Significant differences were found between the manipulative techniques used for all the items
378 at the grid and on the platform (Exact multinomial tests, $p<0.001$ except for the large items
379 on the platform: $p=0.036$ and all the items on the ground).

380 Technique 0 (mouth manipulation) was significantly associated with small items on the
381 platform (Binomial *ad hoc* test, $p<0.001$) while technique 1 (associated with PCG) was
382 significantly associated with cooked rice (on the grid and the platform) (Binomial *ad hoc* tests,

383 p<0.001). Technique 2 (associated with WT) was the least frequently used (N=64/766). It
384 seemed to be prevalent for small items on all substrates (especially ground) but the difference
385 is not significant. Technique 3 (associated with TL) was predominant especially for small items
386 (Binomial *ad hoc* tests, p<0.001), except on the ground where it was well represented but the
387 difference was not significant, and for large items on the grid (Binomial *ad hoc* test, p<0.001)
388 and the platform (Binomial *ad hoc* test, p<0.010). Technique 4 (associated with PMG, MFM
389 and OG) was significantly associated with cooked rice on the platform (Binomial *ad hoc* test,
390 p<0.001). Grid manipulations (all items) were also well represented in this technique 4 (PMG,
391 MFM and OG) but the difference was not significant. Finally, cooked rice was more frequently
392 manipulated using techniques 1 (at the grid) and 4 (at the grid and on platform), large items
393 were more frequently manipulated with technique 3/TL (at the grid and on platform) and
394 small items with technique 0/mouth (on platform) and technique 3/TL (on all substrates)
395 (Table 1).

396

397 **3.2. Handling score and manipulative effectiveness according to the food items** 398 **and the substrate**

399 **3.2.1. Handling score**

400 Figure 3a shows how the handling score varied among item-substrate modalities
401 (Kruskal-Wallis test: $\chi^2=328.15$, $df=8$, $p<0.001$). The large items manipulated at the grid
402 required more manipulations than other items: the difference was significant when compared
403 to the cooked rice at the grid (Wilcoxon test, $p=0.034$), and to the small items on the platform
404 (Wilcoxon test, $p<0.001$) and on the ground (Wilcoxon test, $p<0.001$). Large items were more
405 rarely manipulated on the ground (N=4 sequences/57 involving large items) and on the
406 platforms (N=8/57 sequences). On these two substrates, the differences of the handling score

407 between the large items and the others were not significant (i.e., no difference or too small
408 class size). Only the handling score of the large items manipulated on the platform was
409 significantly higher than for the small items on the ground (Wilcoxon test, $p < 0.001$).

410 Cooked rice, whatever the substrate, was the second item that involved more
411 manipulations, especially compared to the small items on the platform (Wilcoxon test,
412 $p < 0.001$ for the three substrates) and on the ground (Wilcoxon test, $p < 0.001$ for the three
413 substrates). The handling score appeared lower at the grid than on the platform (Wilcoxon
414 test, $p = 0.014$) for this item (Figure 3a).

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

421

422 **3.2.2. Manipulative effectiveness**

423 The manipulative effectiveness was significantly different between some item-
424 substrate modalities (Kruskal-Wallis test: $\chi^2 = 254.94$, $df = 8$, $p < 0.001$) (Figure 3b). The
425 effectiveness was lower for cooked rice whatever the substrate compared to the small items
426 on the platform (Wilcoxon test, $p < 0.001$ for the three substrates) and on the ground (Wilcoxon
427 test, $p < 0.001$, for the three substrates). A lower effectiveness was also observed on the
428 platform compared to the grid (Wilcoxon test, $p = 0.009$).

429 Manipulation of large items at the grid was less effective than the manipulation of the
430 small items on the platform (Wilcoxon test, $p=0.005$) but there was no significant difference
431 between the different substrates for the large items.

432 Finally, the manipulation of small items appeared significantly more effective than
433 manipulation of cooked rice (except at the grid where the difference is not significant) and
434 also more effective than manipulation of large items on the grid (except at the grid and on the
435 ground where the differences are not significant; Figure 3b). We also observed a difference
436 in the manipulation of small items, being less effective at the grid versus platform (Wilcoxon
437 test, $p<0.001$) and ground (Wilcoxon test, $p<0.001$), while effectiveness was lower on the
438 ground than on the platform (Wilcoxon test, $p<0.001$).

439

440 **Discussion**

441 The use of innovative methodologies (i.e., the sequential analysis by optimal matching
442 the handling score and the effectiveness score) allowed us to study food manipulation as a
443 dynamic process in zoo-housed bonobos. Our results validate our hypotheses that the use and
444 effectiveness of different manipulative techniques are dependent on the environmental
445 context and the physical characteristics of food items. The following discussion details the
446 implications of our findings with regard to the behavioral flexibility, depending on the
447 decision-making context.

448

449 **1. Manipulative techniques**

450 Our first hypothesis was that bonobos have different manipulative techniques adapted
451 to the physical properties of the food and the environmental context (i.e., substrate). First,
452 our results showed that bonobos could use different manipulative ways to gain access to food.

453 The use of pedal grasping postures did not constitute a specific technique in this study and
454 only occurred rarely but it was necessary to consider it in our analysis as an integral part of
455 the manipulative process, in the same way as rare manual postures. Our hypothesis was
456 confirmed since some manipulative techniques were significantly more frequently used for
457 one or several kinds of food, according to the substrate used for stabilizing the body during
458 feeding. Cooked rice was more frequently manipulated using technique 1/PCG (at the grid)
459 and 4 (at the grid and on platform), large items were more frequently manipulated with
460 technique 3/TL (at the grid and on platform) and small items with technique 0/mouth (on
461 platform) and technique 3/TL (on all substrates).

462 The results showed a trend to manipulate cooked rice preferentially using *Palm grips*,
463 *Manipulative Finger Movement* or *Other grips* (technique 4) used alone or in association with
464 *Precision grips* (technique 1) when the substrate was more complex (i.e., at the grid). This can
465 be explained by the fact that the individuals can reach the cooked rice contained in the tubes
466 by hitting it on the ground or on the platform (*Palm grips*), by probing with their fingers
467 (*Manipulative Finger Movement*) or by using a tool (*Precision grips* and *Other grips* for storage,
468 i.e., keeping a tool in the hand or foot without using it) (Figure 1). The two last cases are
469 bimanual manipulation as it required to stabilize the tube with the other hand (*Palm grips* or
470 *Other grips* categories).

471 The *Without thumb grips* (technique 2) and *Thumb lateral grips* (technique 3) were
472 less specific to one kind of food or substrate. In contrast, manipulation with only the mouth
473 (technique 0) occurred almost exclusively with small items on the platform. This can be
474 explained by the absence of dirt and sand on this substrate, allowing an easier grasping of the
475 small items as suggested in the study of Christel et al. (1998) in which grasping small objects
476 on a cleaner ground required less time than on grassy/sandy ground.

477 Our result show that the manipulative technique can differ between the substrates for
478 the same kind of item (i.e., cluster), depending on the substrate and confirming the necessity
479 to consider the interaction between the two parameters. Furthermore, while some
480 techniques were strongly associated with some modalities of item and substrate (e.g.,
481 technique 1/PCG for the rice manipulated at the grid for instance), we observed different
482 manipulative techniques for the same item-substrate modality. This result is consistent with
483 both the stability and variability showed in Borel et al. (2017) where the subjects modified
484 their technique in order to find new solutions to perform a tool-task when experimental
485 parameters were changed. These results show that in hominids, manipulative abilities are not
486 only depending on the size and diversity of the repertoire but also on its flexibility of use and
487 adaptability to different situations.

488

489 **2. A trade-off between complexity and gain**

490 Our second hypothesis was that the physical parameters of the manipulated food and the
491 substrate influence the handling score (i.e., the complexity of manipulation based on the
492 number of distinct manual postures used and the number of manual posture changes during
493 a feeding sequence) and the effectiveness (i.e., the food intake related to the manipulative
494 investment). We considered that a food that is complex to manipulate and requires many
495 changes of manual postures could be less interesting than a food that requires few
496 manipulations. Our results showed that this rule was not strictly generalizable however, as the
497 great number of manipulations for large items seemed to be compensated by a large number
498 of mouthfuls ingested. This result suggests the existence of a trade-off between the
499 manipulation investment and the food intake, trade-off that could also relate to nutrient or
500 energy intake, but we did not consider these parameters in this study. It may be as efficient

501 to process many small items (i.e., multiple lower investment) with many low intake ratios as
502 to manipulate few large items (i.e., higher investment) with a high intake ratio.

503 The lower effectiveness for the manipulation of the tubes containing cooked rice on
504 the platforms compared to the grid can be explained by the fact that the individuals at the
505 grid tended to stabilize the enrichment device rather than turning it and hitting it on a surface
506 like on the platforms. The handling score was lower at the grid but the number of mouthfuls
507 remained the same on the two substrates so the effectiveness was higher on the platforms.
508 We did not observe any difference in effectiveness between the different substrates for the
509 large items. This finding can be explained by the fact that the largest items do not pass through
510 the bars of the grid without manipulation. During our observations, the large items were more
511 rarely manipulated on the ground and on the platforms. In contrast, we observed a difference
512 of effectiveness for small items where manipulation at the grid appears significantly less
513 effective than on the platform and ground. Contrary to the large items, the complexity of
514 manipulation imposed by the grid (i.e., suspended body posture and passage of the food
515 through the bars of the grid) would not be compensated by the low number of mouthfuls. This
516 structure on the top of the cages and the distribution of large foods on it then appears to be
517 an effective enrichment by extending the time spent for processing foods (Yamanashi &
518 Hayashi, 2011). A lower effectiveness is also observed on the ground compared to the
519 platform. This can be explained by the presence of dirt and sand inducing a greater number
520 of manipulations to isolate the item. Finally, even if the grid makes manipulation more
521 complex, it has a significant advantage related to the presence of the majority of the largest
522 foods (79%, Table 1). However, it remains significantly less effective than the manipulation of
523 small items on the platform. Although it contains a majority of small items (75%), the platform
524 has the advantage to present a substrate making manipulation simpler (stability and rarity of

525 dirt and sand). This link between the substrate choice and the position of the food has already
526 been shown in other primates (*Microcebus murinus*, Toussaint et al., 2015).

527 This study didn't take into account the interindividual variability in the size of the
528 mouthfuls. Our calculation of the effectiveness score could be biased by smaller mouthfuls, in
529 juveniles for instance. But the precise classification of the food items, based on their size, is
530 thought to limit that bias. Competition, with the presence of other individuals within
531 immediate vicinity, could also induce variability in this score. These two limitations could
532 participate to explain the variability of manipulative techniques observed in the same item-
533 substrate modality.

534

535 **3. How to choose a manipulative technique?**

536 The use of one specific technique by an individual bonobo is presumed to enhance the
537 access to the targeted food. The variability observed in the choice of the manipulative
538 technique for each item and substrate, and the effectiveness of the chosen technique could
539 be linked to the individual decision-making process in bonobos. Indeed, primate foragers face
540 daily challenges for which they have to regulate the balance between the costs and benefits
541 for accessing the food (Garcia et al., 2021). As shown in research about primate decision-
542 making, foraging decisions require the integration of multiple sources of information, both
543 ecological (food type and quantity, travelling distance, temporal information, eventuality of
544 predation) and social (presence and identity of congeners, including kinship and social status)
545 (Garber et al., 2009; Rosati & Hare, 2012). Depending on the set of conditions, the foraging
546 decisions can then differ for a same kind and amount of food, leading to divergent behavioral
547 tactics and, in our study, to variable manipulative techniques. From the few studies available
548 about decision-making process in bonobos, we know that compared to chimpanzees, they

549 have a lower tolerance for risk in choices about food (Heilbronner et al., 2008), hypothetically
550 linked to a less competitive and variable environment (Doran et al., 2002; Furuichi et al., 2015;
551 Hohmann & Fruth, 2003) (but see also Koops, et al., 2015). But in the context of zoo-housing,
552 where the intragroup competition is high and the food is available only when distributed,
553 carrying out a more complex manipulation is not always compensated by the quantity of
554 ingested food and induces a higher risk of theft by congeners, and avoidance of risk could be
555 enhanced. The individual parameters also are of critical importance in this decision process,
556 as suggested by the inter-individual differences found in previous manipulative studies in zoo-
557 housed bonobos (Bardo et al., 2016) and chimpanzees (Pouydebat et al., 2011). Besides the
558 physiological state of the individual such as its satiation level and energy status (see the risk-
559 prone choices in chimpanzees during periods of high diet quality; Gilby & Wrangham, 2007),
560 age, sex and/or social status could induce different manipulative techniques for a given food
561 item. Moreover, the manipulative behavior, as part of the whole foraging behavior, could be
562 reinforced by social learning and/or operant conditioning and become more precise with
563 growing age (Bouton, 2007). The experience of subject has also been shown to enhance
564 consistency and accuracy of tool task in human (Borel et al., 2017). Further studies will need
565 to incorporate not only the ecological context but also the individual and social parameters,
566 as they seem to influence manipulative techniques.

567

568 **Conclusion**

569 In this study, we identified several manipulative techniques depending on the
570 manipulated food and the environmental context. Variability in manipulative techniques for a
571 given food and substrate could be explained by the multifactorial aspect of individual making-
572 decision process, relying on both ecological and social parameters and highlighting the need

573 to frame these techniques within the whole ecological and social context. Finally, the
574 innovative methodologies used in this study, and applicable to any sequential behavioral data,
575 enabled us to broaden our approach on the bonobo manipulative capacities by investigating
576 manipulation as a more complete dynamic process. Our results bring new information
577 contributing to our understanding of the evolution of manual abilities in primates in
578 association with different ecological contexts and both terrestrial and arboreal substrates.

579

580 **Acknowledgements**

581 We thank the “Vallée des Singes” (France), the general director Y. Decker for his hospitality,
582 for allowing us to implement our protocols in his park. We also thank the keepers of the
583 bonobos, C. Michelet, F. Alexieff, and M. Lebrun. We also thank the “Action Transversale du
584 Muséum National d’Histoire Naturelle » (ATM2020-MNHN) for funding as part of the MALBO
585 project. C. Gérard thanks the doctoral school « Sciences de la Nature et de l’Homme : écologie
586 et évolution” for the PhD funding.

587 The data that support the findings of this study are available from the corresponding author
588 upon reasonable request. All authors have no conflict of interest (any potential sources of
589 conflict of interest that could inappropriately influence their work and objectivity) to declare.

590

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Tables:

Table 1. Detailed distribution of the manipulative techniques in each item-substrate modality (Exact multinomial and binomial *ad hoc* tests: number in red are significantly higher than a homogeneous distribution, number in blue are significantly lower, $p < 0.05$)

Item-substrate modality	Multinomial test	Technique 0 (mouth)	Technique 1 (PCG)	Technique 2 (WT)	Technique 3 (TL)	Technique 4 (PMG, MFM and OG)	Total
Rice-grid	$p < 0.001$	1	48	0	7	12	68
Rice-platform	$p < 0.001$	0	44	2	3	38	87
Rice-ground	ns	0	3	2	1	1	7
Small-grid	$p < 0.001$	0	13	13	40	10	76
Small-platform	$p < 0.001$	128	14	12	140	1	295
Small-ground	ns	1	56	29	89	1	176
Large-grid	$p < 0.001$	1	4	5	21	14	45
Large-platform	$p < 0.05$	0	0	1	5	2	8
Large-ground	ns	0	1	0	3	0	4
Total		131	183	64	309	79	766

Figures:

Figure 1. Uni and bimanual manipulations of tubes filled with cooked rice (enrichment devices), at the ceiling grid (left) and on a platform (right) (©M. Anne).

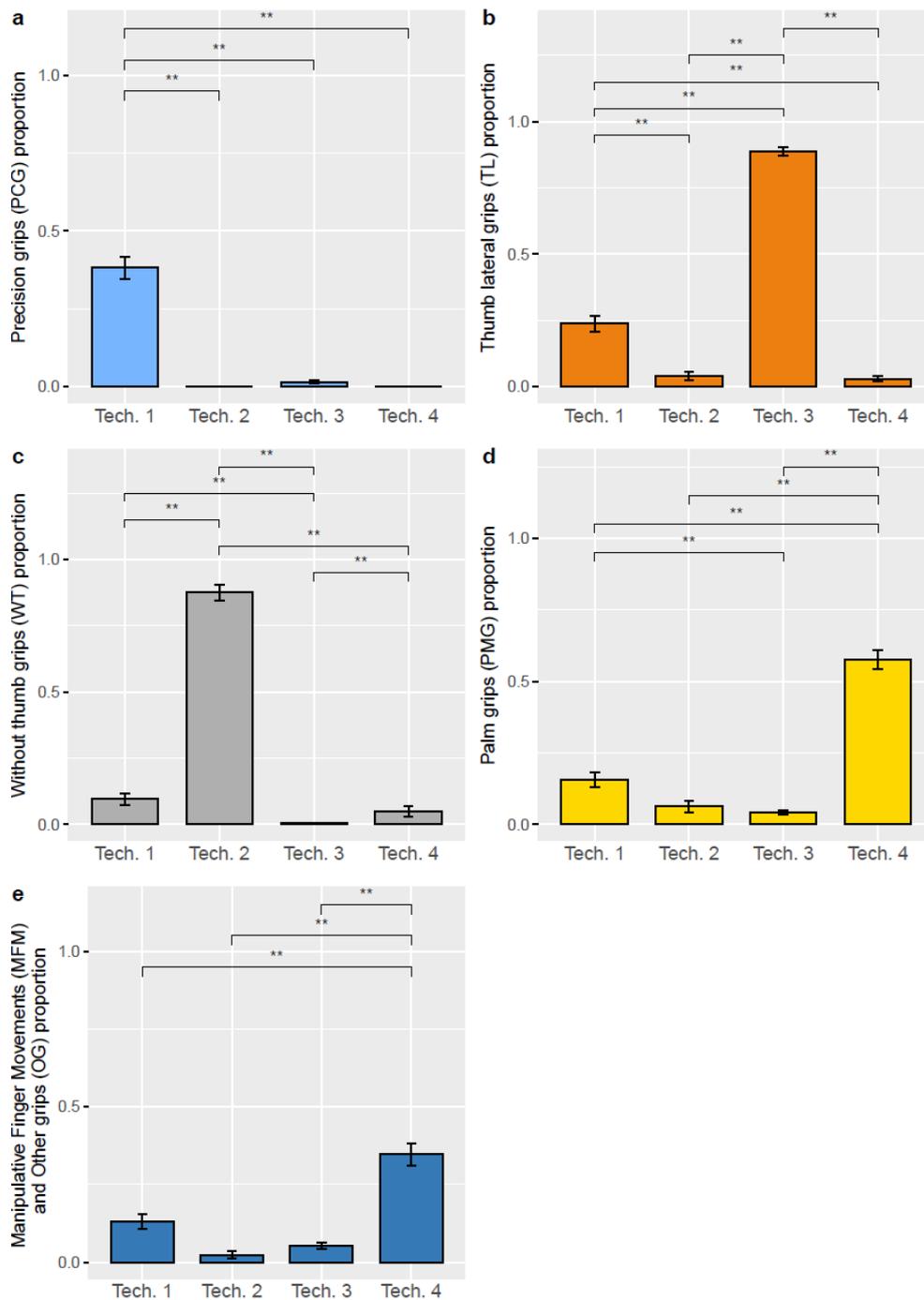


Figure 2. Barplots presenting the means of every grip category proportions in the sequences of each manipulative technique. (Wilcoxon rank sum test with Bonferroni continuity correction, **: $p < 0.001$. Error bars represent standard error of the mean (SEM))

(N technique 1 (PCG) = 183 sequences, N technique 2 (WT) = 64 sequences, N technique 3 (TL) = 309 sequences, N technique 4 (PMG, MFM and OG) = 79 sequences)

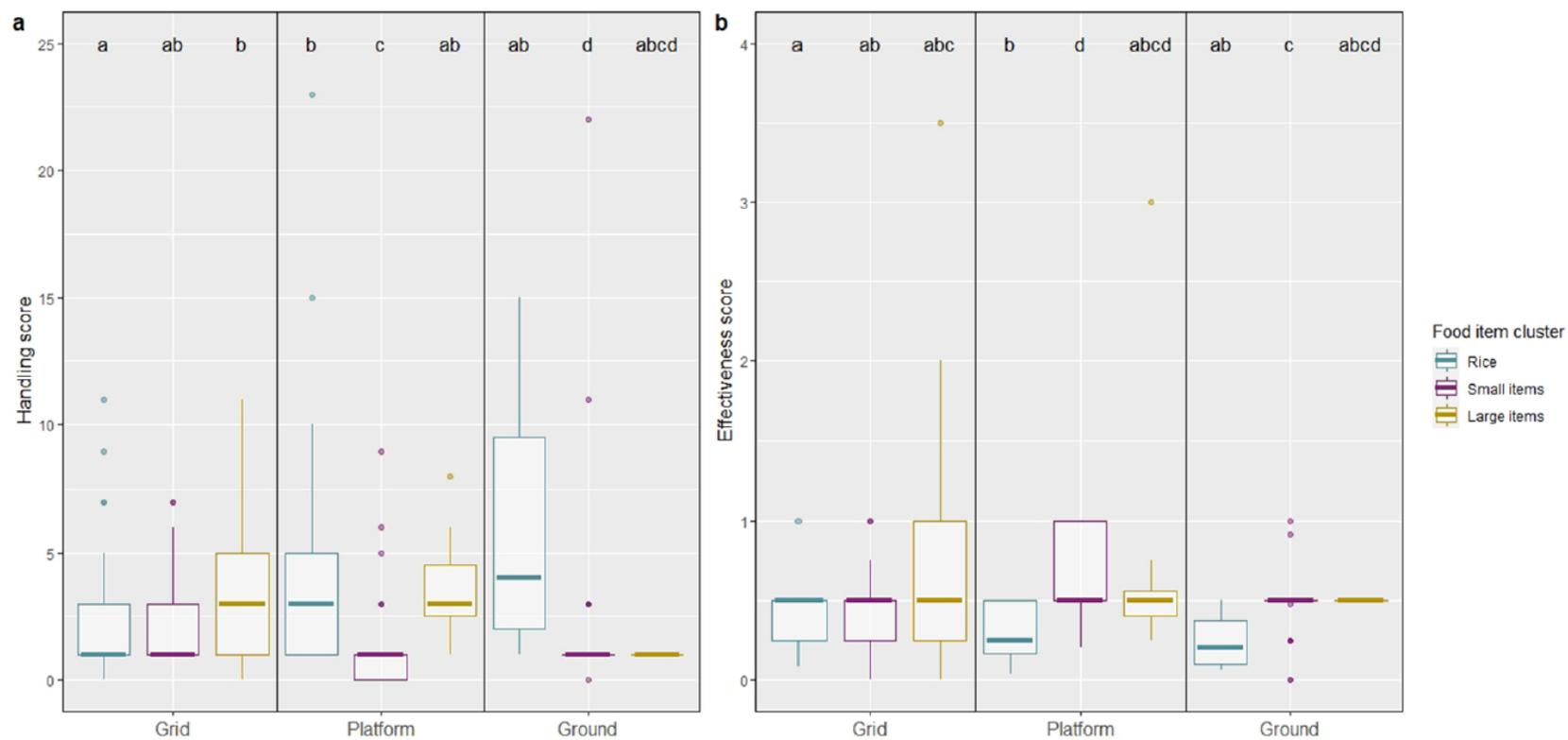


Figure 3. Boxplot representing the handling score (a) and the effectiveness (b) of the sequences in each of the item-substrate modalities (Wilcoxon rank sum test with Bonferroni continuity; modalities that share a letter within and between substrate types do not differ significantly, on average, from each other: $p < 0.05$). Bold horizontal bars represent median values.

Supporting information

Appendix 1. Physical 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	Length (cm)		Width (cm)		Height (cm)		Volume (cm ³)		Mass (gr)		Hardness (N)	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Black radish Cat2	3	6.0	0.0	5.5	0.0	27.0	3.6	10.5	0.8	1.0	0.0	33.0	0.0
Broccoli Cat1	3	14.5	0.3	6.0	0.0	42.0	6.1	23.5	0.6	5.0	0.3	435.0	30.9
Broccoli Cat2	3	6.0	0.3	6.0	0.0	18.0	2.5	20.5	0.5	5.0	0.0	180.0	8.7
Broccoli Cat3	6	2.5	0.3	2.0	0.4	3.0	0.6	0.0	0.0	1.5	0.0	7.5	2.6
Cake	3	15.0	0.0	4.0	0.0	110.0	3.0	0.0	0.0	4.0	0.0	240.0	0.0
Carrot Cat2	5	10.5	0.6	4.0	0.5	53.0	12.7	37.5	0.9	3.5	0.4	147.0	33.3
Carrot Cat3	2	17.5	2.0	3.5	0.0	41.0	1.0	31.0	1.2	2.0	0.0	122.5	14.0
Carrot Cat4	3	14.0	0.0	2.0	0.4	22.0	2.5	31.0	1.2	2.0	0.0	56.0	8.1
Carrot Cat5	2	6.0	0.0	2.5	0.7	11.0	5.0	31.0	1.2	2.5	0.0	37.5	7.5
Cauliflower Cat1	3	13.0	1.5	8.0	0.7	122.0	5.3	14.0	0.4	4.0	0.5	416.0	54.6
Cauliflower Cat2	3	17.0	1.2	8.5	1.1	78.0	4.0	26.0	0.6	2.0	0.3	289.0	54.6
Cauliflower Cat3	4	7.0	0.4	6.0	0.6	50.0	9.5	14.0	0.4	3.0	0.4	126.0	36.4
Cauliflower Cat4	3	6.0	0.3	3.0	0.7	17.0	4.0	8.5	0.5	1.5	0.0	27.0	6.2
Cauliflower Cat5	2	4.0	0.0	3.0	0.0	10.0	1.0	26.0	0.6	1.0	0.0	12.0	0.0
Cauliflower Cat6	9	2.0	0.3	2.0	0.3	2.0	0.6	0.0	0.0	1.0	0.1	4.0	1.8
Celery Cat1	2	14.0	0.0	6.0	0.0	63.0	12.0	14.5	1.0	6.0	0.5	504.0	42.0
Celery Cat2	7	21.5	1.7	6.5	1.4	19.0	2.6	14.5	1.0	1.0	0.0	139.8	35.1
Celery Cat3	3	7.0	0.0	1.5	0.0	9.0	1.5	14.5	1.0	1.5	0.0	15.8	0.0
Celery Cat4	5	13.5	0.7	6.0	0.8	2.0	0.0	0.0	0.0	0.5	0.0	40.5	7.2
Cucumber Cat1	3	11.0	0.0	3.0	0.4	32.0	1.0	11.5	0.4	2.0	0.0	66.0	6.4
Cucumber Cat3	4	7.0	1.1	3.0	0.5	21.0	3.0	11.5	0.4	2.0	0.2	42.0	14.1
Endive Cat3	1	13.0	NA	5.5	NA	11.0	NA	8.7	0.4	0.5	NA	35.8	NA
Endive Cat4	2	9.5	0.5	5.0	0.0	3.0	0.0	8.7	0.4	0.5	0.0	23.8	1.3
Green cabbage Cat1	3	19.5	0.0	9.5	1.3	167.0	11.5	34.5	0.4	6.0	0.9	1111.5	308.3
Green cabbage Cat2	5	24.0	0.9	19.0	0.7	34.0	2.9	26.0	0.9	0.5	0.0	228.0	16.3
Green cabbage Cat3	1	7.5	NA	6.5	NA	37.0	NA	34.5	0.4	6.0	NA	292.5	NA
Green cabbage Cat4	3	13.5	0.9	7.5	0.5	7.0	1.7	0.0	0.0	0.2	0.0	20.3	2.5

Green cabbage Cat5	5	6.0	0.5	3.5	0.4	1.0	0.0	0.0	0.0	0.2	0.0	4.2	0.6
Hazel bark	3	8.5	0.5	1.0	0.0	1.0	0.0	16.0	0.9	0.1	0.0	0.9	0.1
Hazel catkins	10	3.0	0.2	0.5	0.0	0.2	0.0	0.0	0.0	0.5	0.0	0.8	0.0
Leek Cat1	3	19.5	0.8	3.0	0.4	52.0	5.9	17.5	0.6	3.0	0.3	175.5	36.5
Leek Cat2	2	3.5	0.5	2.0	0.0	10.0	2.0	8.0	0.3	2.0	0.0	14.0	2.0
Leek Cat3	3	30.0	1.2	3.0	0.9	15.0	3.1	0.0	0.0	0.2	0.0	18.0	5.4
Leek Cat4	5	14.0	0.2	1.0	0.0	2.0	0.5	0.0	0.0	0.1	0.0	1.4	0.3
Lettuce Cat2	4	10.5	0.7	10.0	1.6	10.0	0.6	0.0	0.0	1.0	0.0	105.0	10.9
Lettuce Cat3	4	9.0	0.6	7.0	0.8	3.0	0.6	0.0	0.0	0.5	0.0	31.5	5.1
Oak leaf Cat4	7	7.0	0.7	5.0	1.0	1.5	0.1	0.0	0.0	0.1	0.0	3.5	0.8
Onion Cat2	2	8.0	0.0	3.5	0.7	20.0	1.0	15.0	0.0	2.0	1.0	56.0	36.0
Onion Cat3	3	6.0	0.0	2.0	0.0	4.0	1.2	5.5	0.0	0.5	0.0	6.0	0.0
Pepper Cat3	3	10.5	0.3	4.5	0.0	36.0	7.6	8.5	0.8	1.5	0.3	70.9	13.1
Pepper Cat4	4	8.5	1.2	4.0	0.7	14.0	1.6	8.5	0.8	1.0	0.2	34.0	9.1
Seeds	10	0.8	0.1	0.5	0.1	0.2	0.0	39.0	0.4	0.2	0.0	0.1	0.0
Zucchini Cat2	3	4.4	0.2	4.5	0.4	18.0	4.5	7.5	0.5	1.0	0.0	19.8	1.9

Appendix 2. 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 (small)	Cluster 2 (large)
Length (cm) (mean \pm SEM)	NA	8.2 \pm 1.0	15.3 \pm 1.4
Width (cm) (mean \pm SEM)	NA	3.7 \pm 0.4	6.6 \pm 1.1
Height (cm) (mean \pm SEM)	NA	1.0 \pm 0.2	3.6 \pm 0.5
Volume (cm ³) (mean \pm SEM)	NA	29.6 \pm 5.7	309.8 \pm 70.7
Mass (gr) (mean \pm SEM)	NA	11.8 \pm 2.3	61.3 \pm 11.7
Hardness (N) (mean \pm SEM)	NA	8.7 \pm 1.8	23.2 \pm 2.8
Food items	Cooked rice	Broccoli Cat3	Broccoli Cat1
Food items	Cooked rice	Black radish Cat2	Broccoli Cat2
Food items	Cooked rice	Carrot Cat5	Cake
		Cauliflower Cat3	Carrot Cat2
		Cauliflower Cat4	Carrot Cat3
		Cauliflower Cat5	Carrot Cat4
		Cauliflower Cat6	Cauliflower Cat1
		Celery stalk Cat3	Cauliflower Cat2
		Celery stalk Cat4	Celery stalk Cat1
		Cucumber Cat1	Celery stalk Cat2
		Cucumber Cat3	Green cabbage Cat1
		Endive Cat3	Green cabbage Cat2
		Endive Cat4	Green cabbage Cat3
		Green cabbage Cat4	Leek Cat1
		Green cabbage Cat5	Leek Cat1
		Hazel bark	Leek Cat1
		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			

Appendix 3. Box-plots presenting the 6 physical variables of the items in each of the clusters 1 (small items, N=29) and 2 (large items, N=14) obtained by Hierarchical Cluster Analysis (HCA) (Wilcoxon rank sum test with Bonferroni continuity correction, *: $p < 0.05$, **: $p < 0.001$).

