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Computerized assessment of dominance hierarchy in baboons (*Papio papio*)

Julie Gullstrand, Nicolas Claidière, and Joël Fagot

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Abstract

Dominance hierarchies are an important aspect of Primate social life, and there is an increasing need to develop new systems to collect social information automatically. The main goal of this research was to explore the possibility to infer the dominance hierarchy of a group of Guinea baboons (*Papio papio*) from the analysis of their spontaneous interactions with freely accessible automated learning devices for monkeys (ALDM, Fagot & Bonté, 2010). Experiment 1 compared the dominance hierarchy obtained from conventional observations of agonistic behaviours to the one inferred from the analysis of automatically recorded supplanting behaviours within the ALDM workstations. The comparison, applied to three different datasets, shows that the dominance hierarchies obtained with the two methods are highly congruent (all $r_s > 0.7$). Experiment 2 investigated the experimental potential of inferring dominance hierarchy from ALDM testing. ALDM data previously published in Goujon & Fagot (2013) were re-analysed for that purpose. Results indicate that supplanting events within the workstations lead to a transient improvement of cognitive performance for the baboon supplanting its partners and that this improvement depends on the difference in rank between the two baboons. This study therefore opens new perspectives for cognitive studies conducted in a social context.

Keywords: monkey, supplanting behaviours, dominance hierarchy, automatized testing, social cognition

41

42 Agonistic behaviours are widely present in the animal kingdom. These behaviours
43 usually occur between group members in a context of competition for limited resources (e.g.,
44 King, 1973) and are relevant to understand a variety of phenomena such as adaptive fitness
45 (e.g., Neat, Taylor & Huntingford, 1998) or dominance style (e.g., Flack, De Waal & Waal,
46 2004). The structure of dominance hierarchies and their mode of computation has been amply
47 discussed in the literature (Bang, Deshpande, Sumana & Gadagkar 2010; Balasubramaniam et
48 al., 2013; Hemelrijk, Wantia & Gygax, 2005; De Vries, 1998; De Vries, Stevens, & Vervaecke,
49 2006). However, this domain of research has witnessed very little evolution regarding the
50 methodology used for data recording. Agonistic behaviours can differ depending on the
51 dominance style of the considered species (e.g., Flack et al., 2004) and their outcome and
52 frequency can both potentially be used to infer group dominance hierarchies. According to
53 David (1987), in linear dominance hierarchies the most dominant individuals emit more
54 agonistic behaviours than they receive, increasing their proportion of contests won. In such
55 situations, dominance hierarchies can therefore be inferred from the difference in frequencies
56 of agonistic behaviours emitted and received by each individual within the group (Dugatkin,
57 1997). In animals with a less linear social organization, the analysis of dominance hierarchies
58 is often more difficult to establish due to a smaller number of agonistic behaviours emitted and
59 received, especially in species with more egalitarian styles (Watts, 1994). Fischer et al. (2017)
60 for instance reported in the male-male tolerant Guinea baboons (*Papio papio*) that they were
61 not able to establish a significant linear rank hierarchy because of the low number of agonistic
62 interactions, and despite the fact that agonistic interactions were mostly unidirectional (see also
63 Patzelt, 2013).

64 Another difficulty encountered in previous studies is that agonistic behaviours require
65 serious efforts to be recorded. In most studies on dominance hierarchies, data are collected by

66 effortful and time-consuming observations, either directly (Barton, Byrne & Whiten, 1996) or
67 based on video recordings (Foris, Zebunke, Langbein, & Melzer, 2019). With the development
68 of modern technologies, new methods have emerged for automatic identifications of animals
69 (e.g., GPS tracking in baboons, Strandburg-Peshkin et al., 2015; bar code tracking in birds,
70 Alarcón-Nieto et al., 2018; deep learning in birds, : Ferreira et al., 2019), but the use of
71 automated identification methods remains limited in social studies on dominance hierarchy. In
72 rare noticeable exceptions, authors inferred dominance hierarchies from the combination of
73 video tracking with (1) RFID data (in mice: Weissbrod et al., 2013), (2) identity data obtained
74 from automated reading of ear-tags (in cows: Foris, Thompson, Keyserlingk, Melzer & Weary,
75 2019), or (3) automated barcode or GPS reading (in pigeons: Nagy et al., 2013), but these
76 methods remain time consuming because of video processing. In another study with olive
77 baboons (*Papio anubis*) the author used supplanting behaviours to assess dominance hierarchy
78 to overcome the lack of the other agonistic behaviours (Packer, 1979).

79 The main goal of the current research was to explore a new method to infer dominance
80 hierarchies automatically. Fagot and Bonté (2010) have implemented novel test systems to
81 study cognition in semi-free baboons. In this study, a colony of Guinea baboons has free access
82 to a battery of ten ALDM (for Automated Learning Devices for Monkeys) test systems. The
83 ALDM test systems are automatized operant conditioning systems equipped with touchscreen
84 on which the cognitive tasks are presented, as well as a RFID tag reader for the identification
85 of the subject. With this technology, each test system reads the identifying RFID microchip
86 implanted in each arm of the baboon when it enters a workstation. This allows the self-paced
87 presentation of the cognitive tasks to the members of the colony, without any social isolation
88 or physical capture. Claidière, Gullstrand, Latouche and Fagot (2017) reported that the spatial
89 use of these ten ALDM test systems provides information on the social structure of the baboon
90 colony: the social network inferred from the co-presence of individuals within the spatially

91 adjacent workstation correlated strongly and reliably with the social network inferred from the
92 affiliative behaviours (e.g. grooming or greeting behaviours) observed inside the enclosure
93 where the group of baboons lived. In this study, we assessed if the use of ALDM systems can
94 also provide information on dominance hierarchy, therefore complementing our previous
95 studies on affiliative network (Claidière et al., 2017; Gelardi, Fagot, Barrat & Claidière, 2019).

96 Following Packer (1979), we considered in our research that supplanting behaviours are
97 interesting behavioural markers of the dominance hierarchy. A supplanting behaviour can be
98 defined as a sequence of behaviour in which one animal A approaches another individual B
99 who then leaves. Supplanting behaviours have the advantage over many other agonistic
100 behaviours to have a clear winner (individual A). According to Johnson (1989), supplanting
101 behaviours lead to the establishment and maintenance of dominance hierarchies in olive
102 baboons (*Papio anubis*), and these behaviours are observed in this species regardless of food
103 quality and rarity, between individuals closer in ranks, avoiding greater risks in escalation of
104 more aggressive displays. To the best of our knowledge, our study is the first study in which
105 dominance hierarchy was inferred from supplanting behaviours in Guinea baboons.

106 Given the proposed relation between supplanting behaviours and dominance hierarchy,
107 our study investigated the dominance hierarchy in Guinea baboons considering supplanting
108 behaviours within the ALDM test systems. In Experiment 1, we first assessed dominance
109 hierarchy from conventional observations of agonistic behaviours expressed within the
110 enclosure where the baboons lived. Secondly, we extracted hierarchy from ALDM dataset,
111 considering supplanting behaviours within the testing workstations and compared the
112 hierarchies obtained with the two methods. Using three different datasets, we found that the
113 dominance hierarchy converged with the two methods. Thirdly, experiment 2 aimed at
114 documenting the experimental potentials of inferring dominance hierarchy from automatically
115 recorded ALDM supplanting behaviours. Supplanting behaviours were extracted from a

116 previous data set already published in Goujon and Fagot (2013) and used as a factor for
117 reanalysing the cognitive performance of the baboons in this study. We found that supplanting
118 events lead to a transient improvement of cognitive performance for the baboon supplanting its
119 partner, confirming the potential usefulness of inferring dominance hierarchies to study
120 cognitive processes.

121

122 **Experiment 1: Assessing dominance hierarchy from ALDM testing**

123 Experiment 1 aimed at comparing dominance hierarchies inferred from the ALDM
124 supplanting behaviours with those obtained from more naturalistic observations of the social
125 behaviours spontaneously expressed in the baboon's enclosure.

126 **Methods**

127 **Participants and living conditions**

128 All participants belonged to the same group of Guinea baboons (*Papio papio*) from the
129 CNRS primate Centre, Rousset-sur-Arc, France. The group consisted of males and females
130 from different families living with their offspring in a large enclosure. The entire group was
131 housed inside a 25 x 30 m² outdoor enclosure connected to an indoor area and to two
132 experimental trailers providing access to computerized (ALDM) test systems (see below). The
133 group had *ad libitum* access to water, and feeding was provided daily at 5 pm.

134 Individuals from this group were studied during three study periods, between 2013 and
135 2015. The size of the group varied among these periods, from 21 to 22 individuals, due to births
136 or deaths from natural causes. The subjects retained for our research were those who were old
137 enough to participate in computerized testing. Supplementary table 1 reports the name, sex,
138 year of birth and participation of the individuals in each test period.

139 **Ethics statements**

140 This research was carried out in accordance with European Union and French ethical
141 standards and received approval from the French Ministère de l'Éducation Nationale et de la
142 Recherche (approval no. APAFIS-2717-2015111708173794-V3).

143 **Behavioural observations in the enclosure**

144 The baboons' spontaneous behaviour in their outdoor enclosure were recorded during
145 three observation periods, which were approximately evenly interspersed within a 3-year time
146 window (from 2013 to 2015, see supplementary table 1). These three periods will be referred
147 to below as the main-, control-1 and control-2 study periods. The method used for behavioural
148 recording during each period is described below.

149 ***Observational methods: main study period.*** Data were recorded during the main study
150 period from the 21st of September to the 21st of October 2015. Behavioural observations in that
151 period used a focal sampling method (Altmann, 1974). The coding scheme contained a long list
152 of affiliative and agonistic behaviours but the current paper will only consider the following six
153 behaviours which are all known to occur in agonistic contexts: “aggression”, “chase”, “threat”,
154 “supplanting behaviour”, “avoidance” and “yakking”, see supplementary table 2 for
155 definitions). Every day of observation was composed of three sessions during which two
156 experimenters observed the baboons. In every other observation session one experimenter was
157 assigned the role of observing the baboons (in order to identify the behaviour performed, its
158 producer and receiver) while the other simultaneously monitored timing and entered the data in
159 the Behavioural Observation Research Interactive Software (BORIS) program (Friard &
160 Gamba, 2006). The observer had to observe each baboon during five minutes in a predefined
161 randomized order varying from sessions to sessions, for a total of 120.8 hours of observation.
162 We recorded a total of 934 agonistic events during this observation period.

163 Inter-observer reliability was assessed using two hours of video recordings of the
164 baboons' behaviours. These videos contained sequences of five minutes of observation per
165 subject and were recorded at the beginning (one hour) and end (one hour) of the observation
166 periods. Each experimenter coded independently the behaviours observed in the video using
167 the same protocol as defined above. The concordance between the two observers was coded
168 using Kappa-Cohen's method (Cohen, 1960; Landis & Koch, 1977). Inter-observer agreement
169 was high regarding the category of the behaviour ($K_{\text{session1}}=0.68$; $K_{\text{session2}}=0.85$), and the identity
170 of the baboons ($K_{\text{session1}}=0.88$; $K_{\text{session2}}=0.85$).

171 ***Observational method: control periods 1 and 2.*** The database from control period-1
172 (from the 2nd to the 29th of July 2014) contained a total of 300 hours of behavioural observation
173 which were recorded in the context of Claidière et al. (2017). The data published in Claidière
174 et al. (2017) only concerned affiliative behaviours, and therefore used a scanning procedure
175 (Altman, 1974) adapted for that purpose. Information on the agonistic behaviours collected in
176 this study has remained thus far unpublished. The dataset from control period-2 (from the 2nd
177 to the 16th of May 2013) used a total of 180 hours of observation (unpublished data) previously
178 collected for the same purpose and with the same method as in period-1. In control periods 1
179 and 2, the observers used the same coding scheme as in the main study period, the only
180 difference being therefore that the data were collected with a scan instead of the focal sampling
181 method. The datasets for control periods 1 and 2 contained a total of 600 and 351 agonistic
182 events respectively, with known agonistic dyads. The difference in the number of agonistic
183 events in periods 1 and 2 is explained by the difference in duration of these periods.

184 **ALDM testing**

185 In our laboratory, the baboons have a permanent access to ten Automated Learning
186 Device for Monkeys (ALDM) systems, and this was also true during the three study periods of
187 this research. The ALDM test systems are described in detail in Fagot & Paleressompouille

188 (2009) and Fagot & Bonté (2010). In short, each ALDM workstation consisted of a 70 cm × 70
189 cm × 80 cm test chamber equipped with (1) a RFID microchip scanner aimed at reading
190 subjects' identity from RFID microchips implanted in their arms; (2) a 19 inches' computer
191 touch screen displaying the task, and (3) a food dispenser delivering a reward inside the test
192 chamber when the subject responded correctly to the task. In practice, the baboons could freely
193 enter and leave each experimental chamber via opened doors installed in the wire mesh of their
194 enclosure.

195 When a baboon voluntarily entered an ALDM test system, it was identified via the
196 forearms' microchip and this identification triggered the initiation of the test program. All
197 ALDM trials were recorded with detailed information regarding the baboon and its
198 performance, including the date and time of the trial, as well as the workstation used. This
199 information was used to detect supplanting behaviours within the ALDM test systems, and to
200 infer the dominance hierarchy from these behaviours (see below). In practice, the baboons
201 received several different computerised cognitive tasks (e.g., Wisconsin task) of varying
202 durations during the three study periods. However, for Experiment 1 we will consider that the
203 type of cognitive test is unimportant for our current scientific purpose, because our primarily
204 goal is to determine if we can use ALDM computerised data to determine the group hierarchy.

205 **Assessing dominance hierarchy**

206 To assess the dominance hierarchy from behaviours observed in the enclosure, we built
207 three “winner/loser” files from the original data, one per study period. Whenever an agonistic
208 behaviour was observed, the individuals displaying aggression, chase, threat, or supplanting
209 behaviour was considered “winner” in each dyad, while the baboons receiving these behaviours
210 were considered “losers”. The coding was reversed for the avoidance and yacking behaviours,
211 which correspond to social submission.

212 To assess dominance from the data collected in the ALDM test systems, we reasoned
213 that supplanting behaviours in the ALDM test systems should be indicated by a very short
214 interval between the last trial of the supplanted subject (“loser”) and the first trial of the
215 supplanting subject (“winner”). Based on this reasoning, we analysed the ALDM data in two
216 steps. Firstly, we defined a “run” as a succession of trials by the same individual within the
217 same workstation, and with inter-trial interval of less than 30 seconds (i.e. not exceeding twice
218 the average delay between two consecutive trials). A run therefore represents a succession of
219 trials corresponding to a single foraging bout. Secondly, to identify supplanting behaviours
220 within the workstations (i.e. cases in which the foraging bout was disrupted), we computed the
221 time interval between the last trial of one baboon within a given workstation and the first trial
222 of the next individual in the same workstation. We considered that this behavioural sequence
223 corresponded to a supplanting behaviour when this interval between two individuals was
224 smaller than 30 seconds (i.e. the foraging bout had been disrupted). Using this procedure, we
225 obtained an ALDM winner/loser files for each observation period, which had the same structure
226 as the winner/loser file from the spontaneous behaviour in the enclosure. This procedure
227 allowed the identification of 7844 cases of supplanting behaviours (for 22132 runs considered)
228 during the main study period (in 2015), and 7700 (22769 runs) and 7479 (17634 runs) during
229 the control periods 1 and 2 respectively.

230 The Elo-rating method (Elo, 1978) was used to calculate dominance hierarchy from the
231 sets of the winner/loser files described above. Interested readers are referred to Elo (1978) for
232 a detailed description of this method. In short, each individual started with the same score with
233 this method, and at each new contest the score of the winner increased by a certain amount
234 while it decreased for the loser by the same amount. To calculate the dominance hierarchy, we
235 used RandomElo function from the Elo-rating package (Neumann et al., 2011) that ran on the
236 statistical environment R (R version 4.0.2 ; R Core Team, 2015), and followed Neumann &

237 Kulik (2014)'s procedure, with starting value of 1000 and a constant k optimized using
238 maximum log-likelihood (provided in supplemental table 4). For each inferred dominance
239 hierarchy, through the 3 sampling periods and both types of data sets, we assessed triangle
240 transitivity and linearity index using Elo-rating package viewable in supplemental table 4.
241 Finally, we ensured the repeatability of the hierarchies by computing repeatability scores using
242 AniDom package (Sánchez-Tójar, Schroeder & Farine, 2018), using the same constant k
243 optimized and 1000 randomisations.

244 **Statistical analyses**

245 *Correlational analyses.* A first way to validate our approach is to directly compare the
246 correlation between the dominance hierarchies obtained through behavioural observations and
247 through computerised testing. We used two different correlation tests on Elo-scores: Spearman
248 and Kendall correlations. The non-parametric Spearman correlation test compares the relative
249 order of dominance hierarchies (for example if A is above B in one hierarchy and B above A
250 in the other) and is widely used in the literature (Balasubramaniam et al., 2013; Hunter, Broom,
251 Edwards & Sibly, 1988; Williamson, Lee & Curley, 2006). The Kendall correlation test is less
252 frequently used (Bang et al., 2010; Hemelrijk et al., 2005) but compares the strict value of the
253 ranks of individuals in the hierarchy (for example if A is +3 ranks above B in one hierarchy and
254 -1 rank in another) and therefore seems more precise. For the purpose of exhaustivity, we report
255 below the results of both tests.

256 *Modelling.* A high correlation between the two hierarchies would show that both
257 hierarchies are similar but would not inform us on the cause of this similarity. For instance, it
258 is possible that dominant individuals are more frequently involved in cognitive testing than
259 subordinate individuals, and that a higher number of comings and goings in the workstations
260 increases the rank of individuals in the hierarchy calculated from ALDM testing. Exact
261 permutation tests (Fisher, 1954) were used to assess the contribution of such variables to our

262 measurement of dominance hierarchies. In an exact permutation test, we perform a large
263 number of permutations of the variables that may not account for the observed correlation while
264 maintaining the variable of interest constant, every time calculating the correlation between the
265 hierarchy obtained from the randomly permuted computerised data and the one obtained from
266 observed data. This generates a distribution of correlation coefficients obtained under the null
267 hypothesis that the factors that have been permuted do not account for the correlation. If the
268 observed correlation falls outside the 95% confidence interval of the distribution of simulated
269 coefficients, the null hypothesis can be rejected, and we can conclude that the factors that have
270 been permuted are important in explaining the correlation.

271 Two main parameters can influence the position of the individuals in the dominance
272 hierarchy, they include the frequency of agonistic interactions (i.e. supplanting behaviours)
273 each baboon has in the workstation (which could be linked to proportion of contest in traditional
274 hierarchy assessment; David, 1987) and the identity of the winner-loser dyads involved in each
275 agonistic interaction. We therefore used two random models, one testing each variable. This
276 modelling approach was applied to the analysis of the data collected during the main study
277 period only, because this dataset was the largest.

278 ***Random model 1.*** In the first model, the identity of individuals between two recordings
279 was randomly permuted before supplanting behaviours computation (we performed 50 000
280 permutations for 22132 runs for each of the 500 simulations). Each monkey maintained in
281 random model 1 the same frequency of participation in cognitive tasks, but the permutation of
282 the subjects' identity in the dataset altered the proportion of supplanting behaviours performed
283 by each participant as well as the identity of the winner-loser dyads. If the dominance hierarchy
284 obtained from the ALDM is determined mostly by the baboons' frequency of participation in
285 experiments, then we expect the correlation obtained from the simulations to be similar to that
286 obtained with the untransformed ALDM data.

287 **Random model 2.** The aim of the second model was to examine if the hierarchy can
288 depend on the frequency of contests won, irrespective of the identity of the dyad involved in
289 the supplanting behaviour. We performed 500 simulations in which we performed 50 000
290 permutations of the identity of the winners of two different supplanting behaviours (making
291 sure the same individual did not appear both as winner and loser). Each individual therefore
292 maintained the same number of contests won but with different losers. If the hierarchy is mostly
293 determined by the number of contests won and not by the winner-loser identity, then we expect
294 the correlation between the hierarchy obtained from the simulations to be similar to that
295 obtained with untransformed data.

296 **Results**

297 **Reliability and repeatability of the hierarchies**

298 The hierarchies obtained for the three periods and two types of data are highly repeatable
299 and reliable (Repeatability index were very high: $r_{\text{obs}} = 0.92$ and $r_{\text{ALDM}} = 0.96$ for the main study
300 period; $r_{\text{obs}} = 0.88$ and $r_{\text{ALDM}} = 0.97$ for the Control period-1 and $r_{\text{obs}} = 0.94$ and $r_{\text{ALDM}} = 0.95$
301 for the Control period-2). Summary table in the appendix present the sets of Elo-scores and
302 ranks for each baboon (supplemental table 3), as well as the linearity and transitivity indices of
303 the triangles for each hierarchy (supplemental table 4).

304 **Main study period**

305 The correlation between the hierarchies obtained with observational and computerised
306 data is shown on the left-hand panel of Figure 1. It is high and different from chance (Kendall
307 correlation: $\tau = 0.75$, $\text{CI} = [0.59; 0.89]$, $N = 21$, $p < 0.001$; Spearman correlation: $r_s = 0.91$, CI
308 $= [0.76; 0.97]$, $N = 21$, $p < 0.001$). Individual Elo-scores and ranks are presented in

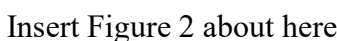
309 supplementary table 3. The absolute difference in rank between the ALDM and observational
310 dominance hierarchies remained relatively low, with an average equal to 2.04 ranks (max = 6).

311  Insert Figure 1 about here

312

313 **Random model 1**

314 For this model, we found that the correlation between the simulated hierarchies obtained
315 by permutations and the observation's hierarchy was not significantly different from 0 (see
316 Figure 2, mean Kendall correlation: $\tau_{\text{sim}} = 0.15$, 95% CI = [-0.16; 0.43]; mean Spearman
317 correlation: $r_{s \text{ sim}} = 0.21$, 95% CI = [-0.19; 0.60]), and significantly smaller than the correlation
318 obtained with untransformed ALDM data ($\tau = 0.75$, CI = [0.59; 0.89], $p < 0.001$; $r_s = 0.91$, CI
319 = [0.76; 0.97], $p < 0.001$). This result shows that the mere variations in the frequency of the
320 baboons' participation to cognitive testing were not at the origin of the strong correlation that
321 we observed.

322  Insert Figure 2 about here

323 **Random model 2**

324 For random model 2, the distribution of simulated correlation coefficients was
325 significantly different from 0 (see Figure 2, mean Kendall correlation: $\tau_{\text{sim}} = 0.64$, 95% CI =
326 [0.60; 0.68]; mean Spearman correlation: $r_{s \text{ sim}} = 0.83$, 95% CI = [0.81; 0.86]). Additionally, the
327 distribution of simulated correlated coefficients was also significantly smaller than the
328 correlation obtained with untransformed ALDM data ($\tau = 0.75$, CI = [0.59; 0.89], $p < 0.001$; r_s
329 = 0.91, CI = [0.76; 0.97], $p < 0.001$), showing that ALDM dominance hierarchies reflect the
330 social assortment of the individuals in each supplanting dyad.

331 **Correlational analyses: all three study periods**

332 Figure 1 illustrates the correlations obtained between the observational and ALDM
333 dominance hierarchies in the three study periods. As indicated above, that correlation was high
334 and significant for the main study period (Figure 1, left panel). This was confirmed by the
335 analysis of the two other study periods as shown in the middle and right panel of Figure 1
336 (control period-1: Kendall correlation: $\tau_{c1} = 0.76$, CI = [0.57; 0.91], N = 22, $p < 0.001$ and
337 Spearman correlation: $r_{sc1} = 0.9$, CI = [0.71; 0.97], N = 22, $p < 0.001$; control period-2: Kendall
338 correlation: $\tau_{c2} = 0.76$, CI = [0.57; 0.91], N = 21, $p < 0.001$ and Spearman correlation: $r_{sc2} =$
339 0.9, CI = [0.70; 0.98], N = 21, $p < 0.001$). On average, the absolute difference in ranking
340 remained relatively low in both control periods, it was equal to 2.0 ranks (max = 6) and 2.1
341 ranks (max = 8) for the control periods 1 and 2, respectively (Individual Elo-scores and ranks
342 are presented in supplementary table3).

343 **Discussion of Experiment 1**

344 Experiment 1 employed two methods to assess dominance hierarchy, conventional
345 observations on the one hand and the analysis of supplanting behaviours during ALDM testing
346 on the other hand. These two methods presented very similar rankings in all three datasets
347 covering a period of 3 years, considering both Kendall and Spearman correlations and similarly
348 high repeatability indices. Simulations further demonstrate that the hierarchies obtained with
349 the ALDM method reflect the social dominance hierarchy, independently of variations in
350 participation to cognitive testing. Both the frequency of supplanting behaviours and the identity
351 of the individuals involved in the supplantation are crucial factors determining the dominance
352 hierarchy. We believe that such results, at the group and individual levels, demonstrate that
353 dominance hierarchy can be inferred reliably from the analysis of supplanting behaviours
354 within the ALDM workstations

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Experiment 2: Effect of supplanting behaviours on cognitive performance

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The main goal of Experiment 2 is to illustrate the possible use of ALDM hierarchies obtained from supplanting behaviours in the context of cognitive studies. Goujon & Fagot, (2013) have previously published data on the cognitive performance of our group of baboons in the ALDM test system. This research used the so called “contextual cueing” task (Chun & Jiang, 1998), in which the baboons had to detect a target in two types of visual displays, first on non-predictive backgrounds providing no information on target location, and second on predictive backgrounds which have been associated by training to specific target location on the computer screen. Results indicated a strong effect of the background on the speed of target detection, with faster response times (RTs) in the predictive compared to the non-predictive condition. In Experiment 2, we reanalysed Goujon and Fagot’s (2013) data in order to assess if the ALDM supplanting behaviours recorded during that research had subtle (but previously undetected) effects on the baboon’s cognitive performance.

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Methods

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Participants

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The study used the same baboon colony as in Experiment 1. However, because this study was conducted in 2012, and therefore one year before the control period 2 of Experiment 1, this colony had a slightly different composition. The data set therefore contained information on a total 20 baboons (5 males and 15 females) whose name and biographical information are indicated in the supplementary section.

376 **Experimental setup, computerized task and database**

377 Experiment 2 used the same ALDM workstations as in Experiment 1. The experimental
378 task is already presented in detail in Goujon and Fagot (2013) and will therefore only be briefly
379 described here. In short, the trials started with the display of a fixation stimulus on the screen.
380 Touching this stimulus triggered the display of 8 items, including one target (the capital letter
381 “T”) and 7 distractors (capital “L” with different orientations). To be rewarded, the baboons
382 had to detect the target on the screen and to touch it. In the predictive condition (P), six patterns
383 of distractors were each associated with a fixed target position. In the non-predictive condition
384 (NP), six different configurations of distractors were presented independently of the target
385 position. The P and NP trials were presented for one month (July 3rd to August 3rd 2012) within
386 a balanced design. Due to a few technical problems, a small number of ALDM test boxes were
387 temporally stopped during testing. Because a too small number of boxes may have affected the
388 monkeys’ turnover and the detection of supplanting behaviours, we only retained the data
389 corresponding to the days when a minimum of 8 boxes were accessible. This criterion lead to a
390 very small rate of rejection (only 3 days), while keeping high the likelihood of detecting
391 supplanting behaviours. The database analysed here contains a total of 411534 trials (mean =
392 20576, median = 21 134, SD = 6355 per baboon).

393 **Data analysis**

394 Investigating the effect of supplanting behaviours on loser of each dyad is difficult,
395 because the subjects either stop temporarily after a supplanting event, or move to a different
396 workstation, with a high variability in time and behaviour between the last trial after the
397 supplantation and the first trial of the next working bout. The analysis therefore focussed on the
398 winner who performed trials immediately after the supplanting event. We considered two types
399 of trials for that subject: those made after the baboon had supplanted another baboon (named

400 “Supplant” trial), and control trials in which it arrived in an empty workstation (baseline trial).
401 Data analysis therefore proceeded in two steps (1) identification of supplanting and baseline
402 trials, and (2) analysis of the baboons’ RT depending on whether the trials were recorded or not
403 after a supplanting event. We used the same procedure as in Experiment 1 to identify runs and
404 instances of supplanting behaviours. A total of 20556 runs were identified with 9310 runs
405 starting after a supplanting event. The dominance hierarchy of the group was computed based
406 on these ALDM supplanting behaviours using the same procedure as in Experiment 1.

407 Because of a very low rate of errors in cognitive test (range: 96%-99%) statistical
408 analyses focused on RTs. Social challenges can induce extremely rapid biological effects in
409 animals (e.g., neuropeptides release, Kelly & Wilson, 2019), with potential consequences on
410 behaviour and cognition (see the discussion of Experiment 2 for additional information). We
411 therefore conducted a preliminary analysis of the data and found that RT differences across
412 conditions were mostly found on the very first trials following supplanting behaviour. On that
413 basis, our next analyses only considered the first 6 trials of each run. The RT of each trial was
414 considered for statistical analyses only if (1) the subject gave a correct response in the trial, and
415 (2) the RT did not exceed three standard deviations from the individual mean RT. This standard
416 filtering procedure avoided consideration of outlier trials resulting from transient inattention
417 (e.g., Lacreuse, Gullstrand & Fagot, 2016). The final dataset contained a total of 99 619 trials.
418 The average number of trials per individuals were as follows for each type of trial: Baseline-
419 NP: mean = 1351, median = 1201, SD = 730; Baseline-P: mean = 1368, median = 1213, SD =
420 743; Supplant-NP: mean = 1129, median = 890, SD = 674; Supplant-P: mean=1133, median =
421 893, SD = 667.

422 Linear mixed-effect models (LMM) were computed to analyse the results, using the
423 lme4 package in R (Bates & Machler, 2010). Goujon & Fagot (2013) have reported that the
424 RTs decreased in this task with the number of days of testing. We therefore included as random

425 factors the “Name” of the subjects with a random intercept and slope depending on the number
426 of “Days” of the experiment. This random factor controlled for repeated measurements and the
427 evolution of RT with learning. We also included a simple random intercept for the “Age” of the
428 subjects, because Goujon & Fagot (2013) reported inter-individual differences between age
429 groups. Based on the above considerations, we report the results of the three way interaction
430 between the following fixed factors: (1) the type of trial (baseline vs supplant trial, referred to
431 as the “Behavioural condition” in this analysis), (2) the type of contextual background (P or
432 NP, referred to as the “Experimental condition”) and (3) the position of the trial in the run (from
433 1 to 6, referred to as “Ntrial” variable).

434 Finally, a last model investigated if the effect on RTs was modulated by the difference
435 of hierarchical position of both protagonists of the supplanting behaviour. In this model, we
436 only considered as dependent variable the RT of the very first trial performed by the winner
437 after a supplanting behaviour in the non-predictive condition, because the effect of
438 supplantation is stronger on the very first trial and then progressively fades. The explanatory
439 variable was the difference of rank between the winner and the loser of the ALDM supplanting
440 behaviour. With 20 individuals in the group, difference in ranks could vary between -19 (if the
441 most subordinated individual supplanted the most dominant) and +19 (if the most dominant
442 individual supplanted the most subordinated).

443 **Results**

444 The results of the three-way interaction model are shown in Table 1. Our results confirm
445 the main effect of experimental condition (P vs NP) previously described, with faster RTs in
446 the predicted condition (on average by 54 ms; RT mean = 541 ms, SD = 214 ms). In addition,
447 there was a small effect of the position of the trial in a run with RTs decreasing on average by
448 1.36 ms with the number of trials performed. Finally, RTs were shorter in trials following a

449 supplanting behaviour compared to trials performed without supplanting behaviours, on
450 average by 20 ms on the first trial. We found no evidence of interactions between these different
451 variables.

452 Insert Table 1 about here

453 Regarding the effect of the difference of hierarchical position (between winner and loser of the
454 supplanting behaviour), we found significant RT differences depending on difference in ranks
455 between the winner and the loser: The most challenging supplanting behaviours, corresponding
456 to the supplanting of a higher-ranking individual by a lower-ranking individual gave rise to the
457 shortest RTs during the ALDM trials immediately following that behaviour, with an estimated
458 difference in RTs of about 1.75 ms (SE = 0.56 ms, t value = 3.12, $p < 0.001$) for each difference
459 in ranks. For instance, when Ewine (10th rank) supplants Angele (4th rank) the estimated RT
460 is 26 ms lower than if she supplants Dream (19th rank), because there is a difference of 15 ranks
461 between Angele and Dream.

462 **Discussion of Experiment 2**

463 Experiment 2 investigated the effect of supplanting behaviours on cognitive
464 performance. We analysed the first six trials of each run performed in the ALDM system,
465 distinguishing those performed after a supplanting behaviour from those without. The results
466 showed a significant effect on baboons' RTs: RTs were shorter in trials following supplanting
467 behaviour, compared to baseline trials. This difference was significant in both predictive and
468 non-predictive conditions. We also found that RTs decreased when the winner supplanted an
469 individual of a higher social rank suggesting that the response speed can be affected by social
470 challenges.

471 Since the goal of the current paper is mostly methodological, we will not discuss at
472 length the behavioural and brain mechanisms by which the supplanting behaviours can affect

497 ALDM data differed from those obtained after a random permutation of the individuals
498 performing the trial, suggesting that the ALDM dominance hierarchies are independent of the
499 frequency of baboon's participation to ALDM testing. Secondly, the dominance hierarchies
500 inferred from untransformed ALDM data also differed from those obtained after random
501 permutation between winners, showing that the dominance hierarchy crucially depends on the
502 identity of the individuals interacting. Thirdly, and most importantly, strong correlations were
503 found between the dominance hierarchies obtained from conventional observations and those
504 obtained from ALDM testing for three independent study periods spanning a total of three years
505 (all correlations' $r > 0.7$). Earlier studies with sows (Hunter et al., 1988), birds (Evans, Devost,
506 Jones, & Morand-Ferron, 2018) and cows (Foris, Thompson et al., 2019) have already shown
507 the interest of computer-controlled identification systems to infer dominance hierarchies.

508 Dominance hierarchies are often difficult to measure in non-human primates, such as in
509 the male-male tolerant Guinea baboons (Fischer et al., 2017; Patzel, 2013). It might be the case
510 that agonistic behaviour are more frequent in captivity (such as in our study) than in the wild,
511 and this could explain why we found a linear dominance hierarchy in our group, while Fischer
512 et al. (2017) did not. Nevertheless, the present study on the same baboon species as in Fischer
513 et al. (2017) highlights the usefulness and reliability of supplanting behaviours in the
514 assessment of the dominance hierarchy. Its findings match perfectly with the previous studies
515 on baboons 'supplanting behaviours (Packer, 1979; Johnson, 1989) that reported that baboons
516 were using supplanting behaviours to reinforce existing social relationships. The consistency
517 of our results, across test periods and methods, opens new perspectives for future studies on
518 dominance hierarchy, and demonstrates that such hierarchies can be inferred from the analysis
519 of supplanting behaviours during ALDM testing.

520 The current study showing that dominance hierarchies can be calculated from
521 automatized ALDM testing also converges with earlier studies demonstrating that *ad-libitum*

522 computerized cognitive testing allows the extraction of social information. Previous studies
523 from our research group have already demonstrated that ALDM cognitive testing permits
524 studies on the static social network (Claidière et al., 2017), on the dynamic of social networks
525 and their instability (Gelardi et al., 2019), as well as on audience (Huguet, Barbet, Belletier,
526 Monteil & Fagot, 2014) and social comparison effects (Dumas, Fagot, Davranche & Claidière,
527 2017). It was also previously found that the cognitive performance measured during ALDM
528 cognitive testing is modulated by socially affiliative and agonistic events in the enclosure
529 (Marzouki, Gullstrand, Goujon & Fagot, 2014). Studies from other laboratories have further
530 shown that the ordering of the interactions with such automatized test systems depends on social
531 factors in Rhesus monkeys (*Macaca mulatta*): monkeys of different ranks tended not to work
532 at the same times to avoid social conflicts (Gaze, Lutz, Meyer, Hassetts & Hampton, 2019).
533 Social effects of freely accessible test systems were also reported in crested macaques (*Macaca*
534 *nigra*) who increased their association with others during the testing days (Whitehouse,
535 Michelatta, Powell, Border & Waller, 2013). From all these studies, we conclude that the
536 spontaneous interactions within automatized test systems presented to groups of individuals
537 should be interpreted as social events, and not only as purely cognitive events. Automatized
538 test systems therefore offer a unique opportunity to conduct experiments on either physical or
539 social cognition in non-human primates, as well as on the interactions between the two. The
540 transient effect of the supplanting behavior on the RTs recorded in the cognitive task of
541 Experiment 2 is a new illustration of the possibility offered by ALDM testing to work at the
542 interface between social and non-social cognition.

543 Modern analyses of behavior tend to be more and more sophisticated and call for the
544 development of new systems to collect social information automatically. The current study
545 shows that the provision of automatized operant conditioning test systems to monkeys
546 maintained in social groups can fulfil that need. One of the most obvious advantage of this

547 method is that extremely large datasets can be collected efficiently to infer dominance
548 hierarchy, in sharp contrast to the more effortful traditional observational methods. Of course,
549 this approach also has some limitations. One of them is that it requires sophisticated
550 technologies that can hardly be accessible to every laboratory working in comparative
551 cognition. The last few years have witnessed the development of freely accessible test systems
552 comparable to the ALDM: in monkeys (e.g., Gazes, Brown, Basile & Hampton, 2012; Fizet et al.,
553 2017; Tulip, Zimmermann, Farningham & Jackson, 2017; Butler & Kennerley, 2018), as well
554 as in other groups such as birds (Huber, Heise, Zenan & Palmers, 2015; Morand-Ferron,
555 Hamblin, Cole, Aplin & Quinn, 2015). We are therefore convinced that such technology will
556 develop even more in the future, opening unprecedented opportunities to grasp the full
557 complexity of animal's social and non-social cognition.

558

559 **Open Practices Statements:**

560 The data analysed in this study are available here: <https://osf.io/w39fr/>

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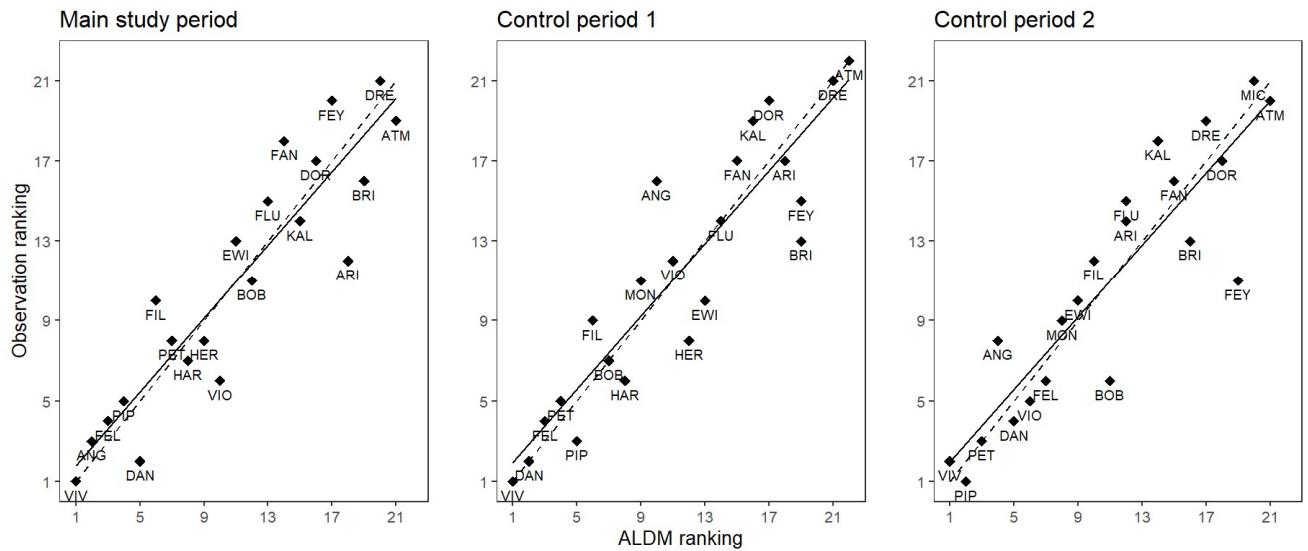
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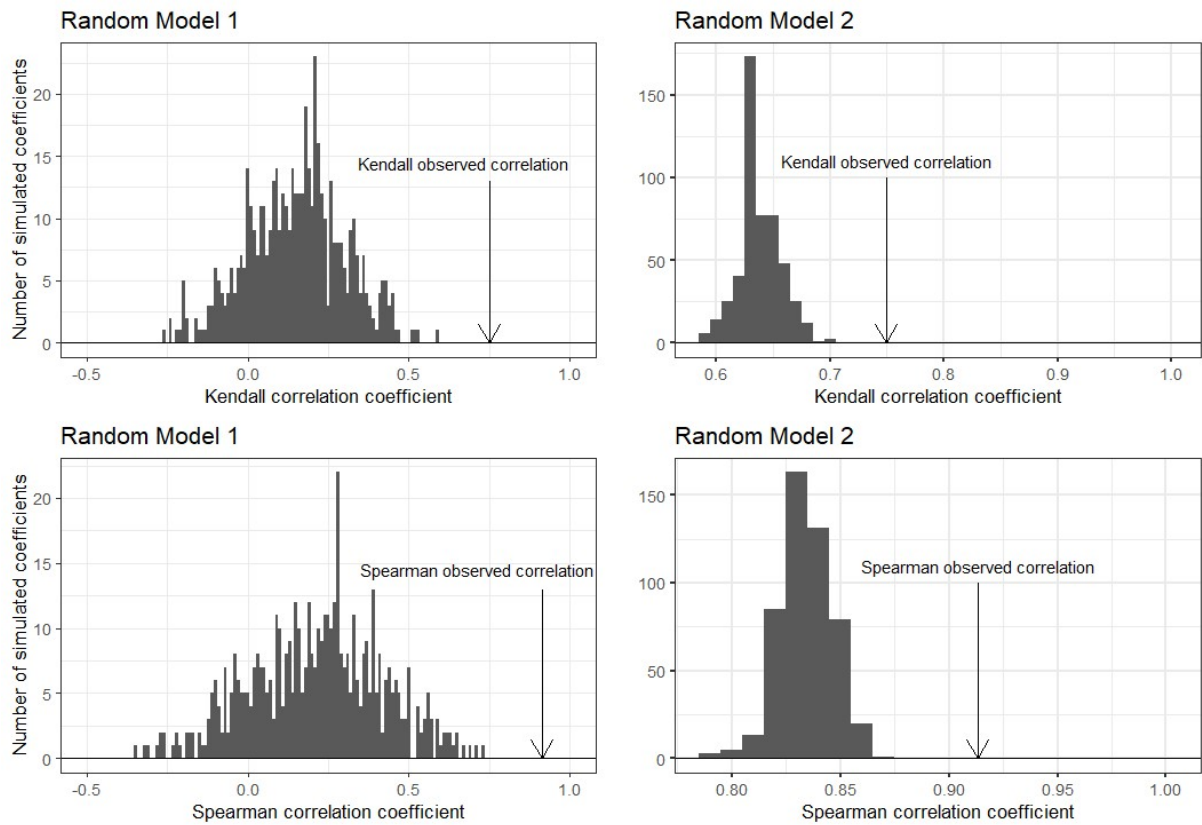
718 Figure 1: Correlation between the dominance ranks of each individual (labelled by the 3 first
 719 letters of their names) obtained from behavioural observations (y-axis) and from computerised
 720 ALDM testing (x-axis) for the three study periods. Bold lines represent the linear regression of
 721 the data and the dotted line a perfect positive ($x=y$) correlation. (Main study period: Kendall
 722 correlation: $\tau = 0.752$, $CI = [0.59; 0.89]$ and Spearman correlation: $r_s = 0.91$, $CI = [0.76; 0.97]$,
 723 Control period-1: Kendall correlation: $\tau_{c1} = 0.7665$, $CI = [0.57; 0.91]$ and Spearman correlation:
 724 $r_{sc1} = 0.9$, $CI = [0.71; 0.97]$, Control period-2: Kendall correlation: $\tau_{c2} = 0.760$, $CI = [0.57; 0.91]$
 725 and Spearman correlation: $r_{sc2} = 0.9$, $CI = [0.70; 0.98]$

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731 Figure 2. Distribution of the simulated Kendall and Spearman correlation coefficients between
 732 dominance hierarchies generated from the random models 1 (left figures) and 2 (right figures)
 733 and the dominance hierarchy from behavioural observations. The arrows indicate the observed
 734 correlation between the dominance hierarchy obtained from untransformed ALDM data and the
 735 one established from behavioural observations (Kendall correlation: $\tau = 0.752$, CI = [0.59;
 736 0.89] and Spearman correlation: $r_s = 0.91$, CI = [0.76; 0.97]).

737

738 Table 1: Results of the linear mixed effects model described in the text.

Random effects:						
Groups:	Name	Variance	SD	Corr		
Name	(Intercept)	620.4	24.91			
	Day	1523.5	39.03	-0.93		
Age	(Intercept)	10395.8	101.96			
Residual		31242.1	176.75			
Fixed effects:						
		Estimate	SE	df	t-value	p-value
Intercept		562.00	23.61	1.92E+01	23.80	<0.001
Experimental condition: Predictive		-54.22	3.32	9.96E+04	-16.31	<0.001
Ntrial		-1.36	0.63	9.96E+04	-2.14	0.03
Behavioural condition: Supplant		-19.73	3.52	9.96E+04	-5.60	<0.001
Beh. cond. by Exp. cond.		8.45	4.93	9.96E+04	1.71	0.09
Beh. cond. by Ntrial		1.70	0.94	9.96E+04	1.82	0.07
Exp. Cond. by Ntrial		0.29	0.89	9.96E+04	0.32	0.75
Beh. Cond. by Exp. Cond. by Ntrial		-0.07	1.32	9.96E+04	-0.05	0.96

739 Note. Number of observations: 99619, number of individuals:20

740

741 Table 2: Results of the linear mixed effects model described in the text.

Random effects:				
Groups:	Name	Variance	SD	Corr
Name	(Intercept)	3402.9	58.334	
	Day	15.5	3.937	0.17
Age	(Intercept)	4966.9	70.476	
Residual		30685.2	175.172	

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Fixed effects:					
	Estimate	SE	df	t-value	p-value
(Intercept)	633.1636	22.5610	18.5753	28.064	<0,001
DiffRank	1.7580	0.5639	4277.7434	3.118	0.00183

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744 Note. Number of observations: 4411, number of individuals: 20

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748 Supplementary table 1: Identity and age of the participants for each study.

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Name	Year of birth	Sex	Experiment 1			Experiment 2
			Main study period (N=21)	Control 1 (N=22)	Control 2 (N=21)	Fagot & Goujon (2013)* (N=20)
KALI	1995	F	+	+	+	+
BRIGITTE	1996	F	+	+	+	+
MICHELLE	1996	F			+	+
MONA	1997	F		+	+	+
ATMOSPHERE	1998	F	+	+	+	+
PETOULETTE	1999	F	+	+	+	+
PIPO	1999	M	+	+	+	+
URANIE	2003	F				+
VIVIEN	2004	M	+	+	+	+
VIOLETTE	2004	F	+	+	+	+
ANGELE	2005	F	+	+	+	+
ARIELLE	2005	F	+	+	+	+
BOBO	2006	M	+	+	+	+
DAN	2008	M	+	+	+	+
DREAM	2008	F	+	+	+	+
DORA	2008	F	+	+	+	+
EWINE	2009	F	+	+	+	+
FANA	2010	F	+	+	+	+
FELIPE	2010	M	+	+	+	+
FEYA	2010	F	+	+	+	+
FLUTE	2010	F	+	+	+	
FILO	2010	M	+	+	+	
HERMINE	2012	F	+	+		
HARLEM	2012	M	+	+		

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751 Note. (+) indicates if the subject is present in the considered study period (*) data in Goujon &

752 Fagot (2013) were collected in 2012.

753

754 Supplementary table 2: Ethogram with the name and definitions of the agonistic behaviours
 755 coded during the observations.

Behaviour	Description/example
Aggression	Hitting, biting, pinching, scratching, slapping another individual
Chase	Pursuing another individual (screaming, ...) during a conflict before or without final aggression
Threat	Threatening another baboon raising its eyebrows with or without screaming and slapping on the ground
Supplanting behaviour	One individual is getting the place of another one, by pushing it
Avoid	Avoiding another individual in his approach (recordable at 2m max between both individuals)
Yak	Yakking behaviour (without avoidance) use to happen in a fear/surprise context or anticipating a conflict

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763 Supplementary table 3: Elo-scores and respective ranks of each individual in the three periods,
764 and for both ALDM and Observation data.

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ID	Main study period		Control period-1		Control period-2	
	Observation	ALDM	Observation	ALDM	Observation	ALDM
ANGELE	1279 (3)	1232 (2)	911 (16)	1058 (10)	1101 (8)	1104 (4)
ARIELLE	1009 (12)	824 (18)	907 (17)	810 (18)	931 (14)	961 (12)
ATMOSPHERE	630 (19)	336 (21)	744 (22)	514 (22)	720 (20)	550 (21)
BOBO	1034 (11)	959 (12)	1015 (7)	1087 (7)	1129 (6)	1014 (11)
BRIGITTE	847 (16)	716 (19)	950 (13)	778 (19)	938 (13)	895 (16)
DAN	1294 (2)	1174 (5)	1156 (2)	1200 (2)	1162 (4)	1079 (5)
DORA	790 (17)	845 (16)	819 (20)	822 (17)	782 (17)	870 (18)
DREAM	509 (21)	557 (20)	772 (21)	729 (21)	749 (19)	874 (17)
EWINE	998 (13)	968 (11)	983 (10)	995 (13)	1025 (10)	1024 (9)
FANA	786 (18)	944 (14)	907 (17)	950 (15)	874 (16)	902 (15)
FELIPE	1155 (4)	1226 (3)	1061 (4)	1165 (3)	1129 (6)	1033 (7)
FEYA	611 (20)	842 (17)	937 (15)	778 (19)	983 (11)	764 (19)
FILO	1068 (10)	1159 (6)	1005 (9)	1101 (6)	971 (12)	1017 (10)
FLUTE	853 (15)	957 (13)	943 (14)	966 (14)	896 (15)	961 (12)
HARLEM	1073 (7)	1127 (8)	1055 (6)	1075 (8)	NA	NA
HERMINE	1070 (8)	1118 (9)	1011 (8)	1007 (12)	NA	NA
KALI	890 (14)	938 (15)	896 (19)	888 (16)	762 (18)	951 (14)
MICHELLE	NA	NA	NA	NA	695 (21)	723 (20)
MONA	NA	NA	969 (11)	1060 (9)	1097 (9)	1028 (8)
PETOULETTE	1070 (8)	1137 (7)	1060 (5)	1163 (4)	1186 (3)	1163 (3)
PIPO	1154 (5)	1179 (4)	1141 (3)	1137 (5)	1297 (1)	1196 (2)
VIOLETTE	1120 (6)	1033 (10)	960 (12)	1029 (11)	1139 (5)	1050 (6)
VIVIEN	1461 (1)	1412 (1)	1213 (1)	1346 (1)	1275 (2)	1206 (1)

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767 Note. NA = Subject non-available for testing during the considered period, for instance due to
768 sickness. Ranks are indicated in parentheses.

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770 Supplementary table 4: Hierarchical indexes through the three periods for both ALDM and
771 observation data.

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Index		Main study period		Control period-1		Control period-2		Exp2
		Observation	ALDM	Observation	ALDM	Observation	ALDM	ALDM
	N	21	21	22	22	21	21	20
Optimal K	optK	101	18	34	12	116	10	10
Triangle	Pt	0.96	0.96	0.85	0.95	0.97	0.94	0.86
transitivity	ttri	0.85	0.83	0.39	0.80	0.88	0.77	0.45
Linearity	h	0.57	0.67	0.16	0.66	0.24	0.69	0.47
	h'	0.59	0.68	0.21	0.67	0.30	0.69	0.47
Repeatability	r	0.92	0.96	0.88	0.97	0.94	0.95	0.91

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774 Note. This table shows OptK: the optimal K used in Elorating procedure of dominance
775 hierarchy assessment, Triangle transitivity (Pt: the proportion of triangles that are transitive,
776 and ttri: this proportion scaled so that it is 0 for the random expectation and 1 for maximum
777 transitivity) and Linearity indices (de Vries linearity index h (Appleby, 1983; de Vries, 1995)
778 and Landau corrected index h'(de Vries, 1998)) from Elorating package and r: the repeatability
779 index (Shizuka & McDonald, 2012) from AniDom package for 1000 randomisations.

780

781 Supplementary references:

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