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

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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 rs >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

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

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

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

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

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

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

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

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

Experiment 1: Assessing dominance hierarchy from ALDM testing

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

Methods

Participants and living conditions

All participants belonged to the same group of Guinea baboons (*Papio papio*) from the CNRS primate Centre, Rousset-sur-Arc, France. The group consisted of males and females from different families living with their offspring in a large enclosure. The entire group was housed inside a 25 x 30 m^2 outdoor enclosure connected to an indoor area and to two experimental trailers providing access to computerized (ALDM) test systems (see below). The group had *ad libitum* access to water, and feeding was provided daily at 5 pm.

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

Ethics statements

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

Behavioural observations in the enclosure

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

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

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

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

ALDM testing

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

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

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

Assessing dominance hierarchy

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

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

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

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

Statistical analyses

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

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

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

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

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

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

Results

Reliability and repeatability of the hierarchies

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

Main study period

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

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

Insert Figure 1 about here

Random model 1

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

Insert Figure 2 about here

Random model 2

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

Correlational analyses: all three study periods

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

Discussion of Experiment 1

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

355

356 **Experiment 2: Effect of supplanting behaviours on cognitive performance**

357 The main goal of Experiment 2 is to illustrate the possible use of ALDM hierarchies
358 obtained from supplanting behaviours in the context of cognitive studies. Goujon & Fagot,
359 (2013) have previously published data on the cognitive performance of our group of baboons
360 in the ALDM test system. This research used the so called "contextual cueing" task (Chun &
361 Jiang, 1998), in which the baboons had to detect a target in two types of visual displays, first
362 on non-predictive backgrounds providing no information on target location, and second on
363 predictive backgrounds which have been associated by training to specific target location on
364 the computer screen. Results indicated a strong effect of the background on the speed of target
365 detection, with faster response times (RTs) in the predictive compared to the non-predictive
366 condition. In Experiment 2, we reanalysed Goujon and Fagot's (2013) data in order to assess
367 if the ALDM supplanting behaviours recorded during that research had subtle (but previously
368 undetected) effects on the baboon's cognitive performance.

369 ## Methods

370 ### Participants

371 The study used the same baboon colony as in Experiment 1. However, because this
372 study was conducted in 2012, and therefore one year before the control period 2 of Experiment
373 1, this colony had a slightly different composition. The data set therefore contained information
374 on a total 20 baboons (5 males and 15 females) whose name and biographical information are
375 indicated in the supplementary section.

Experimental setup, computerized task and database

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

Data analysis

Investigating the effect of supplanting behaviours on loser of each dyad is difficult, because the subjects either stop temporarily after a supplanting event, or move to a different workstation, with a high variability in time and behaviour between the last trial after the supplantation and the first trial of the next working bout. The analysis therefore focussed on the winner who performed trials immediately after the supplanting event. We considered two types 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

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

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

Results

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

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

Insert Table 1 about here

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

Discussion of Experiment 2

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

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

RTs but will only briefly suggest three hypotheses that may account for our findings. A first potential mechanism is a release of steroid hormones which are known to occur in animals after social challenges (e.g., for a review see Kelly and Wilson, 2019). Androgens and especially testosterone are known to affect cognitive performance (e.g., Janowsky, 2006) and to enhance spatial abilities. Alternatively, the release of neuropeptides such as oxytocin could explain our results, knowing their contribution to prosocial and aggressive behaviours. The action of oxytocin has been reported on various types of social behaviours, including social approach (Thompson and Walton, 2004) and aggression (Bosch, 2013). Note that oxytocin releases have rapid effects on the behavioural response (e.g., Knobloch et al., 2012). This may account for the transient effects of supplanting behaviour in our task. Finally, faster RTs after a supplanting behaviour can be accounted for by a winner effect (Chase, Bartolomeo & Dugatkin, 1994). Reeve, Olson & Cole (1985) argued that winning enhances intrinsic motivation in the task relative to loosing. According to this view, the baboon winning the contest would have an enhanced motivation to perform well in the computerized task, even more so if subordinates were supplanting dominants, gaining a time advantage on the task.

Independently of the validity of these different hypotheses, which remains to be tested, Experiment 2 has revealed that the dominance hierarchy can have subtle effects on cognitive performance that would probably remain undetectable with more traditional experimental approaches. We believe that the analysis of such effects can help answering questions regarding the interaction between social and non-social cognition.

General discussion

The main goal of Experiment 1 was to demonstrate that the baboons' supplanting behaviours within the ALDM test system can be used reliably to determine the dominance hierarchy of the group. We showed that the dominance hierarchy inferred from untransformed

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

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

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

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

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

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

Open Practices Statements:

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

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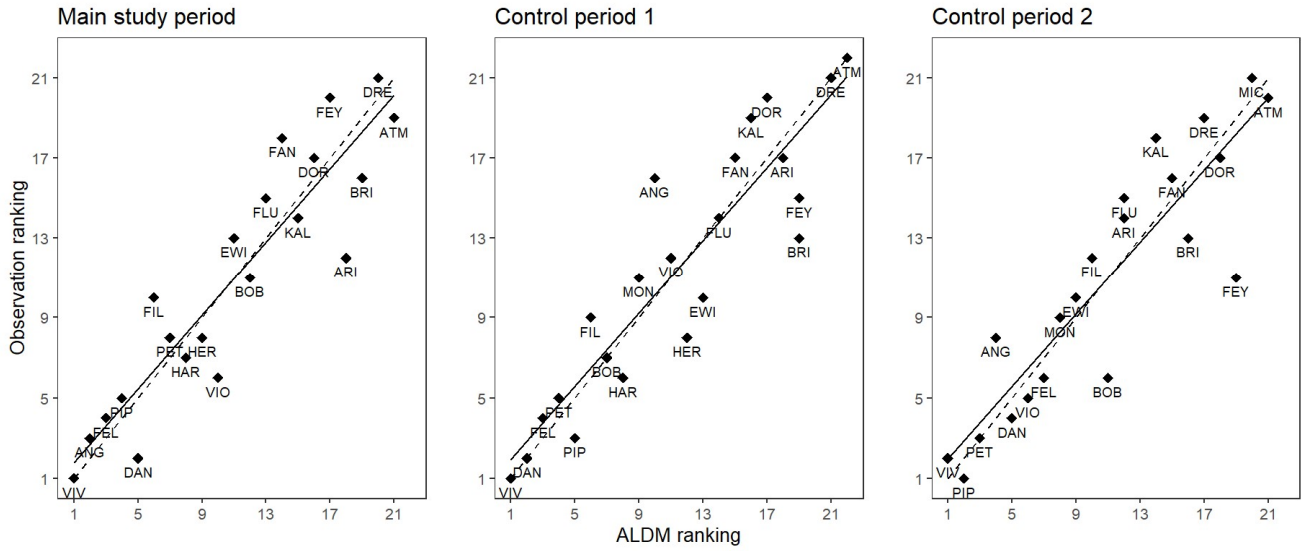
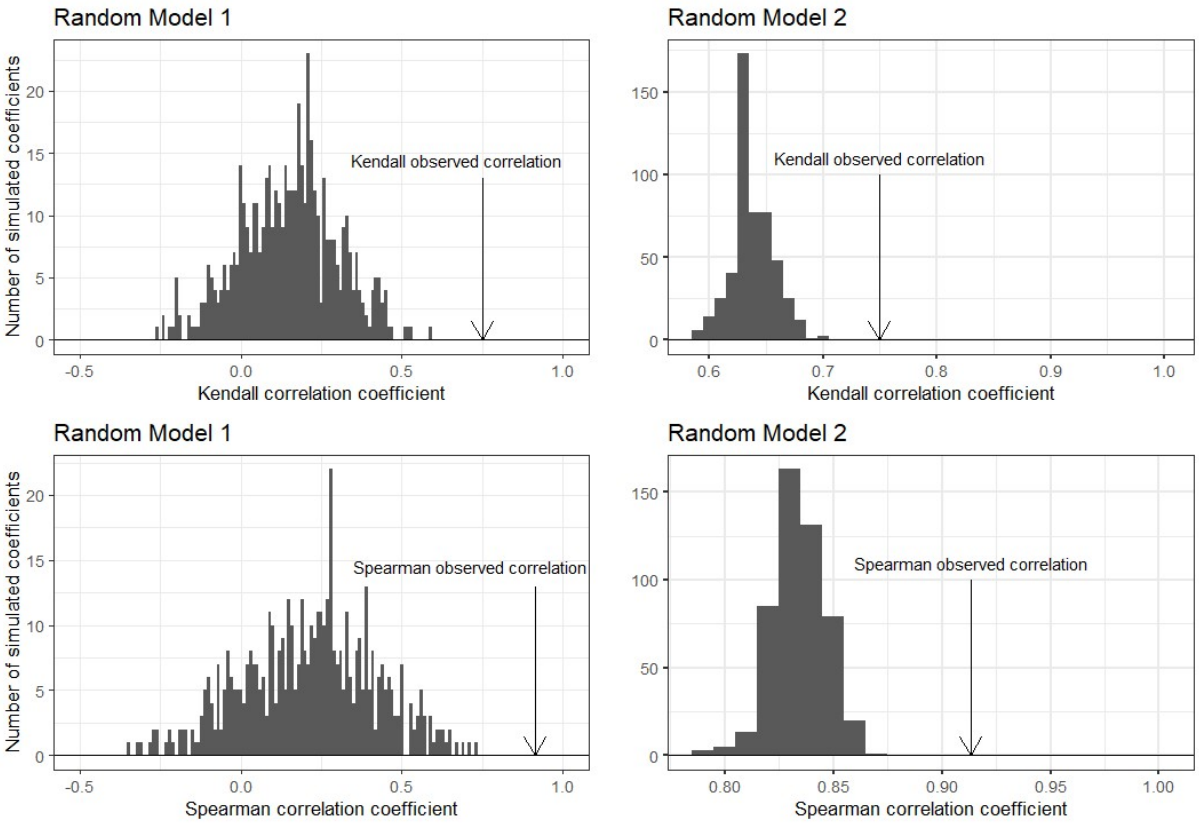


Figure 1: Correlation between the dominance ranks of each individual (labelled by the 3 first letters of their names) obtained from behavioural observations (y-axis) and from computerised ALDM testing (x-axis) for the three study periods. Bold lines represent the linear regression of the data and the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



730

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 effets:					
		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 inidividuals: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	

742

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

743

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

745

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747

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

749

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	+	+		

750

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.

765

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

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 transitivity	Pt	0.96	0.96	0.85	0.95	0.97	0.94	0.86
	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

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

Supplementary references:

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