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## Does a high social status confer greater levels of trust from groupmates? An experimental study of leadership in domestic horses

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1                   **Does a high social status confer greater levels of trust from groupmates?**  
2                   **An experimental study of leadership in domestic horses**

3  
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20  
21

22 **Abstract**

23 In collective movements, specific individuals may emerge as leaders. In this study on the  
24 domestic horse (*Equus ferus caballus*), we conducted experiments to establish if an individual  
25 is successfully followed due to its social status (including hierarchical rank and centrality).  
26 We first informed one horse about a hidden food location and recorded by how many it was  
27 followed when going back to this location. In this context, all horses lead their groupmates  
28 successfully. In a second step, we tested whether group members would trust some leaders  
29 more than others by removing the food before the informed individual led the group back to  
30 the food location. In addition, two control initiators with intermediate social status for which  
31 the food was not removed were tested. The results, confirmed by simulations, demonstrated  
32 that the proportions of followers for the unreliable initiator with highest social status are  
33 greater than the ones of the unreliable initiator with lowest social status. Our results suggest  
34 an existing relationship between having a high social status and a leadership role. Indeed, the  
35 status of a leader sometimes prevail at the detriment of the accuracy of the information,  
36 because an elevated social status apparently confers a high level of trust.

## 37 **1. Introduction**

38 One of the most captivating social displays in the biological world is undoubtedly collective  
39 movements and concerns many species: swarms of invertebrates, shoals of fish, flocks of  
40 birds, herds of ungulates or troops of primates. This polyphyletic phenomenon reflects its  
41 highly adaptive function (Boinski and Garber 2000). However, how such coordination for  
42 moving together is achieved raises several issues. Among them, the possibility that some  
43 individuals exert a disproportionate influence on group decisions, and thus considered as  
44 leaders, is still in debate (Strandburg-Peshkin, Papageorgiou et al. 2018) including in humans  
45 (von Rueden and van Vugt 2015), and raises questions about its sustainability within a social  
46 group. Indeed, confidently following a leader will speed up the collective decision but it  
47 implies that the information is concentrated in this sole individual (Couzin, Krause et al. 2005,  
48 Sumpter and Pratt 2009, Kao and Couzin 2014, Gavrilets, Auerbach et al. 2016). In case of  
49 wrong information, the whole group will suffer the consequences of bad choices (Conradt and  
50 Roper 2005).

51 Even if all group members can initiate collective movements in nearly all species, some of  
52 these initiators are joined more successfully than others. In this context, we wonder why some  
53 individuals are elevated to leadership roles by group members, resulting in a more efficient  
54 decision-making process. These interindividual differences in leadership success can be  
55 accounted for by several factors such as age, sex, temperament, energetic state, dominance  
56 status, or centrality (see Petit and Bon 2010 for a review). Whatever the species, there is not a  
57 unique and consistent factor explaining the success of an initiator. However, it appears that  
58 several parameters underlying social status may play a preponderant role. Indeed, on one  
59 hand, we know that dominant individuals can play a key role in collective decision-making  
60 (Radford 2004, Sueur and Petit 2008, Jacobs, Watanabe et al. 2011). On the other hand, it  
61 seems that the network of affiliative relationships amply explains joining latencies with an  
62 optimization of the process when initiators have high centrality scores (Sueur and Petit 2008,  
63 King, Sueur et al. 2011, Sueur, MacIntosh et al. 2013, Briard, Dorn et al. 2015). All these  
64 factors refer to the social position of an individual among its group mates. It is thus likely that  
65 a favourable social position may lead to a higher social influence on group decisions. This  
66 social influence could reflect the trust that other group mates might place in this conspecific.

67 This study aims to explore the social influence of individuals in explaining successful  
68 leaders and thus focuses on followership which is generally neglected in the literature (Van  
69 Vugt, Hogan et al. 2008). We first predict that potential followers would be more inclined to  
70 follow an initiator proposing an activity if this initiator possess a high social status (including  
71 hierarchical rank and centrality). If this is the case, it might suggest that followers consider  
72 those individuals as more ‘trustable’ leaders, making them more motivated to follow.

73 In naturally occurring complex social systems, correlations between multiple factors result  
74 in feedback effects that make it difficult to distinguish between causes and consequences. It is  
75 therefore necessary to conduct experiments to assess the determining factors of decision-  
76 making. Thus, we conducted experiments simulating natural situations to establish if an  
77 individual is successfully followed due to its social status. By controlling experimentally the  
78 time and place of the group departure, we are able to narrow our focus on the influence of a  
79 leader’s identity itself by discarding the influence of the pre-departure period (Bourjade,  
80 Thierry et al. 2009, Sueur, Deneubourg et al. 2011, Briard, Deneubourg et al. 2017, Briard,

81 Deneubourg et al. 2021). In the first step of this experiment, we informed one individual  
82 about a hidden food location containing highly preferred food and recorded how much and  
83 how rapidly it was followed in comparison to other group members. As a result, the whole  
84 group had access to a great amount of highly preferred food. We tested individuals with  
85 different hierarchical status and centrality scores and compared their performances in terms of  
86 proportion of the group members that followed the initiator. In the second step of the study,  
87 we tested whether group members would trust some leaders more than others with an  
88 extinction procedure. To investigate this extent of trust, we experimentally tested its  
89 perseverance for an initiator for which the reliability is challenged. In this second step, we  
90 informed a single individual about a food location as usual, but food was removed before the  
91 informed individual led the group back to this location. We then measured how this new  
92 unreliability impacted the followers' decision throughout several testing sessions. If group  
93 members no longer trust the informed individuals whatever their identity, we should observe a  
94 decrease of the following rates over the course of the experiment. Conversely, if congeners  
95 continue to follow specific individuals, those with high social status for example, it would  
96 provide the best demonstration that a form of trust from the followers that does not solely  
97 depend on an assessment of a leader's reliability as a keystone factor to determine group  
98 decision-making.

99 We conducted this work in the domestic horse (*Equus ferus caballus*) which is an ideal  
100 model for this experimental study as they are easily trainable. The domestic horse forms  
101 cohesive social groups of both sexes (Cameron, Setsaas et al. 2009, Linklater and Cameron  
102 2009), and shares physiological attributes, cognitive and social characteristics with many  
103 social primates that have been extensively studied when exploring the influence of social  
104 status on decision-making processes.

105

## 106 2. Methods

### 107 2.1. Experimental horses

108 Three groups of 6 females were studied (two in 2014: groups A and B, and one in 2015: group  
109 C). Subjects were Haflinger, Dartmoor and Shetland ponies aging  $7.2 \pm 0.6$  years (mean  $\pm$   
110 SE), housed at the "Elevage du Haut-barr" (Saverne, France) and used for reproduction  
111 purposes (brood mares and their daughters) (see Table 1 for a summary of individual  
112 characteristics). All horses were familiarised with each other for several years within the farm  
113 and studied groups were formed and stabilized at least 6 months before the beginning of the  
114 experiment. Four of the 12 horses studied in 2014 were part of the 2015 group C (ARM,  
115 OTO, SER, and TAK). All horses lived in outdoor pasture all year long with periodical fodder  
116 supplementation and water available *ad libitum*. Each morning when an experiment took  
117 place, all horses were equipped with halters that were removed after the last test.

118 The three groups (A, B, C) were tested for the individual initiation tests (**Experiment 1**) and  
119 only the group C was finally tested for the extinction tests (**Experiment 2**).

120

### 121 2.2. Experiment 1: individual initiations tests

122 We provoked movement initiations with a protocol based of food hiding in order to assess  
123 individual levels of success (Gérard, Valençon et al. 2020). The three groups were tested.  
124 The experiment consisted of 73 valid tests.

125 At each test, we first gathered the whole group into a temporary pen (approximately 5 m x 5  
126 m) at the departure area. Then, an experimenter concealed the food reward (19 carrots) out of  
127 sight at 30 m from the departure area. The tested horse (only one for each test) was then  
128 brought to this hidden food location and was allowed to eat only one carrot so it became  
129 motivated to come back. Then, it was brought back to the group and as soon as it entered the  
130 departure zone, the whole group was released so the informed horse could initiate a  
131 movement to the food location and being eventually followed by others. The 19 carrots were  
132 divided in a pile of 10 carrots at the centre plus 9 carrots randomly distributed at a distance of  
133 2-3m around the centre so all horses can have access to food even when the whole group is  
134 present (*i.e.* non-monopolisable resource).

135 Three experimenters were present to build and rapidly remove the temporary pen made of 6  
136 plastic posts and 20mm-large plastic tape. Three cameras were arranged in order to cover the  
137 departure area, the route taken by the group and the arrival area.

138 The number of followers per initiation was recorded (from direct observations and videos).  
139 Any horse seen moving away (at least 20 steps) from the departure in the same direction as  
140 the initiator was identified as a follower (Briard, Dorn et al. 2015). Only the trials when the  
141 informed horse was the first to move to go directly from the departure zone to the food reward  
142 were analysed. Three trials a day were conducted and we had at least two hours break  
143 between trials.

144

### 145 **2.3. Experiment 2: extinction tests**

146 Extinction tests aimed to assess the perseverance of a group to follow an initiator despite this  
147 initiator not leading them to a food reward. This experiment was conducted on group C only.  
148 The protocol was the same as for individual initiations tests except the reward (with the  
149 exception of two carrots) was removed by an experimenter (discreetly) after the initiator was  
150 informed and before it came back followed by the group. The two carrots were left so the  
151 initiator had still access to a food reward as it arrived first (to keep it motivated to go back to  
152 the reward location), but the rest of the group was not rewarded. Two “unreliable initiators”  
153 (*i.e.* no reward anymore) and two control “reliable initiators” (*i.e.* intact reward) were tested  
154 randomly. The two misinformed initiators were: the horse with the highest social status (HS)  
155 and the one with the lowest social status (LS). The two informed initiators were two horses  
156 with intermediate social status (see paragraph (d) for social status determination).

157 During the first phase, we completed five rewarded initiation tests for each initiator, meaning  
158 the whole reward remained present for the group. Then, in the second phase, we conducted  
159 seven other trials per initiator. These seven trials were extinction trials for the two unreliable  
160 initiators (food reward was removed for the followers) and rewarded trials for the two reliable  
161 initiators (food reward remained present for all). For each initiator, we compared the amount  
162 of followership between the six first trials (five control trials + the 1<sup>st</sup> trial of the second phase  
163 when the group discovered the absence of food reward for misinformed initiators) and the  
164 next six trials (6 rewarded trials for reliable initiators or 6 extinction trials for unreliable  
165 initiators).

166

### 167 **2.4. Assessing social status**

168 Each group was observed and filmed continuously for 6 h daily, distributed between 8a.m.  
169 and 7 p.m., during the four weeks preceding the beginning of experiment 1, for a total of 50  
170 hours.

171 Agonistic interactions were recorded continuously. For each interaction, we recorded the  
172 identity of the emitter of each approach, threat or aggression, and both the identity and the  
173 response of the receiver (offensive behaviour, avoidance or no reaction). Unidirectional  
174 interactions - when only one horse was approaching or emitting offensive behaviour and the  
175 other clearly avoided them - were used to build a dominance hierarchy. We carried out an  
176 analysis of dominance hierarchy using SOCPROG 2.4 (Whitehead 2009) to obtain David's  
177 scores for each rank and then checked for hierarchy linearity (de Vries 1995, de Vries 1998,  
178 de Vries, Stevens et al. 2006).

179 Spatial proximities between horses were recorded every 15min using instantaneous scan  
180 sampling ((Altmann 1974), 200 scans total). Two individuals were considered to be close  
181 when they were <1m apart. Based on these scans, we built a proximity matrix based on the  
182 number of scans where two individuals were observed close to each other, for each possible  
183 dyad. We carried out a social network analysis to obtain a Centrality score for each horse  
184 (Eigen vector) index (Jacobs and Petit 2011)).

185 Dominance and centrality scores have been attributed to each individual (**Table 1**). For the  
186 group C used for the experiment 2, the dominance hierarchy was significantly linear (de Vries  
187 test for linearity,  $h'=0.89$ ,  $P=0.04$ ) and dominance scores and centrality scores were positively  
188 correlated (Spearman correlation test,  $r=1$ ,  $P=0.003$ ). Therefore, the horse (SER) with the  
189 highest David's score and Centrality index was chosen to be the *unreliable initiator with the*  
190 *highest social status* (HS), and the horse (TAK) with the lowest David's score and Centrality  
191 index was chosen to be the *unreliable initiator with the lowest social status* (LS). Horses  
192 ARM and RAT were chosen as control *reliable initiators 1 and 2* due to their intermediate  
193 status.

194

## 195 **2.5. Simulation study**

196 A general probability to follow has been calculated from the first experiment and was the  
197 same for all initiators (0.9). This probability was considered to be degraded by the failures  
198 (i.e. the unrewarded trials) and we made the assumption that this decrease occurred as soon as  
199 the first failure occurred. The probability that an individual will not follow will then be related  
200 to the number of failures by the following relationship:

201

$$P_S = P_0 + \frac{P_m}{1 + \left(\frac{E}{S}\right)^n} \quad (1)$$

202

203 Where  $P_S$  is the probability to follow an initiator. This probability decreases with the number  
204 of failures.  $P_0$  the basic probability to follow an initiator,  $P_m$  the maximal probability to follow  
205 a reliable initiator,  $E$  the number of failures (number of trials with no food) and  $S$  the  
206 threshold for tolerating a failure (depending on the social status in our assumption),  $n$  the  
207 sensitivity to the number of failures. The extreme is an all-or-none response of the potential  
208 followers:

$$P_S = P_0 \quad \text{if } E \geq S. \quad (2, a)$$

$$P_S = P_0 + P_m \quad \text{if } E < S \quad (2, b)$$

209

210  $P_0$  and  $S$  depend on the identity or the status of the initiator: a highly potentially reliable  
211 initiator shows a high value of  $P_0$  and  $S$ . This formula allowed us to calculate the probability  
212 to follow each unreliable initiator for each trial as well as the probability to follow the reliable  
213 initiators. Finally, we obtained a threshold for tolerating failure for the two unreliable  
214 initiators.

215 Eventually, we conducted simulations on the number of followers according to the respective  
216 threshold we obtained for both unreliable initiators to confirm our experimental results.

217

## 218 **2.6. Statistical analyses**

219 Social status analyses (Davids score, linearity tests and Eigenvector centrality scores) have  
220 been performed using SOCPROG 2.4. Statistical analyses were performed using R software  
221 (R Core Team 2019). The level of statistical significance was set at  $P < 0.05$ , and the level of  
222 tendency at  $P < 0.10$ . In the text, we report median and interquartile ranges in the form “ $M =$   
223 (1st interquartile–3<sup>rd</sup> interquartile)”.

224 For experiment 1, inter-individual comparisons have not been statistically investigated due to  
225 a lack of inter-individual variability in the number of followers. For experiment 2, we used  
226 generalised linear model (GLM) with binomial distribution to test how the testing phase,  
227 individual’s identity, and trial number influenced the proportion of the group members that  
228 followed the informed individual. We used *car* package (Fox and Sanford 2019) for this  
229 analysis. We started with the full model that included the testing phase, individual identity,  
230 interaction between these two terms, and trial number as predictor variables.

231 To perform model selection, we relied on the second-order Akaike’s Information Criterion  
232 (AICc) and Relative Variable Importance (RVI) as was suggested by Burnham & Anderson  
233 (2002) and Symonds & Moussalli (2011). As best-fitting models, we considered the model  
234 with the lowest AICc and any model within two AICc units. We then used *model.avg* function  
235 of the *MuMIn* package (Barton 2019) to calculate RVI for our predictor variables. Our best-  
236 fitting model contained variables with an RVI of at least 0.7 and it had the lowest AICc score.  
237 It included testing phase and individual identity as predictor variables. However, the  
238 interaction term between these two variables and trial number were not retained. To compare  
239 performance of different individuals we performed post-hoc analysis on the individual  
240 identity variable in the GLM. We used *emmeans* function of the *emmeans* package (Lenth  
241 2019) to perform multiple pairwise comparisons with a Tukey correction.

242

## 243 **2.7. Ethics statement**

244 The experimental protocols followed EU Directive 2010/63/EU guidelines for animal  
245 experiments and were approved by the Ethical Committee (CREMEAS) under agreement  
246 number AL/01/10/07/11.

247

## 248 **3. Results**

### 249 **3.1. Experiment 1**



250 A total of 73 trials have been analysed (*i.e.* when the informed individual was the first to go  
251 directly to the food location) and resulted in 3 or more trials per initiator for a total of 15  
252 initiators (Table 2). We found no variation in the number of followers according the initiator's  
253 identity since a large majority of the trials was followed by the whole group (Group A:  
254 96.15%, Group B: 100%, Group C: 78.57 %). Three initiators failed to validate the criteria to  
255 be retained in the analysis (DLI in Group A, CHE in Group B and OTO in Group C).  
256

### 257 3.2. Experiment 2

258 During the first six trials (5 trials of phase 1- rewarded - plus the 6<sup>th</sup> trial when followers  
259 discovered the food was missing for the first time, see protocol details above), 4 or 5  
260 followers always followed each one of the four initiators. During the 6 following trials (phase  
261 2), the number of followers ranged from 5 to 1 for the reliable initiators (rewarded trials).  
262 Concerning the unreliable initiators, this number ranged from 4 to 1 for the initiator with  
263 highest social status (extinction trials), and from 2 to 1 for the initiator with the lowest social  
264 status (extinction trials, Fig. 1). The best fitting model was explained by horse's identity and  
265 testing condition (Supplementary Table XXX). There was a significant effect of Phase 2: the  
266 proportion of group members that followed decreased during the unrewarded (second) phase  
267 of the test (GLM,  $N = 48$ ,  $\beta = -3.075$ ,  $SE = 0.525$ ,  $Z = -5.86$ ,  $P < 0.001$ ). The proportion of  
268 group members that followed also depended on the identity of the initiator (**Table 3**).  
269 Specifically, the ability of the two reliable initiators (ARM, *Reliable 1* and RAT, *Reliable 2*)  
270 to recruit the followers was 7 and 10 times respectively greater than the ability of the  
271 unreliable initiator with lowest social status (TAK, *Unreliable 2*) (Ration value  
272  $Reliable1/Unreliable2 = 7$ ,  $z = 3.6$ ,  $P < 0.0001$ ; Ration value  $Reliable2/Unreliable2 = 10.1$ ,  $z = 4.00$ ,  $P <$   
273  $0.0001$ , **Table 2**). On the contrary, the differences between the unreliable initiator with  
274 highest social status (SER, *Unreliable 1*) and the other individuals were not significant  
275 (Ration value  $Reliable1/Unreliable1 = 2.9$ ,  $z = 2.00$ ,  $P = 0.19$ ; Ration value  $Reliable2/Unreliable1 = 4.1$ ,  $z =$   
276  $2.500$ ,  $P = 0.06$ ; Ration value  $Unreliable1/Unreliable2 = 2.4$ ,  $z = 1.800$ ,  $P = 0.25$ , **Table 3**). Finally,  
277 no difference was found between two reliable initiators (Ration value  $Reliable1/Reliable2 = 0.7$ ,  $z = -$   
278  $0.6$ ,  $P = 0.93$ ).  
279

### 280 3.3. Simulation study

281 The probability to follow the unreliable initiator with highest social status (SER) was less  
282 affected by the discovery that food was no longer present than for the unreliable initiator with  
283 lowest social status (TAK) (**Fig. 2**).

284 In our case, after a first failure, for both unreliable initiators (regardless their social status), the  
285 mean number of followers decreases but then remains constant from trial to trial (linear  
286 regression between the number of followers as a function of the successive trials, null  
287 hypothesis the slope is equal to zero,  $P > 0.05$ ). However, the mean number of followers per  
288 trial is greater for the initiator with highest social status than for the other unreliable initiator  
289 (respectively SER: 2.66 and TAK: 1.17). These results suggest that equation 2b is a good  
290 approximation of the individual response to an initiator, the two thresholds (number of  
291 failures) for decreasing the probability to the initiator (S, equation 2) are equal to 1 and  
292 confirm our assumption that an individual with a high social status continues to be trusted  
293 even if it provides false information. On the contrary, an individual with a low social status is

294 poorly followed immediately after the discovery of the food absence. The probability that  
295 each potential follower ( $P_0$  in equation 1) follows the initiator with a low social status is lower  
296 than the  $P_0$  for the initiator with a high social status (respectively  $P_0 = 1.17 / 5 = 0.23$  for TAK  
297 and  $P_0 = 2.66 / 5 = 0.5$  for SER). This result also means that the success of the reliable  
298 initiators was not influenced by the failures experienced by group members in trials with  
299 unreliable initiators.

300 We performed 10000 simulations of 6 successive trials in which we applied the  $P_0$  of each  
301 unreliable initiator,  $P_0$  being the probability that each individual follows the initiator. We  
302 obtained that the proportions of followers for the unreliable initiator with highest social status  
303 (SER) and the unreliable initiator with lowest social status (TAK) are statistically different ( $P$   
304  $< 0.05$ ) (Fig. 2).

305

#### 306 4. Discussion

307 In the first experiment of this study, we provided optimal conditions of departure by giving  
308 the same value to all initiators in terms of food access for the whole group. As a consequence,  
309 we did not observe any difference between the different initiators in the amount of  
310 followership. Such positive influence of possessing right information on followers has already  
311 been found in pigeons (Watts, Nagy et al. 2016) and horses (Andrieu, Henry et al. 2016). This  
312 absence of inter-individual variability contrasts with what is observed in spontaneous  
313 collective movements, where initiators were found to be of unequal value for followers which  
314 join them less quickly or not at all (Leca, Gunst et al. 2003, Sueur and Petit 2008). It suggests  
315 that phenomena that are non-specific to an initiator identity are also at play in the followers'  
316 decisions and emphasises the importance of the pre-departure period. Indeed, we know that  
317 each group member can notify its motivation to move, negotiate or vote during this period and  
318 thus contributes to the collective decision at this early step or that group dispersion and  
319 activity are decisive for moving collectively (Bourjade, Thierry et al. 2009, Ramseyer, Boissy  
320 et al. 2009, Sueur, Deneubourg et al. 2010, Sueur, Deneubourg et al. 2011, Briard,  
321 Deneubourg et al. 2021).

322

323 Since in optimal experimental conditions each horse appears to be able to lead successfully, in  
324 the second experiment, we placed potential followers in a more challenging environment  
325 which mimicked natural cases where an initiator could lead the group to a bad location (in  
326 terms of food expectation). These conditions simulated the crucial impact of a leader on  
327 collective choices. With this experiment, we aimed to reveal the strength of the trust the  
328 followers put into a leader, by asking directly the followers. In such a context, followers  
329 successfully displayed flexibility in their willingness to follow a leader according to its  
330 reliability. Indeed, an immediate drop in the followership was observed within the unreliable  
331 initiator with the lowest social status, while followers kept following both reliable initiators. It  
332 demonstrates that horses are able to assess the reliability of an initiator. This could be  
333 mediated by associative learning mechanisms, especially since it involves the presence or  
334 absence of food reward. Such influence of recent experience on former choice on subsequent  
335 decision has been found in human and non-human primates (Steelandt, Dufour et al. 2012,  
336 Pele, Broihanne et al. 2014). Being able to discriminate social information based on the  
337 reliability of their emitting source has also been shown in other social contexts, such as for

338 alarm calls for instance (vervet monkeys: Cheney and Seyfarth 1988, yellow-bellied marmots:  
339 Blumstein, Verneyre et al. 2004, carrion crows: Wascher, Hillemann et al. 2015). Such ability  
340 is undeniably crucial to optimise the benefit in the use of social information.

341

342 Moreover, our results suggest an even more subtle phenomenon: not only the followers have  
343 been able to adapt their choice to follow -or not- based on the reliability of the initiator, but  
344 the identity of the unreliable initiator played a role in how fast this initiator lost their trust.  
345 Indeed, whereas the number of followers dropped drastically and immediately for the  
346 unreliable initiator with the lowest social status, this was not the case for the unreliable  
347 initiator with the highest social status where the decrease was delayed and more gradual. Our  
348 results, obtained on a limited number of individuals, were confirmed by our simulations  
349 which demonstrated that the proportions of followers for the unreliable initiator with highest  
350 social status differed from the one of the unreliable initiator with lowest social status. These  
351 calculated probabilities may represent a threshold for trusting a group mate, and this threshold  
352 may depend on the leader's social status since our two unreliable initiators occupied the two  
353 most extreme social positions within their group (i.e. the most dominant and central horse *vs.*  
354 the most subordinate and peripheral one). The fact that the extinction pattern is delayed and  
355 more gradual with an unreliable initiator with the highest social status suggest that even if  
356 followers were able to detect its unreliability, as shown before, there was something left to  
357 maintain their motivation to follow and it strongly suggests an existing relationship between  
358 having a high social status and a leadership role. It is often assumed that animals with a high  
359 social status, especially high-ranked individuals (i.e. in dominance hierarchy), are more  
360 successful as a leader because they are usually older and more experienced, and should  
361 therefore possess accurate information about their environment (McComb, Shannon et al.  
362 2011). In many species, age and hierarchical ranks are indeed correlated (e.g. in horses  
363 (Sigurjónsdóttir, Machteld et al. 2003, Briard, Dorn et al. 2015)), and leaders are also often  
364 high-ranking and/or older group members (Sueur and Petit 2008, Sueur and Petit 2008). As a  
365 consequence, from observational studies, it is impossible to disentangle the intrinsic abilities  
366 that contribute to lead groups successfully. On the contrary, our experimental results suggest  
367 that groupmates' decision to follow depends on the social status of the initiator, and not age  
368 since neither centrality or David's scores followed the age order. Moreover, actual signs of  
369 unreliability did not prevent the group to keep following the high-status initiator, suggesting  
370 that a high level of leadership, once acquired, does not depend directly on how well-informed  
371 the leader is, or, at least, that a highly influential leader will benefit from a margin of errors  
372 that a low-status initiator would not benefit from. Altogether, it really emphasises that the  
373 influence of a leader's social status cannot be solely explained by the actual and/or current  
374 reliability of the information it possesses. We now need to explore whether highly influential  
375 individuals are also leaders in other domains like conflict management (Petit and Thierry  
376 1994, Widdig, Streich et al. 2006), group protection and defence (Meunier, Molina-Vila et al.  
377 2012, Strandburg-Peshkin, Clutton-Brock et al. 2020) or observational learning (Frith and  
378 Frith 2012).

379

380 What component of social status explain highest trust in followers and what is their causal  
381 link remain open questions. It is important to notice that in our study, we considered both the

382 affiliative and agonistic dimensions of the social status, that were correlated in our studied  
383 group, but it is not necessarily the case in horses (Cameron, Setsaas et al. 2009). There is a  
384 general tendency to oversimplify the social position of a leader to its dominance status can  
385 lead to miss the point. Bonanni et al. (2010) indeed demonstrated in free-ranging dogs that  
386 leadership is influenced by both affiliative and agonistic relationships. Affiliative  
387 relationships appear to be especially important for trust, as shown by chimpanzees that trust  
388 their friends more than their non-friends in a modified version of the trust game (Berg,  
389 Dickhaut et al. 1995, Tooby and Cosmides 1996, Engelmann and Herrman 2016). In the same  
390 way, Fruteau et al's study suggests that social centrality is more determinant than  
391 dominance's rank to gain the trust of other group members (Fruteau, Voelkl et al. 2009).  
392 Indeed, in their experiment, the authors found that subordinate vervet monkeys were more  
393 groomed after providing food access to group mates, whereas no change in troop hierarchical  
394 order was reported. These results also suggest that a feedback loop between social status and  
395 trust (and thus tolerance to error) should exist even though it is difficult to determine its  
396 direction. In order to understand this causal relationship between social status and trust, we  
397 will need to manipulate again the level of social credibility of leaders by increasing the one of  
398 lower social status individuals.

399 It is important to note that, in our study, we only conducted six tests for each initiator and we  
400 focused on a temporary loss of reliability in a specific food context. This protocol was indeed  
401 designed to prevent any habituation or counterstrategies from group members since they  
402 might have decided to search for food reward on their own. Such process could be seen during  
403 the last trials when followership started to be disrupted even with control initiators. However,  
404 even with those limitations, we believe such extinction paradigm should be tested further, in  
405 more animals and more groups. Studying the contrast in extinction patterns is a good way to  
406 start quantifying this part of trust that animals put into a conspecific and that cannot be solely  
407 explained by trial and error mechanisms.

408  
409 Finally, the flexibility that followers displayed in our experiments also raises interesting  
410 questions for the comprehension of equine social cognition. Indeed, followers appeared to  
411 adapt adequately their responses to contexts and initiators identities, suggesting flexibility  
412 when deciding which individual to follow and when. Such flexibility evokes the concept of  
413 social learning strategies, the *"flexible rules that specify or bias when or how individuals  
414 should use social information, under various circumstances, to meet functional goals"*  
415 (Kendal, Boogert et al. 2018). Social learning strategies likely involve both associative and  
416 social learning (Kendal, Boogert et al. 2018), and eventually sophisticated social cognition in  
417 some cases. The ability of horses to be selective and flexible in what, when, and from which  
418 individual they should get and use social information could explain why many authors  
419 struggled in demonstrating (observational) social learning in this species, despite the strong  
420 assumption they should possess this capacity (classic learning a simple operant: (Lindberg,  
421 Kelland et al. 1999), discrimination: (Baer, Potter et al. 1983, Baker and Crawford 1986,  
422 Clarke, Nicol et al. 1996), instrumental: (Ahrendt, Christensen et al. 2012), or detour spatial  
423 task: (Rørvang, Ahrendt et al. 2015, Burla, Siegwart et al. 2018). Interestingly, the only two  
424 studies that possibly showed premises of copying mechanisms suggest that a demonstrator's  
425 influence depends on its social status (Krueger and Heinze 2008, Schuetz, Farmer et al. 2017).

426 The absence of clear experimental evidence of copying abilities contrasts with the knowledge  
427 we have of the horses' non-social cognitive abilities (reviews: (Hausberger, Stomp et al.  
428 2019)), and the existence of flexible and complex social phenomena that have been studied in  
429 more naturalistic conditions, such as in the context of – like in the present study - collective  
430 movement (Briard, Dorn et al. 2015, Briard, Deneubourg et al. 2017, Gérard, Valenchon et al.  
431 2020) - or third-party interactions and reconciliation (domestic horses (Cozzi, Sighieri et al.  
432 2010), feral horses: (Schneider and Krueger 2012), and Przewalskii horses: (Krueger,  
433 Schneider et al. 2015)). Therefore, our study highlights the importance of including the  
434 flexibility and selectivity factors when considering social phenomena, and that the study of  
435 leadership using experimental paradigms constitutes a great framework to explore this topic.

436

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651

652 **Animal welfare note**

653 The experimental protocols followed the EU Directive 2010/63/EU guidelines for animal  
654 experiments and were approved by the Ethical Committee (CREMEAS) under agreement  
655 number AL/01/10/07/11.

656  
657

**TABLES**

**Table 1. Individual characteristics**

ID	Group	Year of study	Age (yrs)	Breed	David's score	Centrality index
CAN	A	2014	2	Dartmoor	-5.46	0.52
DAY	A	2014	1	Shetland	-5.42	0.32
DLI	A	2014	23	Dartmoor	13	0.48
HAV	A	2014	19	Dartmoor	5	0.54
NOR	A	2014	18	Shetland	-1.78	0.17
TAK*	A	2014	7	Shetland	-5.33	0.28
ARM*	B	2014	4	Dartmoor	-11.57	0.55
CAL	B	2014	2	Dartmoor	-8.63	0.28
CHE	B	2014	2	Dartmoor	6	0.51
CYB	B	2014	2	Dartmoor	-2.71	0.36
OTO*	B	2014	12	Dartmoor	2.33	0.26
SER*	B	2014	8	Haflinger	14.57	0.41
ARM*	C	2015	5	Dartmoor	0.58	0.23
BEL	C	2015	4	Shetland	-9.00	0.09
OTO*	C	2015	13	Dartmoor	4.29	0.67
RAT	C	2015	10	Shetland	0.52	0.15
SER*	C	2015	9	Haflinger	15.00	0.68
TAK*	C	2015	8	Shetland	-15.00	0.07

\* studied in both 2014 and 2015

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**Table 2. Number of followers per initiation according to initiator's identity for each group (A, B, C) during experiment 1**

Group	Initiator	Number of followers						
		Initiation 1	Initiation 2	Initiation 3	Initiation 4	Initiation 5	Initiation 6	Initiation 7
Group A	SER	5	5	5				
	OTO	5	5	5	5			
	ARM	5	5	5	5			
	CAL	5	5	5	5			
	CYB	5	5	5				
	CHE	5						
Group B	CAN	5	4	5	5	5		
	DAY	5	5	5	5	5		
	DLI	5						
	HAV	5	5	5	5	5		
	NOR	5	5	5	5			
	TAK	5	5	5	5	5	5	
Group C	ARM	5	5	5	5	5	4	
	BEL	2	2	5	5			
	RAT	5	3	5	5	5	5	5
	SER	5	5	5	4	5		
	TAK	5	4	5	5	5	5	

664 **Table 3. Comparison of individual performances during the testing phase.** For each  
 665 combination of two initiators, the ration of the proportion of individuals that followed one  
 666 individual over the proportion of individuals that followed another individual has been tested.

<b>Individual A / Individual B</b>	<b>ratio</b>	<b>SE</b>	<b>z.ratio</b>	<b>P Value</b>
Reliable1 / Reliable2	0.7	0.4	-0.600	0.93
Reliable1 / Unreliable1	2.9	1.5	2.000	0.19
Reliable1 / Unreliable2	7.0	3.8	3.600	<0.0001
Reliable2 / Unreliable1	4.1	2.3	2.500	0.06
Reliable2 / Unreliable2	10.1	5.8	4.000	<0.0001
Unreliable1 / Unreliable2	2.4	1.2	1.800	0.25

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