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HAL Authorization

1 **Effects of selection for divergent levels of social motivation on behavioral repertoire and synchronization in**
2 **Japanese quail (*Coturnix japonica*)**

3

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29 **ABSTRACT**

30 Behavioral synchronization occurs when individuals perform the same behavior simultaneously
31 and in close proximity. It is widely recognized as a key mechanism that fosters social cohesion,
32 coordination, and cooperation within groups, providing substantial adaptive benefits. However, since
33 individuals within a group often exhibit inter-individual differences in social tendencies, these variations
34 may influence group organization and the extent to which synchronization occurs. Here, we investigated
35 how genetic selection for social motivation (i.e., an individual's internal drive to seek contact, approach
36 and remain close to a group of conspecifics) in Japanese quail (*Coturnix japonica*) impacts their
37 behavioral repertoire and their behavioral synchronization, by comparing 10 trios (groups of three)
38 constituted of individuals selected for high social motivation (S+) and 10 trios constituted of individuals
39 selected for low social motivation (S-). For this purpose, trios were placed for 24 consecutive hours in
40 an arena filled with wood shavings and providing *ad libitum* access to food and water. Birds' behaviors
41 were recorded and analyzed during four one-hour time windows (hour 1: 8:30–9:30 am, hour 2: 11:00–
42 12:00 am, hour 3: 1:30–2:30 pm and hour 4: 4:00–5:00 pm). Results revealed that S- quail exhibited
43 more locomotion behaviors, while S+ quail displayed more inactivity behaviors and particularly "sit
44 relaxed" behaviors. Also, S+ individuals had a longer total synchronization duration than S- individuals.
45 Specifically, S+ quail performed more synchronized "sit relaxed" behaviors, spent more time in this
46 state and remained synchronized longer during a "sit relaxed" bout compared to S- quail. The S+ group
47 also had a significantly higher Kappa coefficient for this behavior, which differed from 0, suggesting
48 that synchronization in this line was more structured and less random. Notably, during synchronization
49 bouts of the behavior "Sit relaxed", birds reduced inter-individual distances, indicating an active
50 preference for staying closer together during this activity. Overall, these findings suggest that individuals
51 with higher social motivation are more likely to engage in synchronized behaviors, particularly during
52 resting behaviors, which may promote close proximity and strengthen social bonds. Such
53 synchronization may foster social cohesion and lead to more harmonious and stable group dynamics.
54 Further studies will be necessary to better elucidate these effects and confirm these different hypotheses.
55 This research highlights the critical role of individual differences in social motivation in shaping

56 collective behavior. These insights enhance our understanding of animal social dynamics and could
57 inform more effective management strategies in animal husbandry.

58

59 Keywords: Japanese quail; Synchronization; Behavior; Social motivation; Personality; Welfare

60

61 **1. Introduction**

62 Behavioral synchronization (i.e., individuals displaying the same behavior, at the same time and
63 at the same place: Duranton and Gaunet, 2016) plays a crucial role in the organization and dynamics of
64 social groups. It may result from mutual behavioral adjustment between group members (allelomimetic
65 synchronization: Gautrais et al., 2007) and provides numerous adaptive advantages, such an increased
66 offspring survival and protection through the synchronization of reproduction, births and parental care
67 (Duranton and Gaunet, 2016; Hernández-Matías et al., 2003; Ims, 1990); enhanced defense against
68 threats via synchronized anti-predator strategies (Duranton and Gaunet, 2016; Beauchamp, 2015; Roy
69 Nielsen et al., 2008); improved foraging efficiency through cooperative hunting; and strengthened social
70 cohesion (Duranton and Gaunet, 2016; Conradt and Roper, 2005; Engel and Lamprecht, 1997). Group
71 cohesion is considered a precondition of group living (Gautrais et al., 2007). Thus, given the substantial
72 benefits of behavioral synchronization, all socially oriented species can act in synchrony with
73 conspecifics (Lamontagne and Gaunet, 2023; Webster and Hurnik, 1994).

74 Behavioral synchronization is shaped by a complex interplay of external factors, related to the
75 environment, and internal factors, specific to the individual (King and Cowlshaw, 2009). External
76 factors, such as seasonality, along with the temporal and spatial distribution of resources and their
77 availability (Hauschildt and Gerken, 2015a; Engel and Lamprecht, 1997), are key factors influencing
78 behavioral synchronization. Uneven resource distribution, for example, can lead to competition or
79 monopolization, disrupting coordinated behaviors and preventing group synchronization (Vahl et al.,
80 2007). Beyond immediate environmental cues, behavioral synchronization is closely tied to circadian
81 rhythms (Alvino et al., 2009), which can be an important determinant of individuals' internal states and
82 motivations and has more recently been suggested to include social motivations (Asher and Collins,

83 2012; Davidson and Menaker, 2003). Synchronized behavior is also known to be influenced by factors
84 such as group size (Rands et al., 2008), age, body size or sex (Eklund and Jensen, 2011; Ruckstuhl and
85 Neuhaus, 2001). In fallow deer, synchronization appears to be higher in unisex groups than in mixed-
86 sex groups (Villerette et al., 2006), likely due to differences in behavior, motivation (Michelena et al.,
87 2004; Bon, 1992) and activity needs between males and females (Neuhaus and Ruckstuhl, 2004;
88 Conradt, 1998; Ruckstuhl, 1998). Furthermore, social relationships—including hierarchy, affinities, and
89 kinship—can affect an animal’s response to social factors (Favreau et al., 2009). Social status may lead
90 to repulsion between individuals and variations in resource use (Webster and Hurnik, 1994; Syme et al.,
91 1983; Mankovich and Banks, 1982), resulting in behavioral asynchrony.

92 In addition to the more obvious factors influencing behavioral synchronization, a less-explored
93 yet crucial aspect is how intra-group, inter-individual behavioral differences shape this phenomenon.
94 These differences, often referred to as animal personality, are characterized by behavioral traits that
95 remain stable over time and across various contexts or situations (Tang and Fu, 2019; Wolf and
96 Weissing, 2012; Réale et al., 2010). Animal personality not only affects how individuals cognitively
97 perceive and process information but also determines their behavioral responses in social and
98 environmental interactions. One particularly relevant personality trait is exploration, which has been
99 shown to influence both attentional, learning, and memory processes (Guillette et al., 2011; Ferreira et
100 al., 2020, 2019), as well as collective behavior. For instance, Tang and Fu (2019) examined the role of
101 personality in fish shoaling behavior and found that shoals composed of proactive individuals—
102 characterized by higher activity and boldness—exhibited increased movement and enhanced
103 synchronization of speed compared to more reactive shoals with lower activity and boldness. These
104 findings suggest that the collective dynamics of a group are not merely an emergent property of group
105 size or external stimuli but are also shaped by the intrinsic behavioral tendencies of its members.

106 Another fundamental personality axis is sociability, which refers to an individual’s propensity
107 to form and maintain social bonds (Gartland et al., 2022; Réale et al., 2007). Within a group, individuals
108 can exhibit considerable variation in sociability levels, with some actively seeking social interactions
109 while others display a more independent or avoidant disposition (Gartland et al., 2022; Wascher et al.,
110 2018; Nawroth et al., 2017; Cote et al., 2012). Such differences can influence a wide range of social

111 dynamics, including group cohesion, information transfer, and leadership roles (Bevan et al., 2018;
112 Morton et al., 2015).

113 Despite increasing interest in the effects of personality on collective behaviors, the specific role
114 of sociability in shaping behavioral synchronization remains largely unexplored. Given that
115 synchronized behaviors often emerge from repeated social interactions and shared attention
116 mechanisms, we can hypothesize that more sociable individuals act as key facilitators of group
117 coordination, promoting stronger temporal alignment in movement and decision-making. Conversely,
118 less sociable individuals might act as weak links in synchronization, either by lagging behind or
119 disrupting cohesion. In this context, our study aims to deepen the understanding of how individual's
120 social motivation influences behaviors that are critical for the organization and the social cohesion of
121 the group, particularly behavioral synchronization. To investigate this, we observed the behavior of two
122 lines of Japanese quail selected based on their social motivation: the S+ line, consisting of individuals
123 selected for high social motivation and the S- line, consisting of individuals selected for low social
124 motivation (Mills and Faure, 1991). Previous studies have demonstrated that differences in social
125 motivation between S+ and S- quail span across different experimental testing conditions and persist
126 into adulthood and across various situations (Formanek et al., 2008; François et al., 1998; Launay et al.,
127 1993, 1991; Mills and Faure, 1991). Further studies have revealed significant differences between the
128 two lines in various aspects of sociability, beyond social motivation itself. For example, S+ quails were
129 found to be more reactive in situations of social isolation (Formanek et al., 2008, Mills et al., 1993) and
130 social instability (Schweitzer et al., 2011, 2010; Schweitzer and Arnould, 2010) than S- quails. They
131 also exhibited shorter inter-individual distances at an early developmental stage (François et al., 1999)
132 and showed a non-specific social attraction to their peers, whereas S- quails appeared to be preferentially
133 attracted to familiar conspecifics (Schweitzer et al., 2011, 2010, 2009). Taken together, these findings
134 suggest that these quail lines represent a valuable model for exploring how individual differences in
135 social motivation—and perhaps sociability more broadly—influence group behavior and behavioral
136 synchronization. Accordingly, the primary aim of this study was to compare the extent of behavioral
137 synchronization between the S+ and S- lines. In addition, we examined the behavioral repertoires of
138 both lines to further characterize them and gain insight into potential differences in their behavioral

139 synchronization. Because selection for social motivation is expected to enhance social behaviors, we
140 hypothesized that more sociable individuals (S+) would exhibit higher levels of behavioral
141 synchronization than their less sociable counterparts (S-).

142

143 **2. Material and methods**

144 *2.1. Ethical statement*

145 This study was conducted at the Pôle d'Expérimentation Avicole de Tours (UE PEAT, INRAE,
146 Experimental Poultry Facility, <https://doi.org/10.15454/1.5572326250887292E12>) of the INRAE
147 Centre Val-de-Loire, France, from January to March 2024. It was conducted under the approval of the
148 INRAE animal experimentation ethics committee, under the project number CE19 – 2023-3110 - 1, in
149 compliance with the current French legislation.

150

151 *2.2. Lines historic*

152 The experiment was conducted on birds from the 76th generation of a unique model of two lines
153 of Japanese quail, selected since 1984 at the Pôle d'Expérimentation Avicole de Tours (France) for social
154 motivation (i.e., an individual's internal drive to seek contact, approach and remain close to a group of
155 conspecifics, Launay et al., 1991). Until the 45th generation, these quail lines were selected using a
156 treadmill test and from the 46th generation, this test was carried out every 3 years to check the divergence
157 of the lines. In this test, individual chicks (6-8 days old) were placed at the center of a corridor, with five
158 conspecifics from a control line (the social stimuli) at one end in a box. Once a chick began walking or
159 running toward its conspecifics, the treadmill was activated, pulling the chick away. The distance
160 traveled to attempt to approach the conspecifics and the time spent in the end far from them were
161 recorded after 5 minutes. Chicks that traveled the greatest distance to join conspecifics and spent the
162 least time away were considered to have high social motivation, whereas those that traveled the shortest
163 distance and spent the most time away were considered to have low social motivation. Importantly, the
164 selection process ensured that social motivation was independent of tonic immobility responses,
165 meaning that the S+ and S- lines should not differ in their fear levels (Mills and Faure, 1991).

166 2.3. *Animals and housing*

167 The animals used in this experiment were incubated and hatched at the Pôle d'Expérimentation
168 Avicole de Tours. At hatching, birds were fitted with a unique numbered wing tag to allow individual
169 identification and then moved to a rearing facility.

170 Initially, from 1 day to 21 days of age, a total of 252 Japanese quail were housed and reared in
171 four small enclosures designed for chicks (90 × 75 × 40 cm). The group consisted of 100 individuals
172 selected for high social motivation (S+ birds), 100 S- individuals selected for low social motivation (S-
173 birds) and 52 individuals from a non-selected control line with intermediate social motivation (ST birds).
174 The S+ chicks were distributed across two enclosures, separated from the S- chicks, who were housed
175 in the other two enclosures. The ST chicks were evenly distributed across all four enclosures, resulting
176 in each enclosure housing 50 S+ or S- individuals along with 13 ST individuals, at a stocking density of
177 93.3 birds/m². The temperature was initially set at 40°C on day 1 and gradually lowered to 25°C by day
178 21. A 24-hour light-dark cycle was implemented, that started with continuous artificial light (24 hours)
179 on day 1 and progressively reduced to 12 hours of artificial light by day 21.

180 At 22 days of age, when it became possible to visually distinguish males from females (notably
181 on the basis of plumage), the birds were sexed. Because males become aggressive towards each other
182 and exhibit frequent sexual behavior towards females upon reaching sexual maturity around six weeks
183 of age (François et al., 1999) and because the birds were kept longer for this and subsequent experiments,
184 only females were kept for this study. In addition to their wing tag, a colored metal leg ring was placed
185 on their right leg to ensure easy identification.

186 Therefore, 90 females (35 S+, 35 S- and 20 ST) were randomly and evenly chosen from the
187 chicks' enclosures and moved to a bigger rearing room. This room was divided into two pens (450 ×
188 180 × 250 cm) separating S+ from S- birds. We chose not to mix the birds to prevent any potential social
189 influences between the lines (Court et al., 2024). Each pen housed 35 S+ or S- individuals along with
190 10 ST individuals, at a stocking density of 5.6 birds/m². The two pens were separated by plastic panels
191 to prevent physical and visual contact between the groups. The floor was covered with wood shavings
192 and the birds had *ad libitum* access to food and water. Several plastic mesh tubes were placed on the
193 ground to provide environmental enrichment. The temperature was maintained between 20 and 22°C

194 and a 24-hour light-dark cycle was introduced with 16 hours of artificial light (8:00 am to midnight) at
195 an average intensity of 30.5 lx, followed by 8 hours of darkness.

196 To habituate the birds to human presence and handling, experimenters spent 15 to 30 minutes
197 daily in each pen, before the testing phase began.

198

199 *2.4. Behavioral synchronization test*

200 Inspired by the study of Eklund and Jensen (2011), we performed a behavioral synchronization
201 test on 60 Japanese quail (30 S+ and 30 S-), aged between 29 and 39 days. The 60 tested animals were
202 divided into 20 trios (groups of three), each composed of individuals from the same line (10 trios of S+
203 and 10 trios of S-). The trios were formed randomly and remained consistent throughout the test.

204

205 *2.4.1. Test arena*

206 The test was conducted in five adjacent arenas (100 × 140 × 50 cm, Figure 1) located in a testing
207 room near the rearing room. The side and back walls of the arena were made of white opaque expanded
208 PVC, while the frontal wall was made of wire mesh. Each arena was covered with a net to prevent the
209 birds from escaping. As in their rearing pens, the arenas were filled with wood shavings and provided
210 *ad libitum* access to food and water. Three black visual markers (20 cm) were placed on the inner walls
211 of the arenas and later used as reference points to calculate inter-individual distances (see Section 2.4.3).
212 The temperature, light-dark cycle and light intensity in the testing room were similar to those in the
213 rearing room. Cameras (Sony HDR-CX240E or HDR-CX405 and Panasonic HC-VX870 or HC-
214 VX980) mounted above each arena recorded the tests, minimizing interference from experimenters.

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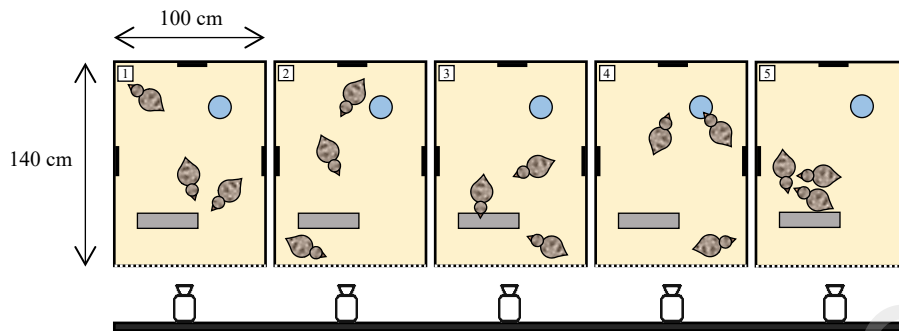


Figure 1. Schematic representation of the testing room with the five adjacent arenas. Each arena contained a water container (blue circle), a food container (grey rectangle) and three black visual markers (strips of black tape measuring 20 cm in length) on the inner walls, used to assess inter-individual distances. Five cameras were mounted above the arenas to record the animals throughout the test duration.

2.4.2. Procedure

The week before the test, when the birds were 29 to 32 days old, each trio underwent progressive habituation to its designated arena over four consecutive days. Each trio spent 15 minutes in the arena on day 1, 30 minutes on day 2, 45 minutes on day 3 and 60 minutes on day 4. As there were five arenas, five trios were tested simultaneously (either three S+ and two S- or vice versa). Trios from the same line were alternated and therefore not placed in adjacent arenas.

The test was conducted the week following habituation, over four consecutive days, when the birds were 36 to 39 days old. Each day, five trios were tested (the same sets of trios as during habituation, placed in the same arenas). The birds remained in the arenas for a total of 24 hours. They were placed in the arenas the evening before the test, around 5 pm, providing additional habituation time. The following day, the trios had their behaviors recorded during four one-hour time windows, each spaced 1.5 hours apart (hour 1: 8:30–9:30 am, hour 2: 11:00–12:00 am, hour 3: 1:30–2:30 pm and hour 4: 4:00–5:00 pm). To minimize disturbance, the experimenters turned on the cameras 15 minutes before each time window and left the room. The cameras were then turned off after each recording session. At the end of the final video recording, the tested quail were returned to the rearing room and the next five trios were placed in the arenas. Two observers (J.S. and M.G.) coded the video recordings collected during

250 the test. Prior to this, they reached a consensus and trained together until achieving at least 90% inter-
251 observer agreement.

252

253 *2.4.3. Behavioral recordings*

254 **Behavioral repertoire and inter-individual distances.** Based on previous studies (Eklund and Jensen,
255 2011), our ethogram included 22 behaviors grouped into eight major behavioral categories: "Feeding",
256 "Foraging", "Exploration", "Vigilance", "Locomotion", "Inactivity", "Comfort" and "Social behaviors"
257 (Table 1). Over the four one-hour observation windows (totaling four hours of recorded video per trio),
258 behavioral data were collected for each individual in the trio using instantaneous sampling every 60
259 seconds, resulting in 180 sampling points per hour and a total of 720 sampling points per trio.

260 Besides the behavioral repertoire, we were also interested in how closely the birds stayed
261 together over time. Using the black markers on the arenas' walls, we recorded inter-individual distances
262 at each instantaneous sampling point, with a precision of a few centimeters. These distances represented
263 the empty space between two individuals, measured from the closest parts of their bodies and thus
264 independent of the birds' body size.

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278 **Table 1.** Ethogram.

279

Behavioral category	Recorded behavior	Description
<i>Feeding</i>	Drink	Drinks from water container.
	Feed	Eats from food container.
<i>Foraging</i>	Explore ground	Walks or stands with head close to the ground.
	Ground peck	Pecks at items on the ground.
	Ground scratch	Scratches the ground.
<i>Exploration</i>	Explore object	Visually inspects an object (food or water containers, walls of the arena).
	Peck object	Pecks an object (food or water containers, walls of the arena).
<i>Vigilance</i>	Sit alert	Sits (with legs bent) in immobile posture with eyes open and alert body stance.
	Stand alert	Stands (with legs upright) in immobile posture with eyes open and alert body stance.
<i>Locomotion</i>	Locomotion	Walks or runs.
<i>Inactivity</i>	Sit relaxed	Sits (with legs bent) with reduced attention.
	Stand relaxed	Stands (with legs upright) with reduced attention.
<i>Comfort</i>	Dust bath	Shakes wings and rubs its own body in litter.
	Feather ruffle	Erects feathers, ruffles and shakes its own body.
	Preen	Uses beak to trim and arrange feathers.
	Scratch body	Uses feet to scratch, clean and preen feathers.
	Stretch leg	Stretches leg straight backwards.
	Stretch wing	Stretches wing straight backwards.
	Wing flap	Flaps wings whilst body is kept upright.
	Yawn	Gapes.
<i>Social behaviors</i>	Non-aggressive peck	Pecks gently at conspecific, without eliciting escape behavior.
	Aggressive peck	Pecks harshly at conspecific, eliciting escape behavior.

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283 **Behavioral synchronization.** Besides the behavioral repertoire and inter-individual distances, our
284 primary focus was on how selection for social motivation may have influenced group synchronization.
285 A synchronization bout was defined as the moment when all three individuals in the trio performed the
286 same behavior simultaneously for more than three seconds. For each trio, all occurrences of
287 synchronization and their duration (in seconds) were recorded for each specific behavior across the four
288 hours of video footage. A synchronization bout was considered to end as soon as one of the three
289 individuals changed behavior. If two synchronization bouts of the same behavior were separated by 10
290 seconds or less, they were treated as a single synchronization bout.

291 Inter-individual distances were measured again, this time to investigate how synchronization
292 influenced the bird's spatial proximity. For this purpose, inter-individual distances were recorded at the
293 beginning of each synchronization bout and again 60 seconds after its conclusion.

294

295 *2.5. Statistics*

296 All statistical analyses were performed using R software version 4.4.2.

297

298 **Behavioral repertoire and inter-individual distances.** A time budget (expressed as a percentage) was
299 calculated for each behavioral category. This was determined by dividing the number of observations
300 for a specific category by the total number of scans (180 per trio per hour) and multiplying by 100. The
301 calculation was performed for each trio and for each of the four testing hours. Due to its low occurrence
302 during the scans (0.2 ± 0.3), the category "Social behaviors" was excluded from the analysis.
303 Furthermore, as "Sit relaxed" was one of the most frequently observed behavior in synchronization and
304 because it revealed interesting differences between the two lines (see below and Results), we conducted
305 a more in-depth analysis of this specific behavior. Finally, the mean inter-individual distances measured
306 during scans were calculated for each trio and for each of the four testing hours.

307

308 **Behavioral synchronization.** The means of the total occurrences and duration of synchronization, as
309 well as the mean inter-individual distances during and after synchronization bouts, were calculated for
310 each trio and for each of the four testing hours. Synchronization bouts predominantly occurred during

311 the behaviors "Sit relaxed", "Stand alert" and "Preen", while other behaviors contributed to less than
312 10% of the total synchronization occurrences and duration. Consequently, further analyses were focused
313 on these three specific behaviors, with particular attention given to "Sit relaxed", for the same reasons
314 mentioned earlier. For the specific behavior "Sit relaxed", a Kappa coefficient (K) was used to calculate
315 a synchronization index for each trio and for each of the four testing hours. According to Asher and
316 Collins (2012), this measure is the most suitable for studying synchronization as it determines whether
317 group behavior is more synchronous than expected by chance. To calculate the Kappa coefficient, we
318 used the following formula:

$$319 \quad K = \frac{P(S) - P(E)}{1 - P(E)}$$

320 where P(S) is the observed proportion and P(E) the expected proportion of synchronization if the activity
321 patterns are random. P(S) was determined by dividing the number of scans in which all three individuals
322 exhibited the behavior "Sit relaxed" simultaneously by the total number of scans (60 per trio per hour).
323 P(E) was determined by dividing the number of observations of the behavior "Sit relaxed" by the total
324 number of scans (180 per trio per hour), then raising the result to the power of 3 to estimate the
325 probability of all three individuals engaging in this behavior simultaneously, based on the probability of
326 one individual of the trio performing the behavior. The coefficient varies between 0 and 1. A value of 0
327 equals either no synchronization or synchronization resulting from chance occurrences and a value of 1
328 indicates perfect, non-random synchronization. As described by Landis and Koch (1977), a Kappa
329 coefficient lower than 0 indicates poor synchronization, a Kappa coefficient between 0 and 0.40
330 indicates slight synchronization, a Kappa coefficient between 0.40 and 0.80 indicates moderate
331 synchronization and a Kappa coefficient higher than 0.80 indicates almost perfect synchronization.

332 All variables were analyzed using Linear Mixed Models (using the lmerTest package). The line
333 (S+ and S-) and the testing hours (hour 1, hour 2, hour 3 and hour 4), along with their interactions, were
334 initially included as fixed factors. For models analyzing inter-individual distances during and after
335 synchronization bouts, the period (during synchronization and after synchronization) was also included
336 as a fixed factor. The trio was included as a random factor to account for repeated measures. Non-
337 significant interactions were excluded from the models, retaining only the main effects. When main

338 effects were significant, post-hoc ANOVA comparisons of the estimated marginal means were
339 performed for multiple comparisons (using the emmeans package with Tukey adjustment). A one
340 sample t-test was also performed to test whether the Kappa coefficient value of the S+ and S- lines
341 significantly differs from zero. We verified all model assumptions, including the normality of residuals
342 and homogeneity of residual variance, through graphical evaluations (using the DHARMA package).
343 The variables "Locomotion", "Synchronization duration in sit relaxed", "Synchronization duration in
344 stand alert", "Synchronization duration in preen" and "Mean duration of one synchronization bout in sit
345 relaxed" were transformed using the square root function to approximate a normal distribution.

346 For all statistical tests, statistical significance was accepted at $p \leq 0.05$. Results are presented as
347 raw means \pm standard deviations.

348

349 **3. Results**

350 **Behavioral repertoire and inter-individual distances.**

351 Only the behavioral categories "Locomotion" ($F = 4.59$; $p = 0.05$) and "Inactivity" ($F = 10.14$;
352 $p = 0.005$), including the behavior "Sit relaxed" ($F = 14.00$; $p = 0.001$), showed a significant difference
353 between the two lines (Figure 2, Table S1). Regardless of the testing hour, individuals from the S+ line
354 exhibited fewer locomotion behaviors, more inactivity behaviors and especially more "sit relaxed"
355 behaviors than individuals from the S- line (S+: $6.7 \pm 5.7\%$; S-: $8.5 \pm 4.2\%$, S+: $35.7 \pm 12.8\%$; S-:
356 $26.7 \pm 12.0\%$, S+: $28.6 \pm 12.0\%$; S-: $18.4 \pm 11.8\%$, respectively). Inter-individual distances measured during
357 scans showed no significant differences between the two lines ($F = 0.83$; $p = 0.37$).

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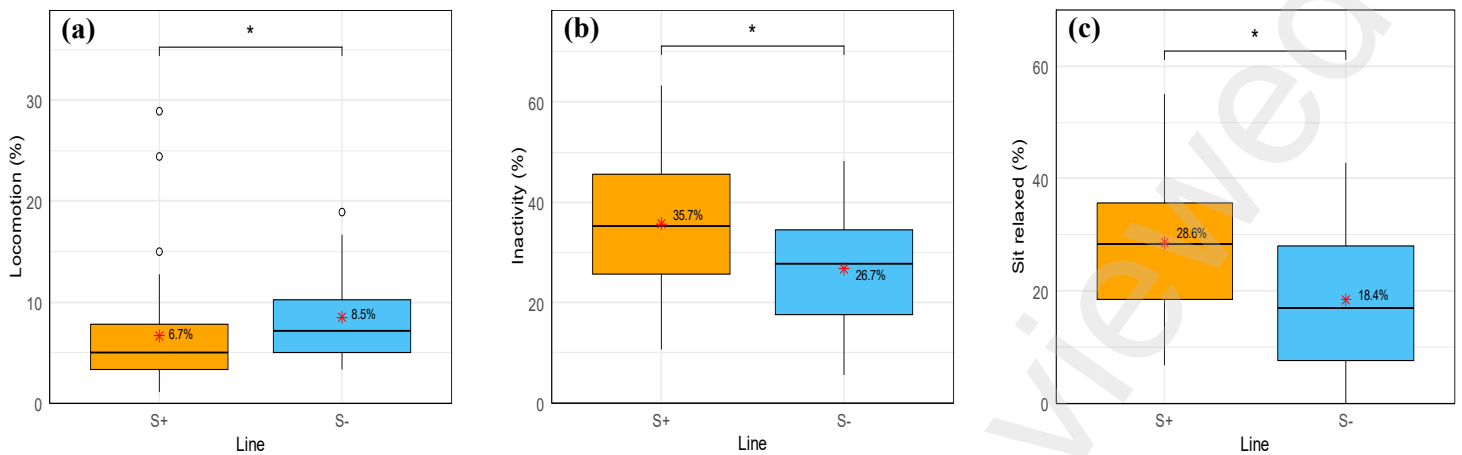
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368 **Figure 2.** Boxplots comparing the mean percentage of observations for (a) the behavioral category
 369 "Locomotion", (b) the behavioral category "Inactivity" and (c) the specific behavior "Sit relaxed",
 370 between individuals with high social motivation (S+, orange boxplots) and those with low social
 371 motivation (S-, blue boxplots). * Indicates a statistically significant difference ($p \leq 0.05$).

372

373 Five of the seven analyzed behavioral categories and the behavior "Sit relaxed" were
 374 significantly influenced by the testing hour (Table S1): "Foraging" ($F = 8.27$; $p < 0.001$), "Exploration"
 375 ($F = 7.38$; $p < 0.001$), "Locomotion" ($F = 11.80$; $p < 0.001$), "Inactivity" ($F = 22.85$; $p < 0.001$),
 376 "Comfort" ($F = 9.77$; $p < 0.001$), "Sit relaxed" ($F = 21.64$; $p < 0.001$). During the early hours of the
 377 test, exploration behaviors were more prevalent, whereas foraging behaviors became more frequent
 378 toward the end. Birds also showed increased inactivity in the middle hours, resulting in reduced
 379 locomotion. Comfort behaviors were most common in the first hour, while "sit relaxed" behaviors was
 380 relatively uncommon during that same period. Inter-individual distances measured during scans were
 381 significantly influenced by the testing hour ($F = 3.16$; $p = 0.03$), with distances being slightly greater at
 382 hour 1 and slightly shorter at hour 3.

383 The interaction between line and testing hour had a significant effect on the behavioral
 384 categories "Foraging" ($F = 5.66$; $p = 0.002$), "Vigilance" ($F = 3.95$; $p = 0.01$), "Locomotion" ($F = 5.60$
 385 ; $p = 0.002$), "Inactivity" ($F = 3.61$; $p = 0.02$) and on the behavior "Sit relaxed" ($F = 4.13$; $p = 0.01$,
 386 Table S1). Individuals from the S+ line foraged less during hours 3 and 4 and moved less during hours

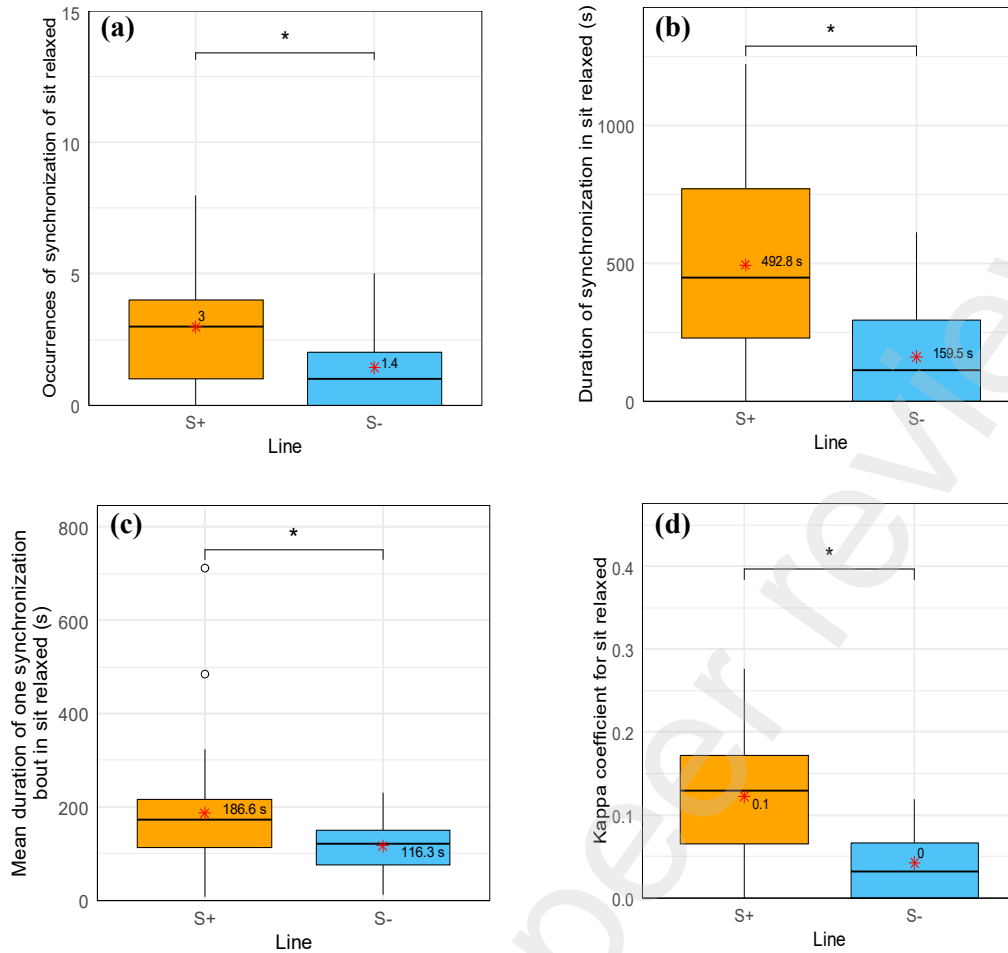
387 1 and 3 compared to individuals from the S- line. In contrast, they displayed more inactivity behaviors,
388 particularly "sit relaxed" behaviors, during hours 1, 2 and 3. No significant interaction effect was found
389 for inter-individual distances measured during scans.

390

391 **Behavioral synchronization.**

392 The total duration of synchronization ($F = 11.18$; $p = 0.004$) and the occurrences of
393 synchronization ($F = 13.57$; $p = 0.002$), the duration of synchronization ($F = 18.32$; $p < 0.001$), the
394 mean duration of one synchronization bout ($F = 6.73$; $p = 0.02$) and the Kappa coefficient ($F = 13.61$;
395 $p = 0.002$) for the behavior "Sit relaxed" were all statistically different between the two lines (Figure 3,
396 Table S2). Regardless of the testing hour, individuals from the S+ line had a longer total synchronization
397 duration than those from the S- line (S+: 675.4 ± 335.2 s ; S-: 418.2 ± 213.8 s). Furthermore, they
398 performed more synchronized "sit relaxed" behaviors (S+: 3.0 ± 2.1 ; S-: 1.4 ± 1.5), spent more time in
399 synchronized "sit relaxed" (S+: 492.8 ± 352.9 s ; S-: 159.5 ± 177.3 s) and remained synchronized for a
400 longer duration during a "sit relaxed" synchronization bout (S+: 186.6 ± 126.7 s ; S-: 116.3 ± 52.7 s).
401 S+ individuals also achieved a significantly higher Kappa coefficient for the behavior "Sit relaxed" (S+:
402 0.106 ± 0.075 ; S-: 0.018 ± 0.066), which differed significantly from 0 ($t = 8.93$; $p < 0.001$), while the
403 Kappa coefficient for the S- line did not ($t = 1.71$; $p = 0.09$). Overall, the Kappa coefficient ranged from
404 -0.14 to 0.28 , with a mean value of 0.06 . No differences between lines were found for the other two
405 most frequently observed synchronized behaviors, "Stand alert" and "Preen". Inter-individual distances
406 during and after synchronization bouts for the behavior "Stand alert" differed significantly between the
407 two lines ($F = 5.23$; $p = 0.03$, Table S3). Regardless of the testing hour and the period, S+ individuals
408 were more distant than S- individuals during stand alert behaviors (S+: 36.4 ± 10.4 cm; S-: 28.9 ± 10.3
409 cm).

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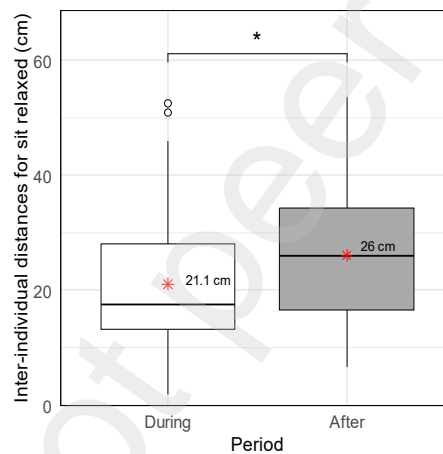
417

418 **Figure 3.** Boxplots comparing (a) the occurrences of synchronization, (b) the duration of
419 synchronization, (c) the mean duration of one synchronization bout and (d) the Kappa coefficient for
420 the behavior "Sit relaxed", between individuals with high social motivation (S+, orange boxplots) and
421 those with low social motivation (S-, blue boxplots). * Indicates a statistically significant difference (p
422 ≤ 0.05).

423

424 The testing hour significantly influenced the total synchronization occurrences ($F = 4.38$; $p =$
425 0.008) and the total synchronization duration ($F = 6.55$; $p < 0.001$), as well as the occurrences and
426 duration of synchronized behaviors "Sit relaxed" ($F = 10.92$; $p < 0.001$, $F = 13.88$; $p < 0.001$,
427 respectively), "Stand alert" ($F = 4.25$; $p = 0.009$, $F = 3.94$; $p = 0.01$, respectively) and "Preen" ($F = 4.45$;
428 $p = 0.007$, $F = 5.03$; $p = 0.004$, Table S2). The Kappa coefficient for the behavior "Sit relaxed" was also
429 significantly influenced by the testing hour ($F = 8.00$; $p < 0.001$). Synchronization occurred more

430 frequently at the beginning of the test, whereas the overall duration of synchronization was greater in
 431 the middle. Specifically, occurrences, duration and the Kappa coefficient for the behavior "Sit relaxed"
 432 were lower during hour 1. For the behaviors "Stand alert" and "Preen", both synchronization occurrences
 433 and duration decreased over time. No hour effect was observed for inter-individual distances during or
 434 after synchronization bouts. However, the period significantly influenced inter-individual distances
 435 during and after synchronization bouts in general ($F = 6.84$; $p = 0.01$) and particularly for the behavior
 436 "Sit relaxed" ($F = 11.80$; $p < 0.001$, Table S3). Regardless of the line and the testing hour, individuals
 437 were closer together during synchronization bouts than one minute after their end, both generally (27.2
 438 ± 8.2 cm; 29.5 ± 7.9 cm, respectively) and especially for the behavior "Sit relaxed" (21.1 ± 11.6 cm;
 439 26.0 ± 11.2 cm, Figure 4).



447 **Figure 4.** Boxplots comparing inter-individual distances during the expression of the behavior "Sit
 448 relaxed", measured during synchronization bouts (white boxplot) and one minute after their conclusion
 449 (grey boxplot). * Indicates a statistically significant difference ($p \leq 0.05$).

451 The interaction between line and testing hour had a significant effect on the total occurrences of
 452 synchronization ($F = 5.04$; $p = 0.004$) and on the occurrences of synchronized behaviors "Sit relaxed"
 453 ($F = 2.71$; $p = 0.05$) and "Stand alert" ($F = 2.83$; $p = 0.05$, Table 3). Individuals from the S+ line exhibited
 454 more synchronization bouts in hour 4 and more "sit relaxed" synchronization bouts in hours 2 and 3
 455 compared to individuals from the S- line. A significant interaction effect was also found on inter-
 456 individual distances during and after synchronization bouts, either generally ($F = 8.06$; $p < 0.001$) or for

457 the behaviors "Sit relaxed" ($F = 5.33$; $p = 0.002$), "Stand alert" ($F = 4.09$; $p = 0.008$) and "Preen" ($F =$
458 3.83 ; $p = 0.01$, Table 4). Regardless of the period, individuals from the S+ line were more distant than
459 those from the S- line in hour 1, both overall and especially for the behavior "Sit relaxed", as well as for
460 the behavior "Stand alert" in hours 1 and 2.

461

462 **4. Discussion**

463 The goal of this study was to investigate how selecting for individual social motivation affects
464 both an individual's social behavioral repertoire and group-level behavioral synchronization, a key
465 process in group organization and social cohesion. To achieve this, two lines of Japanese quail, selected
466 based on their social motivation (the S+ line characterized by high social motivation and the S- line
467 characterized by low social motivation), were subjected to a behavioral synchronization test. The results
468 revealed clear differences between the two lines in both behavioral repertoire and synchronization. S-
469 quail were more active, engaging in more locomotion, while S+ quail spent more time in synchronized
470 behaviors and remained synchronized for longer periods. These differences suggest that social
471 motivation influences both individual activity patterns and group coordination. Below, we explore these
472 findings in greater detail, discussing their implications for the relationship between social motivation
473 and behavioral synchronization.

474

475 **Behavioral repertoire and inter-individual distances.**

476 The test revealed significant behavioral differences between S+ and S- quail. S+ individuals
477 showed less locomotion and more inactivity, particularly sit relaxed behaviors, suggesting lower activity
478 levels. However, this contrasts with previous studies where S+ quail were more active than S- quail,
479 especially under social isolation (Formanek et al., 2008; Mills et al., 1993). These previous findings may
480 be linked to the selection process of the lines, where S+ individuals are those that travel greater distances
481 in the treadmill test (Mills and Faure, 1991), which may have inadvertently favored higher activity
482 levels. Since the quail in our study were tested in trios rather than in isolation, this social context may
483 have influenced their behavioral responses. The limited social presence might have provided a buffering
484 effect for S+ birds, helping them remain more relaxed. In contrast, it may not have been sufficient to

485 alleviate stress in S- birds, which are known for their specific social motivation and preference for
486 familiar conspecifics. Unlike S- quail, S+ quail do not exhibit a strong preference for familiar individuals
487 (Formanek et al., 2008). Thus, despite being reared together, S- quail may have perceived their test
488 companions as unfamiliar, weakening social buffering and increasing stress. This is supported by the
489 fact that differences between the lines were most pronounced at the start of the test, suggesting that
490 stress in S- quail gradually decreased over time, possibly as social bonds strengthened. Additionally, S-
491 individuals maintained shorter inter-individual distances during vigilance synchronization and shortly
492 after, particularly early in the test. This behavior likely reflects heightened stress and a greater need for
493 proximity as a protective strategy.

494 Regarding the inter-individual distances recorded during the scans, no significant differences
495 were found between the two lines. These results are consistent with other studies showing that, although
496 S+ individuals maintain shorter inter-individual distances than S- individuals at a young age, these
497 distances tend to increase over time and become similar to those observed in S- quail around six weeks
498 of age, at sexual maturity. Prior research suggests that although S+ birds exhibit high social motivation,
499 they also tend to become more aggressive over time (François et al., 1999). While no substantial
500 aggressive behavior was observed in S+ individuals during our study, they may have experienced a
501 heightened approach-avoidance motivational conflict, leading to increased inter-individual distances.
502 This could account for the absence of significant differences between the two lines.

503 Overall, beyond the differences observed in locomotion and inactivity behaviors, selection
504 based on social motivation does not seem to lead to major differences in the baseline behavioral
505 repertoire or average inter-individual distances between the two lines. However, our results suggest that
506 more sociable individuals may exhibit greater resilience in stressful situations, likely benefiting from
507 the social buffering effect provided by the presence of conspecifics. This hypothesis warrants further
508 investigation in future studies.

509

510 **Behavioral synchronization.**

511 Our results revealed that individuals from the S+ line had a longer total synchronization duration
512 compared to that from the S- line. This finding supports our initial hypothesis that more sociable

513 individuals tend to synchronize more with their conspecifics and is consistent with results from previous
514 studies. For instance, gregariousness, a potential aspect of sociability defined based on the frequency of
515 having a close neighbor (<3m), was found to result in higher synchronization within a group of highly
516 gregarious sheep compared to a group of less gregarious individuals (Hauschildt and Gerken, 2015b).
517 Similarly, Tang and Fu (2020) showed that highly social schooling fishes were more synchronized in
518 their swimming speeds with other group members than less social ones. Such synchronization could in
519 turn provide benefits in efficient information transfer and collective motion coordination (Krause and
520 Ruxton., 2002), ultimately strengthening group cohesion.

521 More socially motivated individuals likely synchronize more because they form stronger social
522 bonds and are more influenced by their peers. Supporting this, S+ quail are more likely than S- quail to
523 eat novel food after seeing conspecifics consume it (unpublished data). This suggests that their increased
524 synchronization may result from a stronger intrinsic drive to align with others' behaviors. However,
525 further research is needed to clarify the role of social motivation in synchronization and the underlying
526 mechanisms. Future studies could explore how social network dynamics—such as the strength and
527 number of individual connections—influence synchronization or whether more sociable individuals
528 exhibit heightened sensitivity to visual social cues or higher performance in social cognition given that
529 behavioral synchronization could rely on cognitive mechanisms (Lamontagne and Gaunet, 2023;
530 Papageorgiou et al., 2023; Carvalho et al., 2022).

531 A more in-depth analysis of the data revealed that S+ quail exhibited higher levels of behavioral
532 synchronization than S- quail, particularly during the behavior "Sit relaxed", a key resting behavior.
533 Notably, "sit relaxed" was the only behavior associated with a reduction in inter-individual distances
534 during synchronization bouts. This finding highlights a link between synchronization and spatial
535 proximity, suggesting that synchronization in this context is not random but may be modulated by social
536 factors. Previous research supports this notion, showing that inter-individual distances tend to be smaller
537 during resting than during feeding (Bøe et al., 2013; Keeling and Duncan, 1991).

538 Beyond its role in predation avoidance and thermoregulation, resting behavior and social
539 dynamics are closely linked, with each potentially influencing the other (Chakravarty et al., 2024). For
540 example, wild Japanese macaques sleep longer and more peacefully when huddled with natal group

541 members, whereas those in non-natal clusters experience more disturbances and show signs of stress
542 and social anxiety (Mochida and Nishikawa, 2014). This suggests that more sociable individuals may
543 be more inclined to engage in behaviors with strong social significance, strengthening group cohesion
544 and promoting longer, less interrupted rest. During these periods, they may also reinforce their social
545 bonds, which could explain why, in our study, S+ individuals synchronized specifically during the
546 behavior "Sit relaxed" and maintained synchronization for a longer duration within a single "sit relaxed"
547 bout.

548 Another possible explanation for our results is that S+ quail engaged in "sit relaxed" behavior
549 more frequently in their daily activities, naturally increasing the likelihood of synchronization. To
550 account for this, we used the Kappa coefficient (Asher and Collins, 2012), a robust measure of group-
551 level synchronization that is independent of time budget. The Kappa coefficient was significantly higher
552 in S+ quail and differed from 0, whereas no such pattern was observed in S- quail. These findings suggest
553 that "sit relaxed" synchronization in S+ quail was not random and cannot be attributed solely to the
554 higher frequency of this behavior.

555 Overall, selection for social motivation seems to enhance behavioral synchronization, especially
556 in certain behaviors like "Sit relaxed". This suggests that social motivation effect on synchronization is
557 not just a matter of frequency but involves more complex underlying mechanisms. To better understand
558 this process, further research is needed to explore how social motivation shapes individual behavior and
559 what drives these synchronized interactions, ultimately helping to explain their role in social cohesion.

560

561 **Testing hour effect**

562 In addition to the line effect, it is important to consider the influence of testing hour on the
563 analyzed behaviors, as temporal factors can shape activity patterns and behavioral responses. Two
564 general trends emerged. First, quail exhibited higher activity levels at the onset of the test, likely due to
565 the testing environment and potential stress triggered by the experimenters' initial entry into the testing
566 room. Second, quail behavior appeared to follow a daily rhythmicity, with increased activity during the
567 early and late test phases and more resting behaviors during the middle phases. While the hour effect
568 may have interacted with the line effect, the latter remained consistently significant. In cases where line-

569 hour interactions were observed, the same line always predominated, regardless of the observation
570 window. Given the complexity of temporal influences on behavior, future studies should further explore
571 the interplay between circadian rhythms and social tendencies to better understand their role in shaping
572 synchronization and overall activity patterns.

573

574 **5. Conclusion**

575 Our findings provide new insights into the relationship between inter-individual differences in
576 social motivation, behavioral synchronization and group life. They suggest that more sociable
577 individuals are more likely to engage in synchronized behaviors, which could play a crucial role in the
578 organization and social cohesion of the group. Indeed, since behavioral synchronization is a mechanism
579 that fosters social cohesion, more sociable individuals, with their greater tendency to synchronize, may
580 promote more harmonious and stable group dynamics. The results also indicate that selection based on
581 an individual's social motivation can influence more subtle social behaviors that could underlie broader
582 sociability. This phenomenon could have important implications in ecological contexts, where it would
583 contribute to collective survival, but also in husbandry contexts, where it could positively influence
584 animal welfare. This is especially relevant considering that certain major behavioral issues in poultry
585 production systems—such as severe feather pecking and aggressiveness—are linked to social behavior.
586 Further research is needed to refine our understanding of the mechanisms underlying behavioral
587 synchronization and its broader effects on group functioning. Investigating these dynamics in greater
588 detail could provide valuable insights for both animal behavior research and the development of
589 improved management strategies in animal husbandry.

590

591 **AUTHORS' CONTRIBUTIONS**

592

593 J.S., M.G., V.H.B.F. and L.C. conceived the study. F.C., J.L., L.L. and P.J. contributed to improvements
594 on the experimental design and/or with the supply of material for experiments. J.S., M.G. and V.H.B.F.
595 executed the project, collected, analyzed and interpreted data. J.S. was the primary author and drafted
596 the initial manuscript, for which V.H.B.F. and L.C. provided critical revision and improvements.

597 V.H.B.F. and L.C. acquired funds. All authors revised the final draft, approved the final version of the
598 manuscript and agree to be held accountable for the content therein.

599

600

COMPETING INTERESTS

601

602 We declare we have no competing interests.

603

604

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608

609

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE

610

WRITING PROCESS

611

612 During the preparation of this work the authors used ChatGPT in order to enhance readability and
613 language. After using this tool/service, the authors reviewed and edited the content as needed and take
614 full responsibility for the content of the publication.

615

616

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