To Peck or Not To Peck: The influence of early-life social environment on response inhibition and impulsive aggression in Japanese quails

Alizée Vernouillet[1*], Kathryn Willcox[1], Reinoud Allaert[1], Anneleen Dewulf[1], Wen Zhang[1], Camille A. Troisi[1,2], Sophia Knoch[1], An Martel[1], Luc Lens[1], Frederick Verbruggen[1]

1. Centre for Research on Ecology, Cognition and Behaviour of Birds, Ghent University
2. Éthologie animale et humaine (EthoS), UMR 6552, Université de Rennes

Alizée Vernouillet ORCID: https://orcid.org/0000-0003-2525-2936
Kathryn Willcox ORCID: https://orcid.org/0000-0002-3222-2850
Reinoud Allaert ORCID: https://orcid.org/0000-0002-6122-496X
Anneleen Dewulf ORCID: https://orcid.org/0000-0003-4215-0421
Wen Zhang ORCID: https://orcid.org/0000-0001-9120-9763
Camille A. Troisi ORCID: https://orcid.org/0000-0002-4036-3848
Sophia Knoch ORCID: https://orcid.org/0000-0001-9156-5725
An Martel ORCID: https://orcid.org/0000-0001-7609-5649
Luc Lens ORCID: https://orcid.org/0000-0002-0241-2215
Frederick Verbruggen ORCID: https://orcid.org/0000-0002-7958-0719

Correspondence concerning this article should be addressed to Alizée Vernouillet. Email: alizee.vernouillet@gmail.com

1. Summary

Deficits in response inhibition (i.e., the ability to suppress inappropriate responses) may contribute to increased impulsive aggression (i.e., unplanned behaviors that harm others). Since early-life environment might influence the development of response inhibition, it could also indirectly affect impulsive aggression. However, this relationship has rarely been directly examined. Here, we investigated whether response inhibition is associated with impulsive aggression and whether this relationship explains the effects of early-life social environments on impulsive aggression in juvenile Japanese quails (*Coturnix japonica*). Quails (n = 120) were raised in two social conditions: Small groups of five birds or Large groups of 15 birds. Response inhibition was assessed using the Barrier and Cylinder tasks, while impulsive aggression was measured in two contexts - within a group of five familiar individuals and in a dyad with an unfamiliar individual. We found that some aspects of response inhibition were related to impulsive aggression. Furthermore, quails reared in small groups showed significantly poorer response inhibition than those reared in large groups. Yet, impulsive aggression did not significantly differ between the two conditions. These findings suggest that, while impulsive aggression is partly related to response inhibition, other factors mitigate the effects of early social environments on its expression.

Keywords: aggression, early-life social environment, inhibitory control, impulsive behaviour, personality, response inhibition

2. Introduction

Group living brings many benefits, such as reducing predation pressure and increasing foraging efficiency, but can also create conflicts between members due to increased competition (1). These agonistic interactions between individuals may result in *impulsive aggression* (i.e., the unplanned behavioural response of inflicting damage to self or others, (2)), that in turn may sometimes have negative fitness consequences for one or multiple individuals involved (e.g., reduced access to resources, injuries, or even death). While a lot of research has focused on aggression as a personality trait in animals (as reviewed by e.g., (3)), little is known about the cognitive mechanisms underlying aggression.

Some researchers suggest that impulsive aggression results from deficits in *response inhibition* (also referred to in the animal cognition field as *inhibitory control*; (4–6); but see (7)), the suppression of inappropriate pre-potent behavioural responses or actions (8–10). Indeed, inhibition deficits are correlated with increased aggression in rats (11), dogs (12), long-tailed macaques (13), and humans (14–16). Additionally, both increased levels of aggression and decreased levels of response inhibition have been correlated with lower levels of central serotonin (5-HT), a well-conserved neuromodulator of nervous systems in both invertebrates and vertebrates (9,11,17,18). However, most studies investigating the link between response inhibition and impulsive aggression are correlational. This has two important consequences. First, response inhibition deficits could cause or contribute to impulsive aggression, but it is also possible that a common underlying factor simply influences both independently (as suggested by (19)). Second, it has been proposed that environmental factors during early life contribute to response inhibition deficits and impulsive aggression later in life. Yet again, causal relationships have been hard to establish, and systematic research is lacking.

Early-life environmental conditions, both physical and social, can shape an individual's cognitive abilities and personality (e.g., (20–24)). For example, response inhibition is key to

maintain spatial and temporal cohesion between group members (25). Indeed, individuals within a group benefit from being surrounded by others and performing the same activity together, so they need to adjust their activity to that of other group members (e.g., (26,27)). Additionally, within a group, subordinate individuals might inhibit feeding or mating in the presence of dominant individuals to avoid potential aggressive interactions or confrontations (28). Given that social complexity is multi-faceted and highly variable, both within and between species (29), in the present study we focused on one key aspect of the social organization – social group size (30). An increase in group size means an increase in potential interactions with other group members, and therefore an increase in possibilities to learn how to interact with other individuals. Social group size has been shown to correlate with higher levels of response inhibition in Australian magpies (*Cracticus tibicen dorsalis*, (31)), in hyenas (*Crocuta crocuta*, (32)), and in primates (33), but not in guppies (*Poecilia reticulata*, (24,34)). Hence, we expected that a larger group size required individuals to develop better response inhibition due to greater social requirements.

Many studies have found aggression is usually suppressed in larger groups (e.g., calves – (35), chickens – (36,37), fish – (38), pigs – (39)). Based on the same reasoning described in the previous paragraph, with larger groups come a higher number of potential competitors for resources, and individuals might thus benefit to switch to a more socially tolerant strategy (e.g., (37,40), but see e.g., (41)). Yet, methodological differences between studies make it difficult to determine whether, and if so in what direction, early-life social environment shapes an individual's aggressive tendencies (42). Based on previous research and on the theoretical link between inhibition and aggression, and because we predicted that individuals raised in larger groups would have better response inhibition, we expected levels of impulsive aggression to decrease with increasing group size.

In this study, we investigated the link(s) between early-life social environment, response inhibition and aggression in juvenile Japanese quails (*Coturnix japonica*). Japanese quails are a precocial social bird species that is easy to raise in captivity, which enabled us to rear them without

101 the presence of adult quails. This controlled raising environment allowed us to manipulate their
102 postnatal social conditions, while controlling all other environmental parameters. Additionally,
103 Japanese quails have long been recognized as an ideal model for studying aggression, as hierarchies
104 within their social group are established and maintained through frequent aggressive interactions
105 (e.g., (26,43,44)). As a result, their typical behaviors, including aggressive behaviors towards
106 conspecifics, have been extensively documented (e.g., (44–46)). These combined factors were
107 crucial in establishing causal relationships between early-life social environment and an individual's
108 response inhibition and aggression.

109 We evaluated response inhibition in Japanese quails with two commonly used tasks to
110 evaluate an animal's response inhibition: the *Barrier task*, during which individuals must detour
111 around a vertical transparent barrier to reach a reward, and the *Cylinder task*, during which
112 individuals must reach through the openings of a transparent cylinder to obtain a reward. Both
113 tasks are purporting to measure the same aspect of response inhibition and have been referred to
114 as "detouring" tasks or "motoric self-regulation" tasks, as, in both tasks individuals must inhibit a
115 prepotent motor action (i.e., going towards the visible reward) and instead change it into a different
116 one (i.e., detouring around a physical barrier) (47) (but see (48)). Aggression was evaluated in two
117 different contexts: once in a group of familiar individuals (e.g., (44)), and once in presence of an
118 unfamiliar individual (e.g., (49)).

119 The main goal of the study was to experimentally determine the influence of early-life social
120 environment on response inhibition and impulsive aggression in Japanese quails. We focused on
121 three research questions: (A) do deficits in response inhibition cause impulsive aggression at an
122 individual-level, and (B) does social group size during early life shape an individual's response
123 inhibition and (C) impulsive aggression? Based on previous correlational research and on
124 theoretical models, we predicted that, if indeed higher impulsive aggression can be attributed to a
125 deficit in response inhibition, (A) response inhibition and impulsive aggression would be inversely

126 related at an individual-level, and that (B and C) individuals raised in larger groups would have a
127 higher level of response inhibition and be less aggressive than individuals raised in smaller groups.

128 **3. Material and methods**

129

130 *Subjects*

131

132 We used 120 juvenile Japanese quails (*n* = 60 females, *n* = 60 males) in this study. Birds
133 were hatched simultaneously over two days and kept together at the Opvangcentrum Vogels en
134 Wilde Dieren, Ostend, Belgium. Birds were housed in four identical heated lofts, each loft
135 containing four $1m^2$ (1 m length x 1 m width x 2 m height) enclosures. Each enclosure included an
136 electric hen heating plate (25 cm length x 25 cm width, Comfort Chicks), which was replaced with
137 a plastic cover when birds were 16 days old. Outside of the experimental food restriction procedure,
138 birds were provided with *ad lib* grain food mix (Aveve), presented in a single 50-cm long linear
139 chick feeder (Voss Framing). Birds had free access to water. Each loft followed a 12:12 day-night
140 cycle, with light onset at 07:00 am. All birds were visually checked at least twice a day (once in the
141 morning and once in the evening). Measurements (weight and tarsus length) were taken when the
142 birds were 20 days old (before the start of the study) and at 44 days old (at the end of the study).
143 Quail care was performed by AV, KW, RA, AD, WZ, and CT, under AV and RA's supervision.
144 Within each loft, one of the four enclosures housed a large group of 15 individuals (Large),
145 and the three other enclosures housed a small group of five individuals (Small). On day 2 post-
146 hatch, birds were randomly assigned to either a Small or a Large enclosure. Hence, 60 birds were
147 assigned to each experimental condition. Previous research has found differences in social bonding
148 and other social affiliation behaviors between individuals raised in groups of 6 vs 15 (50).
149 Additionally, wild Japanese quails have broods of up to 15 individuals (51,52), and once sexually
150 mature, they can be monogamous or live in small flocks (51). Hence, we predicted that Japanese

151 quails raised in groups of five and 15 would differ in their RI and IA if the early-life social group
152 size influenced the development of cognitive and behavioral traits.
153
154 *General Experimental Procedures*
155
156 Quails were habituated to being handled and to the testing environment during their second
157 and third week. Testing started when birds were 24 days old and ended when they were 41 days
158 old. At that age, juvenile quails are independent and can be socially isolated without showing signs
159 of distress. All 120 individuals underwent the Barrier task, the Cylinder task, the Familiar Group
160 task, and the Unfamiliar Individual task, given in that order for all individuals. Birds were tested
161 individually during the Detour and the Cylinder tasks (i.e., response inhibition tasks) at the age of
162 24-33 days old, and with other individuals during the Familiar Group and the Unfamiliar Individual
163 tasks (i.e., impulsive aggression tasks) at the age of 39-41 days old. Tasks were performed on
164 separate days. A schematic overview of the study timeline can be found in the Supplementary
165 Material (Fig. S1).
166 Testing took place between 08:30 and 14:00 (local time). Food was removed the evening
167 prior testing to ensure motivation to participate in the experiment. On the morning of testing, birds
168 were individually placed in a portable cage with multiple compartments (Ducatillon) and
169 transported to a waiting room, where they were kept before and after testing until all individuals
170 had been tested.
171 All testing occurred in a test box (86 cm length x 146 cm width x 91 cm height). The testing
172 box was lit with LED lights to control for lighting. All trials were recorded using a camera
173 (BASCOM) mounted to the ceiling of the test box. A 'start box' (29 cm length x 45 cm width x 29
174 cm height) was attached to the front of the test box. The start box had two doors – one transparent
175 and one opaque – which slid vertically on rails between the two boxes, and a separate light. Inside
176 the start box was another square piece of wood that served as the back of the box attached to a

handle, which could slide forward and was used to gently push the birds into the test box when required.

Every testing trial followed the same general procedure. First, the bird(s) to be tested was (were) placed in the start box with both start box doors closed. Next, the opaque door was opened, allowing the bird(s) to see within the test box but not enter the test box. After 15 seconds the transparent door was opened, indicating the start of the trial. Birds that did not leave the start box within 30 seconds were gently pushed into the test box. Once the bird(s) either reached the reward location, or the time limit for the trial was reached, the test box lights were turned off, indicating the end of the trial. The bird(s) was (were) given 15 seconds to return to the start box; if it(they) did not, it was (they were) caught by the experimenter and placed back in the start box. Once all birds completed all required trials for a session, they were returned to their home enclosures. Data collection was performed by AV, KW, RA, AD, WZ, CT, and LL, under AV and KW's supervision.

Videos were coded using BORIS v.7.13 (Behavioral Observation Research Interactive Software (53)). All the videos of the response inhibition tasks were coded by one experimenter (KW), who was naïve to the conditions. All the videos of the impulsive aggression tasks were coded by another coder (SK), who was naïve to the conditions and the experimental hypotheses. To assess inter-observer reliability, 20 % of the videos of the response inhibition tasks were coded by one coder (SK), who was naïve to the conditions and the experimental hypotheses, and 20 % of the videos of the impulsive aggression tasks were coded by one experimenter (AV). Inter-rater reliability was calculated using BORIS, and was high, with average Cohen's kappa coefficients of 0.840 and 0.805, for all response inhibition videos and all impulsive aggression videos respectively (54).

Habituation

202 Birds were gradually habituated to the portable cage from 20-days-old onwards and to the
203 test box at 22-23 days old. For the habituation in the test box, a feeder was placed 50cm from the
204 test box entrance. The feeder used was filled with grains and was the same design as those used in
205 the birds' enclosures, but smaller (30cm length). A petri dish with two live mealworms was also
206 placed in front of the feeder. Both rewards were familiar to the birds and were used to entice them
207 to participate in testing. The total trial time was 5 minutes; each bird received one habituation trial.
208
209 *Response inhibition tasks*
210
211 Barrier task
212
213 *Apparatus*. The apparatus for the Barrier task consisted of a square wooden frame (40 cm
214 length x 41.2 cm height) with two horizontal supports (20 cm width) (Fig. 1). The frame was placed
215 55 cm from the entrance of the test box, centrally such that there was 22 cm between it and the
216 test box wall on each side. A reward feeder filled with grains was placed directly behind the barrier,
217 and a petri dish containing two mealworms was placed directly behind the feeder. An opaque
218 barrier was used during the training trials and a transparent barrier was used during the testing trials,
219 so the reward food was visible to the birds through the barrier during the test session (Fig. 1). Both
220 barriers had a strip of green tape on the left side and a strip of yellow tape on the right side (the
221 same colours as the enclosure and reward feeders).
222
223 *Procedures*. This task included a training session and a testing session on two separate,
224 consecutive days.
225 During the training session, the opaque barrier was attached to the frame. During the first
226 trial, the bird was given two minutes to detour around the barrier to reach the food; from the
227 second trial onwards, it had one minute and a half. Trials were repeated until the bird successfully

228 detoured on three consecutive trials, with a maximum of seven trials per bird. If the bird did not
229 detour once within three consecutive trials, the session ended. All birds passed the training session.
230 The testing session on the following day consisted of one training trial and one test trial per
231 bird. The test trial followed the same procedure as during the training trials, but the transparent
232 barrier was used instead of the opaque barrier.
233 'Successful' trials were defined as when the bird detoured around the barrier (opaque or
234 transparent) without interacting (i.e., pecking or pushing) with it.
235
236 Cylinder task
237
238 *Apparatus*. The cylinder apparatus consisted of a transparent Plexiglas tube with open ends
239 (5.4 cm diameter x 13.2 cm length) mounted on a small wooden platform (13 cm length x 3 cm
240 width x 2 cm height; Fig. 1). The wooden base was covered with horizontal strips of yellow and
241 green tape. The apparatus was placed 40 cm from the entrance of the test box, so that the entrances
242 were perpendicular to the start box and secured to the floor with tape. One freshly killed mealworm
243 and 1tsp of grain were placed centrally inside the cylinder. Quails had to put their head within the
244 cylinder to retrieve the food.
245 *Procedures*. The Cylinder task occurred during a single test day. During each trial, the bird
246 had two minutes to reach the food inside the cylinder. Trials were repeated until the bird completed
247 ten trials, which was the maximum number of trials given, or until the bird failed to reach the food
248 for three consecutive trials.
249 'Successful' trials were defined as when the bird reached the food through one of the two
250 open sides of the cylinder without first pecking at the outside of the cylinder. For the purpose of
251 this study, we only focused on the first trial, as we believe it best measure the stopping behaviour
252 of an individual (55). Indeed, the subsequent trials might reflect the inhibitory learning of the
253 individual and is investigated in a different study (56).

Behavioural measures of response inhibition tasks

For each quail, the dependent measures evaluated were (1) trial success (i.e., whether the trial was a success), and (2) time spent 'interacting' with the barrier/cylinder (i.e., time the bird spends actively and repeatedly pecking/pushing the barrier).

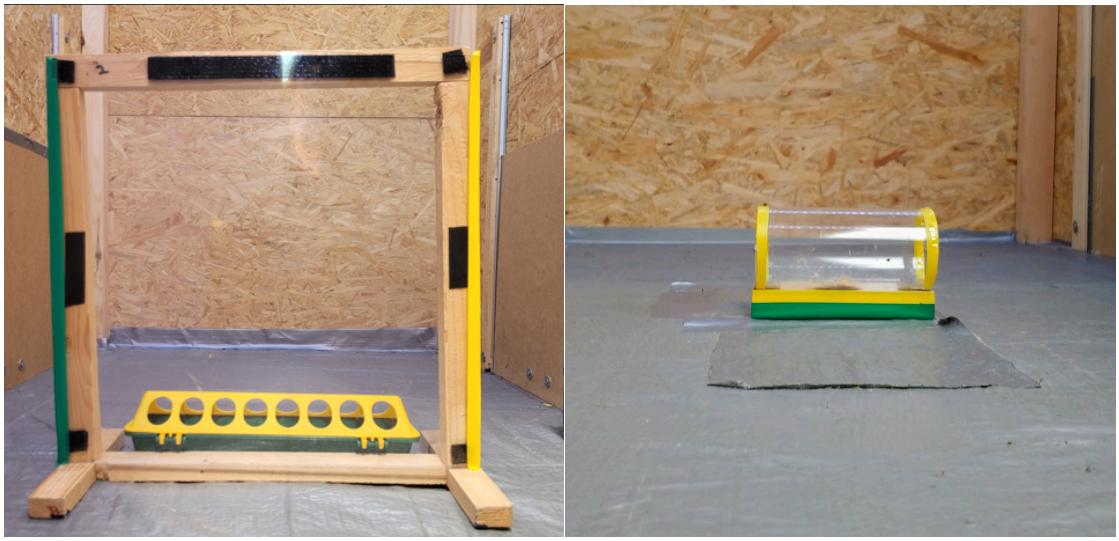

Figure 1. Apparatuses used for the *Barrier task* (left) and for the *Cylinder task* (right) with Japanese quails (n = 120).

Impulsive aggression tasks

Impulsive aggression tasks had multiple trials and different experimental phases, which allowed us to investigate whether quails' aggressive behaviour was repeatable across contexts differing in food availability. The same set of birds were tested for all trials. This repeatability aspect is being investigated in a different project and not analysed in this study (Vernouillet et al. in prep.). Here, we focused on the behaviour of individuals during the first trial.

Familiar Group

Apparatus. A feeder, identical to the one present in the home enclosure of individuals and filled with grains, was placed in the middle of the text box. A sheet of semi-transparent plastic was placed inside the feeder to control access to the food. The feeder was present through the duration of the trial, but access to the food was adjusted during the trial (see Procedures).

Procedures. Five quails from the same enclosure were tested together for two trials on two consecutive days. The five individuals were placed in the start box and, following the same procedure as during the previous tasks, were let into the test box after 15 seconds after the opaque door of the start box was removed. Trials lasted 10 minutes. During the first trial, access to the feeder was completely thwarted for the first five minutes of the trial (No Food phase), with the sheet of plastic blocking access to all the holes in the feeder, then partially thwarted so that only one individual could access the food for the last five minutes of the trial (Limited Access phase), with the sheet of plastic blocking access to all but one hole in the feeder. During the second trial, the procedure was reversed (i.e., Limited Access phase during the first five minutes, No Food phase during the last five minutes).

<u>Unfamiliar Individual</u>

Apparatus. Similar to the Familiar Group task, a feeder, identical to the one present in the home enclosure of individuals and filled with grains, was placed in the middle of the test box. A sheet of semi-transparent plastic was placed inside the feeder to control access to the food. The feeder was placed inside the test box during the trial (see Procedures).

Procedures. Two quails from a different enclosure and loft (but of the same experimental condition) were tested together for three trials on three consecutive days. Two individuals in the start box, and following the same procedure as during the precedent tasks, were let into the test box after 15 seconds from removing the opaque door of the start box. Trials lasted three minutes. The feeder was placed in the test box after one minute. During the first trial, only one bird had

access to food when the feeder was placed in the test box, with the sheet of plastic blocking all but one hole in the feeder. During the second trial, both birds could freely access the food when the feeder was placed in the test box, as there was no sheet of plastic blocking access to the feeder. During the third trial, none of the birds had access to the food, as access was thwarted, with the sheet of plastic blocking all holes in the feeder.

Behavioural measures of impulsive aggression tasks

For each quail, the dependent measures evaluated were (1) number of pecks given, (2) number of pecks received, (3) time spent chasing, (4) time spent escaping, and (5) time spent pushing. Descriptions of each behaviour can be found in Table S1.

Statistical analyses

We first wanted to perform a structural equation modelling approach (SEM) to determine whether response inhibition, as estimated by the measures assessed during the Barrier and the Cylinder tasks, could predict impulsive aggression, as estimated by the behavioral measures assessed during the Familiar Group and the Unfamiliar Individual tasks, and whether early-life social condition influenced response inhibition and impulsive aggression. However, a preliminary Confirmatory Factor Analysis indicated a lack of correlations among measures assessing the latent factors of interest (i.e., response inhibition and impulsive aggression), and none of the models tested had a decent fit (see Supplementary Material, Figures S2 and S3, Table S2 for more details on factors analyses and SEM).

We thus used a different approach for our analyses. First, to determine whether both the Barrier task and the Cylinder task were assessing the same aspect of response inhibition, we correlated (1) first trial success using a tetrachoric correlation (for binary data), and (2) time spent 'interacting' with the barrier/cylinder using a Pearson's correlation. Second, to determine whether

325 both impulsive aggression tasks were assessing the same aspect of aggression, we conducted a PCA
326 with (1) number of pecks given, (2) number of pecks received, (3) time spent chasing, (4) time
327 spent escaping, and (5) time spent pushing for both tasks. PCA was based on a correlation matrix.
328 We only considered components whose Eigenvalues were higher than 1 and for each component,
329 we only considered loadings whose contribution was higher than what was expected if all loadings
330 were of equal weight. Third, as we did not find any significant correlation between the different
331 response inhibition variables (see Results), we assessed whether higher levels of impulsive
332 aggression were linked to response inhibition deficits by evaluating whether aggression scores (as
333 calculated during the PCA) significantly differ between individuals that were successful during the
334 first trial of each response inhibition task using a Student t-test and whether they correlated with
335 time spent 'interacting' with the barrier/cylinder using a Pearson's correlation. Importantly, unlike
336 the SEM approach, this approach does not allow us to infer the direction of the potential link
337 between response inhibition and impulsive aggression.

338 To determine whether early-life social environment influenced an individual's response
339 inhibition and/or impulsive aggression, we used a generalized linear model (GLM) approach, with
340 (1) trial success (i.e., whether the barrier/cylinder testing trial was successful) for each response
341 inhibition task separately, and (2) time spent 'interacting' with the barrier/cylinder (i.e., time the
342 bird spends actively and repeatedly pecking/pushing the barrier) for each response inhibition task
343 separately, as dependent variables associated with response inhibition, and (3) using the PCA scores
344 obtained for the first two axes, as aggressive behaviours during the Unfamiliar Individual task
345 mostly loaded on PC1 and aggressive behaviours during the Familiar Group task mostly loaded on
346 PC2 (see Results) as dependent variables associated with impulsive aggression. Full models
347 included social group condition, as well as morphological factors such as body weight and sex.

348 To assess whether specific factors influenced our dependent variables, we compared full
349 models to a reduced model that did not include the factor that was evaluated (following the

350 procedures described by (57,58)). Parameter estimation was achieved using the residual maximum
351 likelihood ratio test.

352 For trial success during the Barrier and the Cylinder tasks, we used a binomial distribution.
353 For time spent interacting with the barrier/cylinder, we rounded the values to the nearest second
354 and used a Poisson distribution. We first checked the assumptions of the GLMs were met using
355 the *DHARMa* package (59). Models were checked for dispersion and zero-inflation using residual
356 plots. In case residuals were over-dispersed, we added a dispersion parameter (this was the case for
357 the GLM on the second impulsive aggression score). In case there were too many zero in our
358 dataset, we added a zero-inflated model with a constant at the origin, and in the case that the
359 assumptions of the models were still not met, we changed the family to a negative binomial family
360 (this was the case for the GLM on time spent pecking for both response inhibition tasks).

361 Analyses were conducted using R version 4.3.2 (60) with the *glmmTMB* (61), *psych* (62),
362 *FactoMine*R (63), and *factoextra* (64). Descriptive statistics were obtained using the *Rmisc* package
363 (65). Plots were created using the *ggplot2* (66), *ggsignif* (67), *ggpubr* (68), *patchwork* (69), *wesanderson* (70)
364 packages. Alpha was set at 0.05 for all statistical analyses. All statistical analyses were performed by
365 AV, verified by KW and CAT.

366

367 **4. Results**

368

369 *Overview of response inhibition tasks*

370

371 Overview of Barrier task

372

373 During the testing trial, 19 individuals detoured successfully (i.e., without touching the
374 transparent barrier), 93 individuals detoured unsuccessfully (i.e., after touching the transparent
375 barrier), seven individuals touched the barrier but did not detour during the entire duration of the
376 trial, and one did not interact with the apparatus nor detoured around the transparent barrier (view
377 Table S3 for an overview of the response outcomes of the quails based on their social group and
378 on sex). Among individuals who pecked the barrier (n = 100), average time spent pecking the
379 barrier was 17.5 (±*SE*: 1.4) seconds.

380

381 Overview of Cylinder task

382

383 During the first testing trial, 14 individuals detoured successfully (i.e., without touching the
384 transparent cylinder), 46 individuals detoured unsuccessfully (i.e., after touching the transparent
385 cylinder), 36 individuals touched the cylinder but did not detour, and 24 did not interact with nor
386 detoured around the cylinder (view Table S3 for an overview of the response outcomes of the
387 quails based on their social group and on sex). Among individuals who pecked the cylinder (n =
388 82), average time spent pecking the cylinder was 15.0 (±*SE*: 1.6) seconds.

389

390 Repeatability of response inhibition

391

There were 88 individuals who were not successful during either response inhibition task, 18 individuals who were successful during the Barrier task only, 13 individuals who were successful during the Cylinder task only, and only one individual who was successful during both response inhibition tasks.

For this analysis, only individuals who interacted (either by detouring around and/or by pecking the transparent barrier) during both tasks were included (n = 95). Results from the correlations indicated that both tasks were measuring different aspects of RI, as neither success between tasks (tetrachoric correlation coefficient: -0.250) nor time spent interacting with the transparent barrier/cylinder (Pearson correlation coefficient: r = -0.116, t = -1.129, df = 93, p = 0.262, Fig. 2) correlated between tasks.

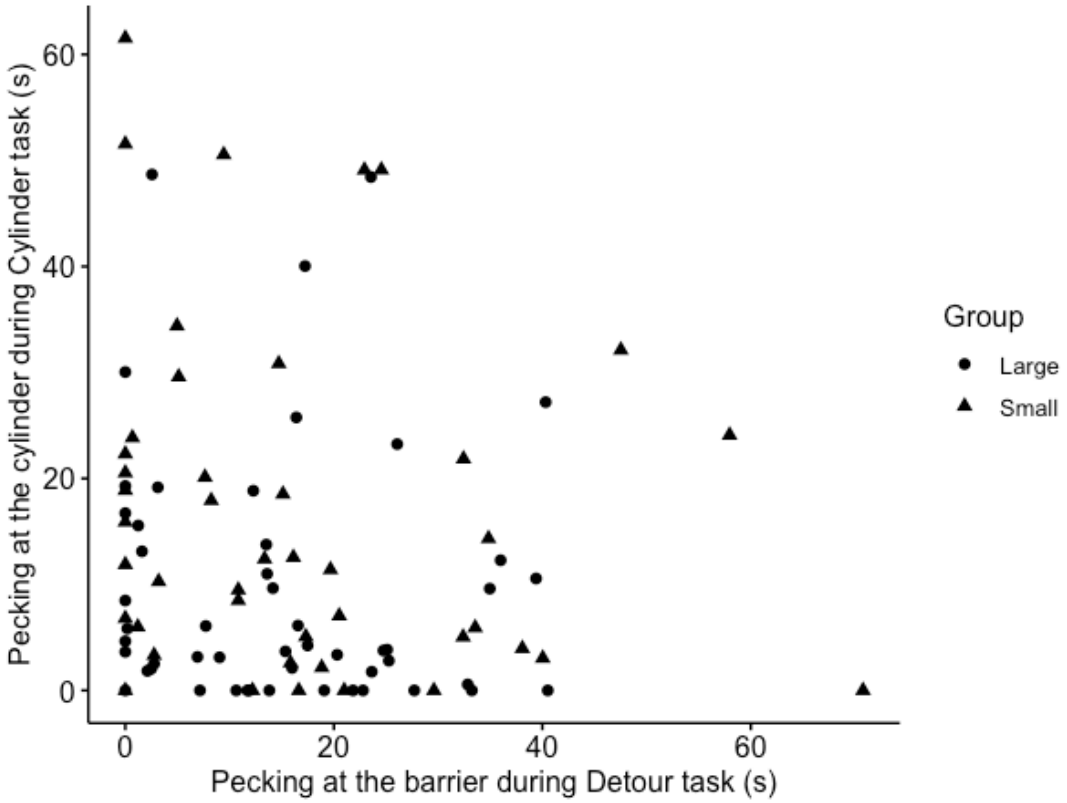

Figure 2. Time spent pecking at the transparent barrier during the Barrier task did not significantly correlate with the time spent pecking the cylinder during the Cylinder task in Japanese quails (Pearson correlation coefficient: r = -0.116, t = -1.129, df = 93, p = 0.262).

407

408 *Overview of impulsive aggression tasks*

409

410 Overview of Familiar Group task

411

412 All 120 individuals participated during the Familiar Group task. Quails gave on average 8.2
413 ± 16.7 pecks, received on average 8.2 ± 9.0 pecks, chased another individual for 1.0 ± 5.0 seconds,
414 escaped for 1.7 ± 4.4 seconds, and pushed others for 2.3 ± 6.0 seconds.

415

416 Overview of Unfamiliar Individual task

417

418 All 120 individuals participated during the Unfamiliar Individual task. Quails gave on
419 average 2.5 ± 5.3 pecks, received on average 2.5 ± 5.3 pecks, chased another individual for 1.8 ±
420 5.7 seconds, escaped for 3.3 ± 7.5 seconds, and pushed the other for 0.3 ± 0.9 seconds.

421

422 Repeatability of impulsive aggression

423

424 All individuals were included in the analysis, as they all participated in both tasks (n = 120).
425 Results of the PCA indicated that there was not a unique impulsive aggression aspect measured
426 during the tasks (Table 1). The first five components had an Eigen value higher than 1 and together
427 explained 78.1 % of the variance in the data. We found that both tasks investigated a different
428 impulsive aggression aspect, as measures related to each task loaded on different components
429 (Table 1). For the subsequent analyses, we used the individual scores obtained on the first two
430 components, as they best represent the aggression scores during each task (PC1 for Unfamiliar
431 Individual, PC2 for Familiar Group).

Table 1. PCA loadings for the measures on impulsive aggression in Japanese quails. Loadings considered important (i.e., whose contribution was higher than what was expected if all loadings were of equal weight) are indicated in bold.

		Dimensions				
		1	2	3	4	5
Eigen values		2.17	1.86	1.48	1.25	1.05
Variance explained (%)		21.7	18.6	14.8	12.5	10.5
Cumulative variance explained (%)		21.7	40.3	55.0	67.6	78.1
Familiar Group	Number of pecks given	0.044	**-0.737**	**0.440**	0.176	0.186
	Time spent chasing	0.148	**-0.644**	0.191	0.300	**0.530**
	Time spent pushing	-0.036	-0.264	**0.606**	0.070	**-0.626**
	Number of pecks received	0.254	**0.563**	**0.488**	0.020	0.310
	Time spent escaping	**0.483**	**0.509**	0.128	0.082	**0.346**
Unfamiliar Individual	Number of pecks given	**0.716**	-0.036	-0.271	**0.457**	-0.148
	Time spent chasing	**0.493**	-0.183	**-0.553**	**0.382**	-0.170
	Time spent pushing	**0.515**	0.310	**0.491**	0.279	-0.264
	Number of pecks received	**-0.624**	0.280	0.058	**0.599**	-0.010
	Time spent escaping	**-0.662**	0.211	-0.059	**0.574**	0.053

Relationship between response inhibition and impulsive aggression

We evaluated whether the different response inhibition behavioural measures were related to the aggression scores of the individuals. For these analyses, we used reduced datasets that included quails that interacted with the apparatuses (either by detouring successfully or by pecking at the apparatus) either during Barrier task (n = 119) for measures associated to that task or during the Cylinder task (n = 96) for measures associated to that task.

Aggression scores for the Unfamiliar Individual task (PC1) significantly correlated with the amount of time spent pecking on the cylinder during the Cylinder task. Individuals that spent more time pecking at the cylinder had a higher aggression score than individuals that spent less time pecking at the cylinder (Pearson coefficient correlation: r = 0.221, t = 2.199, $d.f.$ = 94, p = 0.030; Fig. 3). Unsuccessful individuals tended to have higher aggression scores in in comparison to successful individuals (t = 2.072, $d.f.$ = 18.08, p = 0.053). Response inhibition measures assessed during the Barrier task did not significantly correlate with the PC1 aggression scores for that task (Success during the Barrier task: t = -0.090, $d.f.$ = 38.55, p = 0.929; Time spent pecking the transparent barrier: Pearson coefficient correlation: r = -0.018, t = -0.197, $d.f.$ = 117, p = 0.844).

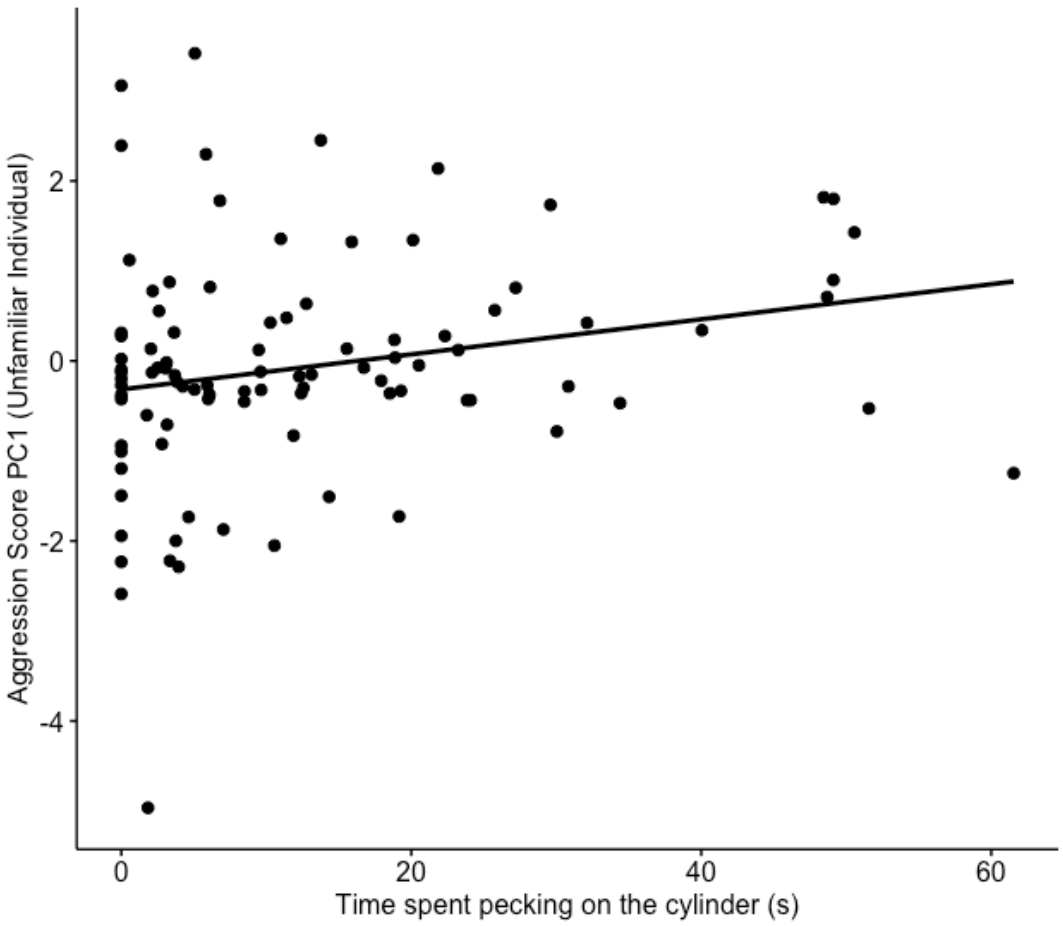

Figure 3. Time spent pecking on the cylinder during the Cylinder task significantly predicted the aggression scores obtained during the Unfamiliar Individual task (Pearson coefficient correlation: $r = 0.221$, $t = 2.199$, $d.f. = 94$, $p = 0.030$).

Aggression scores for the Familiar Group task (PC2) were significantly linked to the success during the Barrier task, with individuals that successfully detoured during the Barrier task being more aggressive than individuals that were unsuccessful ($t = 2.757$, $d.f. = 20.79$, $p = 0.012$; Fig. 4). No other response inhibition measures significantly influenced the PC2 aggression scores (Success during the Cylinder task: $t = 1.588$, $d.f. = 20.54$, $p = 0.128$; Time spent pecking the transparent barrier: $t = -1.757$, $d.f. = 117$, $p = 0.082$; Time spent pecking the transparent cylinder: $t = -1.645$, $d.f. = 94$, $p = 0.103$).

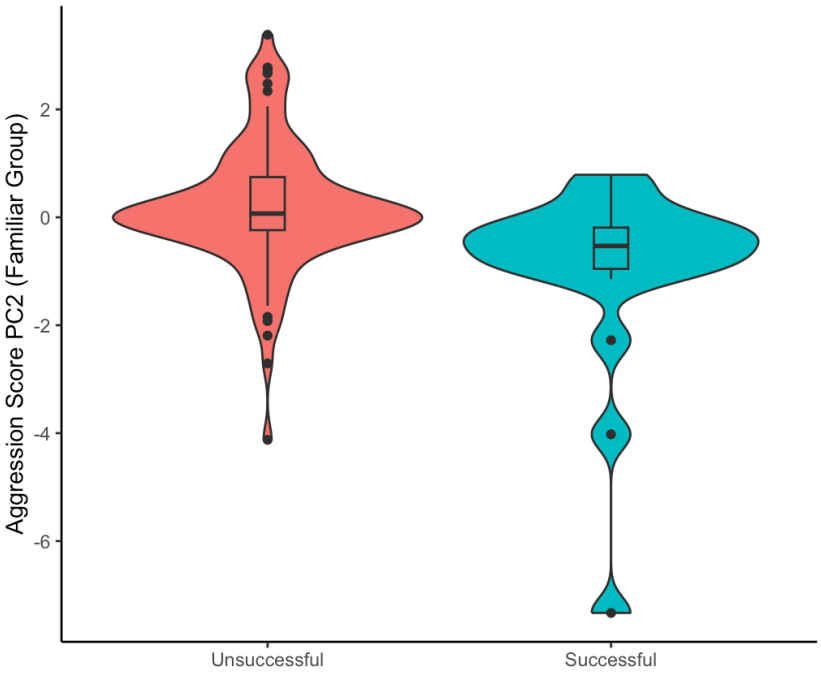

Figure 4. Success during the Barrier task significantly predicted the aggression scores PC2 obtained during the Familiar Group task. Note that for this aggression score, negative scores indicate more aggressive behaviours than positive scores.

Influence of group size on response inhibition and impulsive aggression

<u>Influence of group size on response inhibition</u>

Given the lack of contextual repeatability, we evaluated the effects of Group Size, Sex, and Body Weight on success and on the time spent interacting with the transparent barrier/cylinder for both Response Inhibition tasks separately.

Only individuals who interacted (either by detouring around and/or by pecking the transparent barrier) were included for the analyses on success (n = 119 for the Barrier task, n = 96 for the Cylinder task; see Table S3 for overview of number). Success during the Barrier task and success during the Cylinder task were not explained by Group Size, Sex, nor Body Weight (Table 2).

Table 2. Factors evaluated to explain success (i.e., successfully detouring without touching the barrier or not) and time spent pecking during the Barrier task and during the Cylinder task. Significant factors are indicated in bold.

	Barrier task						Cylinder task					
	Success			Time spent pecking			Success			Time spent pecking		
	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*	χ^2	*d.f.*	*p*
Group Size	0.732	1	0.392	1.608	1	0.205	0.421	1	0.517	**6.256**	**1**	**0.012***
Sex	3.725	1	0.054	0.063	1	0.802	1.410	1	0.235	3.719	1	0.054
Body Weight	1.298	1	0.255	**5.835**	**1**	**0.016***	0.002	1	0.965	**14.268**	**1**	**< 0.001***

Only individuals who pecked at the transparent barrier were included for the analyses on time spent pecking (n = 100 for the Barrier task, n = 82 for the Cylinder task; see Table S3 for overview of number). Time spent pecking at the transparent barrier during the Barrier task was not explained by Group Size (Fig. 5) nor by Sex (Table 2). However, Body Weight significantly influenced time spent pecking at the transparent barrier, with individuals with a lower weight spending more time interacting with the barrier than individuals with a higher weight (Fig. S4). Group Size significantly influenced the time spent pecking at the transparent cylinder during the Cylinder task, with individuals in the Large group spending less time pecking at the transparent cylinder than individuals in the Small group (Time spent pecking at the transparent cylinder $M \pm SE$: Large group: 11.64 ± 1.92 s, Small group: 18.70 ± 2.50 s; Table 2; Fig. 5). Body Weight also significantly influenced time spent pecking at the cylinder, with individuals with a higher weight spending more time interacting with the cylinder than individuals with a lower weight (Figure S4). There was no significant difference between males and females (Table 2).

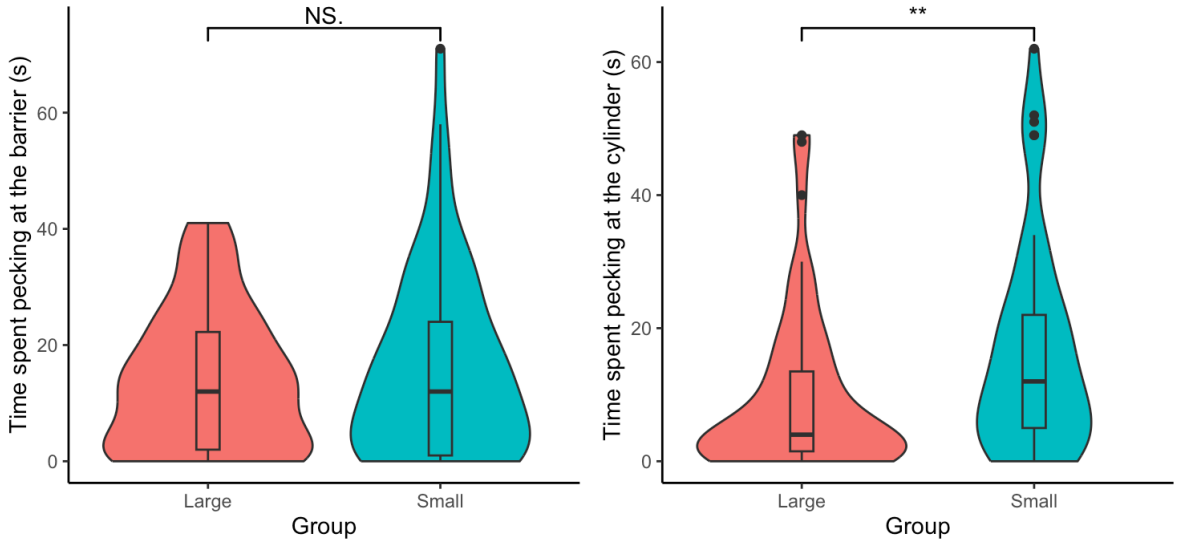

Figure 5. Left. Time spent pecking at the transparent barrier during the Barrier task did not significantly differ between social groups (χ^2 = 1.608, *d.f.* = 1, p = 0.205). Right. Quails in the Large group spent significantly less time pecking at the transparent cylinder than quails in the Small group (χ^2 = 6.256, *df* = 1, p = 0.012).

<u>Influence of group size on impulsive aggression</u>

Given the lack of repeatability in impulsive aggression between contexts, we evaluated the effects of Group Size, Sex, Body Weight on the aggressive scores for both impulsive aggression tasks separately (n = 120 quails).

Aggression scores for the Unfamiliar Individual task (PC1) were not explained by Group Size (χ^2 = 0.001, *d.f.* = 1, p = 0.973; Fig. 6) nor by Body Weight (χ^2 = 1.178, *d.f.* = 1, p = 0.278). However, male quails had a significantly higher aggression score than female quails (Females: -0.28 ± 1.54, Males: 0.28 ± 1.38; χ^2 = 4.318, *d.f.* = 1, p = 0.038; Figure S5).

Aggression scores for the Familiar Group task (PC2) were not explained by Group Size (χ^2 = 0.183, *d.f.* = 1, p = 0.670; Fig. 6). However, males were significantly more aggressive than females (Females: 0.35 ± 0.97, Males: -0.35 ± 1.61; χ^2 = 8.554, *d.f.* = 1, p = 0.004; Figure S5), and quails with a higher weight were significantly more aggressive than quails with a lower weight (χ^2 = 6.002, *d.f.* = 1, p = 0.016; Figure S6).

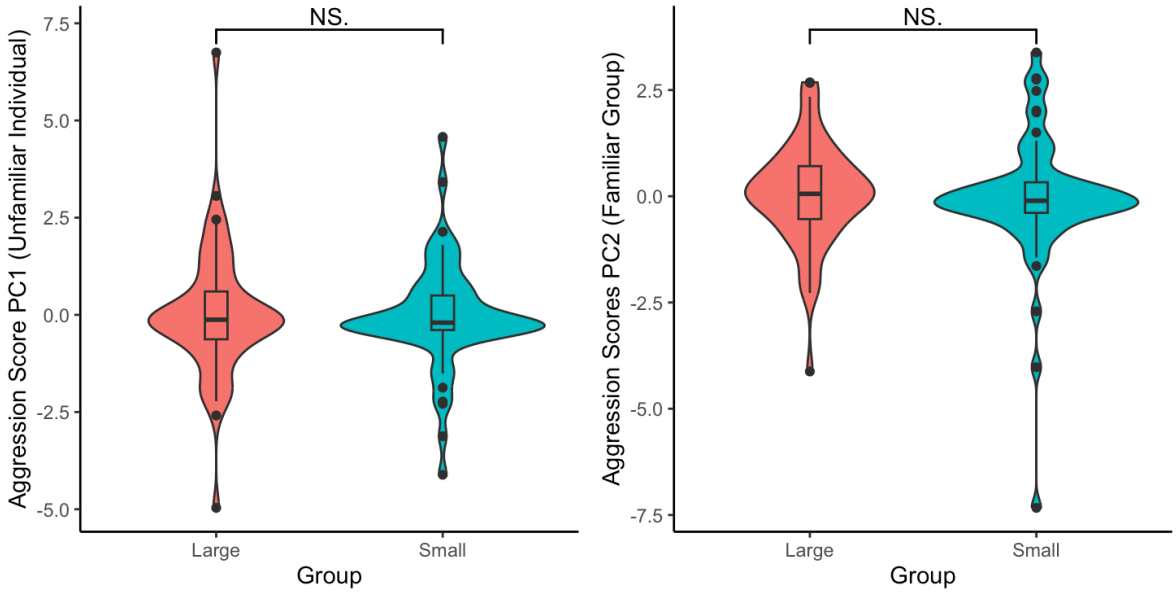

Figure 6. There were no significant differences in aggression scores between social groups a) during the Unfamiliar Individual (χ^2 = 0.001, *d.f.* = 1, p = 0.973), and b) during the Familiar Group task (χ^2 = 0.183, *d.f.* = 1, p = 0.670). *Note: for the axis PC2, more aggressive individuals have a negative score.

538 **5. Discussion**

539

540 The main goals of this study were threefold: (A) to examine the link between response
541 inhibition and impulsive aggression at an individual level, and (B) to assess whether group size
542 during early-life environment influenced the development of response inhibition and (C) impulsive
543 aggression using juvenile Japanese quails. We found (A) some significant correlations between
544 measures of response inhibition and impulsive aggression, providing some limited support to the
545 theoretical model linking both concepts. We also found (B) evidence that early-life social
546 environment indeed shapes the development of response inhibition, as quails raised in smaller
547 social groups spent more time repeating an inefficient action (i.e., pecking at the cylinder) than
548 those raised in larger social groups. However, contrary to what we expected, (C) we found no
549 evidence that early-life social environment influenced the development of impulsive aggression.

550

551 *Relationship between response inhibition and impulsive aggression*

552

553 In juvenile Japanese quails, we found some evidence that response inhibition was
554 significantly linked to impulsive aggression at an individual level. More specifically, increased
555 perseveration on an unrewarded action towards an unfamiliar object (i.e., time spent pecking at the
556 transparent cylinder) was significantly correlated to increased aggression towards unfamiliar
557 individuals. This result may suggest that individuals tend to interact aggressively towards novelty,
558 be it an object or an individual. The link between higher aggression and lower inhibition has also
559 been found in previous observational studies in mammals (12,13,71,72), as suggested by theoretical
560 models (14). In primates, aggressive individuals with low response inhibition are thought to have
561 an advantage to access and retain food resources (73). A similar observation was found in
562 Australian magpies, where individuals involved in aggressive interactions (both initiating and
563 receiving) performed worse in an associative learning task, possibly due to lower time and/or

564 energy to attend the task (74). While the authors did not test inhibition directly, previous work in
565 that study population has found a significant correlation between inhibition (as assessed with a
566 cylinder) and associative learning (31). Together, these results highlight how the social environment,
567 its dynamics, and cognitive performance are tightly linked with one another.

568 Interestingly, we also found that individuals that successfully fully cancelled a discrete action
569 (i.e., by detouring without pecking at the transparent barrier) had significantly increased levels of
570 aggression towards familiar individuals. This result goes in the opposite direction to what we
571 predicted, and contrast with previous studies that investigated the link between inhibition and
572 aggression. One potential explanation for this seemingly contradictory result could be by viewing
573 the adaptive significance of aggression (3). Indeed, aggressive individuals are more likely to initiate
574 contests and to subsequently win them (75), which potentially gives them higher fitness payoffs.
575 Hence, individuals with better response inhibition may use the most advantageous coping strategy
576 in response to the social environment demands.

577 These contradictory results may suggest three things: a) that the mechanisms involved during
578 the cancellation of an action depend on whether the individuals are already engaged in the action
579 they need to inhibit, and/or b) that the tasks are not assessing response inhibition or aggression,
580 but rather pecking tendency (whether it is towards an object or an individual), and/or c) that
581 response inhibition and aggression depends highly on the social context.

582 Indeed, when examining in detail the requirements of both the Detour and the Cylinder tasks,
583 individuals may have to inhibit two actions: first, the prepotent response of going directly at the
584 food, thus pecking at the transparent barrier, and second, the repetitive action of pecking along the
585 barrier if they failed to inhibit the first action (76). The lack of correlations between the different
586 measures of the two response inhibition tasks occurred despite both tasks requiring individuals to
587 detour around a transparent barrier (47) and despite both tasks having a similar "go" stimulus (i.e.,
588 the visible food reward) and a similar "stop" stimulus (i.e., the transparent barrier) present at the
589 same time (76). Rather, the characteristics of the stop stimulus itself, such as the shape (e.g., (77))

590 and the motor action required to successfully detour, might influence the individual's response: the
591 transparent barrier in the Barrier task is large and requires individuals to move their entire body
592 around it, whereas the transparent barrier in the Cylinder task is small and requires individuals to
593 place their head through the openings (55). Even when carefully choosing tasks purporting to
594 assess the same aspect of response inhibition, our results suggest that response inhibition is multi-
595 faceted and context-dependent (55,78–80). Not only the nature of the action to be stopped, but
596 the overall task context in which actions need to be stopped could thus involve different
597 mechanisms.

598 Alternatively, training differences and learning may explain the lack of repeatability in
599 performance we observed. For the Barrier task, individuals were trained to go around the opaque
600 barrier and might have learned the detouring solution (81), explaining the high success of
601 individuals in this task during the first transparent trial. In comparison, quails were not trained with
602 an opaque cylinder during the Cylinder task. Hence, quails had to not only inhibit pecking at the
603 transparent cylinder, but also to successfully "solve" the task (i.e., learning the detouring solution
604 (55,56,82). This may also explain why the number of quails who successfully detoured during the
605 Cylinder task was lower than during the Barrier task. Thus, the cognitive processes involved during
606 both tasks may have differed. Additionally, unlike what was found with pheasants (78), there was
607 no evidence that Japanese quails used their previous experience of detouring around a transparent
608 barrier, as detouring success and time spent pecking during the Cylinder task did not improve from
609 during the Barrier task, supporting once more the idea that response inhibition is context-
610 dependent. Understanding how and why exactly there is such a low reliability between tasks is
611 beyond the scope of the current study but warrants further investigation (83).

612 Similarly, the contradictory results we obtained regarding the link between aggression and
613 response inhibition may be due to the contextual differences between both aggression tasks.
614 Individuals' behaviour may differ when they are in the presence of familiar and of unfamiliar
615 individuals (e.g., (84), "winner and loser effects" – (85), "dear enemy" hypothesis – as reviewed by

616 (86); but see (44) for a counter-example with male Japanese quails). Because agonistic interactions
617 between individuals can be costly, familiarity is thought to play a key role in the formation of
618 hierarchies, both within species (87) and between species (88). For this reason, aggression is usually
619 reduced within the group once hierarchies are established (3). Yet, the lack of repeatability in
620 individual aggression scores is surprising as it goes against the idea of aggression as a personality
621 trait (e.g., (89–91)). Instead, this result suggests that aggression is subject to high intra-individual
622 variation (92). Plasticity in aggressive responses could depend on the outcome of past antagonistic
623 interactions (93) and on the traits of the other individual, such as status signals or signals of fighting
624 ability (reviewed by (94)) or use social information to assess the costs of engaging in an antagonistic
625 behaviour towards another individual (95).

626 Regardless of the lack of correlations in aggressive behaviours between tasks, we found that
627 behaviours associated with individuals that were the target of aggressive behaviours (as assessed by
628 the time spent escaping and the number of pecks received) were less likely to engage in aggressive
629 behaviours (as assessed by the time spent chasing and pushing, and the number of pecks given)
630 within each task context. While we did not assess hierarchical dominance directly, this behavioral
631 trend suggests differences in social rank between individuals. Hierarchical dominance has been
632 found to influence, or even suppress, the expression of certain cognitive abilities and to affect brain
633 morphology ((96–99), but see (100)), and may contribute to the duality in our results linking
634 response inhibition and aggression.

635 The social context of the task may also explain this duality in our results. Aggression was
636 assessed in a group context whereas response inhibition was assessed in a solitary context. The
637 social context may exert different inhibitory pressures on individuals. For instance, in the presence
638 of a more dominant or more aggressive group member, an individual might inhibit going towards
639 the food reward to reduce the risk of receiving directed aggression (101). However, when alone,
640 that same individual may or may not have lower response inhibition levels towards the food

641 rewards. This possibility suggests, once again, the importance of accounting for the social context
642 when evaluating impulsivity generally.
643
644 *Influence of early-life social environment on response inhibition and impulsive aggression*
645
646 The importance of the social environment on the development of cognition has been
647 suggested in many species (20,21,23,30,74,102). More specifically, social group size, a key
648 component of the social environment, has been found to correlate with higher levels of inhibition
649 in hyenas (32) and in Australian magpies (31), but not in guppies (34,103) nor in horses (104). Here,
650 we found that quails raised in larger groups inhibited a repetitive unrewarded action (i.e., pecking
651 at the transparent cylinder) faster, on average, than quails raised in smaller groups. This result aligns
652 with those from previous studies evaluating intraspecific variability in response inhibition using the
653 Cylinder task on Australian magpies and on hyenas (31,32), and support what we predicted.
654 However, we found no significant effect of social group size on the overall success rate for both
655 tasks, nor on the time spent pecking on the transparent barrier during the Barrier task. As we
656 previously mentioned, both tasks may not measure the same aspect of response inhibition or may
657 measure pecking tendency in one or the other. Therefore, the influence of the social environment
658 might be mediated differently depending on which aspect of response inhibition is considered.
659 Early-life social environmental conditions have strong effects on aggressive behaviour in
660 many species ((42,105–107)), with usually a decrease in aggression and higher social tolerance as
661 group size increases (e.g., (37,40,49)). Unlike previous research, we found no significant difference
662 in levels of aggression between groups during our aggression tasks. This lack of significant results
663 might be caused by the increase in density associated with the increase in group size, as individuals
664 of both conditions were given the same size enclosure. Higher population density has been
665 associated with higher aggression levels (e.g., lizards – (108)), as individuals switch to a resource
666 defence strategy (36,37). Yet, unlike group-living species in the wild that may encounter limited

667 amount of food, our quails were provided with *ad lib* access to food (outside of food restriction
668 procedures). Resource availability and competition for food should have been the same for both
669 groups, independently of group density and size. In such circumstances, theoretical models suggest
670 that aggression levels should be low for both groups (109), and that individuals should be socially
671 tolerant (i.e., tolerance hypothesis; (110)). Disentangling the effects of group size and group density
672 on aggression as well as on response inhibition is a promising next step.

673 Social group size is not the only aspect of social complexity. Group dynamics and stability,
674 as well as the nature of the relationships between group members, are other important aspects that
675 contribute to the variation in social complexity within and between groups (29,50). Further
676 investigation is needed to determine which aspects of the social life influence the development of
677 aggression and of response inhibition (111).

678

679 *Intra- and inter-individual variation in response inhibition and in impulsive aggression*

680

681 Research on non-human animals had, until recently, tried to minimize the importance of
682 inter-individual variation in cognition (112,113). Now, there is a general effort in pinpointing which
683 factors may underlie individual differences in cognition generally (114,115). Despite controlling the
684 early-life physical and social environment of our quails, as well as the acclimatation, habituation
685 and testing procedures, we still observed pronounced individual differences in the success and time
686 spent performing a repetitive unrewarded action during the response inhibition tasks and in the
687 aggressive behaviours during the impulsive aggression tasks that were not explained by the
688 difference in group size.

689 These inter-individual differences in response inhibition and impulsive aggression may be
690 due to differences in motivation and attention (116–118). Some individuals might have greater
691 motivation to participate during the tasks due and interact with apparatuses and/or other
692 individuals due to high exploration/low neophobia (119–123) or due to higher basal energetic

693 demands than others (124). The latter could explain why we found an effect of body weight on
694 time spent pecking at the transparent barrier (125). However, given that the direction of that effect
695 was opposite for both response inhibition tasks, we cannot confirm this explanation as to why or
696 how it might be the case. Additionally, in group-living domestic species, more aggressive individuals
697 often outcompete less aggressive individuals for limited resources and have a higher weight as a
698 result (e.g., (126)), which support our findings on heavier individuals being more aggressive towards
699 familiar individuals. Concurrently, being aggressive might be less costly and more beneficial for
700 larger individuals, as they are more likely to physically outcompete smaller ones.

701 Cognitive abilities and personality traits have also been known to differ between females and
702 males in some species (127–131). Despite not finding any differences in response inhibition
703 between males and females, we found that males were significantly more aggressive than females
704 (44,132–136). We found such a sex difference in aggression when the quails were between 5- and
705 6-weeks old, at the onset of sexual maturity in Japanese quails (between 6- to 8-weeks old). Little
706 is known regarding aggression in immature, non-sexually active or castrated quails, but it is usually
707 assumed they have lower aggressive tendencies than sexually mature ones (43,137). Hence, inter-
708 individual variation in aggression that we observed might also be due to inter-individual differences
709 in reaching sexual maturity, despite keeping all other parameters constant for all individuals
710 (photoperiod, temperature, food). Similarly, in our study, response inhibition was assessed in
711 juvenile quails. Previous research on other species show that inhibition follows a developmental
712 period (138,139). While there has not been a study directly investigating the development of
713 inhibition in Japanese quails, domestic chicks (*Gallus gallus*), a closely related precocious species
714 who follows a similar developmental pattern (both species reaching maturity at six to eight weeks
715 old), can already detour when they are two weeks old (138). As quails were at least three weeks old
716 at the time of testing, we expected them to have fully completed the developmental period in
717 response inhibition, but that assumption might be erroneous. Hence, the lack of consistent

correlations we found between measures in response inhibition and aggression may be due to one or both traits not being fully developed when assessed.

Finally, a large inter-individual variation in inhibiting a behavioral response might indicate a lack of strong selection on a given trait (e.g.,(140)), or alternatively, that it might be favored in certain environments or contexts, but not in others (141,142). Similar arguments can be made to explain intra-individual variation in response inhibition and in aggression. Indeed, the lack of repeatability in response inhibition at an individual level may suggest that individuals are flexible in their cognitive ability and in their social behavior, depending on the context. For instance, impulsive actions might be more adaptive in an unstable or unpredictable environment or when travel time between resources increase (143). Understanding in which contexts extreme values of response inhibition might be favored and why such variation in cognitive traits and in personality exists within the population is a topic that warrants further investigation.

6. Conclusion

In summary, our study provides one of the first experimental evidence that early-life social environment can influence the development of response inhibition. We also experimentally showed that certain aspects of aggression are linked to deficits in response inhibition, especially regarding perseverating in performing an unrewarded action towards novelty (objects and/or individual). Hence, our study shed some light regarding the mechanisms underlying impulsive aggression using Japanese quails. Yet, contrary to what was expected based on previous literature, group size, a key aspect of early-life social environment, did not influence aggression in our quails, despite it influencing certain aspects of response inhibition (the same ones that were linked to aggression). Aggression is a multifaceted and complex behaviour that involves multiple processes (144,145). Thus, despite controlling the physical and social environment, intrinsic factors such as genetics, motivation, non-social personality traits (i.e., neophobia, exploration, activity), and the ability to get social information might explain inter-individual variability in aggression that we

744 witnessed and mediate the link between response inhibition and aggression. Regarding the
745 influence of sociality on the emergence of aggressive behaviors, other social factors, such as group
746 dynamics and stability, and further research is warranted to fully understand how sociality, response
747 inhibition, and aggression relate to one another.

Acknowledgements

We thank the staff of the Wildlife Rescue Centre Ostend for general project support and Harry Suter for insightful discussions and comments on the draft of the manuscript. We also thank two anonymous reviewers for their critical and insightful comments.

Ethical Statement

The experiment was performed in accordance with the Association for the Study of Animal Behaviour ethical guidelines under permission of the ethical committee of animal experimentation (VIB Site Ghent, Universiteit Gent): EC2022-005.

Funding Statement

Research support was provided by a BOF postdoc fellowship (#BOF.PDO.2021.0035.01) to AV, a FWO (Flemish Research Foundation) PhD Fellowship grant (No. 11F0823N) to AD, a CSC (China Scholarship Council) PhD Scholarship (No. 202106180023) to WZ, a Marie Skłodowska-Curie Action fellowship ('UrbanCog', project number: 101062662) under the European Union's Horizon Europe Programme to CAT, a FWO (Flemish Research Foundation) PhD Fellowship grant (No. 11P3G24N) to SK, an ERC Consolidator grant (European Union's Horizon 2020 research and innovation programme, grant agreement No 769595) to FV, and a Methusalem Project 01M00221 (Ghent University) to FV, LL, and AM.

Data Accessibility

All videos of the experiment can be found on Zenodo (https://zenodo.org/records/13361318). R codes and extracted data from BORIS can be found on OSF (https://osf.io/2b5uy/).

Competing Interests

None to declare.

Author contributions

Based on the CRediT system, the contributions of the authors are as follow: 'Conceptualization' – AV, LL, FV; 'Data curation' – AV, KW; 'Formal analysis' – AV; 'Funding acquisition' – AV, AD, WZ, CAT, AM, LL, FV; 'Investigation' – AV, KW, RA, AD, WZ, CAT, SK, LL, FV, 'Methodology' – AV, KW, RA, AD, LL, FV; 'Project administration' – AV, FV; 'Resources' – FV, 'Supervision' – AV, LL, FV; 'Validation' – AV, KW, SK, CAT; 'Visualization' – AV, 'Writing—original draft' – AV, and 'Writing—review & editing' – AV, KW, RA, AD, WZ, CAT, AM, LL, FV. In the Methods section, we followed the MERIT system (Nakagawa et al. 2023).

References

1. Hamilton WD. Geometry for the selfish herd. J Theor Biol. 1971 May 1;31(2):295–311.
2. Barratt ES, Stanford MS, Dowdy L, Liebman MJ, Kent TA. Impulsive and premeditated aggression: a factor analysis of self-reported acts. Psychiatry Res. 1999 May 31;86(2):163–73.
3. Holekamp KE, Strauss ED. Aggression and dominance: an interdisciplinary overview. Curr Opin Behav Sci. 2016 Dec;12:44–51.
4. Breuer J, Scharkow M, Quandt T. Sore losers? A reexamination of the frustration–aggression hypothesis for colocated video game play. Psychol Pop Media Cult. 2015;4(2):126–37.
5. Osumi T, Nakao T, Kasuya Y, Shinoda J, Yamada J, Ohira H. Amygdala dysfunction attenuates frustration-induced aggression in psychopathic individuals in a non-criminal population. J Affect Disord. 2012 Dec 15;142(1):331–8.
6. Tremblay RE. Developmental origins of chronic physical aggression: An international perspective on using singletons, twins and epigenetics. Eur J Criminol. 2015 Sep;12(5):551–61.
7. Chester DS. Aggression as successful self-control. Soc Personal Psychol Compass. 2024 Feb;18(2):e12832.
8. Verbruggen F, Logan GD. Response inhibition in the stop-signal paradigm. Trends Cogn Sci. 2008 Nov 1;12(11):418–24.
9. Bari A, Robbins TW. Inhibition and impulsivity: Behavioral and neural basis of response control. Prog Neurobiol. 2013 Sep;108:44–79.
10. Diamond A. Executive Functions. Annu Rev Psychol. 2013 Jan 3;64(Volume 64, 2013):135–68.
11. Homberg JR, Pattij T, Janssen MCW, Ronken E, De Boer SF, Schoffelmeer ANM, et al. Serotonin transporter deficiency in rats improves inhibitory control but not behavioural flexibility: Serotonin transporter knockout and impulse control. Eur J Neurosci. 2007 Sep 25;26(7):2066–73.
12. Gobbo E, Zupan Šemrov M. Dogs Exhibiting High Levels of Aggressive Reactivity Show Impaired Self-Control Abilities. Front Vet Sci. 2022 Mar 24;9:869068.
13. Overduin-de Vries AM, Vermande MM, Hessen DJ, Sterck EHM. The ability to inhibit impulses is related to social behavior in long-tailed macaques. Am J Primatol. 2024 Feb;86(2):e23587.
14. Vigil-Colet A, Codorniu-Raga MJ. Aggression and inhibition deficits, the role of functional and dysfunctional impulsivity. Personal Individ Differ. 2004 Nov;37(7):1431–40.
15. Hoaken PNS, Shaughnessy VK, Pihl R o. Executive cognitive functioning and aggression: Is it an issue of impulsivity? Aggress Behav. 2003;29(1):15–30.
16. Van Den Bergh F, Spronk M, Ferreira L, Bloemarts E, Groenink L, Olivier B, et al. Relationship

820 of delay aversion and response inhibition to extinction learning, aggression, and sexual
821 behaviour. Behav Brain Res. 2006 Nov;175(1):75–81.
822 17. Bacqué-Cazenave J, Bharatiya R, Barrière G, Delbecque JP, Bouguiyoud N, Di Giovanni G, et
823 al. Serotonin in Animal Cognition and Behavior. Int J Mol Sci. 2020 Feb 28;21(5):1649.
824 18. Miyazaki K, Miyazaki KW, Doya K. The Role of Serotonin in the Regulation of Patience and
825 Impulsivity. Mol Neurobiol. 2012 Apr 1;45(2):213–24.
826 19. Puiu AA, Wudarczyk O, Goerlich KS, Votinov M, Herpertz-Dahlmann B, Turetsky B, et al.
827 Impulsive aggression and response inhibition in attention-deficit/hyperactivity disorder and
828 disruptive behavioral disorders: Findings from a systematic review. Neurosci Biobehav Rev.
829 2018 Jul 1;90:231–46.
830 20. Foraita M, Howell T, Bennett P. Environmental influences on development of executive
831 functions in dogs. Anim Cogn. 2021 Jul;24(4):655–75.
832 21. Johnson D, Policelli J, Li M, Dharamsi A, Hu Q, Sheridan MA, et al. Associations of Early-Life
833 Threat and Deprivation With Executive Functioning in Childhood and Adolescence: A
834 Systematic Review and Meta-analysis. JAMA Pediatr. 2021 Nov 1;175(11):e212511.
835 22. Kotrschal A, Taborsky B. Environmental Change Enhances Cognitive Abilities in Fish. PLOS
836 Biol. 2010 Apr 6;8(4):e1000351.
837 23. Nettle D, Bateson M. Adaptive developmental plasticity: what is it, how can we recognize it and
838 when can it evolve? Proc R Soc B Biol Sci. 2015 Aug 7;282(1812):20151005.
839 24. Triki Z, Zhou T, Argyriou E, Sousa De Novais E, Servant O, Kolm N. Social complexity affects
840 cognitive abilities but not brain structure in a Poecilid fish [Internet]. Animal Behavior and
841 Cognition; 2023 Aug [cited 2024 Feb 7]. Available from:
842 http://biorxiv.org/lookup/doi/10.1101/2023.08.20.554009
843 25. Dunbar RIM, Shultz S. The Social Role of Inhibition in Primates and Other Animals [Internet].
844 bioRxiv; 2022 [cited 2024 Dec 19]. p. 2020.10.26.354852. Available from:
845 https://www.biorxiv.org/content/10.1101/2020.10.26.354852v3
846 26. Alcala RS, Caliva JM, Flesia AG, Marin RH, Kembro JM. Aggressive dominance can decrease
847 behavioral complexity on subordinates through synchronization of locomotor activities.
848 Commun Biol. 2019 Dec;2(1):467.
849 27. Papageorgiou D, Farine DR. Group size and composition influence collective movement in a
850 highly social terrestrial bird. Díaz-Muñoz SL, Rutz C, Díaz-Muñoz SL, editors. eLife. 2020 Nov
851 10;9:e59902.
852 28. Byrne RW, Whiten A. Cognitive Evolution in Primates: Evidence from Tactical Deception.
853 Man. 1992;27(3):609–27.

29. Kappeler PM. A framework for studying social complexity. Behav Ecol Sociobiol. 2019 Jan;73(1):13.
30. Croney CC, Newberry RC. Group size and cognitive processes. Appl Anim Behav Sci. 2007 Mar;103(3–4):215–28.
31. Ashton BJ, Ridley AR, Edwards EK, Thornton A. Cognitive performance is linked to group size and affects fitness in Australian magpies. Nature. 2018 Feb;554(7692):364–7.
32. Johnson-Ulrich L, Holekamp KE. Group size and social rank predict inhibitory control in spotted hyaenas. Anim Behav. 2020 Feb;160:157–68.
33. Amici F, Aureli F, Call J. Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. Curr Biol. 2008 Sep 23;18(18):1415–9.
34. Lucon-Xiccato T, Montalbano G, Reddon AR, Bertolucci C. Social environment affects inhibitory control via developmental plasticity in a fish. Anim Behav. 2022 Jan;183:69–76.
35. Færevik G, Andersen IL, Jensen MB, Bøe KE. Increased group size reduces conflicts and strengthens the preference for familiar group mates after regrouping of weaned dairy calves (Bos taurus). Appl Anim Behav Sci. 2007 Dec;108(3–4):215–28.
36. Estevez I, Newberry RC, Keeling LJ. Dynamics of aggression in the domestic fowl. Appl Anim Behav Sci. 2002 Apr 2;76(4):307–25.
37. Estevez I, Keeling LJ, Newberry RC. Decreasing aggression with increasing group size in young domestic fowl. Appl Anim Behav Sci. 2003 Dec;84(3):213–8.
38. Syarifuddin S, Kramer DL. The effect of group size on space use and aggression at a concentrated food source in blue gouramis, Trichogaster trichopterus (Pisces: Belontiidae). Environ Biol Fishes. 1996 Jul 1;46(3):289–96.
39. Turner SP, Horgan GW, Edwards SA. Effect of social group size on aggressive behaviour between unacquainted domestic pigs. Appl Anim Behav Sci. 2001 Nov;74(3):203–15.
40. Pagel M, Dawkins MS. Peck orders and group size in laying hens: `futures contracts' for non-aggression. Behav Processes. 1997 Apr 1;40(1):13–25.
41. Van Loo PLP, Mol JA, Koolhaas JM, Van Zutphen BFM, Baumans V. Modulation of aggression in male mice: influence of group size and cage size. Physiol Behav. 2001 Apr 1;72(5):675–83.
42. Haller J, Harold G, Sandi C, Neumann ID. Effects of Adverse Early-Life Events on Aggression and Anti-Social Behaviours in Animals and Humans. J Neuroendocrinol. 2014 Oct;26(10):724–38.
43. Caliva JM, Falkenburger Melleu F, Marino-Neto J, Marin RH, Kembro JM. Expression of aggressiveness modulates mesencephalic c-fos activation during a social interaction test in

Japanese quail (Coturnix japonica). Behav Brain Res. 2019 Jul;367:221–9.
44. Pellegrini S, Condat L, Caliva JM, Marin RH, Guzman DA. Can Japanese quail male aggressions toward a female cagemate predict aggressiveness toward unknown conspecifics? Livest Sci. 2019 Apr;222:65–70.
45. Mills AD, Crawford LL, Domjan M, Faure JM. The behavior of the japanese or domestic quail Coturnix japonica. Neurosci Biobehav Rev. 1997;21(3):261–81.
46. Millman ST, Duncan IJ, Widowski TM. Male broiler breeder fowl display high levels of aggression toward females. Poult Sci. 2000 Sep;79(9):1233–41.
47. Kabadayi C, Bobrowicz K, Osvath M. The detour paradigm in animal cognition. Anim Cogn. 2018 Jan;21(1):21–35.
48. van Horik JO, Langley EJG, Whiteside MA, Laker PR, Beardsworth CE, Madden JR. Do detour tasks provide accurate assays of inhibitory control? Proc R Soc B Biol Sci. 2018 Mar 28;285(1875):20180150.
49. Samarakone TS, Gonyou HW. Domestic pigs alter their social strategy in response to social group size. Appl Anim Behav Sci. 2009 Oct;121(1):8–15.
50. Schweitzer C, Lévy F, Arnould C. Increasing group size decreases social bonding in young Japanese quail, Coturnix japonica. Anim Behav. 2011 Mar;81(3):535–42.
51. Cheng KM, Bennett DC, Mills AD. The Japanese Quail. In: The UFAW Handbook on the Care and Management of Laboratory and Other Research Animals [Internet]. John Wiley & Sons, Ltd; 2010 [cited 2025 Apr 24]. p. 655–73. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1002/9781444318777.ch42
52. Lukanov H, and Pavlova I. Domestication changes in Japanese quail (Coturnix japonica): a review. Worlds Poult Sci J. 2020 Oct 1;76(4):787–801.
53. Friard O, Gamba M. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol. 2016;7(11):1325–30.
54. McHugh ML. Interrater reliability: the kappa statistic. Biochem Medica. 2012 Oct 15;22(3):276–82.
55. Vernouillet AAA, Stiles LR, Andrew McCausland J, Kelly DM. Individual performance across motoric self-regulation tasks are not correlated for pet dogs. Learn Behav. 2018 Dec;46(4):522–36.
56. Willcox K, Vernouillet A, Lens L, Verbruggen F. Early-life group size influences response inhibition, but not the learning of it, in Japanese quails. Learn Behav [Internet]. 2024 Sep 19 [cited 2024 Nov 21]; Available from: https://link.springer.com/10.3758/s13420-024-00643-2
57. Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, et al. A

brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ. 2018 May 23;6:e4794.

58. Tredennick AT, Hooker G, Ellner SP, Adler PB. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology [Internet]. 2021 Jun [cited 2022 May 18];102(6). Available from: https://onlinelibrary.wiley.com/doi/10.1002/ecy.3336

59. Hartig F, Lohse L, leite M de S. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Internet]. 2024 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/DHARMa/index.html

60. R Core Team. R: The R Project for Statistical Computing [Internet]. [cited 2024 Dec 19]. Available from: https://www.r-project.org/

61. Brooks M, Bolker B, Kristensen K, Maechler M, Magnusson A, McGillycuddy M, et al. glmmTMB: Generalized Linear Mixed Models using Template Model Builder [Internet]. 2024 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/glmmTMB/index.html

62. Revelle W. psych: Procedures for Psychological, Psychometric, and Personality Research [Internet]. 2024 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/psych/index.html

63. Husson F, Josse J, Le S, Mazet J. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining [Internet]. 2024 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/FactoMineR/index.html

64. Kassambara A, Mundt F. factoextra: Extract and Visualize the Results of Multivariate Data Analyses [Internet]. 2020 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/factoextra/index.html

65. Hope RM. Rmisc: Ryan Miscellaneous [Internet]. 2022 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/Rmisc/index.html

66. Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, et al. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics [Internet]. 2024 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/ggplot2/index.html

67. Ahlmann-Eltze [aut C, Patil (@patilindrajeets) I. ggsignif: Significance Brackets for "ggplot2" [Internet]. 2022 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/ggsignif/index.html

68. Kassambara A. ggpubr: "ggplot2" Based Publication Ready Plots [Internet]. 2023 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/ggpubr/index.html

69. Pedersen TL. patchwork: The Composer of Plots [Internet]. 2024 [cited 2024 Dec 19]. Available

from: https://cran.r-project.org/web/packages/patchwork/index.html
70. Ram [aut K, cre, Wickham H, Richards C, Baggett A. wesanderson: A Wes Anderson Palette Generator [Internet]. 2023 [cited 2024 Dec 19]. Available from: https://cran.r-project.org/web/packages/wesanderson/index.html
71. García-Forero C, Gallardo-Pujol D, Maydeu-Olivares A, Andrés-Pueyo A. Disentangling impulsiveness, aggressiveness and impulsive aggression: An empirical approach using self-report measures. Psychiatry Res. 2009 Jun 30;168(1):40–9.
72. Rudebeck PH, Walton ME, Millette BHP, Shirley E, Rushworth MFS, Bannerman DM. Distinct contributions of frontal areas to emotion and social behaviour in the rat. Eur J Neurosci. 2007;26(8):2315–26.
73. Overduin-de Vries AM, Vries H de, Vermande MM, Reijntjes AHA, Sterck EHM. Both aggressive and affiliative behaviour facilitate resource access in high-ranking female long-tailed macaques (Macaca fascicularis). Behaviour [Internet]. 2020 Mar 20 [cited 2024 Dec 19];157. Available from: https://brill.com/view/journals/beh/157/3-4/article-p267_3.xml
74. Speechley EM, Ashton BJ, Thornton A, King SL, Simmons LW, Woodiss-Field SL, et al. Aggressive interactions influence cognitive performance in Western Australian magpies. Proc R Soc B Biol Sci. 2024 Jun 5;291(2024):20240435.
75. Garnham LC, Porthén SA, Child S, Forslind S, Løvlie H. The role of personality, cognition, and affective state in same-sex contests in the red junglefowl. Behav Ecol Sociobiol. 2019 Nov 19;73(11):149.
76. Troisi CA, Vernouillet A, Allaert R, Knoch S, Martel A, Lens L, et al. Beyond a unitary construct: Dissecting stopping behaviour in two bird species. bioRxiv;
77. Zucca P, Antonelli F, Vallortigara G. Detour behaviour in three species of birds: quails (Coturnix sp.), herring gulls (Larus cachinnans) and canaries (Serinus canaria). Anim Cogn. 2005 Apr;8(2):122–8.
78. Van Horik JO, Langley EJG, Whiteside MA, Laker PR, Madden JR. Intra-individual variation in performance on novel variants of similar tasks influences single factor explanations of general cognitive processes. R Soc Open Sci. 2018 Jul;5(7):171919.
79. Brucks D, Marshall-Pescini S, Wallis LJ, Huber L, Range F. Measures of Dogs' Inhibitory Control Abilities Do Not Correlate across Tasks. Front Psychol. 2017 May 24;8:849.
80. Fagnani J, Barrera G, Carballo F, Bentosela M. Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. Anim Cogn. 2016 Nov 1;19(6):1165–72.
81. Marshall-Pescini S, Virányi Z, Range F. The Effect of Domestication on Inhibitory Control:

990 Wolves and Dogs Compared. PLOS ONE. 2015 Feb 25;10(2):e0118469.
991 82. Vernouillet A, Anderson J, Clary D, Kelly DM. Inhibition in Clark's nutcrackers (Nucifraga
992 columbiana): results of a detour-reaching test. Anim Cogn. 2016 May 1;19(3):661–5.
993 83. Cauchoix M, Chow PKY, van Horik JO, Atance CM, Barbeau EJ, Barragan-Jason G, et al. The
994 repeatability of cognitive performance: a meta-analysis. Philos Trans R Soc B Biol Sci. 2018 Sep
995 26;373(1756):20170281.
996 84. Doran C, Bierbach D, Laskowski KL. Familiarity increases aggressiveness among clonal fish.
997 Anim Behav. 2019 Feb;148:153–9.
998 85. Dugatkin LA, Earley RL. Individual recognition, dominance hierarchies and winner and loser
999 effects. Proc R Soc Lond B Biol Sci. 2004 Jul 22;271(1547):1537–40.
1000 86. Werba JA, Stuckert AM, Edwards M, McCoy MW. Stranger danger: A meta-analysis of the dear
1001 enemy hypothesis. Behav Processes. 2022 Jan;194:104542.
1002 87. Marler P. On animal aggression: The roles of strangeness and familiarity. Am Psychol.
1003 1976;31(3):239–46.
1004 88. Leighton GM, Drury JP, Small J, Miller ET. Unfamiliarity generates costly aggression in
1005 interspecific avian dominance hierarchies. Nat Commun. 2024 Jan 6;15(1):335.
1006 89. Sih A, Bell A, Johnson JC. Behavioral syndromes: an ecological and evolutionary overview.
1007 Trends Ecol Evol. 2004 Jul 1;19(7):372–8.
1008 90. Bell AM. Future directions in behavioural syndromes research. Proc R Soc B Biol Sci. 2006 Dec
1009 21;274(1611):755–61.
1010 91. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. Integrating animal temperament
1011 within ecology and evolution. Biol Rev Camb Philos Soc. 2007 May;82(2):291–318.
1012 92. Briffa M, Sneddon LU, Wilson AJ. Animal personality as a cause and consequence of contest
1013 behaviour. Biol Lett. 2015 Mar;11(3):20141007.
1014 93. Hsu Y, Earley RL, Wolf LL. Modulation of aggressive behaviour by fighting experience:
1015 mechanisms and contest outcomes. Biol Rev Camb Philos Soc. 2006 Feb;81(1):33–74.
1016 94. Tibbetts EA, Pardo-Sanchez J, Weise C. The establishment and maintenance of dominance
1017 hierarchies. Philos Trans R Soc B Biol Sci. 2022 Feb 28;377(1845):20200450.
1018 95. Hobson EA. Differences in social information are critical to understanding aggressive behavior
1019 in animal dominance hierarchies. Curr Opin Psychol. 2020 Jun;33:209–15.
1020 96. Matzel LD, Kolata S, Light K, Sauce B. The tendency for social submission predicts superior
1021 cognitive performance in previously isolated male mice. Behav Processes. 2017 Jan;134:12–21.
1022 97. Guadagno A, Triki Z. Executive functions and brain morphology of male and female dominant
1023 and subordinate cichlid fish. Brain Behav. 2024;14(5):e3484.

98. Barnard CJ, Luo N. Acquisition of dominance status affects maze learning in mice. Behav Processes. 2002 Oct 31;60(1):53–9.
99. Colas-Zelin D, Light KR, Kolata S, Waas C, Denman-Brice A, Rios C, et al. The imposition of, but not the propensity for, social subordination impairs exploratory behaviors and general cognitive abilities. Behav Brain Res. 2012 Jun 15;232(1):294–305.
100. Boogert NJ, Reader SM, Laland KN. The relation between social rank, neophobia and individual learning in starlings. Anim Behav. 2006 Dec;72(6):1229–39.
101. Hector AK, Raleigh MJ. The effects of temporary removal of the alpha male on the behavior of subordinate male vervet monkeys. Am J Primatol. 1992;26(2):77–87.
102. Lambert CT, Guillette LM. The impact of environmental and social factors on learning abilities: a meta-analysis. Biol Rev. 2021 Dec;96(6):2871–89.
103. Triki Z, Zhou T, Argyriou E, Sousa De Novais E, Servant O, Kolm N. Social complexity affects cognitive abilities but not brain structure in a Poeciliid fish. Le Roux A, editor. Behav Ecol. 2024 May 1;35(3):arae026.
104. Brucks D, Härterich A, König Von Borstel U. Horses wait for more and better rewards in a delay of gratification paradigm. Front Psychol. 2022 Jul 22;13:954472.
105. Ruploh T, Henning M, Bischof H, Von Engelhardt N. Effects of social conditions during adolescence on courtship and aggressive behavior are not abolished by adult social experience. Dev Psychobiol. 2015 Jan;57(1):73–82.
106. Rodenburg TB, Koene P. The impact of group size on damaging behaviours, aggression, fear and stress in farm animals. Appl Anim Behav Sci. 2007 Mar;103(3–4):205–14.
107. Middlebush CW, Mountjoy PT, Riley V. Unconditioned aggression in the Japanese quail, Coturnix coturnix japonica. Psychon Sci. 1968 Mar;11(3):113–4.
108. Cooper Jr WE, Dimopoulos I, Pafilis P. Sex, Age, and Population Density Affect Aggressive Behaviors in Island Lizards Promoting Cannibalism. Ethology. 2015;121(3):260–9.
109. Dubois F, Giraldeau LA, Grant JWA. Resource defense in a group-foraging context. Behav Ecol. 2003 Jan 1;14(1):2–9.
110. Estevez I, Andersen IL, Nævdal E. Group size, density and social dynamics in farm animals. Appl Anim Behav Sci. 2007 Mar;103(3–4):185–204.
111. Lambert CT, Sewall KB, Guillette LM. Questioning the developmental effects of group size on cognitive abilities. Learn Behav. 2019 Dec 1;47(4):280–3.
112. Shaw RC, Schmelz M. Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. Anim Cogn. 2017 Nov 1;20(6):1003–18.

1058 113. Boogert NJ, Madden JR, Morand-Ferron J, Thornton A. Measuring and understanding
1059 individual differences in cognition. Philos Trans R Soc B Biol Sci. 2018 Sep
1060 26;373(1756):20170280.
1061 114. Thornton A, Lukas D. Individual variation in cognitive performance: developmental and
1062 evolutionary perspectives. Philos Trans R Soc B Biol Sci. 2012 Oct 5;367(1603):2773–83.
1063 115. Völter CJ, Tinklenberg B, Call J, Seed AM. Comparative psychometrics: establishing what
1064 differs is central to understanding what evolves. Philos Trans R Soc B Biol Sci. 2018 Aug
1065 13;373(1756):20170283.
1066 116. Brucks D, Marshall-Pescini S, Range F. Dogs and wolves do not differ in their inhibitory
1067 control abilities in a non-social test battery. Anim Cogn. 2019 Jan;22(1):1–15.
1068 117. Rowe C, Healy SD. Measuring variation in cognition. Behav Ecol. 2014 Jan 1;25(6):1287–
1069 92.
1070 118. Smulders TV. Smarter through group living? Learn Behav. 2019 Dec 1;47(4):275–6.
1071 119. Lucon-Xiccato T, Montalbano G, Bertolucci C. Personality traits covary with individual
1072 differences in inhibitory abilities in 2 species of fish. Carere C, editor. Curr Zool. 2020 Apr
1073 1;66(2):187–95.
1074 120. Dougherty LR, Guillette LM. Linking personality and cognition: a meta-analysis. Philos
1075 Trans R Soc B Biol Sci. 2018 Aug 13;373(1756):20170282.
1076 121. Webster MM, Rutz C. How STRANGE are your study animals? Nature. 2020
1077 Jun;582(7812):337–40.
1078 122. Ferreira VHB, Reiter L, Germain K, Calandreau L, Guesdon V. Uninhibited chickens:
1079 ranging behaviour impacts motor self-regulation in free-range broiler chickens (*Gallus gallus*
1080 *domesticus*). Biol Lett. 2020 Jan;16(1):20190721.
1081 123. Verbeek MEM, Boon A, Drent PJ. Exploration, Aggressive Behaviour and Dominance in
1082 Pair-Wise Confrontations of Juvenile Male Great Tits. Behaviour. 1996;133(11–12):945–63.
1083 124. Szabo B, Hoefer S, Whiting MJ. Are lizards capable of inhibitory control? Performance on
1084 a semi-transparent version of the cylinder task in five species of Australian skinks. Behav Ecol
1085 Sociobiol. 2020 Oct;74(10):118.
1086 125. Shaw RC. Testing cognition in the wild: factors affecting performance and individual
1087 consistency in two measures of avian cognition. Behav Processes. 2017 Jan;134:31–6.
1088 126. Hanas AK, Guigueno MF, Fernie KJ, Letcher RJ, Ste-Marie Chamberland F, Head JA.
1089 Assessment of the effects of early life exposure to triphenyl phosphate on fear, boldness,
1090 aggression, and activity in Japanese quail (Coturnix japonica) chicks. Environ Pollut. 2020
1091 Mar;258:113695.

127. Lucon-Xiccato T. The contribution of executive functions to sex differences in animal cognition. Neurosci Biobehav Rev. 2022 Jul;138:104705.
128. Vinogradov IM, Jennions MD, Van Veen E, Fichtel C, Kappeler PeterM, Fox RJ. The effect of sex, age and boldness on inhibitory control. Anim Behav. 2022 Nov;193:133–43.
129. Lacreuse A, Gullstrand J, Fagot J. Sex differences in inhibitory control in socially-housed baboons (Papio papio). Behav Brain Res. 2016 Oct;312:231–7.
130. Junttila S, Huohvanainen S, Tiira K. Effect of Sex and Reproductive Status on Inhibitory Control and Social Cognition in the Domestic Dog (Canis familiaris). Animals. 2021 Aug 20;11(8):2448.
131. Lucon-Xiccato T, Bisazza A. Discrimination reversal learning reveals greater female behavioural flexibility in guppies. Biol Lett. 2014 Jun 30;10(6):20140206.
132. Ophir AG, Persaud KN, Galef BG. Avoidance of Relatively Aggressive Male Japanese Quail (Coturnix japonica) by Sexually Experienced Conspecific Females. J Comp Psychol. 2005;119(1):3–7.
133. Rutkowska J, Place NJ, Vincent S, Adkins-Regan E. Adrenocortical response to mating, social interaction and restraint in the female Japanese quail. Physiol Behav. 2011 Oct;104(5):1037–40.
134. Schlinger BA, Palter B, Callard GV. A method to quantify aggressiveness in Japanese quail (Coturnix c. japonica). Physiol Behav. 1987 Jan;40(3):343–8.
135. Abuoghaba AAK, Ali F, Selim DAF, Abdelwahab AAM, Abdelfattah MG. Impact of male-female cohabitation period on behavioral aspects, fertility, hatchability, and hormonal estimates of Japanese quail. Poult Sci. 2022 Jan;101(1):101530.
136. Pellegrini S, Orso GA, Marin RH, Guzman DA. The insemination status and social context influences quail laying and social behavior: A novel experimental set up. Poult Sci. 2023 Feb;102(2):102328.
137. Georgelin M, Ferreira VHB, Cornilleau F, Meurisse M, Poissenot K, Beltramo M, et al. Short photoperiod modulates behavior, cognition and hippocampal neurogenesis in male Japanese quail. Sci Rep. 2023 Jan 18;13(1):951.
138. Scholes NW. Detour learning and development in the domestic chick. J Comp Physiol Psychol. 1965;60(1):114–6.
139. Kabadayi C, Jacobs I, Osvath M. The Development of Motor Self-Regulation in Ravens. Front Psychol [Internet]. 2017 Nov 29 [cited 2025 Apr 24];8. Available from: https://www.frontiersin.orghttps://www.frontiersin.org/journals/psychology/articles/10.3389/fpsyg.2017.02100/full

1126 140. Garnham LC, Boddington R, Løvlie H. Variation in inhibitory control does not influence
1127 social rank, foraging efficiency, or risk taking, in red junglefowl females. Anim Cogn [Internet].
1128 2022 Feb 4 [cited 2022 May 18]; Available from: https://link.springer.com/10.1007/s10071-
1129 022-01598-5
1130 141. Madden JR, Langley EJG, Whiteside MA, Beardsworth CE, van Horik JO. The quick are
1131 the dead: pheasants that are slow to reverse a learned association survive for longer in the wild.
1132 Philos Trans R Soc Lond B Biol Sci. 2018 Sep 26;373(1756):20170297.
1133 142. Suter H, Houston AI, Radford AN. Self-control: waiting longer is not necessarily better.
1134 ISBE 2024; 2024 Oct 3; Melbourne, Australia.
1135 143. Stevens JR, Stephens DW. The adaptive nature of impulsivity. In: Madden GJ, Bickel WK,
1136 editors. Impulsivity: The behavioral and neurological science of discounting [Internet].
1137 Washington: American Psychological Association; 2010 [cited 2022 May 18]. p. 361–87.
1138 Available from: http://content.apa.org/books/12069-013
1139 144. Kelly AM, Wilson LC. Aggression: Perspectives from social and systems neuroscience.
1140 Horm Behav. 2020 Jul;123:104523.
1141 145. Flanigan ME, Russo SJ. Recent advances in the study of aggression.
1142 Neuropsychopharmacology. 2019 Jan;44(2):241–4.
1143