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1 **Maternal styles in a precocial bird**

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6

7 Care provided by females of many mammal species varies naturally between
8 individuals; these differences in turn influence the phenotypic development of their offspring.
9 When individual maternal behavioural traits are consistent over a number of breeding periods,
10 maternal styles can be defined. These styles have been studied in a large range of mammalian
11 species. Nevertheless, mammals rarely offer the possibility to dissociate mothers' behavioural
12 influence from their genetic influence or their physiological influence via lactation. Here, we
13 provide, for the first time, evidence of the existence of a precocial bird species' maternal styles.
14 By using an adoption procedure we evaluated how maternal style affected the behaviour of
15 Japanese quail, *Coturnix coturnix japonica*, chicks, via exclusively nongenomic mechanisms.
16 As well as evidence for the existence of maternal styles in this species, we also found
17 correlations between females' temperaments, maternal styles and their fostered chicks'
18 development. Our findings indicate that maternal styles are key features that help understand
19 nongenomic transmission of behavioural characteristics whose vectors have remained poorly
20 understood.

21 Key-words: *Coturnix coturnix japonica*, Japanese quail, maternal styles, nongenetic influences,
22 temperament

23 ***INTRODUCTION***

24 The way in which individuals behave in challenging situations can have significant fitness
25 consequences (Dingemanse, Both, Drent, & Tinbergen, 2004; Réale, Reader, Sol, McDougall,
26 & Dingemanse, 2007; Smith & Blumstein, 2008). In a wide range of species, individual
27 differences in behavioural reactions when facing challenges can remain consistent over time
28 and situations (Réale et al., 2007; Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011). These
29 behavioural consistencies have been studied mainly in nonreproductive contexts, focusing on
30 several dimensions of fearfulness, exploration and sociality and have been termed
31 temperaments or personalities (see Réale et al., 2007 for a review). Nevertheless, many
32 vertebrates can also present individual differences related to reproductive behaviours. Maternal
33 (or mothering) styles can be defined as the individual differences in the dimensions of care
34 expressed by a female towards her young that remain consistent over several periods of
35 maternal care (Albers, Timmermans, & Vossen, 1999; Dwyer & Lawrence, 2000). Maternal
36 styles thus constitute an individual signature of maternal care that must be evaluated over
37 several maternal care periods to make sure that individual differences in care are not due to
38 individual differences in offspring characteristics. These styles are defined by dimensions of
39 care, identified by the relationships between the behaviours of the maternal repertoire. For
40 instance, consistent individual differences in the maternal behaviour of many nonhuman
41 primate species appear in two dimensions of care: protection and rejection. These dimensions
42 of care are independent and both are defined by several correlated care items (see Fairbanks,
43 1996; Groothuis & Maestripieri, 2013). So far, maternal styles have been described in humans
44 (van Ijzendoorn et al., 2000), nonhuman primates (Fairbanks, 1996) and altricial (Champagne,
45 Francis, Mar, & Meaney, 2003) and precocial (Dwyer & Lawrence, 2000; Spinka et al., 2000)
46 nonprimate mammals. Identifying and understanding the relationships between individual
47 differences within and outside the family context to understand their coadaptation remains a

48 key challenge (Roulin, Dreiss, & Kölliker, 2010). By investigating the biological causes and
49 consequences of these individual differences in the maternal care of several mammalian
50 species, researchers have reported a link between maternal style and temperament. Mothers'
51 temperaments influence maternal styles (Fairbanks, 1996; Maestriperi, 1993; Plush, Hebart,
52 Brien, & Hynd, 2011) and, in turn, maternal styles are reported to have a strong impact on
53 offspring temperament (Schino, Speranza, & Troisi, 2001; Weaver et al., 2004). For instance,
54 anxious baboon, *Papio* spp. (Altmann, 1980) and rhesus monkey, *Macaca mulatta*
55 (Maestriperi, 1993) females show high levels of protection of their infants, whereas rejection
56 rates of Japanese macaques, *Macaca fuscata*, are reported to affect their infants' sociality
57 (Schino et al., 2001). So far, mothering styles and their relationship with temperament have
58 been studied only in mammalian species.

59 Maternal styles, as defined above, have never been rigorously identified in a bird species.
60 Nevertheless, consistency of a particular parental care behaviour has been described in altricial
61 birds, suggesting the potential existence of parental styles. For example, food provisioning by
62 a male house sparrow, *Passer domesticus*, can be consistent across broods and is not influenced
63 by his partner's efforts (Schwagmeyer & Mock, 2003). Moreover, parents' temperaments can
64 affect such care behaviour, thus suggesting a potential relationship between temperament and
65 parenting style in birds. For example, the food provisioning and nest defence of titmice
66 (Paridae) are related to their exploratory and aggressive behaviours (Hollander, Van Overveld,
67 Tokka, & Matthysen, 2008; Mutzel, Dingemanse, Araya-Ajoy, & Kempenaers, 2013). Finally,
68 bird mothers can strongly modify the behavioural development of their offspring via nongenetic
69 influences occurring during the early postnatal period. In particular, these maternal effects have
70 been reported to be strong in precocial birds, in which mothers can transmit nongenetically
71 some of their temperament traits to chicks, including fearfulness (Houdelier, et al., 2011;
72 Richard-Yris, Michel, & Bertin, 2005) and traits related to sociality (Formanek, Houdelier,

73 Lumineau, Bertin, & Richard-Yris, 2008). Precocial birds are currently becoming the models
74 of choice to investigate such maternal effects because the absence of lactation and the
75 opportunity to carry out adoption procedures enable researchers to disentangle behavioural
76 from physiological (Catalani et al., 2000; Hinde & Captanio, 2010), genetic (Schino et al., 2001)
77 and prenatal (Stamps & Groothuis, 2010) influences. Nevertheless, the mechanisms associated
78 with these influences remain unknown. In these precocial bird species, as in most mammals,
79 mothers are the only caregivers and express a rich maternal behavioural repertoire to provide
80 warmth and protection to their offspring and to stimulate their feeding behaviour until they can
81 look after themselves (Nelson, 1995). Nevertheless, the implication of individual differences in
82 the maternal behaviour of precocial hens has never been investigated in relation to these
83 maternal influences.

84 We investigated the existence of maternal styles in a precocial bird species, the Japanese
85 quail, *Coturnix coturnix japonica*, and the link between maternal styles and both mothers' and
86 their offspring's temperaments. Using a recently described procedure to evaluate maternal care
87 in this species (Pittet, Coignard, Houdelier, Richard-Yris, & Lumineau, 2013), we analysed the
88 maternal behaviour of 20 adult female Japanese quail over three consecutive maternal periods
89 and evaluated their temperament and the temperament of their offspring. We asked the
90 following questions: (1) can maternal styles be defined in a bird species and if so, (2) can a
91 female's temperament predict her maternal style and (3) can maternal styles predict offspring
92 behavioural characteristics?

93

94

95

96 **METHODS**

97 Housing conditions

98 The quail studied originated from an industrial farm (Les Cailles de Chanteloup, Corps-
99 Nuds, France). In our laboratory, they were kept at 20 ± 1 °C on a 12:12 h light:dark cycle
100 (lighting = 500 lx). Food provided was a high-protein cereal diet in the form of a mix of pellet
101 for chicks and granulates for adult females (VEGAM, Cesson-Sévigné, France).

102 Twenty adult females arrived at the laboratory when they were 5 weeks old and were placed
103 singly in wire-mesh cages (100x70 cm and 62 cm high) with opaque walls 7 weeks before their
104 first brood to habituate them to their experimental environment. The cages contained a feeder
105 and a water source with food and water available ad libitum. Water was available for drinking
106 only and not for bathing. The females were 12, 37, 44 and 51 weeks old, respectively, for the
107 first, second, third and fourth breeding periods (denoted BP0, BP1, BP2 and BP3) and stayed
108 under the same constant environmental conditions throughout the experiment.

109 Chicks were from the same broiler line. For each breeding period, 120 1-day-old chicks
110 (total sample = 480 chicks) arrived at the laboratory and were placed in groups of 30 in four
111 plastic cages (98x35 cm and 42 cm high) with wood shavings covering the floor and equipped
112 with a heater (38 ± 1 °C) and food and water provided ad libitum.

113 After each breeding period, chicks were either used for other experiments or kept in boxes
114 (200x200 cm and 280 cm high) with wood shavings covering the floor, at 20 ± 1 °C and under a
115 12:12 h light:dark cycle, until they could be used for breeding. The 20 females were used for
116 other behavioural experiments and then placed in an outdoor aviary (500x500 cm and 300 cm
117 high) with tall grass and several shelter areas.

118 Fostering protocol and general procedure

119 In the evening of the arrival of chicks, for each breeding period, females were shut in their
120 nestbox (20x20x20 cm) and the light was immediately switched off. One hour later (2100
121 hours) we placed four chicks underneath each female. Chicks' solicitations during the night
122 induce the females to become maternal (Richard-Yris, Michel, & Bertin, 2005) by the following
123 morning when the boxes are opened (0800 hours) . Females that did not accept the chicks (i.e.
124 absence of warming behaviour after the release of the brood, expression of rejection behaviours)
125 were excluded from the experiment; three females were excluded from BP0, one from BP1,
126 two from BP2 and six from BP3. Any chick in a female's brood that showed signs of
127 hypothermia (closed eyes, trembling, motionless) on the first day of each breeding period was
128 replaced by a new chick (so that all broods included four chicks for all the females). The new
129 chicks were ringed and of the same age but were not tested later as they did not spend the whole
130 breeding period with a mother: 18 chicks were replaced for BP0, 23 for BP1, 11 for BP2 and
131 21 for BP3. After the first day, chicks quickly learn to warm one another (Pittet, Coignard,
132 Houdelier, Richard-Yris, & Lumineau, 2012) and we noted no further signs of hypothermia.
133 We could not monitor signs of hypothermia at night since our presence in the breeding room
134 during the dark phase would have disturbed the birds. We nevertheless checked for the absence
135 of distress calls 30 min after the beginning of the dark phase.

136 Behavioural measurements

137 **Observation of maternal behaviour**

138 Maternal behaviour was observed on posthatching days (PHD) 2, 3, 4, 5, 7 and 9 of each
139 maternal care period. The observation procedure was similar to that used by Pittet et al. (2013).

140 Both instantaneous scan sampling and focal animal sampling were equally distributed
141 between the morning and afternoon periods and were carried out from behind one-way mirrors.
142 The 20 adult females were observed using the instantaneous scan sampling method (interval: 4

143 min, 60 observations/female/day) for 4 h on each observation day. The experimenter noted
144 whether or not the female was warming the chicks, whether or not her warming posture covered
145 the chicks entirely and her distance to each chick using five distance classes: close (chick in
146 contact with hen), near (at no more than one chick length from the hen), far (chicks between
147 one chick length and half a cage from the hen), distant (chick between half a cage and a cage
148 length from the hen) and opposite (at one cage length). From these data, several indexes were
149 calculated: (1) mean distance index = $[N_{\text{opposite}} + 0.75 \times N_{\text{distant}} + 0.5 \times N_{\text{far}} + 0.25 \times N_{\text{near}}] / \text{total chicks}$
150 observed while not being warmed; (2) proportion of time spent warming = scans in which
151 warming occurred/total scans; and (3) index of warming posture quality = scans in which
152 warming occurred in a covering posture/scans in which warming occurred.

153 These observations were associated with two 5 min focal animal sampling observations on
154 each observation day for each cage. The experimenter noted aggressive behaviour that included
155 attacks (the mother attacks a chick while making threat vocalizations), pecking (the mother
156 pecks at a chick with her beak closed), trampling of chicks and breaks in warming including
157 the initiator of these breaks (mother or chick). The proportion of warming breaks initiated by
158 the mother was calculated as warming breaks initiated by mother/total warming breaks
159 observed.

160 On PHD10, to evaluate maternal reactivity, chicks were separated from their mothers whose
161 reactions were assessed by a 5 min focal observation recording their vocalizations and latencies
162 to return to feeding and resting.

163 **Temperament assessment of females and foster chicks**

164 Mothers were tested before and chicks were tested after the first breeding period. We
165 applied tests commonly used to assess shyness, neophobia and social motivation in Japanese
166 quail. We evaluated shyness by the time (maximum: 3 min) mothers and chicks took to emerge

167 from a dark shelter box into a novel well-lit environment in the emergence test (Jones, Satterlee,
168 & Cadd, 1999), and neophobia by their reactions to a novel object in a familiar environment,
169 measured during a 10 min focal animal sampling observation. A 5 min open-field test evaluated
170 the way individuals responded to both an unknown open environment and their first social
171 isolation, and their social motivation was evaluated by their aptitude to approach three
172 unfamiliar conspecifics in the runway test (Formanek et al., 2008). For more details on the tests
173 see the Appendix.

174 Data analyses

175 As most data were not normally distributed we applied nonparametric statistics. The overall
176 effects of maternal experience and age of chicks on maternal traits were investigated by
177 Friedman tests followed by Nemenyi post hoc tests with Bonferroni alpha corrections to
178 compare pairs. This initial analysis was carried out to determine the periods when maternal
179 variables were not strongly influenced by maternal experience or by the chicks' age. It showed
180 (see Appendix Table A1) that maternal variables differed strongly between the first and later
181 breeding periods and that maternal traits on PHD7 and PHD9 differed from those on previous
182 days of the breeding period. BP0 was excluded from analysis because of this strong effect of
183 experience already reported (Pittet et al., 2013) and, to obtain a mean of each variable for each
184 breeding period for each female, we averaged data from PHD2 to PHD5.

185 A principal component analysis (PCA) including maternal care variables (see above) was
186 used to determine dimensions of maternal care. We focused on mother–chick interactions in
187 the home cage to identify maternal styles, as described in the literature. Thus, we did not
188 consider the results of the separation tests as a care variable to include in the PCA, since this
189 test presents an artificial situation with disturbance of the brood and was carried out at the end
190 of the care period. Kendall concordance tests were used to describe the consistency of

191 individual differences across breeding periods. Kendall's coefficient of concordance analysing
192 agreement among behavioural trait data or scores obtained by a PCA analysis is a classic
193 statistical method to investigate maternal styles when more than two periods of care are
194 involved (Albers et al., 1999; Dwyer & Lawrence, 2000). As an analysis of concordance
195 requires at least three repetitions, data for the six females that did not accept chicks for one of
196 the last three breeding periods were excluded from the analysis. Kendall correlation tests were
197 computed to analyse the relationship between maternal styles and temperament data. Data
198 analyses were computed using XLStat (www.xlstat.com) and R (The R Foundation for
199 Statistical Computing, Vienna, Austria, www.r-project.org).

200 Ethical note

201 All experiments were approved by the departmental direction of veterinary services (Ille-
202 et-Vilaine, France, permit number 005283) and were performed in accordance with the
203 European Communities Council Directive of 24 November 1986 (86/609/EEC). Our breeding
204 procedure and tests were approved by the regional ethics committee (agreement number: R-
205 2011-SLU-02).

206 Twenty adult females and 480 chicks were used for the four breeding experiments. As some
207 females failed to adopt chicks, 20 was the minimum sample size needed to obtain sufficiently
208 robust statistical results. We used a brood size of four chicks as a compromise between the size
209 of a natural brood (5 - 10 chicks, Taka-Tsukasa 1935), which would be too large to handle, and
210 a smaller brood size that might not elicit maternal care in females.

211 Birds were transported by car and the journey lasted 20 min. Adult females were transported
212 in aluminium crates (70x30 cm and 22 cm high), each containing six individual boxes, and
213 chicks in groups of 30 in plastic boxes (40x40 cm and 15 cm high) with wood shavings covering
214 the floor. Temperature was 20 °C for the female transport and 30 °C for the chicks.

215 Our females were housed singly because, under natural conditions, they generally stay some
216 distance from one another and remain in social isolation while they incubate and care for their
217 chicks which they do alone (Guyomarc'h & Saint-Jalme, 1986). Housing females singly is
218 consequently the usual laboratory procedure for breeding experiments (Bertin & Richard-Yris,
219 2005; Houdelier et al., 2011). We did not provide hiding places because we needed to be able
220 to observe all the five quail in a cage continuously to estimate interindividual distances and
221 maternal behaviour. Nevertheless, the cages were behind one-way mirrors, and we checked that
222 the females showed no stereotypies, distress calls or flight attempts, and that they carried out
223 normal comfort behaviours such as dust bathing, which was facilitated by plastic netting
224 covering the cage floor.

225 We observed some cases of maternal aggression. Two females that were excluded from
226 BP0, BP2 and BP3 not only neglected chicks but also consistently attacked them soon after we
227 opened the nestboxes in these three breeding periods. We detected these attacks on hearing the
228 females' threat vocalizations and their chicks' loud vocalizations and therefore removed the
229 chicks immediately. Chicks that were attacked showed only a slight feather loss on their neck
230 but no bleeding or inflammation except during BP0 when three chicks' heads bled slightly.
231 Injured chicks as well as all the excluded chicks (chicks of nonmaternal females and chicks that
232 had to be replaced) were all put under a heater in plastic cages (98 x 35 cm and 42 cm high) for
233 the rest of the experiment. Chicks that showed signs of hypothermia swiftly recovered (in less
234 than 1 h). Chicks that were injured during BP0 were treated with an antiseptic (Vetidine) and
235 an aerosol bandage (Aluspray) before they were placed in the cages. Signs of the attacks were
236 no longer visible 1 week later. Aggressive (i.e. pecking and aggression) and abusive (trampling)
237 behaviours towards chicks by females in the later part of the breeding period did not cause any
238 feather loss, bleeding or inflammation and consequently did not justify any intervention.

239

240 **RESULTS**

241 Evidence for the existence of maternal styles

242 Maternal traits were objectively summarized by two dimensions of a PCA. Given the loadings
243 of variables on the two factors (Fig. 1), they were respectively labelled ‘aggression’ and
244 ‘rejection versus warming’ (see Fig. 1 legend for explanations). Females’ scores on the two
245 dimensions were not correlated (Kendall correlation test: $P > 0.05$), demonstrating that maternal
246 behaviour was truly multidimensional. We found a significant concordance of both females’
247 aggression (Kendall concordance test: $\omega = 0.62$, $N = 14$, $P = 0.03$; Fig. 2a) and rejection ($\omega =$
248 0.72 , $N = 14$, $P = 0.008$; Fig. 2b) scores over the breeding periods, demonstrating that
249 interindividual differences revealed by these two dimensions were strong and consistent across
250 care periods. We also tested directly the consistency of interindividual differences for each of
251 the seven maternal variables recorded and found a significant concordance across breeding
252 periods for each maternal trait (Kendall concordance test: $P < 0.05$).

253 Females’ reaction to separation from their chicks was related to their maternal style. The more
254 rejection the mothers showed, the less they reacted to separation from their chicks, producing
255 fewer distress calls ($\tau = -0.22$, $N = 42$, $P = 0.05$) and resuming feeding more rapidly ($\tau = -0.26$,
256 $N = 42$, $P = 0.03$).

257 Relationships between maternal styles and temperament

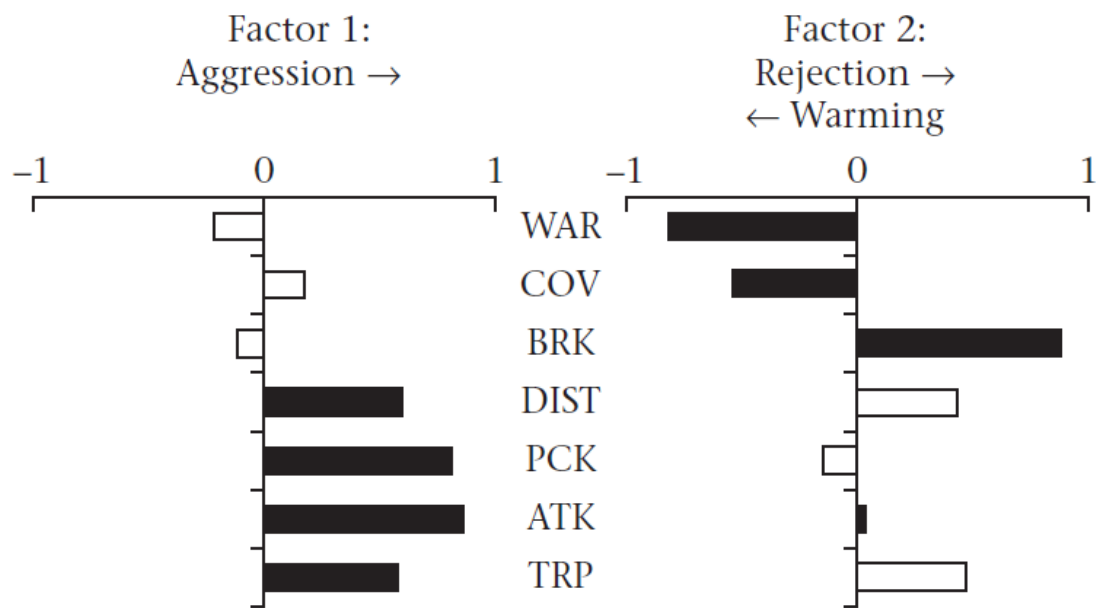
258 **Maternal temperament**

259 Maternal styles were correlated with several maternal temperament traits. Aggression scores
260 were correlated with reaction-to-novelty scores. The more aggressive the mothers were towards
261 chicks, the more they reacted to and avoided a novel object (Kendall correlation $\tau = 0.43$, $N =$
262 19 , $P = 0.012$; Fig. 3a) and the fewer fear postures they adopted ($\tau = -0.40$, $N = 19$, $P = 0.02$;

263 Fig. 3b). In addition, the more socially motivated the females behaved the more they rejected
264 their chicks: the time they spent in contact with a social stimulus in the runway test was
265 positively correlated with their rejection scores ($\tau = 0.34$, $N = 19$, $P = 0.04$; Fig. 3c).

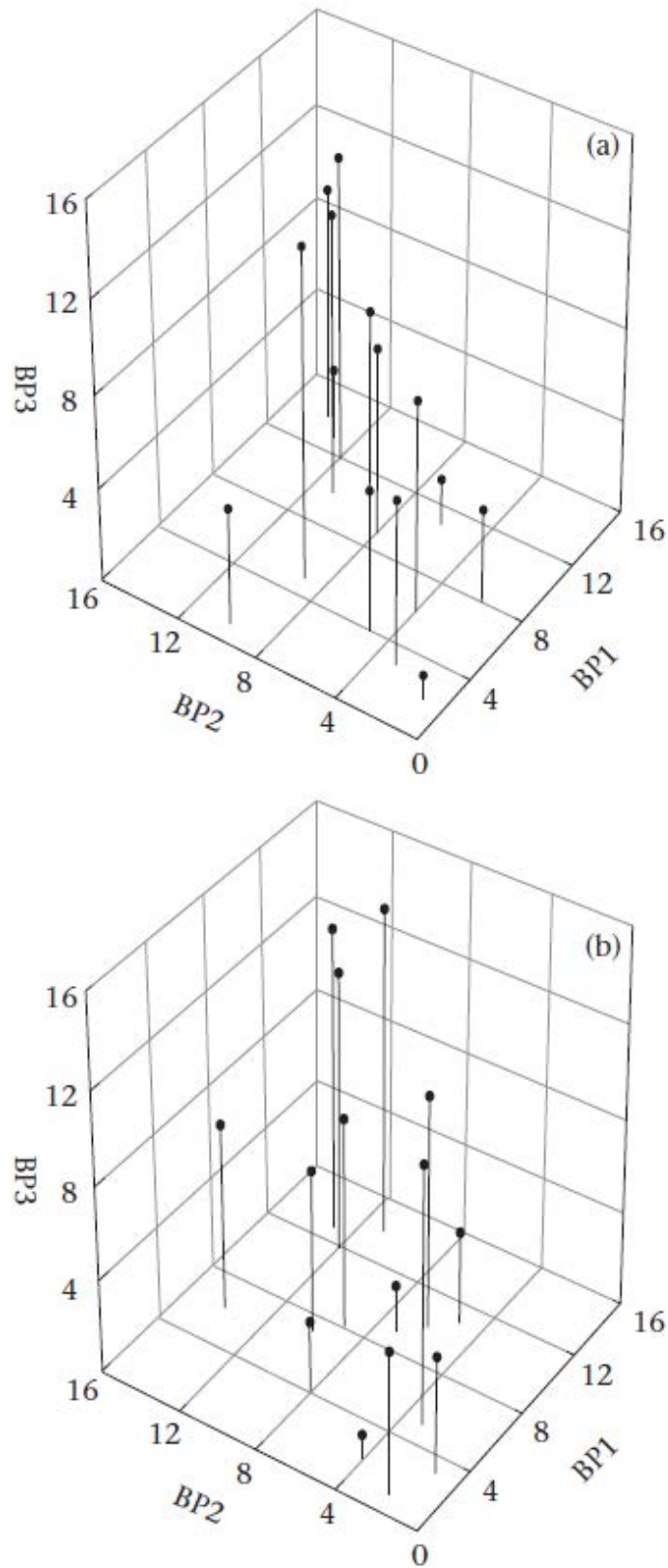
266 **Chicks' temperament**

267 As we found many significant correlations between chicks' behavioural data and the females'
268 maternal styles, we summarized chicks' behavioural responses to our tests using a PCA to avoid
269 type I errors. Chicks' behavioural traits were summarized by three axes, representing 65.56%
270 of the variability. The first two factors represented two dimensions of their sociality: there were
271 positive loadings for the vocalizations of socially isolated chicks in the open-field and
272 emergence tests (23.6% of variability) and their motivation to move closer to unfamiliar
273 conspecifics in the runway test (23.4% of variability). The third axis (18.6% of variability)
274 represented chicks' reactivity in a novel environment; there were positive loadings for the
275 number of steps in an open field and negative loadings for latencies to emerge from a shelter
276 into an unfamiliar cage. We found that maternal rejection scores were positively correlated with
277 socially isolated chicks' vocalization scores ($\tau = 0.23$, $N = 57$, $P = 0.013$) and with their scores
278 for proximity to unfamiliar conspecifics ($\tau = 0.22$, $N = 57$, $P = 0.016$), so that the more rejected
279 the chicks were, the more socially motivated they were subsequently. We found no correlation
280 between care scores and chicks' reactions to novelty scores ($P > 0.05$).



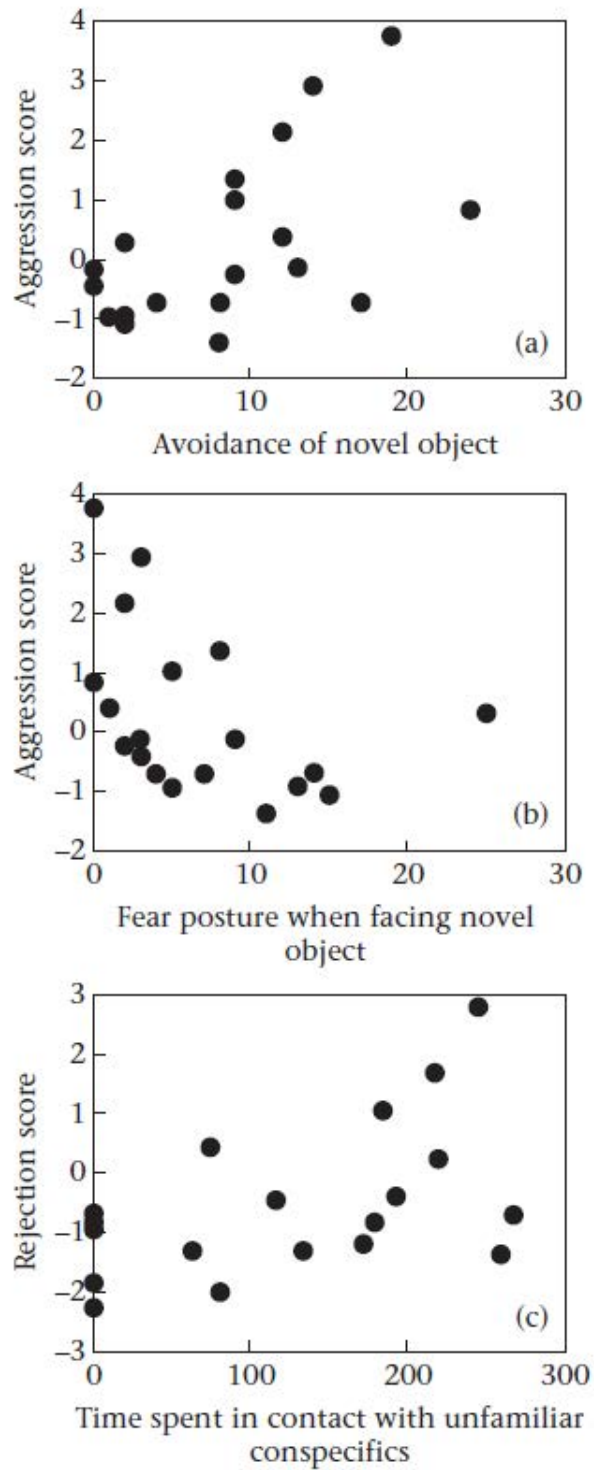
281

282 **Figure 1.** Maternal behaviour evaluated by the loadings of the seven maternal traits on the
 283 first two axes of a PCA ($N = 14 \times 3$ repetitions). Factor 1 accounted for 29.9% of the total
 284 variation and had large positive loadings for pecks (PCK), attacks (ATK), trampling (TRP) and
 285 distance to chicks (DIST) and was thus labelled ‘aggression’. Factor 2 accounted for 28.0% of
 286 the total variation and was labelled ‘rejection versus warming’ as it indicated large negative
 287 loadings for time spent warming (WAR) and proportion of covering posture (COV) and large
 288 positive loadings for maternal initiation of warming breaks (BRK).



289

290 **Figure 2.** Consistency of individual differences. Females' (a) aggression and (b) rejection
 291 scores (ranked) plotted on a three-dimensional graph for BP1, 2 and 3 ($N=14$).



292

293 **Figure 3.** Females' personality and maternal styles. Females' aggression scores when
 294 maternal in relation to (a) active (frequency of avoidances) and (b) passive (frequency of fear
 295 posture) reactions towards a novel object and (c) rejection scores in relation to sociality towards
 296 unfamiliar conspecifics ($N = 14$).

297 **DISCUSSION**

298 Our results provide evidence for the existence of maternal styles in Japanese quail and illustrate
299 close links between mothers' temperaments and their maternal style. They also show marked
300 consequences of maternal styles for the chicks' temperaments.

301

302 **Existence of mothering styles in Japanese quail**

303 First, our study revealed that naturally occurring individual differences in the characteristics of
304 maternal care can be summarized by two principal independent dimensions: mothers'
305 aggressiveness and their propensity to warm or reject their chicks. The consistency of these
306 individual differences demonstrates the existence of individual signatures of maternal care that
307 remain resistant to differences between broods and to the effects of maternal age and increased
308 experience already reported for this species (Pittet et al., 2012, 2013). The present work is, to
309 our knowledge, the first reported case of maternal styles in a nonmammalian species.

310 **Mothers' temperament and maternal style**

311 Our results indicate that the way females react to a novel object (other than their general
312 fearfulness) is related to their aggressiveness towards chicks. Maternal behaviour could be
313 driven by neophobia during the first few days of a breeding period: females that reacted actively
314 to a novel object also reacted actively to chicks, attacking and pecking them and made flight
315 attempts (leading to increased mother–chick distances and trampling). Conversely, females that
316 reacted to novelty more passively also showed restrained reactions to chicks' solicitations.
317 Fearfulness and particularly neophobia have also been reported to affect the quality of
318 mammals' first interactions with their offspring and subsequently to affect their survival

319 (Dwyer 2008; Harris & Gonyou 2003; Kikusui, Isaka, & Mori, 2005; Murphy, Lindsay, & Le
320 Neindre, 1998).

321 We also found that females that stayed at some distance from the social stimulus in the runway
322 test rejected their offspring less. This is analogous to behaviour reported in the mammalian
323 literature. Primates' maternal styles have been reported to depend on social context (see
324 Fairbanks, 1996 for review), but also on mothers' sociality level (Murray, Cooper, Creswell,
325 Schofield, & Sack, 2007). Indeed, primate females showing social anxiety and avoiding social
326 contact delay their infants' emancipation by being overprotective, which can be considered the
327 converse of maternal rejection (Schino et al., 2001). In our study, this link between rejection
328 and emancipation, at least on the mothers' side, is confirmed by our separation test results: less
329 social and less rejecting females remained reactive to separation from their chicks when they
330 were removed at an age when they naturally disperse. Obviously, this link between maternal
331 sociality and rejection is most relevant in rich social environments when offspring risk
332 aggression from conspecifics. Further investigations, testing maternal care of precocial birds in
333 richer social environments, should yield interesting results concerning this relationship. From
334 a neurohormonal point of view, oxytocin is involved in the expression of mammals' social and
335 maternal behaviour (Donaldson & Young, 2008; Nowak, Keller, & Lévy, 2011); in birds this
336 link could be provided by the nonapeptide mesotocin which is implicated in both social flocking
337 behaviour and maternal behaviour (Chokchaloemwong et al., 2013; Goodson, Kelly, &
338 Kingsbury, 2012; Goodson, Schrock, Klatt, Kabelik, & Kingsbury, 2009).

339 The relationships between temperament traits related to neophobia or sociality and maternal
340 styles evidenced here in birds show interesting similarities with reports on mammals. Given the
341 common points in the set-up of maternal styles and personalities (consistency of individual
342 differences mainly defined by genetic and early experience) and the implication of
343 neuroendocrine systems, we hypothesize that the association between maternal styles and

344 personalities could be a universal vertebrate trait, as the maternal care period is a challenging
345 situation particularly fitted for the expression of individual differences.

346 Maternal styles and chicks' temperament

347 Agreeing with reports on mammal species, our study demonstrates that maternal behaviour can
348 influence offspring personality. We showed that chicks' social motivation levels were
349 correlated with their foster mother's rejection scores. Filial imprinting could be involved here.
350 Indeed, hens' behaviour can influence the establishment of a filial bond (ten Cate, 1989) and
351 previous observations indicated that poorly warmed chicks quickly shift their thermoregulation
352 strategies to warming one another (Pittet et al., 2012). If the establishment of imprinting implies
353 mechanisms similar to those involved in associative learning (van Kampen, 1996), the more-
354 rejected chicks should logically develop a weaker bond with their mothers but a stronger bond
355 with the rest of the brood more likely to meet their physiological needs. A similar relationship
356 between rejection and development of sociality has been reported for several primate species.
357 Indeed, maternal rejection (within a normal range) has been reported to reduce nonhuman
358 primates' fearfulness expressed towards a social stimulus (Schino et al., 2001), and humans'
359 overprotective behaviour can induce social anxiety disorders (Spokas & Heimberg, 2009). Our
360 present experiment does not allow us to draw any conclusions about whether maternal styles
361 are involved in the transmission of emotional reactivity, probably because the chicks' reactions
362 to stressful situations are mainly socially oriented at this age or because individual differences
363 between mothers were not sufficient. We could also consider that females' reactions to stressful
364 situations are acquired by chicks via observational learning. This mechanism would imply that
365 fear reactions are not transmitted via maternal care but via fear reactions expressed by females
366 during the breeding period. Further investigations using divergently selected females (Mills &
367 Faure, 1991) should highlight more precisely the influences of maternal fearfulness on chicks'
368 behaviour.

369 Finally, precocial birds' maternal effects are known to be strong as some of the behavioural
370 traits of mothers are transmitted to their foster chicks (Formanek et al., 2008; Richard-Yris et
371 al., 2005). Our study demonstrates, for the first time, that maternal styles are implied in these
372 influences in birds. Our results show that care characteristics enable the transmission of social
373 motivation from mothers to foster chicks through a pattern of successive influences: a female's
374 social motivation influences her rejection score during the maternal stage, a maternal dimension
375 that, in turn, affects chicks' social motivation.

376 Conclusion

377 Mammals' maternal styles have been a key focus for the investigation of maternal behaviour,
378 its influence on offspring behaviour and associated mechanisms in a large range of fields. Our
379 present findings demonstrate for the first time the existence of maternal styles in birds and their
380 relationships with females' temperaments. Our results also highlight influences of maternal
381 styles on chicks' development and demonstrate that maternal care is involved in the nongenetic
382 transmission of behavioural characteristics. Given the current need to develop new models to
383 investigate the impact of early experience on neurological and behavioural development
384 (Lupien, McEwen, Gunnar, & Heim, 2009), we anticipate this study to be a starting point for
385 the integration of precocial birds into investigations of these issues.

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516

517

518

519

520 **APPENDIX**

521 Details of behavioural tests

522 *Emergence test*

523 Each test subject was removed from its home cage and transported in the dark, in a
524 wooden box (18x18x18 cm). This box was then placed on the left side of the apparatus: a large
525 and well-lit wooden box (62x60 cm and 33 cm high) with wood shavings covering the floor
526 and an observation window. When the transport box was placed in the apparatus, it was kept
527 closed for 1 min. Then, the door was left open for 3 min. Latencies for the subject to pass its
528 head out of the box and to emerge completely were recorded.

529 *Novel-object test*

530 This test assessed neophobia by the reactions of subjects to the presence of an unfamiliar
531 object. Mothers were tested in their home cage, but chicks had to be socially isolated and were
532 consequently tested in a polyhedral open field (1 m², 60 cm high) after a 10 min habituation.
533 The novel stimulus was an unfamiliar plastic T-shaped object. During a 10 min focal sample
534 the experimenter recorded latency to approach the object, frequency of locomotion (walks,
535 runs) and frequency of fear behaviours including escape, withdrawal (slowly approach the
536 object and then walk away while keeping it in sight), jumps and fear postures (freezing in
537 crouching posture).

538 *Open-field test*

539 Chicks were placed individually in the dark in the centre of a polyhedral arena (1 m², 60 cm
540 high) with white plastic walls and a linoleum floor. The experiment started when the light was
541 switched on, and, hidden behind a one-way mirror, the experimenter recorded latency of the

542 first distress call, the number of distress calls, the latency of the first step, the number of steps
543 and the frequency of observation, exploration and maintenance activities for 5 min.

544 *Runway test*

545 The apparatus was a 100 cm long plastic tunnel with walls 20 cm high. Test subjects were
546 transported individually in a wooden box (18x18x18 cm), which was then placed at the tunnel
547 entrance. At the other end of the tunnel was a cage (20x35 cm and 20 cm high) containing three
548 unfamiliar conspecifics of the same age as the tested individual, representing a social stimulus.
549 The corridor was divided into four zones: the closest zone to the social stimulus, ‘one bird long’
550 (zone P) and three equal 32 cm long zones called, from the entrance to zone P: zones A
551 (beginning of the tunnel), B (middle) and C (end of the tunnel). One minute after the transport
552 box had been put in place, the door was opened and the subject was observed for 5 min. The
553 experimenter noted the time spent in each zone.

554

555 Table A1

556 **Table A1.** Friedman tests measuring effects of age of chicks and experience of mother on
557 maternal traits

	Effects of age of chicks			Effects of maternal experience		
	<i>F</i>	<i>P</i>	PHD pair comparison	<i>F</i>	<i>P</i>	BP pair comparison
Warming chicks	47.87	<0.0001	PHD2,3 > PHD 7 - PHD2,3,4,5>PHD9	18.69	<0.0001	BP1,2 < BP0
Attacks	5.96	0.31	-	1.10	0.78	-
Breaks from warming	7.73	0.17	-	5.40	0.14	-
Pecks	8.83	0.12	-	8.39	0.04	-
Distance from chicks	25.63	<0.0001	PHD2,3 < PHD7 - PHD2,3 < PHD 9	28.20	<0.0001	BP1,2,3 > BP0
Covering posture	32.08	<0.0001	PHD2,3,4,5 > PHD 9	6.91	0.075	-
Trampling	0.96	0.96	-	3.39	0.34	-

558 Age of chicks (PHD): $N = 14$, $df = 5$, $F_{crit} = 11.07$. Pair comparison: Nemenyi method

559 with Bonferroni alpha correction: $P = 0.003$. Maternal experience (BP): $N = 14$, $df = 3$, $F_{crit} =$

560 7.82. Pair comparison: Nemenyi method with Bonferroni alpha correction: $P = 0.008$.