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1 **Motherless quail mothers display impaired maternal behaviour and**
2 **produce more fearful and less socially motivated offspring**

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7 ***Running title: Maternal deprivation in Quail***

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20 Early maternal deprivation impairs the behavioural development of young individuals.
21 Recently, strong differences between mothered and maternally-deprived chicks have been
22 reported concerning their emotionality, sociality, and spatial skills. Here we investigated long-
23 term and cross-generational impacts of maternal deprivation by comparing the characteristics
24 of the non-reproductive and the maternal behaviour of 22 mothered and 22 non-mothered
25 adult female Japanese quail (*Coturnix c. japonica*) and by comparing the behaviour of their
26 respective fostered chicks. We reveal that non-brooded mothers were more fearful and less
27 competent in spatial tasks and expressed impaired maternal care, characterized by more
28 aggression towards chicks, higher activity rates and more abnormal pacing during the first
29 days of the care period. Chicks' behaviour was clearly affected by maternal care inducing
30 strong differences in their fearfulness and social motivation. Our results show both long-term
31 and cross-generational impacts of early maternal deprivation in precocial birds.

32 **Key-words: Fearfulness; Japanese quail; maternal behaviour; maternal deprivation;**
33 **maternal effects; precocial bird; sociality; spatial skills.**

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41 The behavioural development of animals is strongly influenced by early post-natal living
42 conditions, particularly interactions with the first care-giver between birth and emancipation
43 (Champagne & Meaney, 2001; Fleming, O'Day, & Kraemer, 1999). During this period, a
44 mother's behaviour affects her offspring's neuronal and physiological development with often
45 long-term consequences on their social and emotional behaviour (Berman, Rasmussen, &
46 Suomi, 1997; Caldji, Francis, Sharma, & Plotsky, 2001; Francis & Meaney, 1999) and their
47 cognitive skills (Bredy, Grant, Champagne, & Meaney, 2003; Liu et al., 2000). These
48 influences can occur through various social learning processes (Holmes & Mateo, 1998) or
49 via more passive mechanisms through which mothers directly modify the neurophysiologic
50 development of offspring by tactile stimulations (Champagne & Curley, 2009). Maternal
51 deprivation paradigms have been widely used to investigate the influence of mothers on the
52 subsequent behaviour of their offspring (see Fleming et al., 2002). Early deprivation can be
53 either partial, caused by precocious weaning (see Latham & Mason, 2008; Livia Terranova &
54 Laviola, 1995) or repeated separations (Dettling, Feldon, & Pryce, 2002; Millstein, Ralph,
55 Yang, & Holmes, 2006), or complete (Albers, Timmermans, & Vossen, 1999a; Bertin &
56 Richard-Yris, 2005; Gonzalez, Lovic, Ward, Wainwright, & Fleming, 2001; Melo et al.,
57 2006). Early repeated separations of young mammals from their care-giver affect their
58 emotional behaviour (Ogawa et al., 1994; Wigger & Neumann, 1999), sociality (Livia
59 Terranova & Laviola, 1995; Seay & Harlow, 1965; Tsuda & Ogawa, 2012), sexual behaviour
60 (Rhees, Lephart, & Eliason, 2001) and cognitive skills (Aisa, Tordera, Lasheras, Del Rio, &
61 Ramirez, 2008; Aisa, Tordera, Lasheras, Del Río, & Ramírez, 2007; Garner, Wood, Pantelis,
62 & van den Buuse, 2007).

63 Complete maternal deprivation of mammals has been comparatively less used. Nevertheless,
64 several studies report that subsequent adult behaviour can be strongly impacted by maternal
65 deprivation, such as reproduction (see Fleming et al., 2002; Gonzalez et al., 2001).

66 Most specifically, early social environment has strong effects on the quality and intensity of
67 rodents' and primates' parenting behaviour expressed in adulthood: maternal deprivation
68 impairs the expression of maternal behaviour. Harlow's famous studies showed that most of
69 the macaque "motherless mothers" either appeared ignorant or were abusive to their infant
70 (Arling & Harlow, 1967; Harlow, Harlow, Dodsworth, & Arling, 1966; Harlow & Suomi,
71 1971). Similarly, only 14% of the female chimpanzees reared by humans became competent
72 mothers (Brent, Williams-Blangero, & Stone, 1996) and maternal deprivation led to
73 impoverishment of rats' maternal behaviour (see A. S. Fleming et al., 2002; Gonzalez et al.,
74 2001; Melo et al., 2006) even towards fostered pups (Palombo, Nowoslawski, & Fleming,
75 2010) confirming the direct effects of maternal deprivation on maternal care.

76 Without entirely reconsidering these results, several authors pointed out that mammals do not
77 offer the possibility to measure rigorously the impact of complete maternal deprivation.
78 Indeed, some care must be artificially provided by human interventions and the characteristics
79 of this artificial care is likely to influence pups' development (Fleming et al., 2002).
80 Comparatively, maternally deprived precocial birds can be reared correctly with human
81 intervention limited to providing heat, and consequently they constitute perfect models to
82 investigate the influences of complete maternal deprivation. Complete deprivation procedures
83 have shown that fearfulness and social motivation (Bertin & Richard-Yris, 2005; Fält, 1978;
84 Perré, Wauters, & Richard-Yris, 2002; Roden & Wechsler, 1998; Shimmura et al., 2010),
85 spatial skills (De Margerie et al., 2012) and rhythmicity (Formanek, Richard-Yris, Houdelier,
86 & Lumineau, 2009; Wauters, Perré, Bizeray, Leterrier, & Richard-Yris, 2002) differ strongly

87 between artificially reared and mothered chicks. Nevertheless, these differences have been
88 evidenced only during the first weeks after hatching and comparatively far less is known
89 about long-term consequences of maternal deprivation on precocial birds. The influence of
90 maternal deprivation on the expression of precocial birds' maternal care remains
91 comparatively unknown whereas other aspects of their reproduction behaviour are known to
92 be affected by early experience (Immelman, 1972).

93 This study aimed to evaluate the long-term influences of total maternal deprivation on adult
94 female precocial birds' emotional reactivity, sociality and spatial skills and on the way they
95 subsequently care for their own chicks. Our model is Japanese quail (*Coturnix coturnix*
96 *japonica*), a domestic precocial bird. Mothers are the only care givers in this species, and care
97 lasts only for a short 11-day period. We first evaluated the behavioural characteristics of
98 mothered and non-mothered females using well-established ethological tests (Bertin &
99 Richard-Yris, 2004; Forkman, Boissy, Meunier-Salaün, Canali, & Jones, 2007; Formanek,
100 Houdelier, Lumineau, Bertin, & Richard-Yris, 2008). We then induced maternal behaviour in
101 these females and evaluated the maternal care expressed by mothered and non-mothered
102 females. As differences in maternal behaviour are known to influence the behavioural
103 development of Japanese quail offspring (Pittet, Coignard, Houdelier, Richard-Yris, &
104 Lumineau, 2012), our last goal was to determine whether these potential maternal care
105 differences impacted the way chicks subsequently behaved by comparing the behavioural
106 characteristics of chicks fostered by females that developed either with or without a mothering
107 hen. We hypothesized that, as for mammals, effects of maternal deprivation would still be
108 observable in adult precocial birds, that their maternal behaviour would be impaired by this
109 early deprivation and that this would subsequently affect chicks' behaviour.

110 **Methods**

111 Ethic Statement

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

117

118 Animals and Housing

119 All the subjects were from a broiler line and were provided by an industrial farm (Les Cailles
120 de Chanteloup, Ille et Villaine, France). Food was available *ad libitum* and conditions were
121 LD (light/dark) 12/12 and $20\pm 1^{\circ}\text{C}$.

122 Grandmothers: 8-week-old adult females ($n=22$) were acquired by the laboratory, individually
123 marked by a numbered ring on a wing and placed individually in wire mesh breeding cages
124 ($51\times 40\times 35\text{cm}$) with a drinker and a feeder. They were left in their cage for 3 weeks before
125 being given chicks for adoption, to become habituated to their environmental conditions. The
126 breeding room contained 44 cages and the females were distributed so that two females were
127 never in neighbouring cages. The other cages were equipped with a heater ($38 \pm 1^{\circ}\text{C}$) for
128 rearing non-brooded chicks.

129 Mothers: They were 176 chicks that had been either adopted by “grandmothers” (brooded) or
130 artificially reared (non-brooded). Male and female chicks were acquired by the laboratory
131 when they were 1 day old. They were immediately placed in groups of 44 in 4 large plastic
132 cages ($98\times 35\times 42$) equipped with a feeder, a drinker and a heater ($38\pm 1^{\circ}\text{C}$). In the evening of
133 their arrival they were divided into two groups: 22 sets of 4 chicks (brooded chicks) were

134 given to the 22 “grandmothers” and 22 sets of 4 chicks (non-brooded chicks) were placed in
135 similar cages equipped with a heater. During this first breeding period, although cages with
136 mothers needed more care interventions, we systematically intervened in all the cages to
137 avoid differences between B and NB related to interactions with humans.

138 Adoptive mothers and warming lamps were removed when chicks were 11 days old, when
139 they disperse naturally (Orcutt & Orcutt, 1976). Sex was determined when they were 3 weeks
140 old and one female was chosen randomly from each cage, individually marked with a
141 numbered ring on a wing and left in her breeding cage until she was 3 months old. When a
142 brood did not include a female (5 broods), we took a female from another brood that included
143 two or more females. Brooded females are noted B (n=22) and females that developed
144 without mothers are noted NB (n=22). Emotional reactivity, sociality and spatial abilities of B
145 and NB were assessed using several well-established poultry behavioural tests during the
146 three weeks before they adopted chicks.

147 Chicks: 200 one-day-old newly acquired chicks were placed in groups of 40 in 5 large plastic
148 cages (98x35x42) equipped with a feeder, a drinker and a heater ($38\pm 1^{\circ}\text{C}$). In the evening,
149 176 of these chicks were randomly selected to be adopted either by B (22 sets of 4 chicks: B-
150 c) or by NB (22 sets of 4 chicks: NB-c). After they were separated from their mothers, the
151 emotional reactivity, sociality and spatial skills of B-c and NB-c were evaluated.

152 **Fostering procedure and observation of maternal Behaviour**

153 Fostering procedure

154 The same fostering procedure was used to induce maternal behaviour in both grandmothers
155 and mothers.

156 Maternal behaviour was induced using the induction procedure described by Richard-Yris
157 (1994). At the beginning of the dark phase (20:00), 4 one-day old chicks were placed gently
158 underneath each female who had been shut up in her nest box (18x18x18cm) one hour before.
159 Boxes were shut up again for the whole night (12 hours) during which the chicks' vocal and
160 physical solicitations induced rapid expression of maternal behaviour by the adult females.
161 The next morning, all the boxes were opened and removed from the cages at 08:00. During
162 the first day that the mothers spent with this first brood, their maternal behaviour was
163 monitored and females that did not express any warming behaviour of the young chicks or
164 that expressed aggression resulting in injuries of chicks were excluded from the experiment:
165 none of the 22 females had to be excluded from the initial breeding period (grandmothers
166 breeding mothers), but 4 B and 2 NB were excluded from the second breeding (B and NB
167 breeding respectively B-c and NB-c) period.

168 Chicks that showed signs of hypothermia (motionless, eyes closed and trembling) when
169 leaving the boxes or later during the breeding period were discarded from the experiment.
170 They were immediately placed under heaters where they recovered swiftly. These chicks were
171 replaced by chicks of the same age, identified by a leg ring, so that they were not tested later.
172 At the end of the breeding period, 60 NB-c and 57 B-c had spent the whole breeding period
173 with their mother. Numbers of chicks replaced did not differ significantly between NB and B
174 (NB: 1.15 ± 0.33 , B: 0.67 ± 0.21 , $U=206$, $p=0.4$) and as many NB as B broods involved at least
175 one replacement during the breeding period (NB: 13/20, B: 11/18, $\chi^2=0.06$, $p=0.8$).

176 Mothers were removed from the cages on post-hatching day (PHD) 11. Chicks then remained
177 with their siblings for two more weeks during which the fearfulness, the social motivation and
178 the spatial skills of two chicks from each cage were evaluated (when two chicks that spent the
179 whole breeding period with the mother were available: n NB-c = 32; B-c = 33). As

180 morphological sexual dimorphism appears only at 3 weeks (Mills, Crawford, Domjan, &
181 Faure, 1997), chicks were chosen randomly, but sex ratios did not differ significantly between
182 B-c and NB-c (sex ratios: B-c=0.88, NB-c=0.89; $\chi^2=0.00$, $df = 1$, $p=0.99$). During this test
183 period, chicks were weighed when they were 14 and 28 days old.

184 Observations of maternal behaviour

185 Maternal behaviour was recorded on PHD 3, 5, 7 and 9. During the breeding period when B
186 and NB females adopted chicks, we evaluated maternal behaviour using instantaneous scan
187 sampling to establish mothers' time-budgets and, simultaneously, focal animal sampling to
188 note complete behavioural sequences (see below for details). The observer stood behind a
189 one-way mirror.

190 *Instantaneous scan sampling:* Each day we recorded 60 scans at 5-minute intervals: 30 scans
191 in the morning and 30 in the afternoon. Each scan recorded whether the mother was warming
192 chicks and if she was, we recorded her posture and how many chicks were being warmed. We
193 also recorded the mother's activity and the distance between each chick and its mother. An
194 index of distance was calculated as the average score of all chicks that were not being
195 warmed. The five classes of distances and associated scores were: on opposite sides of the
196 cage (1), more than half a cage away (0.75), less than half a cage away (0.5), one chick length
197 away (0.25) and in contact (0). The higher the index was, the further from the mother the
198 chicks were when not being warmed. We also recorded whether chicks were warming one
199 another. Data were sampled using an ipod Touch (Apple©) and the application "scan
200 sampling" (Vincent Richard ©).

201 *Focal sampling:* Each cage was observed for two 5-minute sessions when the mother's entire
202 behavioural sequence was recorded. The experimenter noted the frequency of interactive

203 behaviours (aggression: the mother attacked chicks while producing threat vocalizations followed
204 by the chick moving away, pecking: the mother pecked at the chick with her beak closed, trampling
205 chicks and contact breaks) and non-interactive behaviours (locomotion, exploration,
206 observation and maintenance).

207 Separation test

208 To assess the strength of the bond between mothers and chicks, we removed chicks from each
209 cage for 5 minutes on PHD 6 and placed them in similar cages without their mother. Mothers'
210 reactions to this separation were observed behind a one-way mirror and the observer recorded
211 vocalizations and latencies to resume comfort behaviours (eating and resting). At the same
212 time, the reactions of 2 chicks a cage were videotaped to assess latency and frequency of their
213 distress calls and steps.

214 **Behavioural characteristics of foster mothers and chicks**

215 Procedures assessing fearfulness

216 Behavioural tests assessed the levels of fearfulness of both B and NB mothers before they
217 adopted chicks and of their chicks after separation. As fearfulness is a multidimensional trait
218 (Mignon-Grasteau et al., 2003) that cannot be estimated by a single procedure, several tests
219 presenting different environmental conditions and various fear-inducing stimuli were realized.
220 We investigated fearfulness using the procedures described below to assess shyness,
221 neophobia and reactions to humans.

222 All observations except reactions to humans were recorded behind a one-way mirror.

223 *Emergence test:* This test followed a protocol similar to that described by Jones et al. (1991).
224 Quail were individually transported in a wooden box (18x18x18cm) with a removable wall.
225 This box was placed against the apparatus: a large and well-lit wooden box (62x60x33cm)

226 with wood-shavings covering the floor and an observation window. The transport box was
227 kept closed for 1 minute before the door was opened to allow access to the apparatus. The
228 experimenter noted the latency between raising of the door and the emergence of the subject's
229 head out of the box, and its total emergence.

230 *Novel object test:* This test assesses neophobia by the reactions subjects express in the
231 presence of an unfamiliar object (R. B. Jones, 1996). Mothers were tested in their home cage,
232 but chicks had to be socially isolated and were consequently tested in a polyhedral openfield
233 (1m², h=60cm) after a 5-minute habituation. The novel stimulus was an unfamiliar plastic T-
234 shaped object. During a 10-minute focal sampling the experimenter recorded latency to
235 approach the object, frequency of locomotion (walks, runs) and frequency of fear behaviours
236 expressed towards the novel object including escape, withdrawal (slowly walk away from the
237 object keeping it in sight), jumps, fear postures (crouching) and freezing (Jones, 1996; Mills
238 et al., 1997). The experimenter also recorded the frequency of defecation, observations and
239 explorations of the object (pecking at the object), of the apparatus (pecking at a wall or at the
240 floor). Scan samples, at 10-second intervals, recorded at the same time the position of the
241 subject in relation to the object. During observations of mothers, the cages were virtually
242 divided into two zones and the experimenter noted whether the female was in the half of the
243 cage containing the object or not. During observations of chicks, the openfield was divided
244 into three equal zones and the experimenter noted whether the chick was in the object zone, in
245 a middle zone or in the zone opposite to the object.

246 *Human observer test:* This test assesses reactions to humans (Jones, 1993). Subjects were
247 tested in their familiar environment. The experimenter, using instantaneous scan sampling,
248 passed in front of each cage at 5-minute intervals recording a total of 32 scans for each cage.
249 Each time he passed in front of a cage, he stopped for few seconds and recorded the

250 instantaneous activity of all subjects: fear reactions (subject interrupts its ongoing activity and
251 moves away from the observer), observation of the observer, explorations, feeding, resting or
252 maintenance behaviours (resting, self-preening).

253 **Procedures to assess sociality**

254 *Inter-individual distances in home-cage:* When they were 21 days old, inter-individual
255 distances between each chick and its nearest conspecific were recorded by 32 scans of each
256 cage, made at 4-minute intervals. We used the same distance classes and scores as those used
257 to describe distances between mothers and chicks during the brooding period.

258 *Runway test:* This test is an adaptation of the treadmill test (Mills & Faure, 1990) that
259 evaluates subjects' motivation to reach a social stimulus (Formanek et al., 2008). The
260 apparatus is a 100cm-long wire-netting tunnel. Test subjects were transported individually in
261 a wooden box (18x18x18cm), which was then placed at the tunnel entrance. At the other end
262 of the tunnel was a cage (20x35x20cm) containing three unfamiliar conspecifics of the same
263 age as the tested individual, representing a social stimulus. The corridor was divided into four
264 zones: the closest zone to the social stimulus, "1 bird long" (zone P) and 3 equal 32cm-long
265 zones called, from the entrance to zone P: zones A (beginning of the tunnel), B (middle) and
266 C (end of the tunnel). One minute after the transport box had been put in place, the door was
267 opened and the subject was observed for 5 minutes. The experimenter noted latency to emerge
268 completely from the box, to reach zone P, number of crossed zones and time spent in each
269 zone. An index of sociality was calculated using the following formula:

270 $\text{Index of sociality} = \text{Time (s) in zone P} + 0.66 \cdot \text{time in zone C} + 0.33 \cdot \text{time in zone B}.$

271 The higher the index is, the closer the individual remained to the social stimulus. The
272 experimenter also recorded latency to emit a distress call, frequency of distress calls,

273 exploration of the cage containing conspecifics (number of soft pecking against the
274 conspecifics' cage), aggressive behaviour (number of violent pecking against the
275 conspecific's cage, associated with threat vocalizations), fear postures, and jumps.

276 *Reaction to a stuffed conspecific:* Only adult females were tested to assess their reactions to a
277 model adult Japanese quail. The social stimulus was a stuffed female quail. Test subjects were
278 first placed in the centre of a plastic arena (Ø120x60cm) with a linoleum floor, for a 5
279 minutes habituation period. Then the light was switched off for one minute when the lure was
280 placed in the centre of the apparatus. When the light had been switched on again they were
281 observed for a 5-minute focal sequence with the lure and, after a one minute without light, for
282 another 5-minute focal sequence without the lure. During each sequence, the experimenter
283 recorded latency of first distress call, number of distress calls, latency of first step, number of
284 steps and frequencies of observation, exploration and maintenance activities. When exposed
285 to the lure, latencies to approach and to contact the stuffed female were also recorded.

286 **Spatial skills test**

287 *Detour task:* The apparatus was a cross between Zucca & Sovrano's (2008) and Zucca,
288 Antonelli & Vallortigara's (2005) detour apparatuses (Fig. 1). Test mothers and chicks were
289 food deprived for 12h by presenting food for only 2 minutes at middle of the restriction period
290 but water was available continuously. The apparatus was a rectangular arena with an obstacle
291 through which a feeder placed just behind it could be seen. Test subjects were placed in the
292 dark in front of the obstacle and had to go round it to reach the feeder. The experimenter
293 noted latency to take first step, to get round the obstacle, to reach the feeder, which side of the
294 obstacle the subject went and all the subject's behavioural activities (vocalizations,
295 locomotion, jumps, observations, fear posture and maintenance).

296 *Figure 1*

297 **Statistical analyses**

298 As most of our data were not normally distributed, we used non-parametric tests to compare
299 NB's and B's, as well as, NB-c's and B-c's behavioural data, separately per each behavioural
300 variable. Mann-Whitney tests were performed to compare frequencies, latencies and
301 proportions of time (spent in a particular area or performing a particular behaviour) between
302 sets, and Chi-square tests were performed to compare proportions of quail of each set that
303 expressed or did not express a behaviour.

304 For bivariate data (repeated measurements), we computed ANOVAs on repeated
305 measurements after checking response variable and residual normalities by Kolmogorov-
306 Smirnov tests and the homogeneity of variances by Mauchly's sphericity test. Data analyses
307 were computed using Statistica® and XLStat®.

308 **Results**

309 **Long-term effects of mother deprivation on adult behaviour**

310 Effects on emotional reactivity

311 During the emergence test, NB put their head out of the shelter earlier than did B (NB: $5.68 \pm$
312 2.09 s, B: 20.81 ± 8.10 s; Mann-Whitney U-test: $U = 132$, $P = 0.01$), but latencies to emerge
313 completely from the shelter did not differ between the two sets of females ($P > 0.05$). When
314 facing a novel object, latencies to approach and to explore the object did not differ
315 significantly between NB and B ($P > 0.05$). Nevertheless, NB moved more frequently (NB:
316 35.0 ± 2.7 , B: 26.7 ± 3.0 ; $U = 153$, $P = 0.04$), avoided the object more ($U = 120$, $P = 0.004$;
317 Fig. 2a) and defecated more than did B (NB: 0.77 ± 0.11 , B: 0.45 ± 0.13 ; $U = 168.5$, $P =$

318 0.05). The frequencies of other behaviours did not differ significantly between B and NB ($P >$
319 0.05). More B than NB spent a significantly higher proportions of time near the object (NB:
320 8/18, B: 13/17; $\chi^2_1 = 3.73$, $P = 0.05$). NB females expressed more fear postures in reaction to
321 humans ($U = 159$, $P = 0.04$; Fig. 2b). The proportions of scans spent in other activities did not
322 differ significantly between B and NB ($P > 0.05$).

323 *Figure 2*

324 Effects on sociality

325 NB took longer to approach the lure than did B (NB: 79.41 ± 13.47 s, B: 48.18 ± 13.05 s, $U =$
326 159 , $P = 0.05$). After removal of the lure, NB took longer to take their first step (NB: $85.77 \pm$
327 13.03 s, B: 27.59 ± 9.75 s; $U = 111.5$, $P = 0.002$) and tended to take less steps (NB: 25.5 ± 7.68 ,
328 B: 38 ± 8.74 ; $U = 162$, $P = 0.06$). The other behavioural traits measured in this test did not
329 reveal significant differences between NB and B ($P > 0.05$). The runway test revealed no
330 significant differences between females' behavioural expressions or the times they spent in
331 the apparatus' different zones ($P > 0.05$).

332 Effects on spatial skills

333 Fewer NB than B were successful in the detour task (NB: 4/22, B: 13/22; $\chi^2_1 = 7.76$, $P =$
334 0.005). None of the other behavioural traits measured in this test, including latency to take
335 first step and frequency of locomotor acts differed significantly ($P > 0.05$).

336

337 **Effects of mother deprivation on maternal behaviour**

338 Reaction to induction

339 The first interactions with chicks (aggressive behaviour, warming parameters) of females that
340 were maternal after the induction procedure and the number of chicks showing signs of
341 hypothermia during the first day following induction did not differ significantly between B
342 and NB (Mann-Whitney U-test: $P > 0.05$).

343 Maternal traits

344 Brooding parameters (time spent warming chicks, number of chicks warmed and posture
345 preferences), contact breaks or distance to chicks did not differ significantly between B and
346 NB during the whole breeding period (Mann-Whitney; $P > 0.05$).

347 Nevertheless, aggressive behaviours towards chicks and time-budgets showed several
348 differences between the two sets of females.

349 Indeed, NB were more aggressive towards chicks than B at the beginning of the brooding
350 period (PHD3: NB: 2.15 ± 0.71 ; B: 0.39 ± 0.23 ; Mann-Whitney U test: $U = 119.5$, $P = 0.04$)
351 and pecked them more on PHD 7 (NB: 1.15 ± 0.45 , B: 0.11 ± 0.08 ; $U = 132$, $P = 0.03$).
352 Frequencies of chick trampling did not differ between B and NB females on any day of the
353 breeding period ($P > 0.05$). NB's and B's time-budgets differed. NB spent more time active
354 than B (see Fig. 3 for details), but their activity was not affected by chicks' age and we found
355 no significant interaction between set of females and age of chicks (Fig. 3). More NB than B
356 expressed stereotypic pacing (abnormally repeated flight attempts with exaggerated
357 locomotion and pecking against the cage walls) on PHD3, PHD5 and tended to on PHD7 (Fig.
358 4), and NB spent higher proportions of time pacing on these days (PHD3: NB: $4.16 \pm 1.56\%$,
359 B: $2.50 \pm 2.50\%$; Mann-Whitney U-test: $U = 96.5$, $P = 0.003$; PHD5: NB: $2.16 \pm 0.46\%$, B:
360 $1.57 \pm 1.13\%$; $U = 112.5$, $P = 0.03$).

361 *Figure 3*

362 *Figure 4*

363 Reactions to separation

364 Reactions (latencies and frequencies of behaviours and vocalizations) to separation from
365 chicks did not differ significantly between B and NB on PHD6 ($P > 0.05$). Similarly,
366 reactions to separation from their mother did not differ significantly between NB-c and B-c (P
367 > 0.05)

368 **Chicks' growth and behaviour**

369 Weights of NB-c and B-c did not differ significantly on PHD 14 or on PHD 28, but we found
370 an interaction between age and set due to B-c's faster weight gain (Fig. 5).

371 *Figure 5*

372 Emotional reactivity

373 Emergence test data indicated that NB-c's mean latencies were more than twice as long as B-
374 c's for both emergence of the head (NB-c: 18.5 ± 6.54 s, B-c: 5.53 ± 2.26 s; $U = 354.5$, $p =$
375 0.005) and full emergence (NB-c: 21.76 ± 6.78 s, B-c: 8.47 ± 3.34 s; $U = 307$, $P = 0.0007$).
376 When exposed to the observer, NB-c spent less scans self-preening (NB: 0.76 ± 0.33 scans; B:
377 2.16 ± 0.63 scans; $U = 462$, $P = 0.04$). We could find no other significant differences between
378 NB-c's and B-c's behavioural expressions during the emergence test and the reaction to the
379 observer test ($P > 0.05$). NB-c's and B-c's behaviours did not differ significantly in the novel-
380 object test ($P > 0.05$).

381 Sociality

382 Observations of NB-c in their cages indicated that they tended to be more frequently in parts
383 of their cage opposite to their nearer conspecific (NB-c: $4.1 \pm 0.7\%$, B-c: $2.9 \pm 0.6\%$, $U = 490$, P
384 $= 0.09$). Distance scores did not differ significantly between NB-c and B-c ($P > 0.05$).

385 Our distance index indicated that NB-c were further from the social stimulus in the runway
386 test (NB: 160.9 ± 16.0 , B: 204.8 ± 16.1 , $U = 378$, $P = 0.034$). Moreover in this test, NB-c
387 crossed more zones (NB-c: 17.8 ± 1.77 , B-c: 11.31 ± 1.25 ; $U = 321.5$, $P = 0.004$) and
388 emitted distress calls earlier than did B-c (NB-c: 188 ± 21.27 s, B-c: 254.81 ± 15.43 s; $U = 392$,
389 $P = 0.032$).

390 Spatial skills

391 As many NB-c as B-c were successful in the detour task (NB-c: 24/32, B-c: 24/33; $\chi^2_1 = 0.04$,
392 $P > 0.05$) and the latencies of the successful subjects to reach to the feeder did not differ
393 between the two sets (Mann-Whitney U-test: $P > 0.05$).

394 Discussion

395 This study evaluated the modifications induced by maternal deprivation on females'
396 subsequent non-reproductive and maternal behaviour in adulthood. We found that maternally
397 deprived females displayed higher fearfulness and impaired spatial skills. When maternal,
398 these motherless mothers were more aggressive towards chicks and more active during the
399 first half of the care period when they also expressed more stereotypic behaviours than did
400 mothered females. When assessing consequences of these maternal care differences on chick
401 development, we found strong differences between NB-c and B-c as NB-c's fearfulness was
402 higher and their social motivation was lower.

403 Effects of maternal deprivation on adult behaviour

404 First we showed that maternal deprivation impacts the non-reproductive behaviour and spatial
405 skills of females when adult. Although previous reports have shown differences between
406 mothered and non-mothered precocial birds, these reports assessed their behaviour only
407 during the first weeks after hatching and no conclusions could be drawn concerning the long-
408 term influences of this early experience (Bertin & Richard-Yris, 2005; de Margerie et al.,
409 2012; Formanek et al., 2009; Perré et al., 2002; Roden & Wechsler, 1998; Shimmura et al.,
410 2010).

411 In the present study, NB were clearly more fearful than B, they were more neophobic in the
412 presence of a novel object and more fearful in the presence of humans. These results are
413 consistent with Roden's (1998) and Perré's (2002) reports concerning domestic chicks, but
414 contradict reports concerning Japanese quail chicks (Bertin & Richard-Yris, 2005). This last
415 inconsistency might be related to the age or sex of test subjects (adult females vs. mixed-sex
416 chicks), but we think they result from the adoptive mothers. Indeed, the females Bertin &
417 Richard-Yris (2005) used as adoptive mothers for the brooded chicks had been selected for a
418 particular level of emotionality (Mills & Faure, 1991). As maternal emotional reactivity is
419 transmitted to fostered chicks (Houdelier et al., 2011; Richard-Yris, Michel, & Bertin, 2005),
420 using mothers from different lines can affect chicks in such a way that they appear either
421 more or less fearful than non-brooded chicks.

422 Another reported consequence of maternal deprivation is impairment of development of
423 sociality (Dettling et al., 2002; Livia Terranova & Laviola, 1995; Seay & Harlow, 1965;
424 Tsuda & Ogawa, 2012). We found that NB reacted more fearfully to a stuffed conspecific
425 than did B. This reaction could be considered either as a lesser social competence or as a
426 neophobic reaction because they had never been exposed to an adult. The fact that the runway
427 test results revealed no differences in proximity with unfamiliar conspecifics between the two

428 sets, led us to favour the second explanation. Non-brooded chicks were reported to behave
429 less socially than chicks that developed with a mother (Bertin & Richard-Yris, 2005; Perré et
430 al., 2002), but we did not find a similar difference when they were adult. We do not suggest
431 that this result indicates no differences in sociality between B and NB, but rather that
432 characteristics of this species are involved (Guyomarc'h & Saint-Jalme, 1986), as adult
433 females display solitary phases whereas chicks are highly gregarious, making differences in
434 sociality much harder to highlight in adults than in chicks.

435 NB's detour results suggest that their spatial skills have been impaired. Exploratory behaviour
436 of these subjects was assessed when they were chicks (in mixed-sex flocks of 4 mothered or
437 non-mothered chicks), and the exploratory skills of non-mothered chicks already showed a
438 deficit (De Margerie et al., 2012) that seems to be still observable in adulthood. This
439 impairment of spatial skills is consistent with the literature reporting the necessity of maternal
440 stimulation to promote mammals' hippocampal synaptogenesis and spatial learning (Liu et al.,
441 2000). Early maternal deprivation experiments highlighted delayed or impaired spatial
442 learning (Aisa et al., 2007; Garner et al., 2007). As suggested by de Margerie (2012), NB's
443 spatial skills could also be a by-product of their higher fearfulness as fear-related behaviour
444 can inhibit exploration (Murphy, 1978), and NB behaved more fearfully in other tests.
445 Nevertheless inhibition of NB's exploration is not supported by our results since latencies to
446 move and frequencies of moving, freezing or flight attempts did not differ significantly
447 between NB and B. We consequently consider that the impoverishment of spatial stimulations
448 due to maternal deprivation during NB's early life induced their poorer spatial ability.

449 Effects of maternal deprivation on maternal behaviour

450 Our results indicate that the maternal behaviour of maternally deprived females was impaired,
451 at least at the beginning of the breeding period. This impairment is characterized by more

452 aggression, more activity and more frequent pacing stereotypies. The negative impact of
453 maternal deprivation has already been reported in mammals. The maternal behaviour of hand-
454 reared female primates is greatly deficient. Brent (1996) reported that only 14% of hand-
455 reared chimpanzee females were able to provide adequate care and ensure the survival of their
456 infants. Maternally-deprived female primates also behave aggressively towards their offspring
457 (Harlow & Suomi, 1971). Artificially reared rats retrieved fewer pups during a retrieval test
458 and exhibited reduced pup licking and crouching behaviours (Gonzalez et al., 2001).
459 Currently, we cannot draw any conclusion about a direct influence of early experience on
460 aggression of chicks as this could also be the expression of NB's higher fearfulness. High
461 levels of activity when facing stressful situations and expression of stereotypic behaviours are
462 also a known particularity of maternally-deprived mammals (Gonzalez et al., 2001; Latham &
463 Mason, 2008). Interestingly, differences between NB and B females were only measurable
464 during the first half of the breeding period. Contrary to all expectations, primate motherless
465 mothers' brutality or indifference finally decreases in response to infants' persistent
466 solicitations (Harlow & Suomi, 1971). We suggest that, similarly, stimulation of their mother
467 by chicks eventually induces NB mothers to express a maternal behaviour comparable to that
468 of brooded females.

469 Nevertheless, maternal deprivation did not appear to modify several fundamental traits of
470 maternal behaviour, including time spent warming, warming posture preference or the
471 strength of bond with chicks (as reactions to separation from chicks did not differ between NB
472 and B). This result could suggest low plasticity of these traits to experiential factors since they
473 were not clearly influenced by the presence of a mother during the first weeks of the female's
474 life or by the female's breeding experience (Pittet, Coignard, Houdelier, Richard-Yris, &
475 Lumineau, in press). This hypothesis subsequently implies the existence of an important

476 individual determinant that could be highlighted by analysis of mothering styles in our species
477 as reported for many mammals (P. Albers, Timmermans, & Vossen, 1999b; De Lathouwers &
478 Van Elsacker, 2004; Dwyer & Lawrence, 2000; Hill, Greer, Solangi, & II, 2007; Maestriperi,
479 1994), but never investigated in birds. We can also consider that chicks' rearing conditions
480 and particularly the fact that they were reared in social groups strongly influenced this result.
481 Several studies dissociate the confused effects of early social isolation and maternal
482 deprivation in mammals and show that deprived individuals reared with social peers had
483 reduced social and maternal deficits (Melo et al., 2006). Similarly, social conditions may have
484 limited the impact of maternal deprivation in our study. Another possibility is that the
485 expression of precocial animals' maternal care is less sensitive to early maternal stimulations
486 than that of altricial species. The maternal care of precocial guinea pigs reared in social
487 isolation, with social partners or with a mother and social partners did not differ (P. Albers et
488 al., 1999a; Stern & Hoffman, 1970).

489 Development of chicks brooded by NB and B mothers

490 The fact that our results indicate that the early rearing conditions of mothers did not influence
491 chicks' survival rates appears logical as most of the fundamental maternal behaviour traits did
492 not differ between B and NB mothers and our laboratory conditions were non-restrictive. We
493 nevertheless found that chicks brooded by B mothers presented a higher weight gain after
494 separation from their mothers. We could consider here that the slightly harsher conditions in
495 which NB-c developed as their mothers were more aggressive and more active probably
496 impaired their weight gains slightly from the first days although differences between NB-c
497 and B-c became significant only a few weeks after separation. Another possibility is that
498 slight maternal behaviour differences did not affect weight directly, but as NB-c were more
499 reactive in several tests, the testing period could have been a more stressful for these chicks

500 and led to a lesser weight gain after separation from the mother since fearfulness and fear
501 behaviour are negatively associated with growth (Jones, Satterlee, & Marks, 1997).

502 Ability to resolve the detour task did not differ between the two sets of chicks and chicks'
503 success was higher than that of their mothers. Our results indicate that the presence of a
504 mother during early development clearly influences the future ability to resolve spatial tasks.
505 Results from mammals indicate that the behavior of mothers can affect the spatial behavior of
506 their offspring (Albers, Timmermans, & Vossen, 2000). Thus we expected the differences
507 between NB's and B's maternal behaviour to induce differences in chicks' detour abilities.
508 Indeed, precocial chicks brooded by a hen tend to follow their mother and hence explore
509 larger areas than non-brooded chicks (Wauters et al., 2002) and show greater ability to
510 explore new environments (De Margerie et al., 2012). NB's higher frequencies of maternal
511 aggression and pacing could have led NB-c to follow their mother less and to be,
512 consequently, less stimulated to explore their cage. The absence of effects of these maternal
513 behaviour differences on NB-c's and B-c's spatial abilities could be related to physical
514 characteristics of their housing environment where distances are limited and individuals never
515 lose sight of one another. We suggest that such maternal stimulations differences could have
516 stronger impacts on chicks' later spatial abilities if the breeding period took place in a larger
517 and structured environment.

518 We found that the emotional and social behaviour differed between chicks brooded by
519 mothered and non-mothered females. This result is in accordance with our previous reports
520 and confirms an influence of maternal care on chicks' subsequent behavioural development.
521 Interestingly, we highlighted maternal behaviour differences between NB and B only during
522 the first half of the care period, but nevertheless chicks' behaviour differed greatly between
523 sets, suggesting that they were more sensitive during this early period. NB-c were more

524 fearful than B-c in both a novel environment and in the presence of humans, traits that clearly
525 paralleled the differences observed between their mothers. NB-c were also less socially
526 motivated, as they were further from both familiar and unfamiliar conspecifics. We did not
527 find evidence of any differences between their mothers concerning their sociality when adult,
528 but, as chicks, B and NB presented similar differences (Bertin & M. A. Richard-Yris, 2005).
529 Altogether, these results describe a clear case of non-genomic transmission of behavioural
530 characteristics from mothers to chicks, similar to that already reported for both emotionality
531 (M. A. Richard-Yris *et al.*, 2005) and sociality (Formanek *et al.*, 2008) in quail.

532

533

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535

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539

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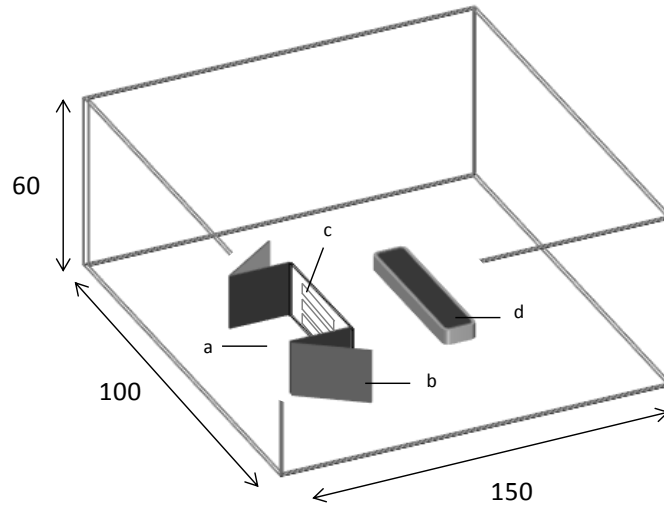
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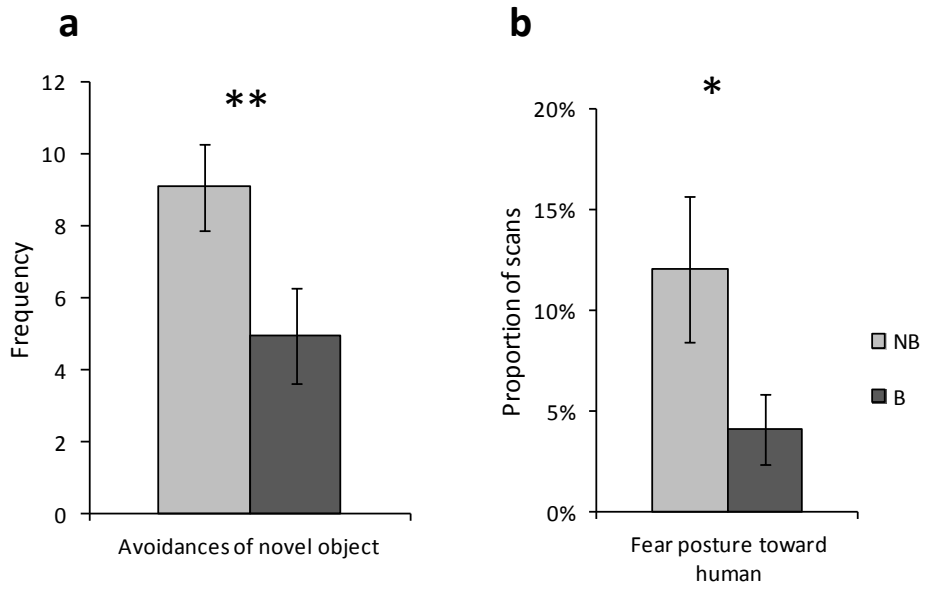
727 **Figures and legends**

728 Figure 1



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730 Figure 2

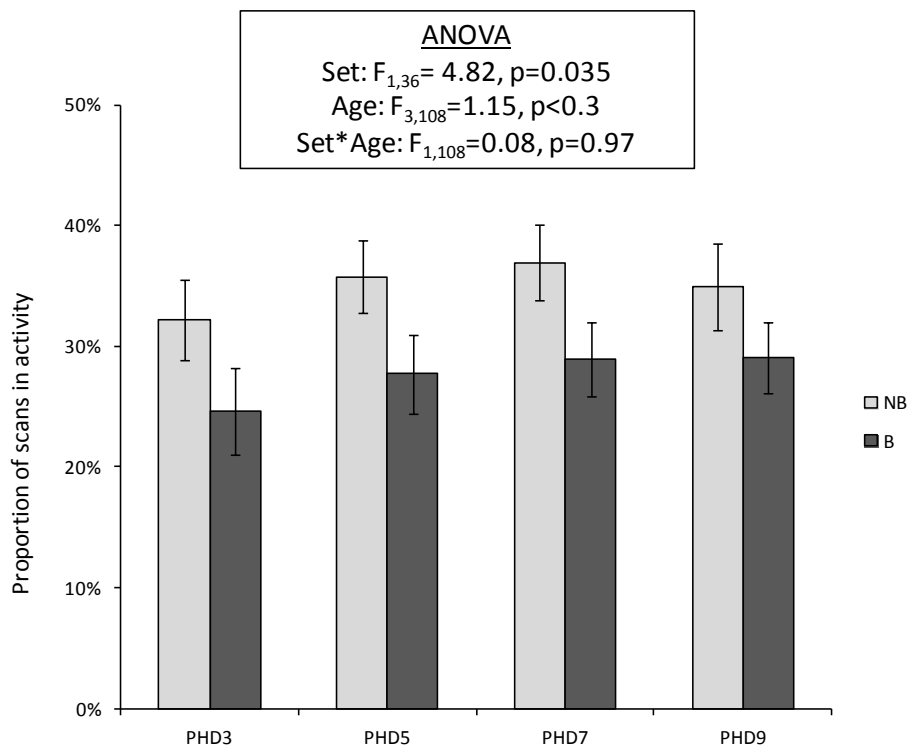


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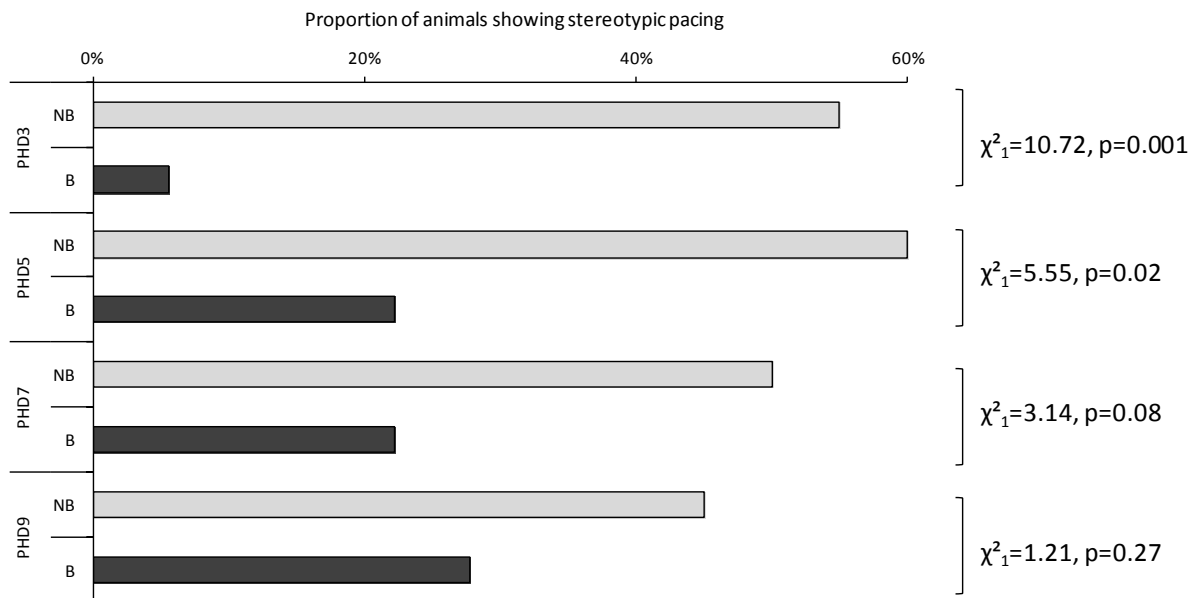
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734 Figure 3



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736 Figure 4



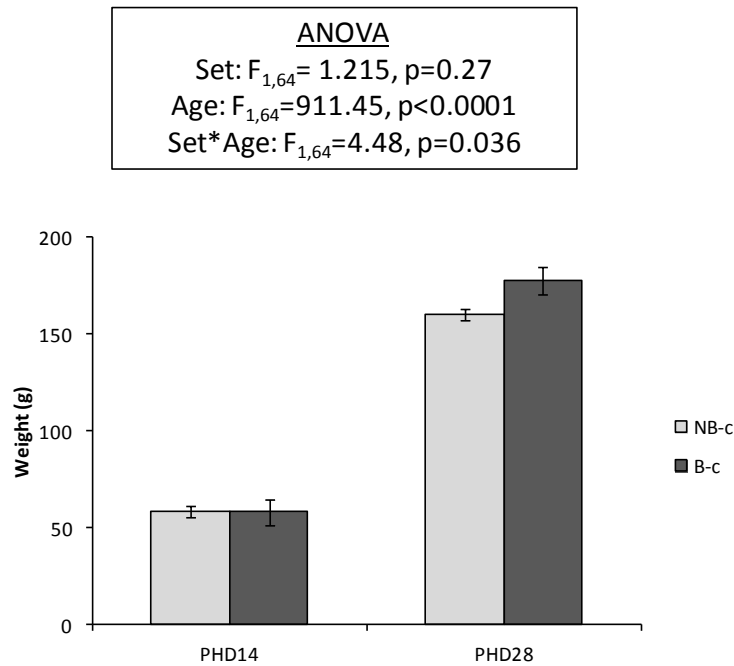
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741 Figure 5



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745 Figure 1. Schematic representation of the detour task with dimensions (in centimetres). a: start
746 location, b: obstacle, c: window, feeder.

747 Figure 2. a: Novel object test. Mean (\pm SEM) frequencies of avoidance of the novel object by
748 NB (grey bar) and B (black bar). b: Reaction to humans test. Mean (\pm SEM) proportions of
749 scans (in % of total number of scans) in fear postures in the presence of a human by NB (grey
750 bar) and B (black bar). Mann-Whitney U-test: ** $p < 0.005$, * $p < 0.05$. (nNB=22, nB=22).

751 Figure 3. Mothers' activity in relation to chick age. Mean (\pm SEM) proportions of scans (in %
752 of total scans) when B and NB were active (including locomotion, exploration, feeding,
753 stereotypic pacing, jumps, alert observations, pecking and aggression). PHD: Days of the
754 breeding period post hatching. Analysis of variance indicated that NB's (n=20) activity level
755 was higher than B's (n=18), but no effect of chicks' age, nor an interaction between set and
756 age of chicks. Grey bar: NB; black bar: B.

757 Figure 4. Mothers' stereotypic pacing in relation to chick age. Proportions of subjects that
758 expressed stereotypic pacing during the breeding period. Chi-square tests indicated that more
759 NB (n=20) than B (n=18) expressed stereotypic pacing at that beginning of the breeding
760 period (PHD3 and PHD5). Grey bar: NB; black bar: B.

761 Figure 5. Chicks' weights in relation to their age. Mean (\pm SEM) weight of NB-c and B-c on
762 PHD14 and PHD28. Analysis of variance indicated an effect of age and an interaction
763 between set and age. (nNB-c=32, nB-c=33). Grey bar: NB-c; black bar: B-c.