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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.

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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

Ethic Statement

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

Animals and Housing

All the subjects were from a broiler line and were provided by an industrial farm (Les Cailles de Chanteloup, Ille et Villaine, France). Food was available *ad libitum* and conditions were LD (light/dark) 12/12 and 20±1°C.

Grandmothers: 8-week-old adult females (n=22) were acquired by the laboratory, individually marked by a numbered ring on a wing and placed individually in wire mesh breeding cages (51x40x35cm) with a drinker and a feeder. They were left in their cage for 3 weeks before being given chicks for adoption, to become habituated to their environmental conditions. The breeding room contained 44 cages and the females were distributed so that two females were never in neighbouring cages. The other cages were equipped with a heater (38 ± 1°C) for rearing non-brooded chicks.

Mothers: They were 176 chicks that had been either adopted by "grandmothers" (brooded) or artificially reared (non-brooded). Male and female chicks were acquired by the laboratory when they were 1 day old. They were immediately placed in groups of 44 in 4 large plastic cages (98x35x42) equipped with a feeder, a drinker and a heater (38±1°C). In the evening of 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±1°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, χ^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

8

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; χ^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

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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).

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 Index of sociality = Time (s) in zone P + 0.66*time in zone C + 0.33*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,

12

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).

Statistical analyses

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

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

Results

Long-term effects of mother deprivation on adult behaviour

Effects on emotional reactivity

During the emergence test, NB put their head out of the shelter earlier than did B (NB: 5.68 ± 2.09s, B: 20.81 ± 8.10s; Mann-Whitney U-test: $U = 132$, $P = 0.01$), but latencies to emerge completely from the shelter did not differ between the two sets of females ($P > 0.05$). When facing a novel object, latencies to approach and to explore the object did not differ significantly between NB and B ($P > 0.05$). Nevertheless, NB moved more frequently (NB: 35.0 ± 2.7, B: 26.7 ± 3.0; $U = 153$, $P = 0.04$), avoided the object more ($U = 120$, $P = 0.004$; 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±13.47s, B: 48.18±13.05s, $U =$

326 159, $P = 0.05$). After removal of the lure, NB took longer to take their first step (NB: 85.77 ±

327 13.03s, B: 27.59 ± 9.75s; 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

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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*

16

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±0.7%, B-c: 2.9±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+79 ± 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 ± 21.27s, B-c: 254.81 ± 15.43s; $U = 392$,

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: $P > 0.05$).

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

19

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; Maestripieri,

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

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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.

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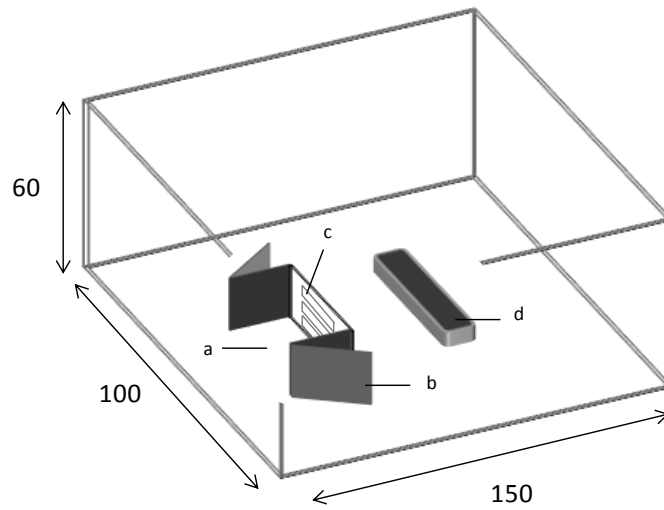720   approaching a stranger. *Cortex*, *44*(1), 13–20.
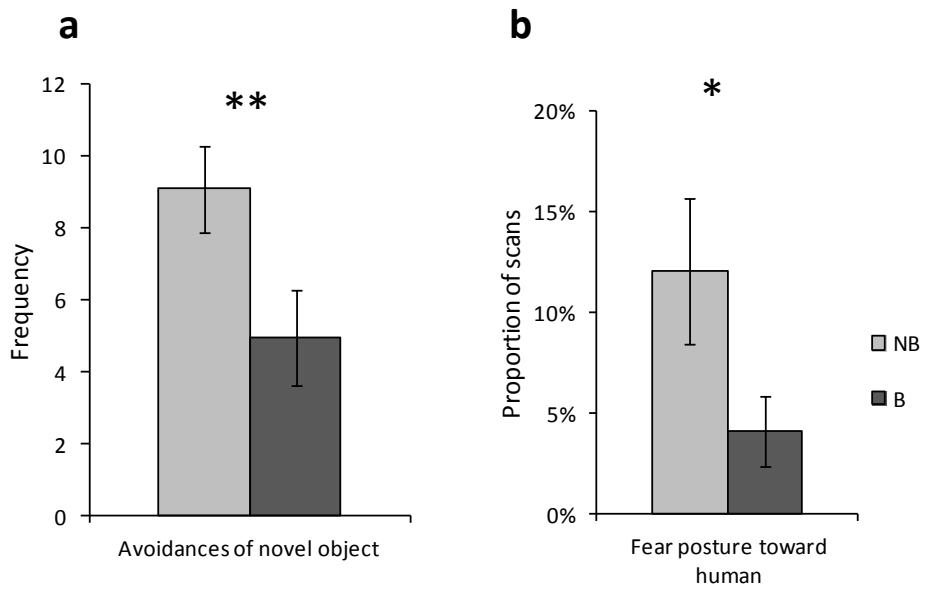
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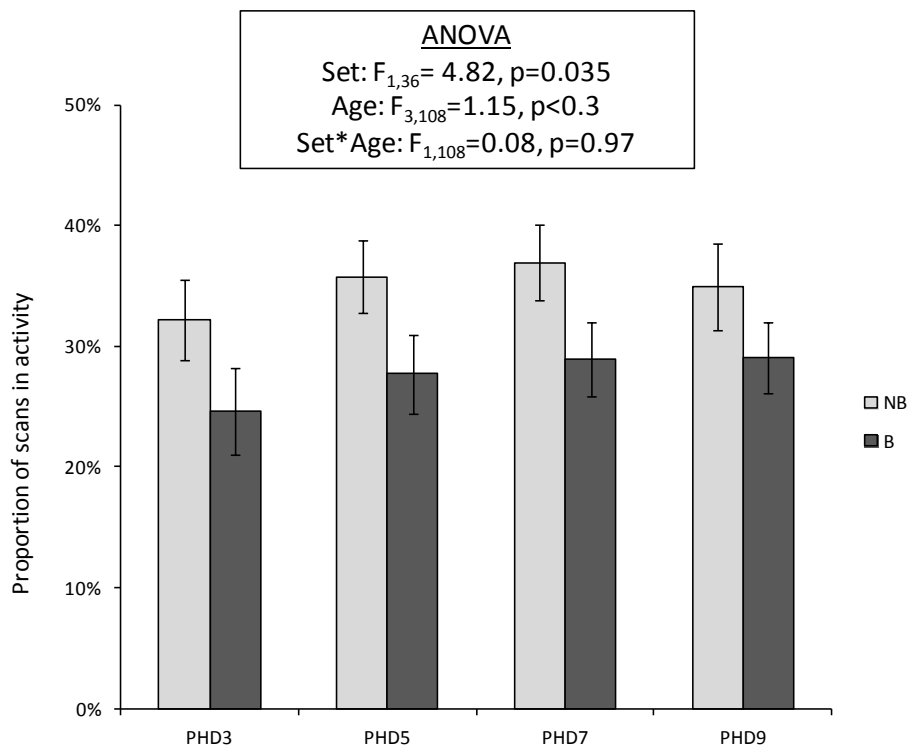
Figures and legends

728 Figure 1

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730 Figure 2

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734   Figure 3

ANOVA
Set: $F_{1,36}$= 4.82, p=0.035
Age: $F_{3,108}$=1.15, p<0.3
Set*Age: $F_{1,108}$=0.08, p=0.97

735

736   Figure 4

Proportion of animals showing stereotypic pacing

χ^2_1=10.72, p=0.001

χ^2_1=5.55, p=0.02

χ^2_1=3.14, p=0.08

χ^2_1=1.21, p=0.27
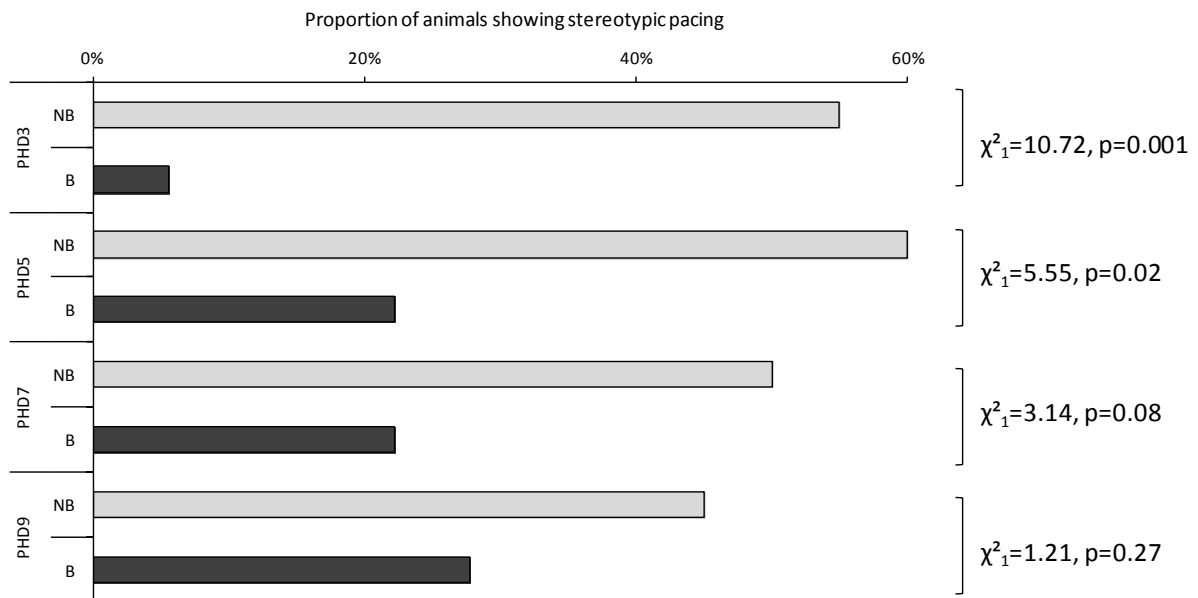
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741   Figure 5

ANOVA
Set: $F_{1,64}$= 1.215, p=0.27
Age: $F_{1,64}$=911.45, p<0.0001
Set*Age: $F_{1,64}$=4.48, p=0.036
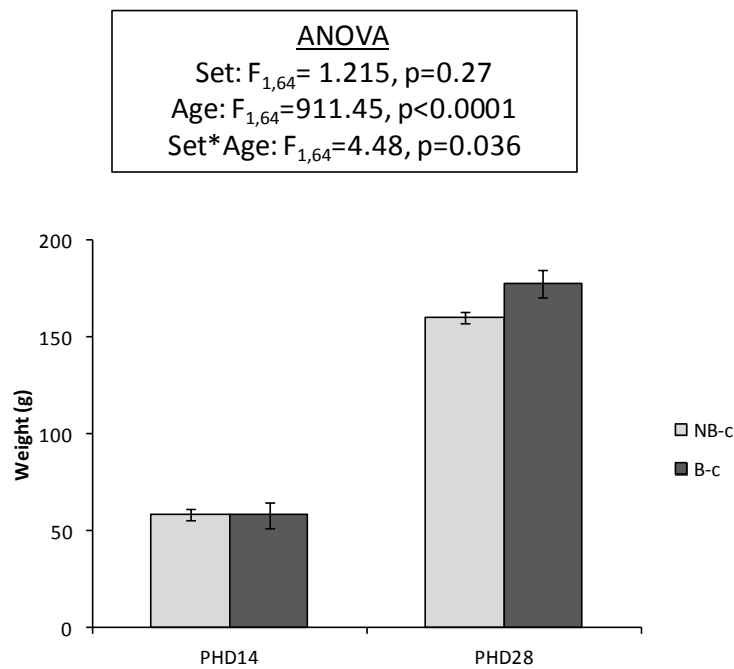
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745   Figure 1. Schematic representation of the detour task with dimensions (in centimetres). a: start
746   location, b: obstacle, c: window, feeder.

747   Figure 2. a: Novel object test. Mean (±SEM) frequencies of avoidance of the novel object by
748   NB (grey bar) and B (black bar). b: Reaction to humans test. Mean (±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 (±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 (±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.