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High social motivation induces deficits in maternal behavior but not plasticity of the subventricular zone in Japanese quail (*Coturnix japonica*)

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ABSTRACT

Maternal behavior develops differently depending on characteristics of the individual, such as age or emotional reactivity. Social motivation, defined as the propensity to establish social contact, has been little studied in relation to maternal behavior in birds. In addition, the transition to motherhood is a time of plasticity in the brain of the new mother in mammals. However, it remains to be determined how maternal brain plasticity is affected in avian species. The present study investigated how a mother's social motivation alters maternal behavior and brain plasticity of the Japanese quail (*Coturnix japonica*). Adult females from lines selected for high and low social motivation were exposed to chicks for 11 days. After maternal care testing, and at matched time points in controls, the brains of females were perfused for assessing immunoreactivity staining of doublecortin, a marker of neurogenesis, in the subventricular zone (SVZ), a neurogenic niche. Our results showed that high socially motivated female quail spent significantly less time in maternal behaviour when exposed to chicks compared to low socially motivated females. Moreover, the high social motivated females warmed chicks with less covering postures and were more rejecting of chicks. Interestingly, the plasticity indicators in the SVZ did not differ between low and high social motivated females and were not associated with differences in maternal caregiving when using doublecortin-immunoreactive staining. Thus, high social motivation in this avian species does not favour maternal behavior and this level of motivation to mother is not related to changes in neuroplasticity in the SVZ of the female quail.

INTRODUCTION

In birds, like in mammals and other vertebrate species, maternal behavior can be defined as any behavior expressed by the female that allows the young to be nourished and protected until they become self-reliant¹. In a few bird species, only the female cares for the young², which in itself is their primary social environment. The mother, therefore, is the main influence on the behavioral development of her young³⁻⁵. In birds, there is also a great diversity of maternal expressions, which vary according to species. For example, in altricial species, such as pigeons, care for young revolves around the nest and chicks are highly dependent on their mother and father, both for feeding and temperature control. In precocial species such as quail, chicks follow their mother from birth. The mother cares for the young for 11 days by warming them, protecting them and offering them food and then the young are independent both in laboratory and semi-natural conditions^{6,7}.

Maternal behavior also shows intraspecific individual variability. Thus, it is likely to be expressed differently depending on a number of individual characteristics such as emotional reactivity or age. For example, in Japanese quail, strong emotional reactivity negatively influences maternal behavior, while aged mothers, who are less reactive give more appropriate maternal care than young mothers^{8,9}. Similarly, the protective behavior of the mare¹⁰ or the percentage of the day spent in contact with the young in the rhesus macaque¹¹ increases with the age of the mother. Ewes selected for their low reactivity to humans and isolation (labeled 'calm') have higher levels of maternal behavior than nervous ewes¹². Surprisingly, social motivation, another characteristic of the individual that can be defined as the propensity to establish social contact¹³, has been little studied in relation to maternal care-giving behaviors in birds. We know that this behavioral trait strongly influences the formation and the strength of the link between familiar conspecifics in the quail¹⁴. Thus, the

possibility that social motivation and the ability to develop maternal behavior are related deserves to be evaluated.

In addition to the onset of maternal behaviors, research in mammals (rodents, sheep and humans) has shown that motherhood is coupled with significant neuroplasticity and remodeling of the maternal brain network, which mediates maternal behavior¹⁵⁻²⁰. Motherhood results in changes in neurogenesis in the maternal brain primarily in neurogenic niches of the hippocampus and subventricular zone (SVZ). For example, the onset of motherhood is associated with a decrease in neurogenesis in the maternal hippocampus (in rodents²¹⁻²³) as well as olfactory bulb (in sheep¹⁹). In non-parturient mammals, offspring exposure resulting in parental behaviors increases neurogenesis in the hippocampus compared to non-offspring-exposed female rodents²³ and male and female prairie voles. Interestingly, non-parental prairie voles exposed to offspring showed significantly elevated rates of neurogenesis compared to those voles that showed parental behaviors when offspring exposed²⁴. It remains to be determined whether social motivation and maternal behaviors may alter neuroplasticity in neurogenic niches of the avian brain.

Japanese quail (*Coturnix japonica*) is an animal model quite appropriate. The social system of Japanese quail changes during the annual cycle. While quail are social during the non-reproductive period, they are monogamous during the reproductive period. After laying, the female incubates the eggs and is the only caregiver of the chicks. She does this without other social contact⁶ indicating that maternal behaviour occurs when the female expresses a low social motivation. In addition, it has been shown that quail selected for a high social motivation showed weaker bond with conspecifics¹⁴. Therefore, the present study hypothesizes that females expressing high social motivation would show lower maternal responsiveness than females showing low social motivation. For this end, we have lines selected for their low (LSR) or their high (HSR) levels of social reinstatement behaviour. The

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selection procedure was described by Mills and Faure¹³: social motivation is measured by the distance made by a chick on a treadmill in order to reach his conspecifics. In addition, this species shows differential maternal styles according to mother's social traits²⁵. Finally, the possibility of inducing maternal behaviour by vocal and tactile stimulation during chick exposure facilitates the use of such a model³.

Therefore, the social motivation of females was evaluated prior to chick exposure in the two lineages low social motivation (LSR) and high social motivation (HSR). Then LSR and HSR quail were paired with three chicks and maternal care was recorded within a period of 11 post-hatching days. After maternal behaviour testing, we tested the hypothesis that maternal behaviors and social motivation are mediators of plasticity in the neurogenic niche of the SVZ, evaluating doublecortin (DCX), a marker of neuroplasticity in avian species, such as quail^{26,27}. We chose the SVZ as it has been shown in mammals to be affected by maternal behaviour and it is an area of the quail brain where there is a high degree of neuroplasticity, as evidenced by the density of DCX-ir fibres and cells.

METHODS

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

Animals. We used 44 adult virgin females from the 61st generation of 2 lines of Japanese quail (*Coturnix japonica*) selected for their high (HSR, n=22) and low (LSR, n=22) social motivation¹³. These lines are selected and maintained at the INRA Research Center (UMR

BOA, INRA, Nouzilly, France). The present experimentation was carried out at the University of Rennes 1 laboratory, where all females were hatched and bred under the same conditions. At the age of 3 months, they were housed in individual wired cage (51×40×35cm) with food and water *ad libitum*. All cages were in the same room maintained to 20±1°C under a 12:12 cycle (lights were on between 8:00am and 8:00pm). Under this photoperiod, females were sexually developed and had stopped laying the week before maternal induction. Before maternal induction, we checked that all females still presented differences in social motivation at adulthood as it is described in Mills and Faure¹³. The 3.5 month-old HSR females spent significantly more time close to conspecifics (within 4 cm zone) than the LSR females when placed in a runway in which 2 females of the same line were placed at one end of the corridor during a 3-min test ($T_{\text{HSR}}=94.6\pm 16.6\text{s}$; $T_{\text{LSR}}=51.6\pm 15.9\text{s}$; $p=0.042$). The females of the 2 lines showed no significant difference in emotional reactivity induced by a brief period of physical restraint (tonic immobility duration: $TI_{\text{HSR}}=157.6\pm 20.5\text{s}$; $TI_{\text{LSR}}=209.7\pm 21.3\text{s}$; $p>0.05$).

For inducing maternal behaviour, we used fertilized eggs bought from a commercial line and hatched in the laboratory (*Les Cailles de Chanteloup*, Corps-Nuds, France). At hatching, 132 chicks were weighed and placed by set of weights (<9.7g, 9.7g-10.3g, >10.3g), in collective cages (98×35×42cm) until the adoption procedure, at the evening of the hatching day. Cages were equipped with a feeder, water and heater (37±1°C).

Maternal behaviour. At 4-months old, females were induced to express maternal behaviour. The day of chicks were hatched, each experimental female had chicks placed in her cage just before night at 8 pm in an opaque nest box (18x18x18cm). Three hatchlings (1 from each weight set) were placed underneath each experimental female. Tactile and vocal stimulations from chicks quickly induced parental response from females²⁸. The following morning, the

nestbox was opened and females were characterized as maternal if they expressed young warming and food offering and maternal calls (cooing and food calls), as it previously done⁷. Brooding lasted 11 days after which mothers and chicks were separated. During the brooding phase, maternal behaviour was observed using instantaneous scan sampling and focal animal sampling on post-hatching days (PHD) 3, 5, 7 and 9^{8,25}.

Female behaviour was scanned every 5 minutes comprising of 20 scans in the morning (from 8.30am to 10am) and 20 scans in the afternoon (from 2pm to 3.30pm) using an iPod Touch (Apple©) equipped with the application “scan sampling” (Vincent Richard©). For each scan, chick feeding, drinking, moving, exploring, pacing were recorded. Warming the chicks as well as the number of warming periods (warming series) was also recorded and a covering posture was differentiated from a non-covering posture i.e. the mother is in high posture or lying on the side not allowing chicks to be warmed. The distance between the female and each chick was classified as follows: “contact” (chick in contact), “near” (\leq one chick length from the foster female), “proximity” (between one chick length and half cage), “distant” (between half cage and one cage length) and “opposite” (at one cage length).

A distance index (ID) was calculated based on²⁹ :

$$ID = \frac{(N^{opposite} + (N^{distant} \times 0.8) + (N^{proximity} \times 0.6) + (N^{near} \times 0.4) + (N^{contact} \times 0.2))}{Total\ Nscan}$$

Focus sampling were performed for 2.5 min in the morning (from 10.30pm to 12pm) and 2.5 min in the afternoon (from 3.30pm to 5pm) to record the number of aggressive behaviours towards chicks (trampling, pecking, attacks), of warming attempts of chicks (accepted or rejected by female), of contact breaks and the identity of the break initiator (mother or chick).

The mother-young bond was also assessed during a separation/reunion test at PDH4. The female was placed alone in a cage similar to her home cage in an isolated room for 3 min

before being reunited to her chicks for 3 min. During the entire test, the female was continuously observed in order to note the latency and frequency of each behaviour and call.

Histology. Because DCX is expressed in proliferating and migrating neuroblasts and is a reliable and specific marker that reflects levels of adult neurogenesis³⁰⁻³², this marker was used to reveal changes in neurogenesis induced by maternal behaviors and social motivation. This marker has been verified in avian species³³⁻³⁵. The last day of maternal care (at PHD 11), a subset of the females used in the maternal behavior study above (n=5 per line) were deeply anesthetized with an overdose of pentobarbital 6% and were transcardially perfused with 4% paraformaldehyde. Brains were post-fixed in 4% paraformaldehyde for 24 h, cryoprotected in 30% sucrose/phosphate-buffered saline solution for up to 1 week, snap frozen on dry ice, and kept at -80°C until further use. Tissue was sliced in 30µm sections on a cryostat (Leica Biosystems, France) throughout the brain in series of 4. Sections were stored in antifreeze cryoprotectant solution and maintained at -18°C.

For immunostaining, one series of tissue was used. This protocol was based on published work²⁶. Tissue was rinsed repeatedly between steps in PBS and PBS-Triton and incubated in 0.6% H₂O₂ for 30 minutes, blocked in serum and incubated overnight at 4°C in goat anti-DCX (1:200, Santa Cruz Biotechnology, Dallas Texas, USA). Sections were incubated for 2h at room temperature in biotinylated rabbit anti-goat (1:500, Jackson ImmunoResearch) and then for 1.5h in avidine-biotine complex (ABC Elite kit; 1:1000; Vector laboratories, France). DAB (3,3-diaminobenzidine; Vector laboratories, France) was used in the final step. Sections were mounted on Superfrost Plus slides (Fischer Scientific, Europe), dried, dehydrated and cover-slipped with Permount (Fischer Scientific, Europe).

In order to investigate the number of immature neurons as well as the area covered by DCX positive fibers and neurons, two sections with areas adjacent to the SVZ were assessed (corresponding to plate 7.8 to 8.2 in the chicken atlas³⁶). This region was observed adjacent to the ventral part of the lateral ventricle, dorsal of the nucleus of the stria terminalis as defined by Aste³⁷. The number of DCX-ir cells were counted under 40x objective (Olympus AX60 microscope) as described^{33,34,38,39}. Cells were considered DCX-ir if cell bodies were darkly impregnated and localized in the area of interest. Area was measured using Axiovision software 4.8.1. Fibres were considered DCX immunoreactive if they were darkly impregnated. Area measurements were taken at 4x objective. We also calculated density of DCX positive cells. For representative photomicrographs see Figure 1.

Statistical analysis.

To analyse maternal behaviour, one principal component analyses (PCA) was performed with the main variables of maternal behaviour from each observation day. Because of the low level of aggressiveness displayed by females, we did not take into account aggressiveness for PCA analysis. We employed a varimax rotation to maximise the independency between components⁴⁰. We chose a criterion of PC loading of |0.5| or higher to consider a variable relevant to a specific component. Factorial scores were thus analysed with an ANOVA on repeated measures to study the influence of time, social line of female and the interaction factor effects. Non-parametric tests (χ^2 test and Mann-Whitney test) were also used for testing efficiency to maternal induction (1 was assigned to successful females, 0 to failed female), call frequencies in response to separation and reunion to chicks and number of DCX-ir cells and area of DCX containing fibres. Pearson correlations were run between maternal behavior scores on each dimension and the area of the SVZ and number of DCX-ir cells in this area. Statistical analyses were performed using the statistical software XLStat

(Addinsoft), Statview (SAS Institute Inc.) or Statistica 13 (Dell Inc.). The level of statistical significance was set at $p \leq 0.05$ (two-tailed tests).

RESULTS

Induction of maternal behaviour.

After the induction procedure, the 22 LSR females expressed maternal behaviours (young warming, food offering and maternal calls), while 5 out of 22 HSR females did not show any maternal care. Thus, significantly more LSR females were induced by chick stimulation than HSR females ($\chi^2 = 5.64$, $p = 0.02$).

Maternal behaviour at PHD3, PHD5, PHD7 and PHD9.

PCA conducted on maternal behaviour explained 64.5% of total variance with 3 main factors. The first dimension of PCA (D1: 29.7% of total variance) was explained by the level of warming behaviour opposite to the distance between mother and chicks is considered as the “protective care”. The D1 scores decreased during the maternal behavior phase ($F_{1,36} = 111.9$, $p < 0.001$). HSR and LSR females showed no significant difference of D1 scores ($F_{1,36} = 1.4$, $p = 0.236$), and no interaction effect was found between line and day ($F_{1,36} = 0.02$, $p = 0.888$).

The second PCA dimension (D2: 19.5% of total variance, labelled as the “non maternal behaviour” axis) was positively correlated with the percentage of uncovering posture (UNCOV) and by the level of activity (Figure 2). The D2 scores decreased during the maternal behavior phase ($F_{1,36} = 34.2$, $p < 0.001$). The HSR females presented higher D2 scores than LSR females ($F_{1,36} = 11.6$, $p = 0.0016$), with no interaction effect found between line and day ($F_{1,36} = 2.1$, $p = 0.153$; Figure 3). The HSR females were more active, and spent less time in uncovering postures over the chicks when warming.

The third PCA dimension (D3: 15.3% of total variance) was mainly explained by rejecting behaviour (contact break by the female and refusal of chick solicitation; Figure 2). The D3 scores decreased during the maternal behaviour phase ($F_{1,36}=4.6$, $p=0.038$). The HSR females showed higher D3 scores than LSR females ($F_{1,36}=4.6$, $p=0.038$), with no interaction effect was found between line and day ($F_{1,36}=0.04$, $p=0.841$; Figure 3). Thus, the HSR females were more rejecting, while the LSR females were more protective.

Response to separation and reunion to chicks at PHD4.

HSR and LSR females did not show any difference of the number of emitted distress calls when separated from their chicks (HSR: 19.2 ± 4.2 ; LSR: 11.3 ± 2.2 ; Mann-Whitney test, $U=145$, $p=0.325$), while LSR females emitted more cooing calls when gathered together (HSR: 4.4 ± 2.1 ; LSR: 7.9 ± 1.8 ; $U=97$, $p=0.014$).

Plasticity in the SVZ.

There were no significant differences between maternal HSR and LSR females with chick exposure in area covered by DCX-ir fibres (Mann-Whitney test, $U=11$, $p=0.8$) or number of DCX-ir cells in the SVZ (Mann-Whitney test, $U=10$, $p=0.6$; Table 1). There were no significant correlations between maternal behaviors on each dimension and the area of the SVZ or number of DCX-ir cells in the SVZ (D1 axis: SVZ area, $r=0.02$, $p=0.9$; DCX+ cells, $r=0.3$, $p=0.2$; D2 axis, SVZ area, $r=0.07$, $p=0.8$; DCX+ cells $r=0.5$, $p=0.1$; D3 axis, SVZ area, $r=0.04$, $p=0.9$; DCX+ cells, $r=0.2$, $p=0.4$).

DISCUSSION

Our results indicate that female quail selected for a low or a high social motivation express differences in maternal care and differences in neuroplasticity in a neurogenic niche, the SVZ. Induction of maternal behaviour by chick exposure was significantly less effective in HSR females than in LSR females. Moreover, while the HSR and LSR mothers expressed the same level of protective care, the HSR mothers expressed more non-maternal behaviours in the presence of chicks than the LSR females. The HSR females also were more rejecting with chicks, while the LSR mothers emitted more calls to the chicks after separation. Interestingly, these differences in motivation and maternal behaviors between HSR and LSR females with chick exposure did not affect the area of the SVZ, as defined by DCX positive fibres, or the number of DCX-ir cells in this area.

Maternal behaviour in LSR and HSR females

Findings from the present study show that LSR females were more easily stimulated by chicks to express maternal care than HSR females. This expands previous work in other avian species showing a relationship between sociality and induction of maternal care. However, this previous work was done in hierarchical species living in a social permanent group, the dominant hens displaying a rapid emergence of maternal behaviour compared to subordinate ones⁴¹, and not in lines bred for social motivation, as in the present study. Thus, the present study suggests how social motivation or affiliative behaviors with a conspecific may relate to maternal care-giving behaviors with chicks. Interestingly, previous work on quail selected for low and high social motivation did not show a difference in maternal care-giving behaviors during an adoption process. However the females in the previous study were older (between 9 to 12 months) than females used in the present study (4 months, at the beginning of reproductive state) and thus there were likely differences in neophobia⁴². Older

females are less neophobic towards chicks and consequently the induction of maternal behaviour is more effective⁸.

In the present study, females of both lines showed similar high levels of protective care. However, HSR female quail expressed less maternal care in presence of chicks. This result indicates that although the majority of HSR females were maternal the quality of their care-giving behaviour was less effective than the behaviours of the LSR females. We also found that HSR females emitted fewer cooing calls after reunion with their chicks compared to LSR females. These cooing calls have been reported to calm the chicks after the stress induced by separation of the mother⁴³ and are a good indicator of a strong mother-young attachment in hens²⁸. Therefore, the decreased vocal response observed in HSR females could indicate a looser bond with their chicks in comparison with LSR mothers. The findings showing that HSR quail show a nonspecific social attraction for conspecifics, whereas LSR quail are able to form bonds with their conspecifics, corroborates this hypothesis¹⁴.

In addition, both HSR and LSR females showed little aggression towards chicks. This can be explained by the fact that both lines are selected for their level of social motivation and that aggressiveness is not correlated to social motivation²⁵.

The main difference between lines selected for social motivation on maternal care-giving behaviours concerns the third dimension of maternal style, *e.g.* rejection behaviour. HSR females expressed more contact breaks and refusal of chick solicitations than LSR females. Our result is in line with data showing, in non-selected quail lines, that there is a positive correlation between social motivation and chick rejection²⁵. Similar conclusions have also been reported in primates in which the more socially motivated females were the less protective of their infants in vervet monkeys⁴⁴, baboons⁴⁵ or in Japanese macaques⁴⁶. In

humans, mothers with social neophobia are more protective of their infant in the presence of strangers than mothers without social neophobia⁴⁷. The poor interactions with chicks displayed by HSR mothers are specifically observed in generic female quail with no brooding experience (housed without a mother)²⁹ or in young females, similar to females tested in the present study. In addition, contrary to the finding that HSR quail are socially more tolerant with their conspecifics than LSR quail¹⁴, HSR females are less tolerant of chicks than LSR females suggesting the hypothesis that high social motivation is not related to the development of maternal care.

SVZ neuroplasticity and maternal behaviors in LSR and HSR female quail

Research in mammals shows that motherhood is coupled with significant remodeling of the maternal brain network, which mediates maternal care-giving behaviors⁴⁸⁻⁵⁰. In addition, a mother's social motivation can affect maternal behaviors and maternal brain plasticity, particularly studied in mammals⁵¹. Our findings show that in an avian species maternal experience (exposure to chicks) for over a week to different social motivated lines (HSR and LSR) does not affect plasticity in the female SVZ as measured by area of the SVZ and number of doublecortin positive cells. To our knowledge, this is the first description of measures of neurogenesis with chick exposure and maternal behaviour in an avian species. Future research in our group is determining whether motherhood, in general, affects female brain plasticity in this avian species.

While a large number of endogenous markers and their combinations are used in mammals to highlight proliferation and differentiation into newly formed neurons, few of these markers are available in birds. The use of DCX, a marker of immature neurons, has been implemented relatively recently and has significantly contributed to a better

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understanding of the regulation of neurogenesis in song birds^{34,35,52,53}. DCX cells and their fibers are also present in the adult telencephalon of non-songbirds but their role is not yet understood⁵⁴. In the present study, differences in social motivation and maternal behaviors after chick exposure with the HSR and LSR lines did not affect DCX-positive fibres or cells in the SVZ area which suggests that this neurogenic niche in the quail brain may not be related to differences in degree of social motivation or maternal care¹⁹. However, it is still not known whether changes in neuroplasticity in the SVZ of avian species who are biological mothers may be affected compared to non-exposed females or whether differences in other neurogenic niches exist with biological or adoptive maternal experience.

A few studies in songbird species show that social factors are strong modulators of neuroplasticity in birds. For example, Alward and colleagues⁵⁵ showed that paired housed male canaries had an increased number of DCX-positive cells in the HVC compared to males housed alone. It should be noted that the opposite pattern of neuroplasticity in a similar study was also reported⁵⁶. These few observations that social context affect neurogenesis, albeit not clearly defined, suggest that in certain interactions with a conspecific neurogenesis is affected. However, we did not find an effect of exposure to chicks on modifying neurogenesis in the SVZ of female quail in the present study. Further research is needed to determine whether aspects of the social environment do affect neuroplasticity in the quail brain and whether these changes are related to differences in social behaviours.

To our knowledge, there is no information about how changes in neuroplasticity and neuroblasts in the SVZ are integrated into neural circuitry in quail. In adult pigeons a significant proportion of new neurons are integrated in the olfactory bulb, as well as to the pallium and dorsal striatum⁵². Although olfaction is not considered as the main sensory input

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in birds, several studies clearly suggest that smell is implicated in the social communication in several bird species (⁵⁷ for review), including Japanese quail⁵⁸. Thus future work should determine the role that these cells have in regards to olfaction and social interaction in the quail brain.

Conclusion

In conclusion, this study shows that socially motivated HSR female quail have deficits in induction and expression of maternal care with chick exposure in comparison with LSR female quail. Thus, it appears that a high motivation to seek contact with adult conspecifics does not imply a high maternal responsiveness to chicks, suggesting counterintuitively that both traits are poorly related. Further work is needed to determine whether a trait for social motivation also affects brain plasticity of biological mothers, leading to the intriguing question of the role of neurogenesis in the maternal brain of birds.

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Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on request

Figure legends

Figure 1. Representative A) schematic representation of the quail brain indicating the location of the subventricular zone (SVZ), and photomicrographs of the B) SVZ delineated by density of doublecortin-ir fibres and indicated with a read line (4x) and C) representative doublecortin-ir cells (40x) in the SVZ of the female quail brain.

Figure 2. Maternal behaviour is described by the main behavioural variables on the dimensions 2 and 3 of PCA with varimax rotation (34.8% of variance). The variables are: frequency of warming (WARM), of chick solicitation (SOLL), index of distance between female and chicks (ID), percentage of uncovering posture when warming (UNCOV), of general activity (ACT), of feeding behaviour (ALIM), of pacing (PACING), of contact break by female (BREAK), of refused solicitation by female (REF) and of warming series (Serie_Warm). A) The second factor represents non-maternal behaviours. B) The third factor represents the level of chicks' rejection by the mother.

Figure 3. Mean (+SEM) scores of HSR and LSR females for A) dimension 2 (D2) which was explained by the percentage of covering posture opposite to the level of activity; for B) dimension 3 (D3) which was mainly explained by rejecting behaviour during the first part (between 3 and 5 post hatching days (PHD)) and the second part (between 7 and 9 PHD) of the maternal behaviour phases.

REFERENCES

1. Rosenblatt JS, Mayer AD, Siegel HI. Maternal Behavior among the Nonprimate Mammals. In: *Reproduction*. Springer, Boston, MA, pp. 229–298.
2. Gowaty PA. Field Studies of Parental Care in Birds: New Data Focus Questions on Variation among Females¹¹Note that scientific names for most species listed are in Table I. For species that do not appear in Table I, scientific names are in the text, after the first appearance of the species. In: Rosenblatt JS, Snowdon CT (eds) *Advances in the Study of Behavior*. Academic Press, pp. 477–531.
3. Formanek L, Houdelier C, Lumineau S, et al. Maternal Epigenetic Transmission of Social Motivation in Birds. *Ethology*. 2008;114:817–826.
4. Formanek L, Richard-Yris M, Houdelier C, et al. Epigenetic Maternal Effects on Endogenous Rhythms in Precocial Birds. *Chronobiol Int*. 2009;26:396–414.
5. Richard-Yris M-A, Michel N, Bertin A. Nongenomic inheritance of emotional reactivity in Japanese quail. *Dev Psychobiol*. 2005;46:1–12.
6. Mills AD, Crawford LL, Domjan M, et al. The behavior of the Japanese or domestic quail *Coturnix japonica*. *Neurosci Biobehav Rev*. 1997;21:261–281.
7. Orcutt F, Orcutt A. Nesting and Parental Behavior in Domestic Common Quail. *Auk*. 1976;93:135–141.
8. Pittet F, Coignard M, Houdelier C, et al. Age Affects the Expression of Maternal Care and Subsequent Behavioural Development of Offspring in a Precocial Bird. *PLOS ONE*. 2012;7:e36835.
9. Pittet F, Houdelier C, Bot OL, et al. Fearfulness Affects Quail Maternal Care and Subsequent Offspring Development. *PLOS ONE*. 2014;9:e102800.
10. Cameron EZ, Linklater WL, Stafford KJ, et al. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav Ecol Sociobiol*. 2000;47:243–249.
11. Hoffman CL, Higham JP, Mas-Rivera A, et al. Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behav Ecol*. 2010;21:972–978.
12. Murphy P, Purvis I, Lindsay D, et al. Measures of temperament are highly repeatable in Merino sheep and some are related to maternal behaviour. *Proc Aust Soc Anim Prod*. 1994;20:247–250.
13. Mills A, Faure J. Divergent Selection for Duration of Tonic Immobility and Social Reinstatement Behavior in Japanese-Quail (*coturnix-Coturnix-Japonica*) Chicks. *J Comp Psychol*. 1991;105:25–38.
14. Schweitzer C, Houdelier C, Lumineau S, et al. Social motivation does not go hand in hand with social bonding between two familiar Japanese quail chicks, *Coturnix japonica*. *Anim Behav*. 2010;79:571–578.
15. Akbari EM, Chatterjee D, Lévy F, et al. Experience-dependent cell survival in the maternal rat brain. *Behav Neurosci*. 2007;121:1001–1011.

- Accepted Article
16. Featherstone RE, Fleming AS, Ivy GO. Plasticity in the maternal circuit: Effects of experience and partum condition on brain astrocyte number in female rats. *Behav Neurosci*. 2000;114:158–172.
 17. Swain JE, Leckman JF, Mayes LC, et al. The neural circuitry of parent-infant attachment in the early postpartum. In: *American College of Neuropsychopharmacology 42nd Annual Meeting*. 2003.
 18. Levy F, Gheusi G, Keller M. Plasticity of the Parental Brain: A Case for Neurogenesis. *J Neuroendocrinol*. 2011;23:984–93.
 19. Brus M, Meurisse M, Keller M, et al. Interactions with the young down-regulate adult olfactory neurogenesis and enhance the maturation of olfactory neuroblasts in sheep mothers. *Front Behav Neurosci*;8. Epub ahead of print 2014. DOI: 10.3389/fnbeh.2014.00053.
 20. Leuner B, Sabihi S. The birth of new neurons in the maternal brain: Hormonal regulation and functional implications. *Front Neuroendocrinol*. 2016;41:99–113.
 21. Leuner B, Mirescu C, Noiman L, et al. Maternal experience inhibits the production of immature neurons in the hippocampus during the postpartum period through elevations in adrenal steroids. *Hippocampus*;17:434–442.
 22. Darnaudéry M, Perez-Martin M, Del Favero F, et al. Early motherhood in rats is associated with a modification of hippocampal function. *Psychoneuroendocrinology*. 2007;32:803–812.
 23. Pawluski JL, Galea LAM. Reproductive experience alters hippocampal neurogenesis during the postpartum period in the dam. *Neuroscience*. 2007;149:53–67.
 24. Ruscio MG, Sweeny TD, Hazelton JL, et al. Pup exposure elicits hippocampal cell proliferation in the prairie vole. *Behav Brain Res*. 2008;187:9–16.
 25. Pittet F, Houdelier C, de Margerie E, et al. Maternal styles in a precocial bird. *Anim Behav*. 2014;87:31–37.
 26. Balthazart J, Charlier TD, Barker JM, et al. Sex steroid-induced neuroplasticity and behavioral activation in birds. *Eur J Neurosci*. 2010;32:2116–2132.
 27. Nkomozezi P, Mazengenya P, Ihunwo AO. Changes in neurogenesis with post-hatching age in the male Japanese quail (*Coturnix japonica*) brain. *Acta Neurobiol Exp (Warsz)*. 2018;78:173–186.
 28. Richard-Yris MA, Leboucher G. Effects of Exposure to Chicks on Maternal Behaviour in Domestic Chickens. *Bird Behav*. 1987;7:31–36.
 29. Pittet F, Coignard M, Houdelier C, et al. Effects of maternal experience on fearfulness and maternal behaviour in a precocial bird. *Anim Behav*. 2013;85:797–805.
 30. Gleeson JG, Lin PT, Flanagan LA, et al. Doublecortin Is a Microtubule-Associated Protein and Is Expressed Widely by Migrating Neurons. *Neuron*. 1999;23:257–271.
 31. Brown JP, Couillard-Després S, Cooper-Kuhn CM, et al. Transient expression of doublecortin during adult neurogenesis. *J Comp Neurol*. 2003;467:1–10.

- Accepted Article
32. Nacher J, Crespo C, McEwen BS. Doublecortin expression in the adult rat telencephalon. *Eur J Neurosci*. 2001;14:629–644.
 33. Balthazart J, Boseret G, Konkle ATM, et al. Doublecortin as a marker of adult neuroplasticity in the canary song control nucleus HVC. *Eur J Neurosci*. 2008;27:801–817.
 34. Balthazart J, Ball GF. Endogenous versus exogenous markers of adult neurogenesis in canaries and other birds: Advantages and disadvantages. *J Comp Neurol*. 2014;522:4100–4120.
 35. Vellema M, Ko M-C, Frankl-Vilches C, et al. What Makes a Marker a Good Marker? *Brain Behav Evol*. 2014;84:5–7.
 36. Kuenzel WJ, Masson M. *A stereotaxic atlas of the brain of the chick (Gallus domesticus)*. Johns Hopkins University Press, <http://agris.fao.org/agris-search/search.do?recordID=US9000051> (1988, accessed 2 October 2018).
 37. Aste N, Balthazart J, Absil P, et al. Anatomical and neurochemical definition of the nucleus of the stria terminalis in japanese quail (*Coturnix japonica*). *J Comp Neurol*. 1998;396:141–157.
 38. Rayen I, Hove DL van den, Prickaerts J, et al. Fluoxetine during Development Reverses the Effects of Prenatal Stress on Depressive-Like Behavior and Hippocampal Neurogenesis in Adolescence. *PLOS ONE*. 2011;6:e24003.
 39. Pawluski JL, van den Hove DLA, Rayen I, et al. Stress and the pregnant female: Impact on hippocampal cell proliferation, but not affective-like behaviors. *Horm Behav*. 2011;59:572–580.
 40. Abdi H. Factor rotations in factor analyses. *Encycl Res Methods Soc Sci Sage Thousand Oaks CA*. 2003;792–795.
 41. Richard-Yris M, Leboucher G. Rate of Emergence of Maternal Responses Varies with Social-Status in the Domestic Hen. *Biol Behav*. 1987;12:207–221.
 42. Richard-Yris M-A. Comportement parental chez les gallinacés: importance du facteur émotivité dans la vitesse d'émergence des réponses parentales. Apports du modèle caille japonaise. In: *Comportement et bien-être animal*. Picard M., Porter R.H., Signoret J.P., 1994, pp. 61–76.
 43. Guyomarc'h J-C, Guyomarc'h C. Vocal communication in European quail; Comparison with Japanese quail. *Comptes Rendus Académie Sci Sér III Sci Vie*. 1996;319:827–834.
 44. Struhsaker TT. Social behaviour of mother and infant vervet monkeys (*Cercopithecus aethiops*). *Anim Behav*. 1971;19:233–250.
 45. Rowell TE, Din N, Omar A. The social development of baboons in their first three months. *J Zool*;155:461–483.
 46. Fairbanks LA. Individual Differences in Maternal Style: Causes and Consequences for Mothers and offspring. In: Rosenblatt JS, Snowdon CT (eds) *Advances in the Study of Behavior*. Academic Press, pp. 579–611.
 47. Murray L, Cooper P, Creswell C, et al. The effects of maternal social phobia on mother–infant interactions and infant social responsiveness. *J Child Psychol Psychiatry*;48:45–52.

- Accepted Article
48. Lonstein JS, Lévy F, Fleming AS. Common and divergent psychobiological mechanisms underlying maternal behaviors in non-human and human mammals. *Horm Behav.* 2015;73:156–185.
 49. Numan M, Insel TR. *The Neurobiology of Parental Behavior*. New York: Springer-Verlag, //www.springer.com/gp/book/9780387004983 (2003, accessed 12 October 2018).
 50. Knobil And Neills Physiology Of Reproduction, <http://gregpdfit.com/knobil-and-neills-physiology-of-reproduction-jimmy-d-neill-ernst-knobil-totally-free-online-books-reading.pdf> (accessed 11 October 2018).
 51. Numan M, Sheehan TP. Neuroanatomical Circuitry for Mammalian Maternal Behaviora. *Ann N Y Acad Sci.* 1997;807:101–125.
 52. Boseret G, Ball GF, Balthazart J. The microtubule-associated protein doublecortin is broadly expressed in the telencephalon of adult canaries. *J Chem Neuroanat.* 2007;33:140–154.
 53. Kim Y-H, Peregrine J, Arnold AP. The distribution of expression of doublecortin (DCX) mRNA and protein in the zebra finch brain. *Brain Res.* 2006;1106:189–196.
 54. Melleu FF, Santos TS, Lino-de-Oliveira C, et al. Distribution and characterization of doublecortin-expressing cells and fibers in the brain of the adult pigeon (*Columba livia*). *J Chem Neuroanat.* 2013;47:57–70.
 55. Alward BA, Mayes WD, Peng K, et al. Dissociable effects of social context on song and doublecortin immunoreactivity in male canaries. *Eur J Neurosci.* 2014;40:2941–2947.
 56. Shevchouk OT, Ball GF, Cornil CA, et al. Studies of HVC Plasticity in Adult Canaries Reveal Social Effects and Sex Differences as Well as Limitations of Multiple Markers Available to Assess Adult Neurogenesis. *PLOS ONE.* 2017;12:e0170938.
 57. Caro SP, Balthazart J, Bonadonna F. The perfume of reproduction in birds: chemosignaling in avian social life. *Horm Behav.* 2015;68:25–42.
 58. Taziaux M, Keller M, Ball GF, et al. Site-specific effects of anosmia and cloacal gland anesthesia on Fos expression induced in male quail brain by sexual behavior. *Behav Brain Res.* 2008;194:52–65.

Table 1. Median [IQ] area of the subventricular zone (SVZ) as defined by doublecortin-ir per mm^2 (DCX), and number of DCX-ir cells in the SVZ in high social motivation (HSR) and low social motivation (LSR) females exposed to chicks. N=5/group. DCX=doublecortin

	Area of SVZ ($\times 10^{-9} \text{mm}^2$)	Number of DCX-ir cells
HSR	7.2 [4.1-11]	50 [30-105]
LSR	8.6 [5.6-9]	62 [47-116]





