



**HAL**  
open science

## Non-genetic Inheritance in Birds: transmission of behaviour from mother to offspring

Cécilia Houdelier, Florent Pittet, Floriane Guibert, Emmanuel de Margerie,  
Sophie Lumineau

► **To cite this version:**

Cécilia Houdelier, Florent Pittet, Floriane Guibert, Emmanuel de Margerie, Sophie Lumineau. Non-genetic Inheritance in Birds: transmission of behaviour from mother to offspring. *Non-Genetic Inheritance*, 2013, 1, pp.62-68. 10.2478/ngi-2013-0007 . hal-01107256

**HAL Id: hal-01107256**

**<https://univ-rennes.hal.science/hal-01107256>**

Submitted on 20 Jan 2015

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Non-genetic Inheritance in Birds: transmission of behaviour from mother to offspring

## Abstract

Understanding the mechanisms of non-genetic inheritance is fundamental as they are involved in evolution processes. One of the paths that non-genetic inheritance can take is via maternal effects. Indeed, we know that mammalian mothers can influence the general development of their offspring both before and after birth. In addition, maternal effects have recently been evidenced in avian species thus opening new possibilities to develop our knowledge of non-genetic inheritance mechanisms. Here, we review the literature on prenatal and postnatal maternal effects on bird behavioural development and we detail recent research that opens new perspectives concerning mechanisms involved in non-genetic inheritance.

## Keywords

Maternal effects • Behavioural development • Phenotypic variability

C. Houdelier\*,  
F. Pittet,  
F. Guibert,

E. de Margerie,  
S. Lumineau

UMR CNRS 6552 Ethologie animale et humaine, Université de Rennes 1, 35042 Rennes, France

© 2013 Houdelier C et al., licensee Versita Sp. z o. o.

This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs license, which means that the text may be used for non-commercial purposes, provided credit is given to the author

Received 11 July 2013

Accepted 04 November 2013

## Introduction

Individual phenotypic variability, first considered as background noise, now appears to play a fundamental role in evolutionary processes and adaptation of species to their environment [1]. An individual's phenotype is the result of both its own genetic factors and, environmental influences [2] that could imply non-genetic inheritance processes. Non-genetic inheritance can be defined as the transmission to offspring of components of the parental phenotype or environment involving factors other than DNA sequences. Such inheritance comprises several proximate mechanisms, such as the transmission to offspring of epigenetic variation (DNA-methylation patterns, chromatin structure or RNA), parental glandular secretion (milk), nutrients (yolk), hormones or behaviors [3]. Non-genetic inheritance encompasses the phenomenon of parental effects [3]. As most mammals and birds depend on their mothers for care early in life, many studies have focused on the role of maternal effects on offspring development.

First, maternal effects can intervene during offspring postnatal development. Maternal deprivation affects many young primates' and rodents' behavioural traits including emotive and social behaviour, cognitive abilities, sexual and maternal behaviour [4-6]. When offspring stay with their mother, their behavioural development is strongly affected by maternal behaviour. Rhesus macaques' with permissive maternal style facilitates their offspring's integration in the social group, whereas a restrictive style, induces a greater timidity in their offspring and

delays their integration into a social group [7]. Frequencies of some of rodents' maternal activities (licking/grooming, arched-back nursing) modulate pups' emotional development [8]. These maternal styles can be transmitted via non-genetic maternal effects [7,9].

Second, maternal effects can intervene prenatally. Mammalian foetuses are exposed to hormones, toxins, immune factors or nutrients that can affect their development [10]. Prenatal exposure to various flavours influences the postnatal olfactory and taste preferences of many species', including humans' offspring [11-13]. Moreover, stressors experienced by gestating females can have deleterious effects on their offspring's behaviour, affecting their emotional reactivity, their social capacities, cognitive abilities and their sexual and parental behaviour [14-16]. These effects on offspring are thought to be mediated by modification of pregnant females' glucocorticoid and androgen plasma concentrations [17,18]. Moreover, these prenatal maternal effects can be transmitted to subsequent generations [19].

The growing amount of research on maternal effects in birds indicates strong parallels between avian and mammalian species. Thus, maternal deprivation and mother's behavioural characteristics modulate precocial species' chicks' behavioural development [20,21]. However, contrary to mammals, few studies have analysed the mechanisms of these postnatal maternal effects. The first section of this article describes recent studies analysing possible mechanisms involved in postnatal maternal effects. The second section focuses on recent developments

\* E-mail: cecilia.houdelier@univ-rennes1.fr

concerning prenatal maternal effects in bird species, especially in relation to transgenerational transmission of such effects.

## Section 1. Postnatal maternal effect mechanisms

Past studies of maternal influences on behavioural development focused largely on the impact of mothers on the social and mating preferences of their offspring [22]. By contrast, recent research has focused on the effects of mothers' characteristics on offspring behavioural development. Females can transmit their feeding preferences [23,24], their emotional and social behaviour in a non-genetic way to their offspring [25,26]. Bird mothers can also transmit the circadian rhythmicity of their feeding activity to their adopted chicks, thus revealing the non-genetic modulation of the ontogeny of offspring circadian rhythm, and by extent, on the functioning of their circadian clock [27].

These studies have revealed that postnatal maternal influences modulate offspring behavioural development. However, the mechanisms of these maternal effects remain, for a large part, unknown. Social learning can be involved in behavioural transmission. Indeed, offspring may learn parental food preference by memorizing the taste/or texture of the food given by a parent [28] or by watching its feeding behaviour [29]. This social learning can be reinforced for example by hens' and quail's maternal behaviour (food calling, food pecking, food dropping and food scratching) that draws the chicks' attention to a food source [30]. Social learning could also be involved in the transmission of some specific-stimulus responses. Thus, young quail reared by fearful mothers could have developed their strong reactivity to humans by watching their mother's behaviour in the presence of humans [20]. However, their responses to a novel environment cannot have developed in this way as their mothers were never confronted to this context [25]. Recently Pittet et al. [31] revealed that the quality of quail mothers' interactions with their chicks affected directly offspring behavioural development. By analysing the effects of females' age on their maternal care, these authors found that older mothers warmed chicks longer and rejected them less than did young females [31]. Consequently chicks of older quail were more fearful and sensitive to social separation than were chicks reared by young mothers. The maternal care of older females (providing more maternal behaviour) could have stimulated the development of a stronger filial imprinting in their chicks. These stronger social bonds with their mother could have increased the effects of separation from their mother as these chicks would have developed higher emotive responses. By contrast, maternal rejection by young females may have induced a less anxious personality in their adopted chicks [31]. Thus the characteristics of mother-chick interactions seem to play a fundamental role in maternal effects. However, in depth understanding of the precise mechanism appears difficult as mother-chick interactions are multimodal and are affected by both mother's and offspring's individual characteristics. In this context, *Ethorobotics* can be an interesting method for analysing the effects of a particular

maternal trait on offspring behavioural ontogeny. Recently, an original report analysed the effects of interactions between young quail and an autonomous mobile robot on the development of chicks' spatial behaviour [32]. Quail chicks spent their first 10 days after hatching with a mobile robot incorporating a heat source and their behaviour was compared to that of chicks confronting the same robot but with its locomotor programme deactivated. Chicks that grew up with a mobile robot presented better spatial abilities than did chicks that grew up with a static robot: they expressed active spatial-search strategies when they were in an arena and solved a detour task more rapidly than the other chicks [32]. Thus, a particular stimulation (that can be extended to a particular maternal trait) perceived during early development can modulate strongly chicks' behavioural development.

## Section 2. Prenatal maternal effects: Transgenerational transmission

As bird embryos develop outside the maternal body, in eggs, prenatal maternal effects were first related to the role of external maternal stimulations (i.e. female's egg rotating rhythm, females' auditory stimulation) on chick development [33,34]. However, Hubert Schwabl's first report [39] showed that the yolk of canaries' and zebra finches' eggs contained important but variable quantities of sexual steroids of maternal origin (testosterone, 5 $\alpha$ -dihydrotestosterone, androstenedione, 17 $\beta$ -oestradiol), thus revealing a new source of prenatal maternal effects. Later, these hormones (as well as progesterone) were identified in the egg yolks of all, both altricial and precocial species, studied to date [35,36]. In parallel, a glucocorticoid, corticosterone, has been identified both in the albumen and in the yolk of many species [36]. Yolk hormone deposition is influenced by many environmental sources, including females' social/sexual context [36], their physical environment [37-39] and/or the females' genetic origin [40,41], social status [42], body condition [43,44], or age [45,46]. Moreover, yolk androgen levels can vary with laying order in a clutch [35,36].

This yolk hormone modulation represents an important path for prenatal maternal effects involved in the emergence of individual variability, and possibly a means to prepare offspring to cope with their environment. Thus, the increase of yolk androgen levels observed in eggs of females living under aversive conditions should modulate their offspring's general phenotype and increase their abilities to cope with this environment. Indeed, prenatal exposure to androgens can increase chicks' growth, immunity, survival rates, their competitive and learning abilities and/or reproduction behaviour [35,36,47,48]. However, prenatal androgens can have negative effects on offspring development [49,50].

Recent reports show that such prenatal maternal influences can have long-term effects on offspring, affecting sometimes the development of following generations. Zebra finch females raised in large broods (i.e. submitted to early developmental stress) produced smaller offspring than did females raised in

small broods [51]. This effect on offspring body growth was similar to that observed for their mothers developing in large broods [52]. Moreover, the reproduction of females whose mothers had been raised in large broods was impaired: hatching success and survival rates of their offspring decreased [53]. Thus the early developmental stress females were subjected to, affected the development of the two following generations. The mechanism of such transgenerational effects could be linked to yolk hormonal modulation, as females reared in large broods laid eggs with lower testosterone levels than did birds reared in small broods [54]. However, parental care could also have been modified by such transmission as the maternal care given by daughters of females reared in large broods appeared deficient [53]. Recently, a study analysed quail's non-genetic maternal transmission across generations of behaviours involving only prenatal factors [55]. Adult female quail were submitted to unpredictable mild stressors during their laying period and the effects of this stress procedure on the development of their offspring and grand-offspring were evaluated. Chicks were incubated artificially and then reared in groups thus excluding postnatal maternal effects. Offspring of stressed females hatched earlier and were heavier than control females' chicks. Moreover they showed higher inherent fearfulness than did control offspring [56]. When they were sexually mature, the sexual behaviour of stressed females' sons was impaired and egg fertilization rates of stressed females' offspring were lower [55]. The effects of this stress were still observable in chicks of the following generation: the inherent fearfulness of grand-offspring (F2) of stressed quail was higher than that of control females' grand-offspring [55]. Surprisingly, the behavioural differences between F2 chicks were similar to those observed between F1 chicks [55,56], thus indicating a transgenerational transmission of stress effects. A potential mechanism of transmission seems to involve yolk hormonal modulation. Indeed, our stress procedures tended to increase

testosterone levels in the egg yolks of stressed quail [56], and in addition modulated the hormonal content of eggs produced by their daughters as yolk testosterone and progesterone levels also increased in their eggs [55].

## Conclusion

Maternal effects play a fundamental role in the behavioural development of young birds both before and after they hatch. As for mammals, they are powerful factors influencing the emergence of phenotypic variability and therefore, the evolution of populations and/or species. However, the mechanisms of bird maternal effects still remain poorly understood and several mechanisms probably interact (Figure 1). First, as mentioned above, social learning processes can be involved in birds' postnatal maternal effects, especially the transmission of feeding preferences, but also of fearfulness, as for mammals [57]. An epigenetic process can also be involved in postnatal maternal effects. The mothering styles of mother rats, especially their levels of tactile stimulation, induced epigenetic modifications (e.g. DNA methylation, modification of chromatin structure) that influenced the expression of glucocorticoid receptors in offspring's hippocampus thus inducing differences in offspring emotional reactivity [58]. Inter-individual differences in quail's maternal care [31,59], reported for the first time for an avian species, can induce epigenetic effects on offspring and explain maternal effects. An epigenetic process could also explain prenatal maternal effects and especially the mechanism of transgenerational transmission. Two hypotheses have been proposed to explain these epigenetic processes [60,61]. The first hypothesis predicts that epigenetic modifications of particular genes (as the result of experience) could be transmitted to offspring. This would imply that epigenetic modifications of germ line cells were not affected by meiosis. The literature provides

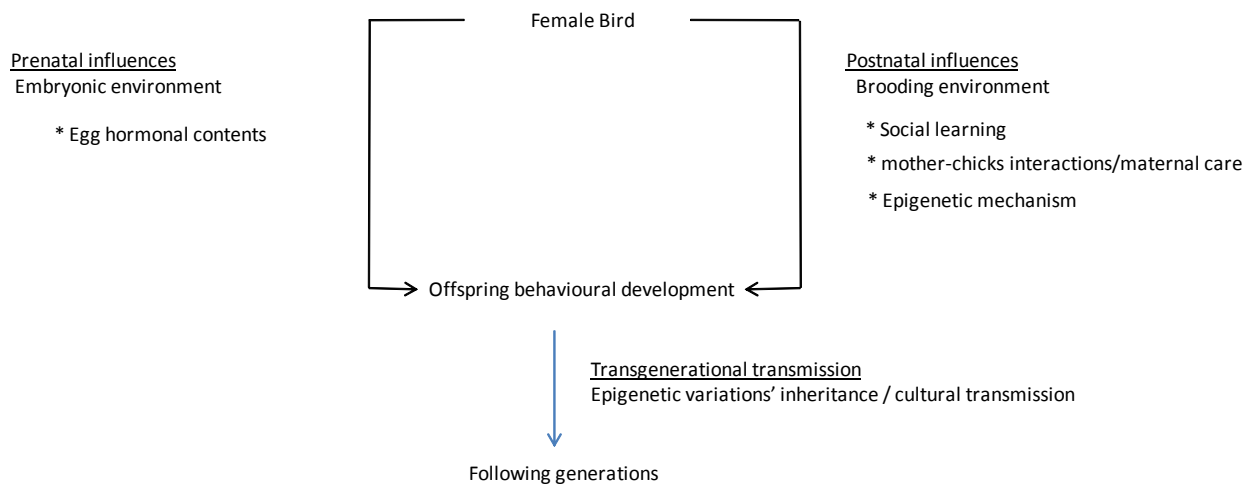


Figure 1. Schema summarizing maternal effects in birds and their possible mechanisms

examples showing that epigenetic modifications can be preserved and transmitted from generation to generation, especially in mammals [62]. A recent study on chickens showed that epigenetic mechanisms could be related to gene expression and DNA methylation. These epigenetic variations are inherited, demonstrating transgenerational stability and revealing their potential role in species evolution. Moreover, some of the methylation differences observed appeared to be tissue-specific whereas others affected a wide range of cells, this revealing the complexity of epigenetic mechanisms [63]. The second hypothesis predicts that epigenetic modifications would be acquired *de novo* in the egg through the action, for example, of steroid hormones of maternal origin. Guibert et al.'s results [55] support this second hypothesis as egg hormonal composition was modified in two successive generations.

Although studies of parental influences have been focused mainly on maternal effects, growing research reveals that paternal effects can also influence mammals' offspring development via non-genetic inheritance [64]. Male birds can also influence sexual traits of their offspring via non-genetic mechanisms. Thus, cultural transmission of Darwin's finches' song from father to their sons has been reported [65]. Moreover, a cross-fostering experience showed that house sparrows' sexual ornamentation (black throat patch) of sons resembled that of their foster father and not that of their biological father [66]. The mechanism of this

paternal effect remains unknown but could imply inter-individual variability in paternal care, the size of the patch appearing to be influenced by nutritional conditions [67]. Paternal effects on offspring development can also be indirect, via males' influence on maternal effects. Indeed, female zebra finches produce larger eggs with higher yolk carotenoids and testosterone levels when mated with less attractive males [68]. Grey partridge females lay eggs with higher yolk testosterone levels when mated with their preferred male [69]. As we know that yolk hormonal contents can influence offspring development, the modulation of egg content by the male's characteristics constitutes an important way for paternal effects and must be taken into account when analysing maternal effects.

Finally, investigations of maternal effect processes appear to overlook the implication of offspring characteristics. However, some studies reveal differences between offspring responses to maternal influence in relation to gender or phenotype. For instance, increase of yolk testosterone levels affected the begging behaviour of zebra finches' female offspring but not of male offspring [70]. Quail postnatal maternal effects were modulated by the emotional phenotype of adopted chicks: the less emotive chicks were more resistant to maternal effects than were the more emotive chicks [71]. Thus these preliminary results stress the fundamental importance of the analysis of maternal effects as a dynamic process involving interactions between mother and offspring.

## References

- [1] Scheiner S.M. 1993 Genetics and Evolution of Phenotypic Plasticity. *Annual Review of Ecology, Evolution and Systematics* 24: 35–68. (doi:10.2307/2097172).
- [2] Gottlieb G. 1991 Experiential canalization of behavioral development: Theory. *Developmental Psychology* 27: 4–13. (doi:10.1037/0012-1649.27.1.4).
- [3] Bonduriansky R., Crean A.J., Day T. 2012 The implications of nongenetic inheritance for evolution in changing environments. *Evolutionary Applications* 5: 192–201. (doi:10.1111/j.1752-4571.2011.00213.x).
- [4] Suomi S.J. 1997 Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin* 53: 170–184.
- [5] Melo A.I., Lovic V., Gonzalez A., Madden M., Sinopoli K., et al. 2006 Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: Tactile stimulation, nest odor, and social rearing prevent these effects. *Developmental Psychobiology* 48: 209–219. (doi:10.1002/dev.20130).
- [6] Hofer M. 1981 Parental contributions to the development of their offspring. *Parental Care in mammals*. New York: Gubernik D & Klopfer P.
- [7] Fairbanks L.A. 1996 Individual Differences in Maternal Style: Causes and Consequences for Mothers and offspring. *Advances in the Study of Behavior*. Academic Press : Rosenblatt J. and Snowdon C. 25: 579–611.
- [8] Francis D., Diorio J., Liu D., Meaney M.J. 1999 Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science* 286: 1155–1158.
- [9] Francis D.D., Meaney M.J. 1999 Maternal care and the development of stress responses. *Current Opinion Neurobiology* 9: 128–134. (doi:10.1016/S0959-4388(99)80016-6).
- [10] Bjorklund D.F. 2006 Mother knows best: Epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Developmental Review* 26: 213–242. (doi:10.1016/j.dr.2006.02.007).
- [11] Hepper P.G. 1988 Adaptive fetal learning: Prenatal exposure to garlic affects postnatal preferences. *Animal Behaviour* 36: 935–936. (doi:10.1016/S0003-3472(88)80177-5).
- [12] Schaal B., Marlier L., Soussignan R. 2000 Human Foetuses Learn Odours from their Pregnant Mother's Diet. *Chemical Senses* 25: 729–737. (doi:10.1093/chemse/25.6.729).
- [13] Simitzis P.E., Deligeorgis S.G., Bizelis J.A., Fegeros K. 2008 Feeding preferences in lambs influenced by prenatal flavour exposure. *Physiology and Behaviour* 93: 529–536. (doi:10.1016/j.physbeh.2007.10.013).
- [14] Braastad B.O. 1998 Effects of prenatal stress on behaviour of offspring of laboratory and farmed mammals. *Applied Animal Behaviour Sciences* 61: 159–180. (doi:10.1016/S0168-1591(98)00188-9).

- [15] Kaiser S., Sachser N. 2005 The effects of prenatal social stress on behaviour: mechanisms and function. *Neuroscience Biobehavioural Review* 29: 283–294. (doi:10.1016/j.neubiorev.2004.09.015).
- [16] Weinstock M. 2008 The long-term behavioural consequences of prenatal stress. *Neurosciences Biobehavioural Review* 32: 1073–1086. (doi:10.1016/j.neubiorev.2008.03.002).
- [17] Welberg L.A, Seckl J.R. 2001 Prenatal Stress, Glucocorticoids and the Programming of the Brain. *Journal of Neuroendocrinology* 13: 113–128. (doi:10.1111/j.1365-2826.2001.00601.x).
- [18] Wewers D., Kaiser S., Sachser N. 2005 Application of an antiandrogen during pregnancy infantilizes the male offsprings' behaviour. *Behavioural Brain Research* 158: 89–95. (doi:10.1016/j.bbr.2004.08.009).
- [19] Pollard I. 1986 Prenatal stress effects over two generations in rats. *Journal of Endocrinology* 109: 239–244.
- [20] Bertin A., Houdelier C., Lumineau S., Formanek L., Richard-Yris M-A. 2008 Influence of early experience with mothers on the development of social and emotional behaviour in Japanese quail. *Biological Psychology: New Research*. Piccard L.N. pp. 193–211.
- [21] de Margerie E., Peris A., Pittet F., Houdelier C., Lumineau S., et al. 2013 Effect of mothering on the spatial exploratory behavior of quail chicks. *Developmental Psychobiology* 55: 256–264. (doi:10.1002/dev.21019).
- [22] Cate ten C., Vos D.R. 1999 Sexual Imprinting and Evolutionary Processes in Birds: A Reassessment. *Advances in the Study of Behavior*. Academic Press, Slater P. 28. pp. 1–31.
- [23] Gajdon G.K., Hungerbühler N., Stauffacher M. 2001 Social Influence on Early Foraging of Domestic Chicks (*Gallus gallus*) in a Near-to-Nature Procedure. *Ethology* 107: 913–937. (doi:10.1046/j.1439-0310.2001.00719.x).
- [24] Wauters A-M., Richard-Yris M-A., Talec N. 200) Maternal Influences on Feeding and General Activity in Domestic Chicks. *Ethology* 108: 529–540. (doi:10.1046/j.1439-0310.2002.00793.x).
- [25] Richard-Yris M-A., Michel N., Bertin A. 2005 Nongenomic inheritance of emotional reactivity in Japanese quail. *Developmental Psychobiology* 46: 1–12. (doi:10.1002/dev.20040).
- [26] Formanek L., Houdelier C., Lumineau S., Bertin A., Richard-Yris M-A. 2008 Maternal Epigenetic Transmission of Social Motivation in Birds. *Ethology* 114: 817–826. (doi:10.1111/j.1439-0310.2008.01536.x).
- [27] Formanek L., Richard-Yris M-A., Houdelier C., Lumineau S. 2009 Epigenetic maternal effects on endogenous rhythms in precocial birds. *Chronobiology International* 26: 396–414. (doi:10.1080/07420520902892433).
- [28] Avery M.L. 1996 Food avoidance by adult house finches, *Carpodacus mexicanus*, affects seed preferences of offspring. *Animal Behaviour* 51: 1279–1283. (doi:10.1006/anbe.1996.0132).
- [29] Mason J., Reidinger R. 1982 Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *The Auk*: 548–554.
- [30] Nicol C.J. 2004 Development, direction, and damage limitation: Social learning in domestic fowl. *Animal Learning Behaviour* 32: 72–81. (doi:10.3758/BF03196008).
- [31] Pittet F., Coignard M., Houdelier C., Richard-Yris M-A., Lumineau S. 2012 Age Affects the Expression of Maternal Care and Subsequent Behavioural Development of Offspring in a Precocial Bird. *PLoS ONE* 7: e36835. (doi:10.1371/journal.pone.0036835).
- [32] de Margerie E., Lumineau S., Houdelier C., Richard-Yris M-A. 2011 Influence of a mobile robot on the spatial behaviour of quail chicks. *Bioinspiration and Biomimetics* 6: 034001. (doi:10.1088/1748-3182/6/3/034001).
- [33] Guyomarc'h J., Yris M-A., Fontenelle G. 1973 Influence de l'expérience prénatale sur le rythme d'activité du poussin domestique. *Bulletin de la Société Scientifique de Bretagne*: 49–57.
- [34] Gottlieb G. 1971 Development of species identification in birds: An inquiry into the prenatal determinants of perception. Oxford, England: U. Chicago Press. 176 p.
- [35] Groothuis T.G.G., Müller W., von Engelhardt N., Carere C., Eising C. 2005 Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neurosciences Biobehavioural Review* 29: 329–352. (doi:10.1016/j.neubiorev.2004.12.002).
- [36] Gil D. 2008 Chapter 7 Hormones in Avian Eggs: Physiology, Ecology and Behavior. *Advances in the study of behavior*. 38: 337–398.
- [37] Schwabl H. 1996 Environment modifies the testosterone levels of a female bird and its eggs. *Journal of Experimental Zoology* 276: 157–163. (doi:10.1002/(SICI)1097-010X).
- [38] Guesdon V., Bertin A., Houdelier C., Lumineau S., Formanek L., et al. 2011 A Place to Hide in the Home-Cage Decreases Yolk Androgen Levels and Offspring Emotional Reactivity in Japanese Quail. *PLoS ONE* 6: e23941. (doi:10.1371/journal.pone.0023941).
- [39] Guibert F., Richard-Yris M-A., Lumineau S., Kotschal K., Guémené D., et al. 2010 Social instability in laying quail: consequences on yolk steroids and offspring's phenotype. *PLoS ONE* 5: e14069. (doi:10.1371/journal.pone.0014069).
- [40] Gil D., Faure J-M. 2007 Correlated response in yolk testosterone levels following divergent genetic selection for social behaviour in Japanese quail. *Journal of Experimental Zoology Part Ecology Genetic Physiology* 307A: 91–94. (doi:10.1002/jez.a.340).
- [41] Bertin A., Richard-Yris M-A., Houdelier C., Richard S., Lumineau S., et al. 2009 Divergent selection for inherent fearfulness leads to divergent yolk steroid levels in quail. *Behaviour* 146: 757–770. (doi:10.1163/156853909X446190).
- [42] Tanvez A., Parisot M., Chastel O., Leboucher G. 2008 Does maternal social hierarchy affect yolk testosterone deposition in domesticated canaries? *Animal Behaviour* 75: 929–934. (doi:10.1016/j.anbehav.2007.08.006).
- [43] Verboven N., Monaghan P., Evans D.M., Schwabl H., Evans N., et al. 2003 Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). *Proceedings*



- of the Royal society of London B Biological Sciences 270: 2223–2232. (doi:10.1098/rspb.2003.2496).
- [44] Tschiren B., Sendecka J., Groothuis T.G.G., Gustafsson L., Doligez B. 2009 Heritable variation in maternal yolk hormone transfer in a wild bird population. *American Naturalist* 174: 557–564.
- [45] Okuliarová M., Skrobánek P., Zeman M. 2009 Variability of yolk testosterone concentrations during the reproductive cycle of Japanese quail. *Comparative Biochemistry and Physiology A Molecular and Integrative Physiology* 154: 530–534. (doi:10.1016/j.cbpa.2009.08.012).
- [46] Guibert F., Richard-Yris M-A., Lumineau S., Kotschal K., Möstl E., et al. 2012 Yolk testosterone levels and offspring phenotype correlate with parental age in a precocial bird. *Physiology and Behavior* 105: 242–250. (doi:10.1016/j.physbeh.2011.08.009).
- [47] Müller W., Dijkstra C., Groothuis T.G.G. 2009 Maternal yolk androgens stimulate territorial behaviour in black-headed gull chicks. *Biology Letters* 5: 586–588. (doi:10.1098/rsbl.2009.0283).
- [48] Bertin A., Richard-Yris M-A., Möstl E., Lickliter R. 2009 Increased yolk testosterone facilitates prenatal perceptual learning in Northern bobwhite quail (*Colinus virginianus*). *Hormone and Behavior* 56: 416–422. (doi:10.1016/j.yhbeh.2009.07.008).
- [49] Sockman K.W., Schwabl H. 2000 Yolk androgens reduce offspring survival. *Proceedings of the Royal society of London B Biological Sciences* 267: 1451–1456. (doi:10.1098/rspb.2000.1163).
- [50] Rubolini D., Martinelli R., von Engelhardt N., Romano M., Groothuis T.G.G., et al. 2007 Consequences of prenatal androgen exposure for the reproductive performance of female pheasants (*Phasianus colchicus*). *Proceedings of the Royal society of London B Biological Sciences* 274: 137–142. (doi:10.1098/rspb.2006.3696).
- [51] Naguib M., Gil D. 2005 Transgenerational body size effects caused by early developmental stress in zebra finches. *Biology Letters* 1: 95–97. (doi:10.1098/rsbl.2004.0277).
- [52] Naguib M., Riebel K., Marzal A., Gil D. 2004 Nestling immunocompetence and testosterone covary with brood size in a songbird. *Proceedings of the Royal society of London B Biological Sciences* 271: 833–838. (doi:10.1098/rspb.2003.2673).
- [53] Naguib M., Nemitz A., Gil D. 2006 Maternal developmental stress reduces reproductive success of female offspring in zebra finches. *Proceedings of the Royal society of London B Biological Sciences* 273: 1901–1905. (doi:10.1098/rspb.2006.3526).
- [54] Gil D., Heim C., Bulmer E., Rocha M., Puerta M., et al. 2004 Negative effects of early developmental stress on yolk testosterone levels in a passerine bird. *Journal of Experimental Biology* 207: 2215–2220.
- [55] Guibert F., Lumineau S., Kotschal K., Möstl E., Richard-Yris M-A., et al. 2013 Trans-generational effects of prenatal stress in quail. *Proceedings of the Royal society of London B Biological Sciences* 280: 20122368.
- [56] Guibert F., Richard-Yris M-A., Lumineau S., Kotschal K., Bertin A., et al. 2011 Unpredictable mild stressors on laying females influence the composition of Japanese quail eggs and offspring's phenotype. *Applied Animal Behavioural Sciences* 132: 51–60. (doi:10.1016/j.applanim.2011.03.012).
- [57] Olsson A., Phelps E.A. 2007 Social learning of fear. *Nature Neuroscience* 10: 1095–1102. (doi:10.1038/nn1968).
- [58] Weaver I.C.G., Cervoni N., Champagne F.A., D'Alessio A.C., Sharma S., et al. 2004 Epigenetic programming by maternal behavior. *Nature Neuroscience* 7: 847–854. (doi:10.1038/nn1276).
- [59] Pittet F., Houdelier C., De Margerie E., Le Bot O., Richard-Yris M., et al. 2013 Maternal styles in birds. *Animal Behaviour*. In press
- [60] Lindqvist C., Janczak A.M., Nätt D., Baranowska I., Lindqvist N., et al. 2007 Transmission of Stress-Induced Learning Impairment and Associated Brain Gene Expression from Parents to Offspring in Chickens. *PLoS ONE* 2: e364. (doi:10.1371/journal.pone.0000364).
- [61] Nätt D., Lindqvist N., Stranneheim H., Lundeberg J., Torjesen P.A., et al. 2009 Inheritance of Acquired Behaviour Adaptations and Brain Gene Expression in Chickens. *PLoS ONE* 4: e6405. (doi:10.1371/journal.pone.0006405).
- [62] Richards E.J. 2006 Inherited epigenetic variation — revisiting soft inheritance. *Nature Reviews Genetics* 7: 395–401. (doi:10.1038/nrg1834).
- [63] Nätt D., Rubin C-J., Wright D., Johnsson M., Beltéky J., et al. 2012 Heritable genome-wide variation of gene expression and promoter methylation between wild and domesticated chickens. *BMC Genomics* 13: 59. (doi:10.1186/1471-2164-13-59).
- [64] Curley J.P., Mashoodh R., Champagne F.A. 2011 Epigenetics and the origins of paternal effects. *Hormone and Behaviour* 59: 306–314. (doi:10.1016/j.yhbeh.2010.06.018).
- [65] Grant B.R., Grant P.R. 1996 Cultural Inheritance of Song and Its Role in the Evolution of Darwin's Finches. *Evolution* 50: 2471. (doi:10.2307/2410714).
- [66] Griffith S.C., Owens I.P.F., Burke T. 1999 Environmental determination of a sexually selected trait. *Nature* 400: 358–360. (doi:10.1038/22536).
- [67] Veiga J.P., Puerta M. 1996 Nutritional Constraints Determine the Expression of a Sexual Trait in the House Sparrow, *Passer domesticus*. *Proceedings of the Royal society of London B Biological Sciences* 263: 229–234. (doi:10.1098/rspb.1996.0036).
- [68] Gilbert L., Williamson K.A., Hazon N., Graves J.A. 2006 Maternal effects due to male attractiveness affect offspring development in the zebra finch. *Proceedings of the Royal society of London B Biological Sciences* 273: 1765–1771. (doi:10.1098/rspb.2006.3520).
- [69] Garcia-Fernandez V., Guasco B., Tanvez A., Lacroix A., Cucco M., et al. 2010 Influence of mating preferences on yolk testosterone in the grey partridge. *Animal Behaviour* 80: 45–49. (doi:10.1016/j.anbehav.2010.03.023).

- [70] Engelhardt N. von, Carere C., Dijkstra C., Groothuis T.G.G. 2006 Sex-specific effects of yolk testosterone on survival, begging and growth of zebra finches. *Proceedings of the Royal society of London B Biological Sciences* 273: 65–70. (doi:10.1098/rspb.2005.3274).
- [71] Houdelier C., Lumineau S., Bertin A., Guibert F., De Margerie E., et al. 2011 Development of Fearfulness in Birds: Genetic Factors Modulate Non-Genetic Maternal Influences. *PLoS ONE* 6: e14604. (doi:10.1371/journal.pone.0014604).