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

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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

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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

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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, 5α-dihydrotestosterone, androstenedione, 17β-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

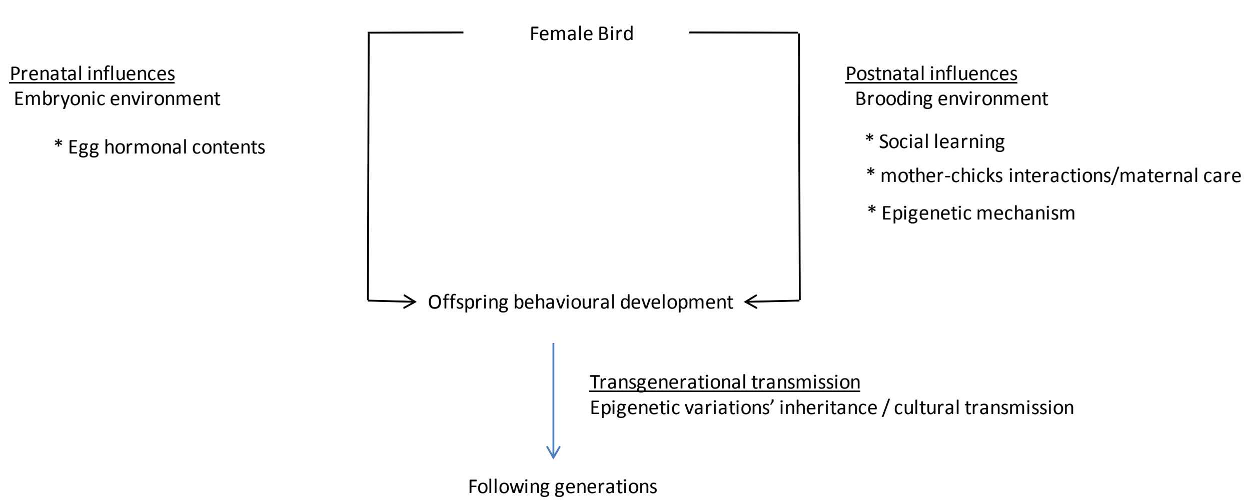

Figure 1. Schema summarizing maternal effects in birds and their possible mechanisms

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 take 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.

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