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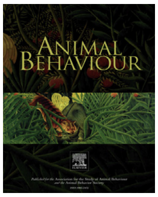

Maternal styles in a precocial bird

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Care provided by females of many mammal species varies naturally between individuals; these differences in turn influence the phenotypic development of their offspring. When individual maternal behavioural traits are consistent over a number of breeding periods, maternal styles can be defined. These styles have been studied in a large range of mammalian species. Nevertheless, mammals rarely offer the possibility to dissociate mothers' behavioural influence from their genetic influence or their physiological influence via lactation. Here, we provide, for the first time, evidence of the existence of a precocial bird species' maternal styles. By using an adoption procedure we evaluated how maternal style affected the behaviour of Japanese quail, *Coturnix coturnix japonica*, chicks, via exclusively nongenomic mechanisms. As well as evidence for the existence of maternal styles in this species, we also found correlations between females' temperaments, maternal styles and their fostered chicks' development. Our findings indicate that maternal styles are key features that help understand nongenomic transmission of behavioural characteristics whose vectors have remained poorly understood.

The way in which individuals behave in challenging situations can have significant fitness consequences (Dingemanse, Both, Drent, & Tinbergen, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Smith & Blumstein, 2008). In a wide range of species, individual differences in behavioural reactions when facing challenges can remain consistent over time and situations (Réale et al., 2007; Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011). These behavioural consistencies have been studied mainly in nonreproductive contexts, focusing on several dimensions of fearfulness, exploration and sociality and have been termed temperaments or personalities (see Réale et al., 2007 for a review). Nevertheless, many vertebrates can also present individual differences related to reproductive behaviours. Maternal (or mothering) styles can be defined as the individual differences in the dimensions of care expressed by a female towards her young that remain consistent over several periods of maternal care (Albers, Timmermans, & Vossen, 1999; Dwyer & Lawrence, 2000). Maternal styles thus constitute an individual signature of maternal care that must be evaluated over several maternal care periods to make sure that individual differences in care are not due to individual differences in offspring characteristics. These styles are defined by dimensions of care, identified by the relationships between the behaviours of the maternal repertoire. For instance, consistent individual differences in the maternal behaviour of many nonhuman primate species appear in two dimensions of care: protection and rejection. These dimensions of care are independent and both are defined by several correlated care items (see Fairbanks, 1996; Groothuis & Maestripieri, 2013). So far, maternal styles have been described in humans (Van Ijzendoorn et al., 2000), nonhuman primates (Fairbanks, 1996) and altricial (Champagne, Francis, Mar, & Meaney, 2003) and precocial (Dwyer & Lawrence, 2000; Spinka et al., 2000) nonprimate mammals. Identifying and understanding the relationships between individual differences within and outside the family context to understand their coadaptation remains a key challenge (Roulin, Dreiss, & Kölliker, 2010). By investigating the biological causes and consequences of these individual differences in the maternal care of several mammalian species, researchers have reported a link between maternal style and temperament. Mothers' temperaments influence maternal styles (Fairbanks, 1996; Maestripieri, 1993; Plush, Hebart, Brien, & Hynd, 2011) and, in turn, are reported to have a strong impact on offspring temperament (Schino, Speranza, & Troisi, 2001; Weaver et al., 2004). For instance, anxious baboon, *Papio* spp. (Altmann, 1980) and rhesus monkey, *Macaca mulatta* (Maestripieri, 1993) females show high levels of protection of their infants, whereas rejection rates of Japanese macaques, *Macaca fuscata*, are reported to affect their infants' sociality (Schino et al., 2001). So far, mothering styles and their relationship with temperament have been studied only in mammalian species.

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Maternal styles, as defined above, have never been rigorously identified in a bird species. Nevertheless, consistency of a particular parental care behaviour has been described in altricial birds, suggesting the potential existence of parental styles. For example, food provisioning by a male house sparrow, *Passer domesticus*, can be consistent across broods and is not influenced by his partner's efforts (Schwagmeyer & Mock, 2003). Moreover, parents' temperaments can affect such care behaviour, thus suggesting a potential relationship between temperament and parenting style in birds. For example, the food provisioning and nest defence of titmice (Paridae) are related to their exploratory and aggressive behaviours (Hollander, Van Overveld, Tokka, & Matthysen, 2008; Mutzel, Dingemanse, Araya-Ajoy, & Kempenaers, 2013). Finally, bird mothers can strongly modify the behavioural development of their offspring via nongenetic influences occurring during the early postnatal period. In particular, these maternal effects have been reported to be strong in precocial birds, in which mothers can transmit nongenetically some of their temperament traits to chicks, including fearfulness (Houdelier et al., 2011; Richard-Yris, Michel, & Bertin, 2005) and traits related to sociality (Formanek, Houdelier, Lumineau, Bertin, & Richard-Yris, 2008). Precocial birds are currently becoming the models of choice to investigate such maternal effects because the absence of lactation and the opportunity to carry out adoption procedures enable researchers to disentangle behavioural from physiological (Catalani et al., 2000; Hinde & Capitanio, 2010), genetic (Schino et al., 2001) and prenatal (Stamps & Groothuis, 2010) influences. Nevertheless, the mechanisms associated with these influences remain unknown. In these precocial bird species, as in most mammals, mothers are the only caregivers and express a rich maternal behavioural repertoire to provide warmth and protection to their offspring and to stimulate their feeding behaviour until they can look after themselves (Nelson, 1995). Nevertheless, the implication of individual differences in the maternal behaviour of precocial hens has never been investigated in relation to these maternal influences.

We investigated the existence of maternal styles in a precocial bird species, the Japanese quail, *Coturnix coturnix japonica*, and the link between maternal styles and both mothers' and their offspring's temperaments. Using a recently described procedure to evaluate maternal care in this species (Pittet, Coignard, Houdelier, Richard-Yris, & Lumineau, 2013), we analysed the maternal behaviour of 20 adult female Japanese quail over three consecutive maternal periods and evaluated their temperament and the temperament of their offspring. We asked the following questions: (1) can maternal styles be defined in a bird species and if so, (2) can a female's temperament predict her maternal style and (3) can maternal styles predict offspring behavioural characteristics?

METHODS

Housing Conditions

The quail studied originated from an industrial farm (Les Cailles de Chanteloup, Corps-Nuds, France). In our laboratory, they were kept at 20 ± 1 °C on a 12:12 h light:dark cycle (lighting = 500 lx). Food provided was a high-protein cereal diet in the form of a mix of pellet for chicks and granulates for adult females (VEGAM, Cesson-Sévigné, France).

Twenty adult females arrived at the laboratory when they were 5 weeks old and were placed singly in wire-mesh cages (100 × 70 cm and 62 cm high) with opaque walls 7 weeks before their first brood to habituate them to their experimental environment. The cages contained a feeder and a water source with food and water available ad libitum. Water was available for drinking only and not for bathing. The females were 12, 37, 44 and 51 weeks old, respectively, for the first, second, third and fourth breeding periods (denoted BP0, BP1, BP2 and BP3) and stayed under the same constant environmental conditions throughout the experiment.

Chicks were from the same broiler line. For each breeding period, 120 1-day-old chicks (total sample = 480 chicks) arrived at the laboratory and were placed in groups of 30 in four plastic cages (98 × 35 cm and 42 cm high) with wood shavings covering the floor and equipped with a heater (38 ± 1 °C) and food and water provided ad libitum.

After each breeding period, chicks were either used for other experiments or kept in boxes (200 × 200 cm and 280 cm high) with wood shavings covering the floor, at 20 ± 1 °C and under a 12:12 h light:dark cycle, until they could be used for breeding. The 20 females were used for other behavioural experiments and then placed in an outdoor aviary (500 × 500 cm and 300 cm high) with tall grass and several shelter areas.

Fostering Protocol and General Procedure

In the evening of the arrival of chicks, for each breeding period, females were shut in their nestbox (20 × 20 × 20 cm) and the light was immediately switched off. One hour later (2100 hours) we placed four chicks underneath each female. Chicks' solicitations during the night induce the females to become maternal (Richard-Yris, Michel, & Bertin, 2005) by the following morning when the boxes are opened (0800 hours). Females that did not accept the chicks (i.e. absence of warming behaviour after the release of the brood, expression of rejection behaviours) were excluded from the experiment; three females were excluded from BP0, one from BP1, two from BP2 and six from BP3. Any chick in a female's brood that showed signs of hypothermia (closed eyes, trembling, motionless) on the first day of each breeding period was replaced by a new chick (so that all broods included four chicks for all the females). The new chicks were ringed and of the same age but were not tested later as they did not spend the whole breeding period with a mother: 18 chicks were replaced for BP0, 23 for BP1, 11 for BP2 and 21 for BP3. After the first day, chicks quickly learn to warm one another (Pittet, Coignard, Houdelier, Richard-Yris, & Lumineau, 2012) and we noted no further signs of hypothermia. We could not monitor signs of hypothermia at night since our presence in the breeding room during the dark phase would have disturbed the birds. We nevertheless checked for the absence of distress calls 30 min after the beginning of the dark phase.

Behavioural Measurements

Observation of maternal behaviour

Maternal behaviour was observed on posthatching days (PHD) 2, 3, 4, 5, 7 and 9 of each maternal care period. The observation procedure was similar to that used by Pittet et al. (2013).

Both instantaneous scan sampling and focal animal sampling were equally distributed between the morning and afternoon periods and were carried out from behind one-way mirrors. The 20 adult females were observed using the instantaneous scan sampling method (interval: 4 min, 60 observations/female/day) for 4 h on each observation day. The experimenter noted whether or not the female was warming the chicks, whether or not her warming posture covered the chicks entirely and her distance to each chick using five distance classes: close (chick in contact with hen), near (at no more than one chick length from the hen), far (chicks between one chick length and half a cage from the hen), distant (chick between half a cage and a cage length from the hen) and opposite (at one cage length). From these data, several indexes were