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Protective mother hens: cognitive influences on the avian maternal response

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We previously demonstrated that domestic hens, Gallus gallus domesticus, show behavioural and physiological responses when witnessing mild chick distress, and possess the underlying foundations of emotional empathy. However, no studies have determined how cognitive influences affect empathic processes in birds. A fundamental question is whether a mother hen's response to chick distress is mediated by her knowledge about the situation or by chick distress cues. We therefore investigated how manipulating hen and chick knowledge influences hens' responses to chick distress. Each hen's brood of chicks was split into three groups, based on whether they had the same, opposite or no knowledge about a potentially threatening situation (environmental cues signalling air puff administration). We compared hens' behavioural, vocal and physiological responses (heart rate, heart rate variability and surface body temperature) to actual and perceived threat to their chicks. Hens increased maternal vocalizations and walking, and decreased preening, when they perceived their chicks to be threatened, regardless of the chicks' reactions to the situation. Hens exhibited signs of stress-induced hyperthermia only when their perception of threat was in accordance with that of their chicks. Chick behaviour was influenced by the hens' expectations, with all chick groups spending more time distress vocalizing and less time preening when in the environment that the hen associated with threat. We conclude that the protective maternal response of domestic hens is not solely driven by chick distress cues; rather, hens integrate these with their own knowledge to produce a potentially adaptive, flexible and context-dependent response.

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Recently, using a carefully controlled experiment, we found that hens witnessing their chicks receiving air puffs at 30 s intervals showed a suite of behavioural and physiological changes (increased alertness, maternal vocalizations and heart rate, and a decrease in preening and eye temperature) indicating behavioural and physiological arousal (Edgar et al. 2011). A fundamental question is whether the observed behavioural and physiological responses are mediated by the hens' state of knowledge about the situation, that is, whether hens can apply knowledge about a situation to their chicks' perspective, or whether the hens' responses are entirely mediated by chick cues (e.g. vocalizations or changes in behaviour).

Domestic chickens have highly developed cognitive abilities, showing evidence of declarative representation (Regolin et al. 1995; Forkman 2000), object permanence (Freire & Nicol 1999; Freire et al. 2004), self-control (Abeyesinghe et al. 2005) and highly developed social-learning abilities (for reviews see Nicol 2004, 2006). These abilities are employed flexibly, depending on the context and the social identity of both the observer and the

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demonstrator. Specifically, hens pay considerable attention to their chicks' behaviour and are sensitive to situations where their chicks make apparent mistakes, altering their maternal feeding display when they perceive their chicks to be eating unpalatable food (Nicol & Pope 1996). This suggests that chickens have a cognitive sensitivity to potential offspring distress, and can apply what they have learnt to conspecifics in the same situation. However, it is not known whether such cognitive sensitivity applies to a less innately driven situation, such as their chicks receiving an air puff.

Indeed, in recent years, there has been a growing interest in whether and to what extent different species of nonhuman animals show emotionally empathic-like responses (see Edgar et al. 2012a for a review). Emotional empathy occurs when one individual (the observer) detects the emotional responses of another individual (the demonstrator), in response to a stimulus, triggering a matching emotional response in the observer. While observers may show elements of emotional empathy without any knowledge of the stimulus that triggered the demonstrator's response, or of the demonstrator's understanding of the situation (e.g. perspective taking), such cognitive empathic processes may, in some cases, integrate with emotional ones (e.g. Davis 1994; Preston & de Waal 2002; Singer 2006; Preston et al. 2007; Edgar et al. 2012a).







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Few previous studies have examined cognitive influences on empathic processes, with the exception of some observational work on postconflict behaviour in corvids. In these studies, apparently affiliative behaviours by a third party were performed at a significantly higher rate in postconflict rather than preconflict periods (Seed et al. 2007) and were dependent upon the strength of the social relationship, indicating a potentially distress-alleviating, or consoling, function (Fraser & Bugnvar 2010), a function considered to indicate more cognitive forms of empathy (de Waal 2008; Fraser & Bugnyar 2010). However, third-party contact rates may simply be more likely when animals are in closer proximity, as they tend to be during postconflict compared with baseline periods (Call 1999). Additional limitations of observational studies are that the presumed purpose of consolation, to alleviate the distress of another, cannot be verified unless parameters associated with distress are measured concurrently in both individuals.

To date, no studies have experimentally determined how cognitive influences might affect empathic processes in birds. Having demonstrated a suite of behavioural and physiological responses of mother hens to chick distress (Edgar et al. 2011), our aim was to investigate to what extent this suite is mediated by the hens' state of knowledge about the threat, and by the chicks' behavioural response. We employed methodology adapted from Nicol & Pope (1996) to investigate whether hens would respond behaviourally and physiologically to perceived, as well as actual, threat to their chicks. This was achieved by splitting each hen's brood of chicks into groups, based on whether they had the same or opposite knowledge to her about a potentially threatening situation. A third chick group that had no knowledge about the situation was included to assess the effects of an overall expectation of danger by the chicks on the chicks' and hens' responses. Hens' behaviour, vocalizations and physiology (heart rate, heart rate variability and surface body temperature) in response to actual and perceived chick distress could then be compared.

METHODS

Animals and Housing

Twelve broody hens (Indian game × Austalorp, aged 50–100 weeks) were obtained from a breeder and were housed individually in a floor pen (1.5×1 m) bedded with 5 cm of wood shavings and with a feeder containing layers mash and a drinker. Upon arrival the hens were allowed to sit on 12 infertile eggs within a cardboard nestbox. If, after 24 h, the hens were still sitting, these eggs were swapped with 12 fertile eggs and the hens were allowed to incubate these until hatching. Throughout this period, hens were encouraged to leave the nestbox daily to feed and drink. This was done by gently lifting and moving the hen from the nestbox to the area near to the feeder and drinker. The temperature in the room was 23 °C and the lighting schedule was 16:8 h light:dark. Brood size ranged from six to nine chicks.

Procedures

Days 1-5

Each hen and her brood of chicks were checked three times per day to ensure they were in good health, but were not handled further until day 6.

Days 6–10: habituation

Each day, for 5 consecutive days, each hen and her brood were habituated to the test procedure and apparatus. To prepare hens for noninvasive heart rate monitoring each hen was fitted with a harness containing material within a pocket, the weight of which was gradually increased until it matched the weight of the heart rate monitor (100 g). The harness was made from elastane, fitted around the back and tail, between the legs and secured behind the neck with hook and loop fastenings, allowing free limb movement and normal behaviour. The pocket was positioned over the hen's back. Hens were closely supervised while they were wearing the elastane harness, to which no adverse reactions were observed. On days 4 and 5 of the habituation phase, self-adhesive electrode sensors (Ambu Blue sensor M-00-S, Ambu, St Ives, U.K.) were applied before fitting the harness; each hen was gently placed on her back, two small sections of skin overlying the pectoralis muscle either side of the sternum were cleaned using surgical spirit and cotton wool and the electrode sensors were applied to the cleaned skin. On day 5 of the habituation period, a noninvasive telemetric logging system (Lowe et al. 2007) was placed in the pocket and connected to the sensors on the hen's skin using two attached wires.

After the fitting process, the hen and her chicks were placed in the habituation apparatus and left undisturbed for 20 min. The habituation apparatus was a wooden structure (100×50 cm and 60 cm high) divided into two sections, the Hen box and the Chick box, which were separated by a clear Perspex screen. After the 20 min period, the harness was removed and the hen and chicks returned to their pen.

Days 11–14: conditioning

Each hen's brood of chicks was split into three notional groups, which would be trained separately from the hen and from each other. Each day, for 4 consecutive days, each hen and chick group were separately trained to associate a particular coloured box (red and yellow) with a particular treatment ('safe' and 'danger'; see below). The conditioning and test apparatus was a wooden structure (100×100 cm and 60 cm high) divided into three sections; a red box, a yellow box and a viewing box (which would be used later during testing; Fig. 1). The red and the yellow boxes were divided using a solid wall and the coloured boxes were separated from the



Figure 1. Conditioning and test apparatus (position of yellow and red counterbalanced between hens).

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