



## Social buffering in a bird



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The presence of a conspecific can ameliorate an individual's stress response. This social buffering is known to be widespread in social mammals but the capacity of birds to act as social buffers has not yet been determined. We previously demonstrated that domestic hens, *Gallus gallus domesticus*, show socially mediated arousal when watching their chicks receiving an aversive air puff. Furthermore, the hens' expectation of the situation strongly influenced the chicks' behaviour. Here we examined whether hens act as a social buffer; reducing their chicks' stress response to an aversive stimulus. Pairs of chicks were exposed to an air puff treatment and a control, each with and without their mothers. Chicks showed a suite of responses to the air puff (including increased standing, reduced eye temperature, preening and ground pecking). Maternal absence exacerbated the chicks' preening and ground-pecking responses to this stressor. Individual hens varied in their effectiveness as a social buffer and this was associated with their socially mediated arousal when (matched pairs of) their chicks received an air puff. Specifically, the hens' heart rate increase was strongly negatively correlated with the degree to which chick preening and ground pecking increased with maternal presence. This is the first demonstration that avian mothers are able to reduce their chicks' stress responses to an aversive stimulus.

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The escalation or de-escalation of arousal and distress within social groups of animals will depend upon a number of potentially opposing social factors, including individual animals' capacities for emotional empathy and the extent to which social buffering occurs. Socially mediated arousal, the behavioural and/or physiological reactions of animals to the responses of conspecifics (demonstrators) showing signs of stress, is one of the component features of emotional empathy (for a review see Edgar, Nicol, Clark, & Paul, 2012). Social buffering is the process by which the presence of a conspecific can ameliorate an individual's response to a stressor. As well as being of fundamental interest, both social phenomena are of high relevance to the welfare of managed animals during exposure to conspecifics' responses to routine procedures, handling and slaughter. While there is opportunity for individuals to buffer a demonstrator's stress response, this may depend on whether, and to what extent, the individual is affected by the demonstrator's stress-related behaviour in the first place. Despite this potential for interaction between the two social phenomena, previous research

on empathy and socially mediated arousal has been conducted entirely in isolation from work on social buffering. Consideration of both social phenomena will shed important light on the spread of stress across groups of animals and is the focus of this paper.

It is important to note that the reduction in stress responses in the presence of a conspecific (social buffering) is distinct from the return to baseline that is seen when social animals are brought together following isolation, or when bonded animals (mating pair or mother/young) are reunited following separation. To date, the literature on animal social buffering can generally be split into studies that focus on stress alleviation through conspecific presence during (e.g. Terranova, Cirulli, & Laviola, 1999; Varlinskaya, 2013) the stressor and those that focus on stress alleviation through social housing prior to and/or following (e.g. Hodges, Green, Simone, & McCormick, 2014; McCormick, Merrick, Secen, & Helmreich, 2007) the stressor (Kiyokawa, Takeuchi, & Mori, 2007). The vast majority of social-buffering studies have focused on mammals and many parameters have been used to measure social buffering. These include traditional stress indicators such as activation of the hypothalamic-pituitary-adrenal axis (e.g. increased heart rate, cortisol; Hodges et al., 2014) and behavioural responses (e.g. escape attempts, Gonzalez et al., 2013), through to neural responses (e.g. Fos gene expression; Kiyokawa et al., 2007;

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Kiyokawa, Hiroshima, Takeuchi, Mod, 2014; Kiyokawa, Honda, Takeuchi, & Mori, 2014), motivation to seek social contact (Geverink et al., 1998; Ishiwata, Kilgour, Uetake, Eguchi, & Tanaka, 2007; Marin, Freytes, Guzman, & Jones, 2001) and recently even changes in ethanol intake (Hostetler & Ryabinin, 2014).

The types of stressors used in social-buffering studies range from anxiety-inducing paradigms such as the elevated plus maze (Grippo et al., 2012), simulated predation (Mommer & Bell, 2013), social defeat (McQuaid, Audet, Jacobson-Pick, & Anisman, 2013), resident intruder tests (Grippo et al., 2012) and conditioned stimuli associated with electric shocks (Kiyokawa et al., 2007; Kiyokawa, Hiroshima, et al., 2014; Kiyokawa, Hiroshima, et al., 2014). Overall, the studies cited above point towards social buffering being a widespread phenomenon in social mammalian species. However, many studies purporting to measure social-buffering effects have used social isolation itself as the stressor (e.g. Hodges et al., 2014; Hostetler & Ryabinin, 2014; Kanitz, Hameister, Tuchscherer, Tuchscherer, & Puppe, 2014; Tuchscherer, Kanitz, Puppe, Hameister, & Tuchscherer, 2014). In this latter case changes in behaviour or physiology are likely to reflect a general return to baseline following separation, rather than a social-buffering effect.

Surprisingly little is known about whether birds can act as social buffers for conspecifics. Studies with starlings, *Sturnus vulgaris*, and zebra finches, *Taeniopygia guttata*, have revealed that social isolation itself is stressful, but found no evidence that a familiar flock member (starlings and zebra finches) or a bonded mate (zebra finches) had any buffering effect on the stress response. Apfelbeck and Raess (2008) showed that, although visual separation of a starling from its group members had strong effects on the bird's behaviour and physiology, the presence of familiar group members did not attenuate the strong neophobic response exhibited during exposure to a novel object. Similarly, when zebra finches were exposed to 10 min of isolation in a novel environment, they showed an elevated corticosterone response, indicating a stress response to isolation. However, when the authors compared the response of isolated pair-bonded individuals with isolated nonpair-bonded birds, surprisingly they found no difference; the presence of their female partners did not attenuate the stress response of bonded male birds, providing no evidence for any social-buffering effect from this type of stressor from the bonded mate (Banerjee & Adkins-Regan, 2011).

However, it would be premature to conclude that birds do not have the capacity to act as social buffers for one another. Domestic chickens, *Gallus gallus domesticus*, are an ideal model avian species to study social buffering; our own studies have shed light on their behavioural and physiological responses to stress, in particular within the mother/offspring bond (Edgar, Lowe, Paul, & Nicol, 2011; Edgar, Paul, & Nicol, 2013). Although the term 'social buffering' has not been directly used in previous chicken studies, there is some literature touching upon the concept of stress reduction through conspecific presence. Brooded domestic chicks show signs of stress, including a high rate of distress calling, when they are separated from their mother (Bermant, 1963; Collias, 1952; Hughes, Hughes, & Covalt-Dunning, 1982). Chicks also show stress responses when separated from same-age conspecifics and are highly motivated to move towards a conspecific (Jones & Williams, 1992; Suarez & Gallup, 1983; Vallortigara, Cailotto, & Zanforlin, 1990). Importantly, studies with broiler chickens have suggested that stress is influential in this 'social reinstatement' response; for example, mechanical restraint increases motivation for chicks to restore contact with conspecifics, especially familiar ones (Guzman & Marin, 2008; Marin et al., 2001). However, a lack of evidence of stress alleviation (provided through the measurement of behavioural and physiological indicators) means that it is unknown whether the presence of conspecifics buffers the stress response.

Additionally, the relevance of the conspecific's role, in terms of both its behaviour and its relationship to the subject, has not yet been determined, but would provide important insight into the extent to which social buffering occurs in birds.

Studies on social buffering in guinea pigs, *Cavia porcellus*, have been pivotal in demonstrating the importance of the relationship between individuals on mammalian social-buffering effects. These studies have found that the mother is a more effective social buffer for her pups than other adult females (Graves & Hennessy, 2000; Hennessy, O'Leary, Hawke, & Wilson, 2002; Hennessy & Ritchey, 1987; Ritchey & Hennessy, 1987; Sachser, Durschlag, & Hirzel, 1998) and that a mate-bonded individual is more effective than other familiar conspecifics for both adult males and females (Graves & Hennessy, 2000; Sachser et al., 1998). However, the mechanisms that underpin the effectiveness of mothers or mates as social buffers have not been explored in mammals or in birds.

We previously demonstrated that while watching their chicks subjected to an air puff, domestic mother hens show increased alertness, maternal vocalizations and heart rate, and reduced preening and eye temperature (which we together term 'socially mediated arousal'; Edgar et al., 2011), phenomena that are not apparent when adult hens watch other familiar adults receive an air puff (Edgar, Paul, Harris, Penturn, & Nicol, 2012). The reduction in eye temperature was likely to be indicative of stress-induced hyperthermia, an increase in core body temperature associated with a decrease in peripheral temperature (Bouwknicht, Olivier, & Paylor, 2007; Busnado et al., 2010; Edgar, Nicol, Pugh, & Paul, 2013). Hens' arousal was influenced, not solely by chick distress cues, but by their own knowledge; mother hens responded behaviourally to expected, as well as actual, threat to their chicks (Edgar, Paul, et al., 2012). In contrast, chicks were strongly influenced by the hens' behaviour; chicks spent more time distress calling and less time preening when their mothers expected a potential threat (Edgar, Paul, et al., 2013). The fact that the hens' expectation of the situation affected the chicks' behaviour suggests that mother hens may influence the chicks' stress responses, raising their stress responses when threat is imminent but also perhaps reducing them when threat has passed and/or protection and care are available.

We therefore aimed to determine whether hens act as social buffers for their chicks. We also aimed to assess the extent of natural variation in mother hens' socially mediated arousal and to examine how this relates to the hens' capacity to act as a social buffer during the same stressor. To do this, in Phase 1 we determined each mother hen's behavioural and physiological responses to their chicks receiving an air puff. Additionally, this phase provided us with information on the chicks' behavioural and physiological response in the presence of their mother, never before recorded. In Phase 2, with naïve chicks, we determined whether the presence or absence of the mother hen influenced the chicks' behavioural and physiological responses during the air puff administration. Using data from Phases 1 and 2, we finally explored whether the mothers' arousal (Phase 1) was correlated with their capacity to act as a social buffer (Phase 2).

## METHODS

### *Ethical Note*

This project was carried out following ethical approval by the University of Bristol (University Investigation Number: UB/07/002) and in accordance with the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching. At the end of the study all animals were rehomed to responsible smallholders.

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