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Effects of domestication on filial motivation and imprinting in chicks: comparison of red junglefowl and White Leghorns

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Domestication has been reported to reduce learning ability and to alter social behaviour. We compared the development of filial behaviour of domestic chickens, *Gallus gallus domesticus*, and the ancestral red junglefowl, *Gallus gallus*. We investigated the tendency of naïve chicks to approach conspicuous stimuli, as a measure of filial motivation, and the development of a preference for familiar stimuli over unfamiliar ones, as a measure of imprinting and hence of social-learning ability. Chicks were placed in an arena containing two stimuli (a red cylinder and a blue ball) after being housed individually with one of these stimuli for 0, 6, 12, 24, 36, 48 or 60 h. During a 20 min trial, observations were made of their latency to approach each stimulus and the amount of time spent close to them. With no prior exposure to either stimulus (0 h), the breeds did not differ in their readiness to approach stimuli, suggesting no difference in filial motivation. However, the breeds differed in their initial preferences between the two stimuli tested and in their ability to imprint on them. Junglefowl chicks showed an initial preference for the red cylinder, but imprinted equally well on both stimuli, whereas Leghorn chicks showed no initial preference but imprinted relatively poorly on the red cylinder. We suggest that junglefowl chicks may be more flexible in their ability to imprint on stimuli than domestic chicks; however, a greater variety of stimulus types must be tested to confirm this.

Keywords: chicken; domestication; domestic fowl; filial motivation; filial imprinting; *Gallus gallus*; learning; preference; red junglefowl; White Leghorn

It has been argued that in many species domestication produces an array of behavioural, morphological and physiological changes that occur together (Trut 1999); these changes have been referred to as ‘the domesticated phenotype’ (Jensen & Andersson 2005). As well as a reduction in brain size (Kruska 2005), there is evidence of increased sociability in some species, including a lower level of intraspecific aggression and an increased willingness to interact with conspecifics (Price 1999). In some cases, such as reduced aggression in domestic rats, *Rattus norvegicus*, this could be environmentally rather than genetically induced (Price 1999); but motivation for social contact in Japanese quail, *Coturnix japonica* (Faure & Mills 1998) and aggressiveness in chickens, *Gallus gallus domesticus* (Craig & Muir 1998) can be manipulated by genetic selection.

The ancestor of the domestic fowl is considered to be the red junglefowl, *Gallus gallus* (Yamashita et al. 1994; Fumihito et al. 1996; Hillel et al. 2003). Domestic chickens show reduced spatial-learning ability compared with junglefowl (Lindqvist et al. 2007). They also show more protracted aggression after regrouping, indicating a poorer social-learning ability (Väisänen et al. 2005). With respect to sociability, the relevant findings are unclear, in part because of a failure to distinguish aggressive from nonaggressive social behaviours. Schütz & Jensen (2001) observed a lower frequency of social (including aggressive) interactions in Leghorns than in junglefowl, whereas Väisänen et al. (2005) reported a lower frequency of some types of social (including aggressive) behaviour but a higher frequency of others, and also observed that Leghorns spent more time in close proximity to one another than junglefowl. Because modern domestic chickens are reared in groups too large for the recognition of all members to be possible, natural

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selection in this environment might be expected to have rendered them more weakly motivated than junglefowl to establish a social hierarchy, but this has not yet been investigated. The social dynamics in large flocks are not well understood and there are a number of possible strategies that chickens might use to cope in such an environment (Mench & Keeling 2001; Estevez et al. 2007). The implications for 'sociability', defined as a tendency or motivation for nonaggressive social interaction, are unclear.

In precocial birds such as chickens, the formation of social attachments occurs in the first few days after hatching. This process is used as a model for the study of learning (Horn 1985) because the chicks' experience prior to hatching can be controlled and standardized. Hence, the period immediately after hatching is likely to be particularly useful for studying social motivation and learning. For these reasons, we decided to compare the development of filial behaviour in domestic chickens and the ancestral red junglefowl.

The development of filial behaviour can be understood in terms of two interacting processes: filial motivation and filial imprinting. Filial motivation causes chicks to approach and follow conspicuous objects with certain general properties (e.g. they show a predisposition for certain colours, shapes and sizes, and for moving objects), which in a natural environment would usually be the hen and other chicks; filial imprinting is a learning process through which the chick comes to restrict this behaviour to a particular stimulus (Bateson 1966; Sluckin 1972; Bolhuis 1991; van Kampen 1996). As chicks become progressively more familiar with an object, they tend to approach this object more and at the same time develop a tendency to avoid dissimilar objects (Horn 1985). This avoidance of novel stimuli restricts the development of social attachments to one or a few types of stimuli encountered in the first few days of life. Thus, filial motivation determines the propensity to make social attachments, while imprinting (in conjunction with unlearned predispositions) determines preference.

We investigated the tendency of naïve chicks to approach conspicuous stimuli, as a measure of filial motivation (experiments 1 and 2), and the development of a preference for familiar stimuli over unfamiliar ones, as a measure of imprinting and hence learning ability (experiment 1). The stimuli chosen were ones between which naïve domestic chicks show no preference (Bolhuis & Bateson 1990), so we anticipated that measures of motivation and imprinting would not be substantially biased by predispositions. We hypothesized that Leghorn chicks would show poorer imprinting than junglefowl chicks. We also tentatively proposed that they might show stronger filial motivation, if the increased sociability that has been reported in some species is a genetic effect of domestication.

METHODS

Experiment 1

Subjects

The subjects of experiment 1 were 54 red junglefowl chicks and 56 White Leghorn chicks. They were hatched and tested in three batches of 28 and one of 26. Junglefowl eggs were obtained from a breeding population consisting of about 60 birds (about 30 of each sex) maintained at Götala Research Station in Skara, Sweden. The population had been in captivity for 14 years; the background of this population is described in more detail by Schütz et al. (2001). The Leghorn eggs were from a commercial laying hybrid, Hyline, purchased when newly laid. The chicks were not sexed after hatching, as this is difficult to do.

Incubation and housing

All eggs were incubated in darkness at 37.8 °C and 55% relative humidity (RH) for 16 days, then transferred to individual compartments in a second dark incubator at 37.4 ± 0.1 °C and $65 \pm 5\%$ RH until hatching on day 19–20 (junglefowl) or 20–21 (Leghorns). The compartments had solid sides that prevented hatched chicks from touching their neighbours. The hatching incubator had a glass lid so we could check the progress of hatching at intervals using a 12 V DC infrared camera (model KPC-S53CNV, KT&C Co. Ltd., Seoul, Korea), operating at 7.5 V to reduce the LED output of red light below the level visible to humans. Because chickens are slightly more sensitive than humans to red light (Prescott et al. 2003), the use of this camera was kept to a minimum, making a mean of seven checks of 1–2 min duration for each batch of chicks.

The chicks remained in the incubator until 24 h after the midpoint of hatch, defined as the time at which half of the viable eggs had hatched. Because most chicks hatch within ±12 h of the midpoint (Tona et al. 2003; Bamelis et al. 2005), subjects would have been approximately 12–36 h old when removed from the incubator. At 12 h of age chicks are mobile (Hess 1959), and they remain highly responsive to imprinting stimuli for a number of days posthatching when reared in darkness (Case & Graves 1978). The chicks were then transferred in dim light to individual cardboard boxes, where they were housed for the remainder of the experiment except during testing. Only chicks that were able to stand were selected for the experiment, thus excluding any individuals that hatched with splayed legs.

Each box measured 330 × 230 mm and 260 mm high. The floor was covered with brown corrugated paper to improve grip. Inside each box were two transparent, colourless plastic bowls mounted on a piece of hardboard, which contained commercial chicken feed (Pullfor: Lantmännen, Stockholm, Sweden) and water. The boxes were arranged side by side in two rows, with a ceramic heat lamp (emitting no light) positioned above each group of four.

Lighting was provided by 60 W incandescent bulbs positioned between the heat lamps, each bulb being shared by a group of four boxes. The experimental room was maintained on a 4:2 h light:dark photoperiod to ensure uniform periods of light and darkness between successive testing times. The short photoperiod also gave a better approximation to the intermittent pattern of light exposure that occurs when chicks are brooded naturally (Workman et al. 1991) than a long photoperiod would have done. Except in the case of control chicks, each box contained a single conspicuous stimulus object. We used two types