



ARTICLES

Response facilitation in the domestic fowl

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Response facilitation is an alternative learning process that could account for some imitative phenomena. It occurs when the presence of a conspecific performing an act temporarily increases the probability that an observing animal will perform the same act. This process could have important implications for social-learning research, because it provides a plausible means by which social learning could occur in animals, yet it superficially resembles imitation and consequently affects the interpretation of current popular 'two-action' tests of imitation. However, there is little good evidence on response facilitation effects, because cases of behavioural synchrony can usually be explained by other factors, so some researchers remain sceptical as to the importance of the process. We conducted an experimental study of social-learning processes in domestic fowl to evaluate whether response facilitation is a plausible explanatory term. Strong behavioural synchrony was observed in hens in preening, sitting and dustbathing behaviour. In the case of preening, we found strong evidence that this synchrony was unlikely to be accounted for by alternative social-learning processes or by external factors influencing birds in the same way. We conclude that there is compelling evidence for response facilitation in the domestic fowl.

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The topic of social learning in animals has attracted much interest among ethologists and psychologists (Heyes & Galef 1996; Galef & Giraldeau 2001; Shettleworth 2001; Galef & Heyes 2004). Social learning is often broadly defined as learning that is influenced by observation of, or interaction with, a conspecific or its products (Box 1984; Heyes 1994). Although social learning does not necessarily result in concordance between the observer's and the demonstrator's behaviour, it is social learning that results in matching behaviour that has attracted most attention. Such learning can potentially result in the social transmission of acquired information through a population (Galef 1976), resulting in increased homogeneity of behaviour that extends beyond the period of interaction (Galef

1988). Examples include the spread of foraging skills or vocalizations through populations of birds and mammals (Lefebvre & Palameta 1988; Heyes & Galef 1996; Fragaszy & Perry 2003). The possibility that these processes could help to maintain simple animal 'cultures' in natural populations has been a topic of major interest, with researchers looking for cases of culture in a wide range of taxonomic groups (e.g. Fleagle 2003; Siegel 2004).

An area of debate in the field of social learning is the extent to which social learning observed in nonhuman animals is homologous to the processes underlying culture in humans. For instance, it has often been argued that imitation and teaching are important in maintaining human but not animal culture (Galef 1992, 2004; Tomasello 1994), although this is contentious (Laland & Hoppitt 2003; Whiten et al. 2004). Although social learning of matching behaviour has been demonstrated numerous times in nonhuman animals, this could occur by many routes besides imitation (or teaching). Consequently, central to the resolution of debates over animal 'cultures' is an understanding of those social-learning processes that can

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generate findings in animals that resemble those resulting from imitation, but that none the less are the result of a different, perhaps simpler, psychological mechanism.

Over the last century, much effort in social-learning research has gone into devising experimental procedures that can isolate imitation from other social-learning processes (Galef 1988), although this research programme is hindered by differences in opinion on how imitation should be defined and demonstrated empirically (e.g. Galef 1988; Tomasello 1990; Heyes 1994, 1996; Byrne & Tomasello 1995; Byrne & Russon 1998; Byrne 2002). Widely regarded as the most successful method for testing for an imitative ability is the 'two-action method' (Dawson & Foss 1965). The experimental subjects must solve a task in one of two ways (e.g. by pushing a bolt or turning a handle to open a box containing food). Half of the subjects observe a demonstrator using one solution, and the other half observe the alternative method. Subjects are then tested to see which method they use, and if each group tends to use the method that they observed more frequently than the other group, then this is taken as evidence of imitation. The best examples of the two-action test have been carefully designed so that each alternative action involves interaction with exactly the same part of the experimental apparatus, to rule out local enhancement as an explanation for differences between groups. Each action should also ideally result in exactly the same movement of the experimental apparatus, to rule out the possibility that the observer is recreating the movements of the experimental apparatus (Custance et al. 1999), rather than the action itself (Akins & Zentall 1996; Zentall et al. 1996). A good example of the two-action method is Zentall et al.'s (1996) study showing that pigeons, *Columba livia*, learned to press a lever for food in the same way that they had observed being demonstrated earlier, either by pushing the lever with their beak or stepping on it with their foot.

The two-action test has been used to test a number of other species for imitative ability, with positive results found in budgerigars, *Melopsittacus undulatus* (Dawson & Foss 1965; Galef et al. 1986), quail, *Coturnix japonica* (Akins & Zentall 1996), starlings, *Sturnus vulgaris* (Campbell et al. 1999; Fawcett et al. 2002), marmosets, *Callithrix jacchus* (Bugnyar & Huber 1997), capuchin monkeys, *Cebus apella* (Custance et al. 1999) and chimpanzees, *Pan troglodytes* (Whiten & Custance 1996). Many view these results as the most convincing cases of animal imitation (Whiten et al. 2004), but others are not convinced. Byrne (2002) defined two types of imitation, production imitation, where the observer learns a new pattern of behaviour, and contextual imitation, where the observer learns to use an existing action in a novel context. The two-action test does not inherently test for production imitation, because it does not show that the alternative actions are novel, although individual cases may be made. However, it potentially provides evidence consistent with contextual imitation.

Byrne (1994, 1999, 2002), however, provided an alternative explanation for the data generated by two-action tasks, i.e. response facilitation, defined as when 'the presence of a conspecific performing an act (often resulting in reward) increases the probability of an animal which sees it doing the same' (Byrne 1994, page 237). So in Zentall et al.'s

(1996) study, the pigeons that observed a demonstrator pecking may not have learned by imitation to peck at the lever, but instead may have been transiently more likely to peck at any object that they encountered as a result of having recently seen another pigeon pecking. To be sure of a case of contextual imitation, it must be shown that the observers have learned to use the target action in that context. One way to eliminate response facilitation as an explanation could be to introduce a significant delay between demonstration and exposure to the task, to let the possible effects of response facilitation wear off. However, it is difficult to know how long a response facilitation effect could last, and consequently how long the delay must be. Another option is to show that learning by observation of the demonstrator is context dependent. So, for example, one could show that pigeon observers learned to peck or step on the lever in response to a light being lit up, after seeing a demonstrator responding in such a way.

Another term with a similar meaning to response facilitation is contagion, which refers to 'matching behaviour limited to those unlearned responses that are typical of a species' (Zentall 1996, page 224). Possible cases of contagion include synchronized predator evasion in flocks and herds of animals (Armstrong 1951) and synchronous courtship behaviour (Nuechterlein & Storer 1982; Zentall 1996). Here we use the more general term 'response facilitation', because such an effect could potentially be a result of experience and need not necessarily be unlearned (Hoppitt 2005). Contagion could be seen as a special case of response facilitation that requires no experience of other individuals' behaviour.

Aside from providing another explanation that must be ruled out in tests of animal imitation, response facilitation seems to be an interesting possibility in its own right (Byrne 1994). Through synchronizing individuals' behaviour, response facilitation might effectively 'teach' animals when and where to perform certain actions. For example, an individual of a frugivorous species might learn that the fruit of a particular tree is good to eat, if the animal is predisposed to eat in the tree with other individuals who are eating the fruit. Response facilitation could result in social learning functionally equivalent to contextual imitation, by a similar process to Suboski's (1990) releaser-induced recognition learning.

Perhaps one reason that the response facilitation explanation has received little attention by imitation researchers is that it is primarily a theoretical construct, and there is little evidence of it. Although numerous cases of behavioural synchrony in many species might be regarded as cases of response facilitation, there are almost always alternative explanations. For example, animals moving around together will encounter the same environments and locations together and may therefore engage in synchronous behaviour. In addition, groups of animals will experience many external factors simultaneously and respond to them in the same way. For example, Armstrong (1951) noted that, although individuals of many species of birds start singing at approximately the same time each morning, this could be explained by a threshold light intensity triggering dawn song. We are aware of no strong empirical evidence that behavioural synchrony is a result of response facilitation and not alternative processes.

Our study attempted to address this question. We tested domestic fowl, *Gallus gallus domesticus*, to evaluate whether response facilitation is a plausible explanatory term for cases of social learning. The domestic fowl is a social species known to be capable of social learning (Nicol 1995, 2004) and so represents a suitable model organism. Observations and preliminary studies of domestic fowl revealed a number of actions that seemed to be performed synchronously within a group. This occurred on a minute-to-minute basis, suggesting that the effect was not a result of daily rhythms, and that these actions might be good candidates for response facilitation. The chickens seemed to be most strongly affected by other individuals engaged in preening, dustbathing and sitting on the ground. We investigated whether the apparent response facilitation effect on these actions still remained when other explanations were ruled out.

METHODS

Experimental Design

If an action, A, is subject to response facilitation, then we would expect the rate with which a bird initiates bouts of A to correlate with the number of visible conspecifics also performing A at that time. However, such a correlation might also be brought about by other factors; for example, external stimuli, such as changes in weather conditions, may affect several birds in the same manner. We controlled such effects by looking at two visually isolated groups of conspecifics exposed to the same external conditions. If behavioural synchrony is stronger within groups than between groups, this result would be consistent with response facilitation affecting their behaviour.

A second alternative explanation would be possible if birds have preferred areas in their enclosures for performing A. If birds moved around their environment together, then they might visit such locations together, resulting in synchrony in A in the absence of response facilitation. To control for this factor, we used as a control the number of birds engaging in another action, B, within the preferred area. If synchrony can be accounted for by a location effect, then the time a bird spends engaging in A would not only correlate with the number of conspecifics in the same area engaging in A, but also the number engaging in B. However, if the within-action effect is stronger than the between-action effect, then this would indicate that response facilitation has occurred.

Subjects and Materials

Subjects were 18 female domestic fowl aged 8–12 months, purchased from Highgate Farm, Willingham, Cambridgeshire, U.K., at 15–16 weeks of age. Birds were subsequently housed at the Sub-Department of Animal Behaviour, University of Cambridge. We used two hybrid breeds. Meadowsweet Ranger are derived from Rhode Island Reds and have a brown plumage; White Star are derived from Leghorns and have a white plumage. Identification was aided by the use of coloured rings attached to the legs. All birds were well accustomed to the presence of human

observers before data were collected. Birds were housed in two adjacent outdoor aviaries (10 × 5 m and 2.5 m high). Aviary 1 housed eight birds ($N = 4$ Meadowsweet Ranger, and 4 White Star); aviary 2 housed 10 birds ($N = 5$ Meadowsweet Ranger, 5 White Star). The aviaries were surrounded by a lawn and hedgerow in a secluded area with minimal influence from other animal housings and human activity. The aviaries were constructed of a wooden frame, covered in wire mesh with holes 5 cm in diameter and with an opaque tarpaulin partition between the two aviaries. Each aviary had a covered area (5 × 2.5 m), the floor of which was lined with wood-chip floor material. This area contained a wooden coop (2 × 1 m and 1 m high), which was lined with straw and had perches 0.3 m high. The remainder of the aviary floor was also regularly lined with straw. Each aviary contained a large tree branch as a perch (about 3.5 m long), a feeder containing layers pellets (French & Sons, Cambridge, U.K.) and a drinker containing water. In addition to the birds' ad libitum food, each aviary was also provided with a bowl containing layers mash mixed with water twice per day at approximately 1000 hours and 1700 hours. The birds' diet was supplemented with lettuce, grit and mealworms; birds also foraged for invertebrates such as earthworms and spiders.

Procedure

We monitored two visually isolated groups of birds in adjacent enclosures over a 1-h period, recording incidents of preening, dustbathing and sitting. The experimenters simultaneously tracked the behaviour of the birds in the two aviaries over 44 1-h sessions, 12 h of which were dedicated to determining interobserver reliability. Two experimenters were present for each session, W.H. and either L.B. or S.H. During experimental sessions, each experimenter watched a different aviary and recorded the time of onset and offset of bouts of preening, dustbathing and sitting for all the birds in that aviary during that time (continuous sampling). Sessions were also run to quantify interexperimenter reliability, where both experimenters watched the same aviary and independently recorded the behaviour of the birds. Observing all the birds in an aviary could have led to inaccuracies in the recorded time of onset, particularly at times of increased activity. The reliability sessions allowed us to quantify this and, most importantly, to check for confounding bias (see Results). Data were collected in two blocks. Between 9 and 27 June 2003, W.H. and S.H. ran two experimental sessions per day for 8 days, starting at 1200 hours and 1500 hours, and a total of four interexperimenter reliability sessions, starting at 1200 hours or 1500 hours, on 3 different days. Between 9 and 31 August 2003, W.H. and L.B. ran two experimental sessions and one interexperimenter reliability session per day for 8 days. On 4 days, the interexperimenter reliability session started at 0900 hours, and the experimental sessions started at 1000 hours and 1200 hours. On the remaining days, the interexperimenter reliability session started at 1300 hours and the experimental sessions at 1500 hours and 1630 hours (Table 1). The second block was structured in this way so that we could also

Table 1. The schedule of experimental (E) and reliability (R) sessions

Block/experimenters	Days	Time (h)					
		0900	1000	1200	1300	1500	1630
1/WH, SH	1, 5 2–4, 6–8, 10–11 9			R(1) E(8) R(1)		E(8) R(1)	
2/WH, LB	12, 15, 16, 18 13, 14, 17, 19	R(4)	E(4)	E(4)	R(4)	E(4)	E(4)

Number of sessions given in parentheses ($N = 32$ experimental sessions and 12 reliability sessions).

investigate daily rhythms in the birds' behaviour, as part of another study.

At the start of the session, stopwatches were synchronized, and each experimenter, seated 1 m outside one aviary, recorded the time of onset and offset of a number of actions occurring within 1 h for all the birds in the aviary. The action patterns recorded were preening, dustbathing and sitting, chosen because observations suggested that these actions would be likely candidates for response facilitation (Table 2; we treated dustbathing as a subset of sitting). We recorded an onset when a bird was observed to fulfil the criteria for that action. For preening and sitting, we recorded an offset if a bird stopped performing the action in question and did not continue within 20 s. An offset was recorded for dustbathing if the bird returned to an upright sitting or standing position and did not throw up any more dirt within 20 s. We also recorded the section of the aviary in which the onset of an action took place (Fig. 1).

Data Analysis

Controlling for common external stimuli

To ensure independence, data from each session were divided into two. Half of these data were used to assess the effect of other birds' behaviour, within the same aviary, on an individual's rate of onset of the three actions, and the other half were used as a control for common external conditions by comparison with the behaviour of birds in the adjacent aviary.

A computer program was written in C to process the raw data; preening, dustbathing and sitting data were processed and analysed separately. We describe the methods used to analyse preening data; those used for sitting were identical, and we made some modifications to the analysis of the dustbathing data, described below.

We defined N_x as the number of birds preening in the same ($x = 1$) or a different ($x = 0$) enclosure, where the

ranges of $N_{x=1}$ and $N_{x=0}$ were 0–7 and 0–10, respectively, for aviary 1, and 0–8 and 0–9, respectively, for aviary 2. We defined the following:

T_{1,N_x} : the time (s) during which N_x other birds were preening in the same ($x = 1$) or different ($x = 0$) aviary;

T_{2,N_x} : the time (s) that the focal individual spent preening when N_x other birds were preening in the same ($x = 1$) or different ($x = 0$) aviary;

N_{o,N_x} : the number of preening onsets when N_x other birds were preening in the same ($x = 1$) or different ($x = 0$) aviary;

T_{3,N_x} : the time (s) during which the focal individual was not preening and N_x other birds were preening in the same ($x = 1$) or different ($x = 0$) aviary (calculated as $T_{1,N_x} - T_{2,N_x}$).

These values were quantified for all birds ($j = 0, 1, \dots, 18$) in both aviaries ($i = 1, 2$) for all sessions ($N = 576$ observations for each set of values of N). N_{o,N_x} and T_{3,N_x} were then pooled across sessions to give a single measure of each variable for each bird.

A different number of birds was in each aviary, so it was necessary to convert N_x to a comparable covariate p , which refers to the proportion of conspecifics preening in the same aviary when $x = 1$, or the other aviary when $x = 0$.

The data were analysed using a Genstat generalized linear mixed model (GLMM) with the model formula:

$$E[r_{o,ijx}] = \mu + a_i + b_j + \alpha_x + \beta p + \gamma_x p \quad (1)$$

$E[r_{o,ijx}]$ is the expected value of r_o (i.e. the probability of onset/for bird j in aviary i), μ is the mean, a_i is a random effect representing aviary i , b_j is a random effect representing individual variation in bird j , α_x is a fixed effect representing a within-aviary comparison ($x = 1$) or a between-aviary comparison ($x = 0$), β is the coefficient of the effect of the covariate p and γ_x is a fixed interaction effect representing a difference in the coefficient of the effect of p between within- and between-aviary comparisons. γ_x is the term of interest here, because it tests for whether an individual's rate of onset of preening depended differently on the proportion of birds preening in the same aviary to the proportion of birds preening in the other aviary. If there were a response facilitation effect, we would expect the slope of the relation to be significantly steeper when $x = 1$ than when $x = 0$, i.e. $\gamma_1 > \gamma_0$.

The error structure was modelled on a binomial distribution, where the binomial totals were taken as $T_{3,ijx}$, and the number of successes as $N_{o,ijx}$ (the number of seconds during which there was an onset). The model assumed that there was a probability r_o that an individual would

Table 2. Definitions of recorded actions

Action	Definition
Preening	An individual's manipulation of its own feathers with its beak
Dustbathing	Lying on the floor pressed into the substrate and using the feet to throw dirt on to the plumage
Sitting	Any position where a bird was on the floor not standing on its feet

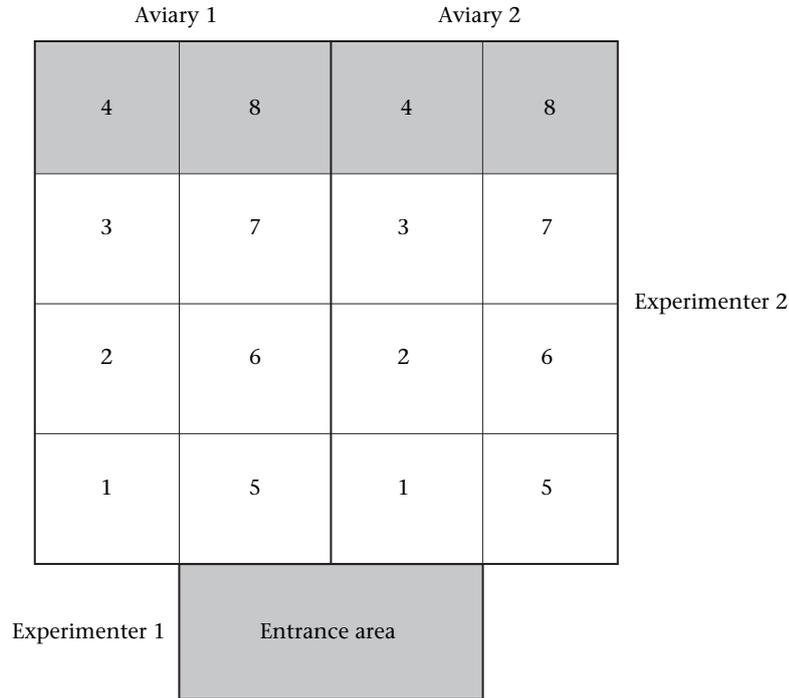


Figure 1. Aviary layout, showing the position of the experimenters and the division of aviaries into sections numbered 1–8. Covered sections are shaded grey. Coops were in section 4 in aviary 1 and in section 8 in aviary 2.

start preening each second that it was not already preening, which depended on the parameters in the model equation above. The dispersion parameter of the error distribution was estimated from the data initially, was found to be close to 1 in all cases and then was fixed to 1 thereafter. The most parsimonious random model was fitted by rejecting any random effect whose variance component did not differ significantly from zero ($\alpha = 0.05$). In the absence of significant random effects, we used a generalized linear model (GLM). A likelihood ratio test (LRT) was used to test for a significant effect of γ_x . This approach follows McCulloch & Searle's (2001, page 149) recommendation that the LRT be preferred to Wald's test.

Dustbathing was relatively rare, so the above model could not be fitted to the dustbathing data. Therefore, the data were pooled further for each bird over all values of $N_x > 0$. Then p became a binary fixed factor, so $p = 0$, $x = 1$, for example, represents the case where no birds were preening in the same aviary, and $p = 1$, $x = 1$ represents the case where there are conspecifics preening in the same aviary. The data were then fitted to a GLMM with the following model formula:

$$E[r_{o,ijxp}] = \mu + a_i + b_j + \alpha_x + \delta_p + \kappa_{xp} \quad (2)$$

Here the model terms are the same as in equation (1), except that δ_p is a fixed effect representing the presence ($p = 1$) or absence ($p = 0$) of preening conspecifics, and κ_{xp} is a fixed interaction effect representing a difference in the effect of the presence or absence of preening conspecifics between within-aviary comparisons ($x = 1$) and between-aviaries comparisons ($x = 0$). If there is a response facilitation effect, we would expect $(\kappa_{11} - \kappa_{10}) > (\kappa_{01} - \kappa_{00})$. The procedure for

model fitting and hypothesis testing was identical to that described above.

Test for interexperimenter reliability

A possible confounding effect is that the coefficient of the relation between the number of birds preening and the dependent variables might be greater with intra-experimenter comparisons (i.e. within aviaries) than with interexperimenter comparisons (i.e. between aviaries). This would make the within-aviary effect appear stronger, and thus suggest a bogus response facilitation effect. To assess whether this was the case, we ran a number of reliability sessions. During these sessions, both experimenters watched birds in the same aviary and independently recorded the behaviour of the birds.

We ran separate tests to assess the reliability of observations made by W.H./S.H. and W.H./L.B. The data were first processed as if testing for a within-aviary effect, using each experimenter's data separately, for the entire 60 min of each session. This analysis yielded values for N_{o,p_w} and T_{3,p_w} for $p_{(w=1)}$, the proportion of other birds preening, in the same aviary, according to the same (primary) experimenter's recordings (i.e. within experimenter). Next, the data were processed for each experimenter as if testing for a between-aviary effect, except that the other (secondary) experimenter's data were recorded from the same aviary, excluding the individual for whom the values were being calculated. This analysis yielded values for N_{o,p_w} and T_{3,p_w} for $p_{(w=0)}$, the proportion of birds preening in the same aviary, according to the secondary experimenter's recordings (i.e. between experimenter).

Data were analysed separately with each experimenter as the 'primary' experimenter, using a GLMM with the model formula:

$$E[r_{o,ijw}] = \mu + a_i + b_j + \varepsilon_w + \beta p + \eta_w p \quad (3)$$

Here the model terms are the same as in equation (1), except that ε_w is a fixed effect representing a within-experimenter ($w = 1$) or between-experimenters ($w = 0$) comparison, and η_w is a fixed interaction effect representing a difference in the coefficient of the effect of p_k between within- and between-aviary comparisons. η_w is the term of interest because it tests for whether the estimate of the effect of p differs between within-experimenter and between-experimenters comparisons. Both experimenters were watching the same birds, so this provides a test of whether the use of different experimenters for each aviary within an experimental session is the source of bias. If $\eta_1 > \eta_0$, this result would indicate a tendency for within-experimenter measurements of the effect of conspecifics' preening to be greater than between-experimenter measurements, and thus result in a spurious response facilitation effect. The procedure for model fitting and hypothesis testing was identical to that described above.

The smaller amount of data for dustbathing led us to analyse these data for reliability by comparing corresponding observations from pairs of observers, and testing for a difference using a paired t test. This approach does not, however, test for a difference in the estimate of the effect of p between within-experimenter and between-experimenters comparisons.

Controlling for a location effect

To assess whether birds in the same aviary tended to preen in the same locations, we calculated the total time spent preening in each section of the aviary for each bird. A preference was tested for using a linear mixed model (LMM) with Location as a fixed factor coding for the section of the aviary and Bird as a random factor to block out between-bird variation. Transformations were applied where appropriate.

The data were then isolated for bouts of behaviour occurring in the preferred area in each aviary, then tested for a response facilitation effect on preening, using sitting as the control action. We analysed the data in a similar manner to that done to control for common external stimuli, to yield measures of N_{o,p_z} and T_{3,p_z} for each bird, where z refers to whether the comparison was within-action ($z = 1$) or between-action ($z = 0$). For the analysis of both sitting and dustbathing, preening was used as the control action. The data were analysed using a GLMM with the model formula:

$$E[r_{o,ijz}] = \mu + a_i + b_j + \phi_z + \delta p + o_z p \quad (4)$$

Here the model terms are the same as in equation (1), except that ϕ_z is a fixed effect representing the difference between within-action ($z = 1$) and between-action ($z = 0$) comparisons, δ is the coefficient of the effect of the covariate p and o_z is a fixed interaction effect representing a difference in the coefficient of the effect of p between within- and between-action comparisons. o_z is the term of interest here, because it tests for whether an individual's rate of

onset of preening depends differently on the proportion of birds preening in the preferred preening area to the proportion of birds sitting in that area. If there were a response facilitation effect, we would expect the slope of the relationship to be significantly steeper when $z = 1$ than when $z = 0$, i.e. $o_1 > o_0$. The procedure for model fitting and hypothesis testing was identical to that described above. The smaller amount of dustbathing data led us to use p as a binary fixed factor, with $p = 0$ representing the absence of preening conspecifics in the preferred preening area, and $p = 1$ representing the presence of preening conspecifics in that area.

RESULTS

Preening

The proportion of visible conspecifics preening increased with the rate of onset of preening (GLMM: LR = 699.69, $P < 0.001$; Fig. 2a). As expected, there was also a significantly stronger within-aviary than between-aviaries effect (GLMM: LR = 10.83, $P < 0.001$; Fig. 2a). In all interexperimenter comparisons, there was a significant difference in the estimate of the effect of p between within- and between-experimenter comparisons. However, the effect always indicated an underestimate of the slope in the within-observer condition. Therefore, it is improbable that the observed effect was a product of a within-experimenter bias, since this would require an overestimate of the slope in the within-experimenter condition.

In both aviaries, birds preferred specific areas for preening (ANOVA, aviary 1: $F_{7,49} = 28.87$, $P < 0.001$; aviary 2: $F_{7,63} = 12.92$, $P < 0.001$). In aviary 1, sections 1, 2 and 4 were preferred for preening, but there was no significant difference in preference between these sections (Tukey's pairwise comparisons: NS). In aviary 2, section 1 was preferred significantly to all other sections (Tukey's pairwise comparisons: $P < 0.05$). Within the preferred preening areas, the time spent preening was more strongly affected by the number of conspecifics preening in that section than by the number that were sitting down there (GLMM: LR = 98.93, $P < 0.001$; Fig. 2b).

Sitting

The number of observable conspecifics sitting increased with the proportion of time spent sitting (GLMM: LR = 377.40; $P < 0.001$; Fig. 2c). The effect was also significantly stronger within aviary than between aviaries (GLMM: LR = 27.16, $P < 0.001$; Fig. 2c).

In both aviaries, birds preferred specific areas for sitting (ANOVA, aviary 1: $F_{7,49} = 23.94$, $P < 0.001$; aviary 2: $F_{7,63} = 26.53$, $P < 0.001$). In aviary 1, sections 2, 4 and 5 were preferred for sitting, but there was no significant difference in preference between these sections (Tukey's pairwise comparisons: NS). In aviary 2, section 1 was preferred significantly to all other sections (Tukey's pairwise comparisons: $P < 0.05$). There was no evidence that, within the preferred sitting areas, the time spent sitting was affected differently by the number of conspecifics sitting down in that section than by the number preening there (GLMM: LR = 2.5, $P = 0.113$; Fig. 2d).

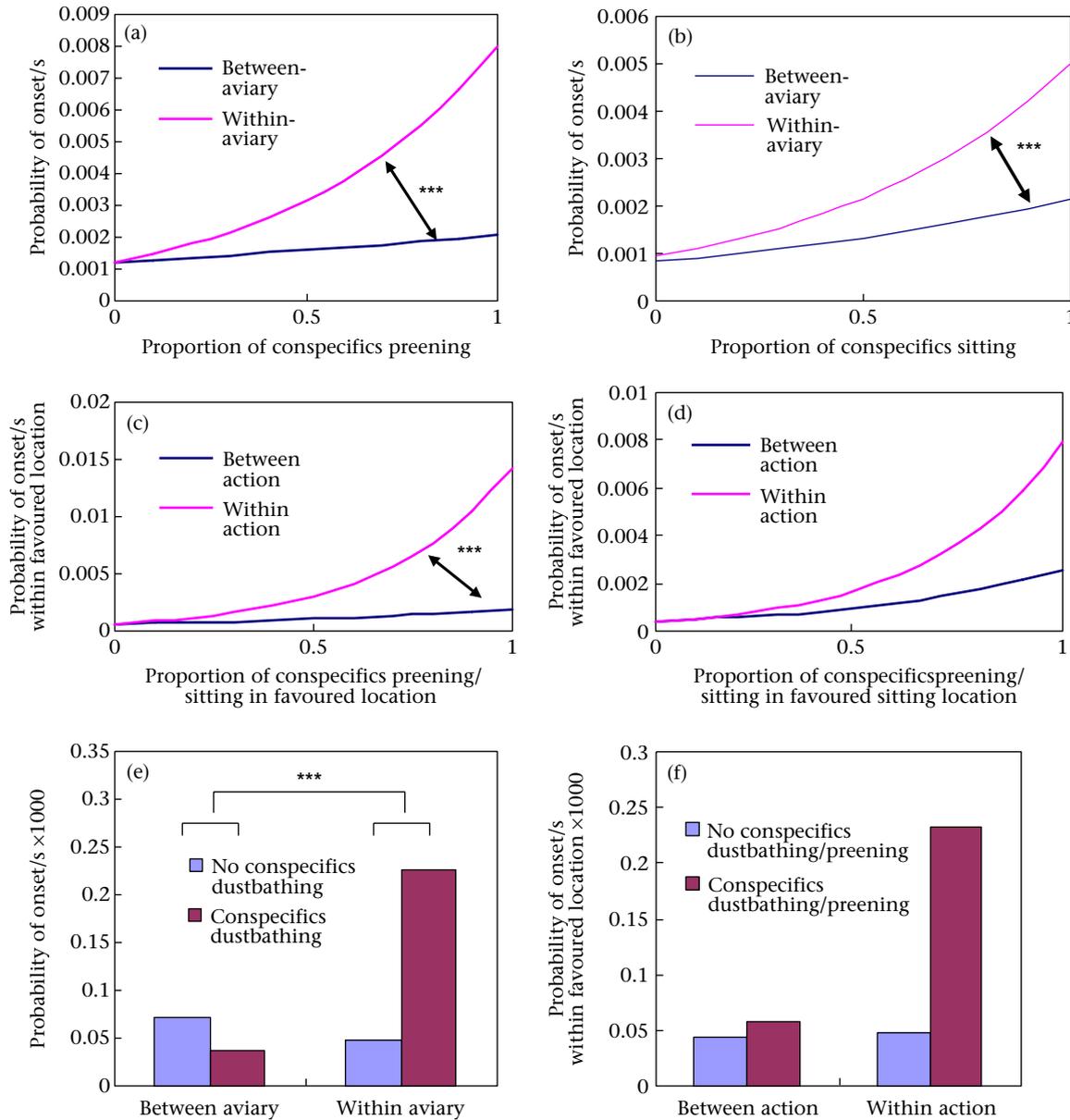


Figure 2. Fitted models showing social effects on the onset of (a, c) preening, (b, d) sitting and (e, f) dustbathing. (a, b, e) Relation between the rate of onset of an action and the proportion of conspecifics engaged in that action in the same and different aviary. Asterisks indicate that the within-aviary effect was greater than the between-aviary effect at the 0.1% level. (c, d, f) Relation between the rate of onset of an action in the preferred location for that action and the number of birds in that location engaged in the same or a different action. Asterisks indicate that the within-action effect was greater than the between-action effect at the 0.1% level.

Dustbathing

The presence of dustbathing conspecifics in the same aviary affected the rate of onset of dustbathing more than did the presence of dustbathing conspecifics in the other aviary (GLM: LR = 30.42, $P < 0.001$; Fig. 2e).

In both aviaries, birds preferred specific areas for dustbathing (ANOVA, aviary 1, $F_{7,49} = 13.88$, $P < 0.001$; aviary 2, $F_{7,63} = 9.73$, $P < 0.001$). In aviary 1, section 8 was significantly preferred to all other sections (Tukey’s pairwise comparisons: $P < 0.05$). In aviary 2, sections 7 and 8 were preferred for dustbathing, but there was no significant difference in preference between these sections

(Tukey’s pairwise comparisons: NS). Within the preferred dustbathing areas, there was a nonsignificant time for the time spent dustbathing to be more strongly affected by the number of conspecifics dustbathing in that section than by the number preening there (GLMM: LR = 3.70, $P = 0.054$; Fig. 2f).

DISCUSSION

The results provide compelling evidence for response facilitation of preening and weaker evidence that it contributes to initiating bouts of dustbathing and sitting.

Individuals' performance of each action was strongly affected by the number of observable conspecifics engaged in that action: birds initiated bouts of preening approximately seven times more often when all other birds were preening than when they were not (Fig. 2a). The monotonic increase as more birds engaged in the action could be explained either by a resulting increase in stimulus strength or by an increased probability that an individual will happen to be paying attention to a bird performing the action in question. The analysis suggests that this trend cannot be accounted for by external stimuli affecting individuals in the same way. External stimuli might operate on a spatial scale small enough that, at any one time, individuals in one aviary are affected, whereas individuals in the other aviary are not. However, no plausible factors seemed to be operating on such a scale likely to cause an effect of the magnitude and consistency observed. The analysis also reveals that a location effect is not sufficient to explain the preening data. The same area of each aviary was favoured for preening and sitting, and within these areas there was a stronger effect within preening than there was between actions, suggesting that the major influence was the behaviour of conspecifics, rather than their location.

We would also expect birds to sit down approximately four times more often when all other birds in the aviary were sitting down than when they were all standing up (Fig. 2c), and the effect on dustbathing seems to be of a similar magnitude (Fig. 2e). Again, the effect remains when common external stimuli are controlled, but we cannot rule out location effect. However, in the case of dustbathing, the effect size appears to be comparable to that for preening, so the nonsignificance might be a result of the low power of the analysis.

The methods used constitute a novel way of analysing animal behaviour to detect response facilitation effects on action. The design could potentially be adapted to any circumstances where animals can be divided into groups that can see each other but not other groups. This is not to say that nonvisual cues, such as vocalizations or other sounds associated with behaviour, might not be important, and the experimental set-up could be modified to investigate this possibility where appropriate. These methods could be useful in identifying the extent of response facilitation in captive and wild animal populations and its contribution to social learning. In addition to the rate of onset of an action, we also analysed the proportion of time spent engaged in an action. In some respects, this measure was more reliable than the rate of onset of an action, since the social effect on the rate of onset seemed to be underestimated in within-experimenter comparisons, which would mask a response facilitation effect. However, problems arise because consecutive seconds are highly nonindependent, so the models used in this study are not appropriate.

Previous approaches to studying social-learning processes have focused on isolating imitation, while ruling out what are assumed to be cognitively simpler processes, such as local enhancement and response facilitation (Zentall 1996). However, it is far from clear that imitation is important in social learning in animal populations

(Galef 1992), and little is known about which psychological processes are important to animal social learning. Understanding such processes requires methods that can distinguish 'simple' social-learning processes such as local enhancement, stimulus enhancement and response facilitation from each other, as well as from imitation (Roitblatt 1998).

To what extent did the methods used in this study allow us to isolate response facilitation? We rule out local enhancement (Thorpe 1956) as an explanation for the preening data because the effect was action-specific. A stimulus enhancement explanation is plausible for the dustbathing findings, because one individual's dustbathing could attract another individual's attention to the loose substrate and so increase the likelihood that the two will interact with it. This explanation seems less plausible for the preening data; attention could be attracted towards feather stimuli, but the effect seemed to be restricted to one's own feathers. Stimulus enhancement seems implausible for the sitting data; if attention were attracted to floor stimuli, we should expect an increase in directed actions, such as pecking at the floor, rather than an increase in sitting.

Whether imitation can explain the observed effects depends on which definition of imitation is used. The effect cannot be explained by production imitation, because the motor patterns required for preening, sitting and dustbathing were not novel, and the effects continued over the course of the experiment. Contextual imitation, where an individual learns by observation to use a specific but not necessarily novel behaviour in a specific context (Byrne 2002), seems equally implausible. This would require birds constantly to form new associations between familiar contextual stimuli and the action in question, as a result of observation of others. Furthermore, none of the behaviour patterns were followed by an obvious reinforcing stimulus, although we cannot rule out the possibility of some kind of social reinforcement. Another view of imitation is that individuals might copy the precise movements or actions of others without the specification that those actions be novel (Bugnyar & Huber 1997; Huber 1998). Such a definition requires the reproduction of a conspecific's behaviour to be fairly exact, and we found no evidence that this was the case among the chickens. For example, individuals did not seem to copy the exact movements of another bird's preening, or even the area of the body that was being preened, but were simply more likely to engage in preening behaviour themselves. Even if the behaviour patterns had been copied exactly, the effect would still be within the definition of response facilitation, but occurring at a fine-grained movement level rather than at the action level. So, for example, if one bird observes another bird preening its primary feathers, it may simply be more likely to preen, or at more fine-grained level, it may be specifically more likely to preen its own primaries.

Another process that could account for some cases of social learning is goal emulation (Whiten & Ham 1992). This term was initially used to refer to cases where the observer understands that the demonstrator's behaviour has certain consequences, but the observer might also

recognize that it can achieve the same goal in a different way. All the actions in question were well established in the behavioural repertoire and were not directed towards any novel stimuli, so it seems unlikely that the birds were learning novel behavioural goals.

Contagion is a term used to refer to 'matching behaviour limited to those unlearned responses that are typical of a species' (Zentall 1996, page 224). We cannot rule out the possibility that the synchrony effects seen in the chickens' behaviour were contagious, because we do not know whether the response is unlearned. However, the responses do not seem to provide *prima facie* compelling cases for contagion because, unlike, say, fleeing in the face of a predator, here there was no obvious adaptive function to the synchrony. Furthermore, we are aware of no case of what is thought to be contagion that has been shown to be unlearned.

Another social-learning process discussed in the literature is social facilitation, although this term has been given a number of different meanings (Zentall 1996). Others have referred to social facilitation in a similar way to contagion (e.g. Visalberghi & Addessi 2000), where one individual's behaviour acts as a releaser for matching behaviour in others, which can be thought of as a subset of response facilitation. Another widely used definition is that of Zajonc (1965), who defined social facilitation as behaviour that is influenced by the mere presence of a conspecific. Nicol (1989) found that the mere presence of conspecifics did cause an increase in chickens' preening, but in the present study, the effect was shown to be action-specific and so cannot be accounted for in the same way.

Response facilitation encompasses a number of more specific processes, where the outcomes are identical. We suggest that the term has both great utility and parsimony, because in most cases the specific mechanisms involved in producing matching behaviour are unknown, and at this stage there is no reason to conclude that such mechanisms are not identical. The definition is based on the observable outcome of the process, so it is relatively easy to isolate it empirically from mutually exclusive social-learning processes. In addition, for those interested in the consequences of social-learning processes in natural populations of animals, what matters is the outcome. Once we have isolated cases of response facilitation, we can then investigate the specific mechanisms involved, whether they are learned or unlearned and how they develop.

In conclusion, our study provides the first clear empirical evidence for response facilitation in animals. This process is able to account for the observed behavioural synchrony in hen preening and also provides the most plausible account for synchrony in dustbathing and sitting. Further investigations are required to determine whether learning is necessary for this social effect to develop and the mechanism involved. None the less, the fact that response facilitation has been empirically demonstrated has implications for interpretation of experimental studies of imitation, particularly those with two-action method designs. In light of these findings, claims of imitation will lack credibility if they fail to rule out a response facilitation mechanism.

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