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The effects of demonstrator social status and prior foraging success on social learning in laying hens

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Opportunities for social learning within a group of animals are likely to be influenced by the social dynamics of that group. Some individuals may be more influential demonstrators than others even when there are no differences in their skill level or performance. In this study of domestic hens, *Gallus gallus domesticus*, differences in demonstrator salience were examined. From 24 separate flocks we selected as demonstrators a dominant cockerel, a dominant hen, a mid-ranking hen or a subordinate hen. Demonstrators were pretrained to perform an operant discrimination task to obtain food. Six observers from each flock individually watched the demonstrator perform the task for four 5-min sessions held on consecutive days. On the fifth day observers were tested individually in the operant chamber. We analysed data from 19 flocks, where there were no quantitative differences in demonstrator performance. Observer hens of relatively high social status performed more correct operant pecks than observer hens of relatively low social status. Demonstrator category also had a significant effect on subsequent observer behaviour. Hens that had observed cockerels performed very few general pecks or operant pecks. Hens that had observed dominant hens performed more operant pecks, but hens that had observed subordinate hens performed more general pecks in the chamber. The results suggested either that there was an interaction between dominance and gender in demonstrator salience or that dominant hens might have been influential because of some factor imperfectly associated with their dominance status. A possible candidate was the foraging ability of the dominant hens. In a second experiment using the same protocol, we manipulated the prior foraging success of dominant hens from four additional flocks but this had no significant effect on their subsequent influence as demonstrators.

The study of social learning is concerned with the ways in which the acquisition of behaviour by naive animals is influenced by social interaction with more experienced individuals, termed 'demonstrators'. One factor influencing social learning is the extent to which different animals are predictors of food (or other) reward. Carlier & Lefebvre (1997), for example, have argued that Zenaida doves, *Zenaida aurita*, form preferences for demonstrators of different species based on local differences in reward contingencies. Opportunities for social learning within a group of animals, however, are also likely to be influenced by the social dynamics of that group. Differences in the extent to which naive individuals are able to approach more skilled individuals, and differences in attentiveness to particular others are likely to result in heterogeneity between group members in the acquisition of new skills and information (Fragaszy & Visalberghi 1996). If so, directed social learning rather than non-specific social learning will occur and information will not spread evenly in time or in extent through a group (Coussi-Korbel & Fragaszy 1995). This has important implications for the development of a theory of animal social learning (Laland et al. 1996). It may also have practical implications if social learning is implicated in the transmission of deleterious patterns of behaviour, such as feather pecking, in domestic animals (Nicol 1995). Despite the general acceptance of these principles there has been very little experimental work that elucidates the extent or nature of the influences of social relationships on social learning.

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Vertical transmission between generations is thought to be a particularly important pathway for the social transmission of new patterns of behaviour. Close contact between parent and offspring facilitates species-specific learning of food preferences and foraging techniques in, for example, cats, *Felis catus* (Caro 1980) and gallinaceous birds (Moffatt & Hogan 1992) and may also provide an optimum environment for juveniles to acquire novel skills and behaviours. However, the relative importance of parents versus nonparents as demonstrators has only recently been addressed. Hatch & Lefebvre (1997) explicitly tested the effectiveness of fathers and unrelated adults as demonstrators of new foraging techniques for juvenile ring-doves. The young birds showed a slight tendency to learn more from unrelated adults than from their fathers, possibly because greater parental tolerance encourages scrounging and thus inhibits learning.

Horizontal transmission between animals of the same age is also thought to be important, particularly when the transmitted information is of only transient value, such as when exploiting different foraging strategies in response to temporary local variations in the environment (Laland et al. 1996). Stable traditions may develop even when the new behaviour is arbitrary, such as in the development of food flavour preferences (Galef & Allen 1995). Again, however, some individuals may be more salient or influential demonstrators than others even when there are no apparent differences in their level of skill, performance rate or value as a predictor of reward. In a previous study of small flocks of laying hens we found that social learning of a keypeck response to obtain food was facilitated more when a dominant hen was used as a demonstrator than when a subordinate hen was used, even though dominant and subordinate demonstrators did not differ in their keypecking rate or accuracy (Nicol & Pope 1994).

There are a number of reasons why dominant hens might be more effective demonstrators. First, dominant birds may attract the continuous attention of subordinates attempting to avoid situations that might result in threat, aggression or attack from them. Second, the appearance of dominant birds might be more striking or noticeable during the performance of specific behaviours. For example, dominant birds may be bigger, adopt a taller body posture, or peck with greater force. Third, dominance may be a correlate of some other indicator of quality such as foraging ability. Thus, dominant birds may receive more attention from conspecifics because of their success in some other domain rather than because of their social position per se.

Our aim here was to confirm and extend our original finding (Nicol & Pope 1994) that dominant hens were more effective demonstrators in a food-related operant task. In experiment 1, we extended the categories of familiar demonstrator to include cockerels and mid-ranking hens in addition to dominant and subordinate hens. We deliberately ensured that reward contingencies and approach distances were held constant in order to examine any effects of demonstrator salience. We also categorized the relative social status of the observer birds, something which has not been done previously. Experiment 2 was designed to determine whether the prior foraging success of dominant hens influenced their subsequent effectiveness as demonstrators.

GENERAL METHODS

Subjects

Floor-reared Isa Brown hens were obtained at 21 weeks of age from a commercial supplier, and mature Maran cockerels from a local smallholder. Birds were randomly divided into flocks of eight hens, or seven hens and one cockerel, and individually marked with leg bands. Each group was housed in a deep-litter pen measuring 3.05×1.2 m with ad libitum food (layers' mash) and water supplied from conventional hoppers. Pens were separated by hardboard partitions to a height of 1 m, and wire mesh to the ceiling. Temperature varied between 18 and 24°C, and light was provided from 0600 to 2000 hours.

Apparatus

The experiments were designed to examine the effects of observation of a trained demonstrator on the strength of acquisition of an operant keypeck response to obtain food. Observation and testing sessions were carried out in a specially constructed two-chamber plywood box (60 cm high). The box was divided, by a sheet of clear Perspex, into a demonstration chamber (30×70 cm) and an observation chamber (46×70 cm). The demonstration chamber contained a red and a green operant key on the front panel, 10 cm apart and 30 cm from the base. Activation of the correct key resulted in access to a food hopper (9.5 cm wide $\times$ 10 cm deep) situated 12 cm beneath the operant keys. The food hopper contained the same layers' mash that was fed in the home pens.

Demonstrator Training

Familiar demonstrators were used because dominance is not an absolute characteristic of hens but a property that emerges through social interaction. In addition hens attempt where possible to avoid unfamiliar conspecifics (Freire et al. 1997). We gave demonstrators an initial pretraining session in which the door to the feed tray was automatically opened for repeated 10-s periods during a total 5-min session. The demonstrators then had six daily sessions in which they were trained by conventional shaping techniques (Leslie 1996) to peck either the green or the red key to obtain access to the food hopper. The correct key for each demonstrator was counterbalanced across treatments. By training day 6, all female demonstrators reliably pecked the key four times for each reinforcement of 10 s of access to food. Cockerels generally required a few extra days of training before they achieved reliable performance.

Social Status of Cockerels

When reared in mixed-sex groups male and female chickens tend to form two separate-sex hierarchies (Wood-Gush 1971). However, when one cockerel interacts with one or more hens he tends to assume a dominant position (e.g. Bshary & Lamprecht 1994). The cockerels in this experiment appeared dominant to the hens in the home pens. The cockerels were not restricted in their movements or in obtaining access to feed, but they appeared to maintain their social position without the use of aggressive pecks or threats, possibly because of the large social distance between the cockerel and the hens. Hens very rarely peck or threaten males (Rushen 1982). The cockerels performed courtship displays and mounted the hens frequently, but they appeared to spend less time than the hens in foraging in the shavings litter of the home pen.

Control Hens

In previous work we found that hens that were exposed to the behaviour of an untrained demonstrator (Nicol & Pope 1993), or to no bird in the demonstration chamber (Nicol & Pope 1994), were extremely unlikely to peck a key in the demonstration chamber during a 5-min test session. When both types of control were directly compared no difference in observer keypecking was noted (Nicol & Pope 1992). In this study we used two control flocks each of eight hens, additional to those reported below. Birds from the control flocks were placed in the observation chamber with no demonstrator present in the demonstration chamber for an equivalent length of time as the observer hens in experiments 1 and 2. They were subsequently placed individually in the demonstration chamber for 5 min and their behaviour monitored by an overhead video camera; any pecks made to the keys were recorded by computer.

Ethical Note

The average rate of aggression observed in the flocks in their home pens was 16.2 pecks/flock per h. Target hens successfully avoided between 70 and 80% of pecks that were directed at them. Aggressive pecks did not result in any injury. Our policy was to intervene if any bird was injured by another, or if any bird was persecuted such that it was reluctant to feed with flockmates. There was no necessity to intervene for these reasons in these experiments. Demonstrator hens were deprived of food for 16 h to ensure consistent operant responding during several consecutive observation sessions. Observers were deprived of food only prior to their test. All hens maintained their free-feeding weights during the course of the experiments as they were allowed access to ad libitum feed after each test session. Hens can adapt to a feeding period of only 2 h per day by increasing the proportion of that time they spend feeding and their rate of feed ingestion (Dawkins 1983).

EXPERIMENT 1: SOCIAL FACTORS

This experiment was designed to examine the influences of demonstrator and observer social status and relationship on social learning of an operant response. Demonstrators were chosen from within each flock of eight.

Methods

In total we used 24 flocks in this experiment. Eight flocks were obtained simultaneously and the experiment was conducted in three sequential replicates. In each replicate two flocks contained a cockerel and seven hens, instead of eight hens. In these flocks the cockerel was selected as the demonstrator. In the remaining flocks within each replicate the demonstrators were the most dominant hen (two flocks), the mid-ranking hen (two flocks) or the most subordinate hen (two flocks).

Social relationships within each flock were determined during a 2-week period before experiments began. During four 1-h observation periods we recorded the identity of each bird involved in a dyadic agonistic encounter, characterized by threats, pecks or avoidances. Social interactions in some flocks were relatively infrequent, and additional observations were conducted on these flocks until we had sufficient information to construct a dominance rank order for each flock. Birds were ranked according to the number of other birds they dominated and the constructed order minimized reversals where individuals dominated birds higher in the rank. Strict linear hierarchies could not be constructed for all flocks. Observer birds were thus classified into two groups: high/mid-ranking (hens that dominated more birds than they were dominated by, and where threats or pecks given exceeded those received) and low/mid-ranking (hens that were dominated by more birds than they dominated and where threats or pecks given were fewer than those received).

Six observer birds were selected from each flock. They observed their trained demonstrator perform the discriminatory operant response to obtain food during four 5-min sessions held on consecutive days. Demonstrators, but not observers, were food deprived before observation sessions, as food deprivation of observers hinders social learning using this procedure with hens (Nicol & Pope 1993). Observers were placed individually in the observation chamber during the demonstration sessions.

On the fourth day food was withdrawn from the observers at 2100 hours. On the fifth consecutive day, starting at 1300 hours, observers were placed individually in the demonstration chamber. Their behaviour was monitored continuously for 5 min via an overhead video camera, and any pecks directed to the operant keys were recorded automatically by the computer. Previous work had shown that most pecks were made during the first minute that hens were placed in the observation chamber and that little additional data could be obtained by extending the test period beyond 5 min. We also knew that observer hens tended to peck the periphery of the demonstrated keys rather than always pecking effectively in the centre. Measures derived from the video and computer recordings and used in subsequent analyses were the number of effective pecks made to the correct key (i.e. pecks registered by the computer), the number of ineffective pecks made to the correct key (i.e. pecks recorded on the video but of insufficient force to activate the computer) the number of effective pecks made to the incorrect key, the number of ineffective pecks made to the incorrect key, the total number of keypecks (effective and ineffective summed), the number of pecks made to the feeder door and the number of pecks directed elsewhere within the demonstration chamber.

Analysis of variance was performed on square-root transformed data to examine the independent effects of the social category of the demonstrator (cockerel, dominant hen, mid-ranking hen or subordinate hen), the relative social rank of the observer (classified as high/medium or low/medium) and batch (replicates 1–3). Data from individual observer hens were treated as independent replicates. Differences between pairs of means were examined using Fisher's least significant difference tests on square-root transformed data.

Results

The 16 birds from the two control flocks directed no pecks to either key and no pecks to the feeder door during the 5-min test sessions. They directed a mean ± SE of 0.12 ± 0.08 general pecks to the demonstration chamber during the test sessions. These data confirm our previous findings that control hens are extremely unlikely to perform a keypeck response if they have received no observational experience. Data from these hens were not included in further analyses.

Five demonstrator birds were not sufficiently reliable throughout the experiment for data from their observers to be included in the analysis. The performance rates of the demonstrators that we retained were very similar and their discrimination accuracy approached 100%. Cockerels appeared to peck the key with considerably more force than the hens although we were not able to quantify force of pecking with the apparatus that was available. We analysed data from four flocks with a dominant hen demonstrator (24 individual observers) and five flocks with a subordinate demonstrator (30 individual observers), a mid-ranking demonstrator (30 individual observers) or a cockerel demonstrator (29 individual observers as one observer died from peritonitis).

Table 1 shows the results of the analyses. There was a significant effect of the social category of the demonstrator on all of the behavioural measures taken with the exception of effective pecks to the correct key and pecks to the feeder door (Table 2). Batch effects had a strongly significant effect on all but one aspect of the behaviour of observers during the test period. The exception was the number of effective pecks made to the incorrect key. The primary cause of the batch effect was the low general occurrence of all types of pecking in birds from batch 3. However, significant interactions between batch and the social category of the demonstrator were also found for some of the behavioural measures taken (Table 1).

Observers that had watched dominant hen demonstrators made more keypecks in total than observers that had watched any other category of demonstrator. Specifically, we found that observers that had watched dominant hens made more ineffective keypecks to the correct key than observers that had watched cockerels or subordinate hens, and more ineffective pecks to the incorrect key than observers that had watched cockerels. Observers that had watched dominant hen demonstrators also made significantly more effective pecks to the incorrect key than observers that had watched cockerels or mid-ranking hens. In the strictest test of task acquisition (the number of effective pecks made to the correct key) observers that had watched a dominant demonstrator performed no better than observers that had observed a subordinate demonstrator (Table 2). Overall, there was a bias in favour of pecking the same key as the demonstrator for all categories of demonstrator. The mean discrimination ratios (number of pecks to same key as demonstrator/pecks to both keys) were 0.72 (dominant demonstrator), 0.65 (mid-ranking demonstrator), 0.86 (subordinate demonstrator) and 0.92 (cockerel demonstrator).

Pecks directed to the feeder door were most frequent in birds that had observed subordinate or mid-ranking demonstrators. General pecks to the walls and floor of the demonstration chamber were most frequent in birds that had observed subordinate demonstrators.

The social status of the observer bird had a significant effect only on the number of effective pecks made to the correct key. Relatively high-ranked birds made an average ± SE of 1.91 ± 0.55 effective pecks to the correct key in the 5-min test period, whilst relatively low-ranked birds made an average of 0.21 ± 0.09 effective pecks to the correct key.

Discussion

The significant effects of the social status of the demonstrator on the degree of social learning by observers extended, and partially confirmed, our previous findings. Birds that had observed dominant hen demonstrators performed more keypecks themselves during test sessions. This type of precise learning may be required to exploit the same food resource as a socially dominant conspecific. However, this effect was weaker than in our previous study (Nicol & Pope 1994) and there was no significant effect on the most exacting task, that is, the number of effective pecks made to the correct key. By contrast, pecking at the feeder door and pecking elsewhere in the chamber were more frequent in hens that had observed subordinate demonstrators than hens that had observed cockerels. It is reasonable to expect that observing a subordinate bird feed would stimulate general pecking activity at the same site. Subordinate birds can be exploited as producers (Caraco et al. 1989) and there may be no need to learn the details of how they obtain their food. Indeed, scrounging from conspecifics has been shown to inhibit learning of novel food acquisition behaviours in pigeons, *Columba livia* (Giraldeau & Lefebvre 1987).

The most consistent result was that the use of cockerels as demonstrators resulted in very little social learning in the hens. This was the case for all the behavioural measures we took and was apparent in all replicates. We cannot conclude that this is a gender effect as the cockerels we used were of a different (albeit closely related) strain, and were also older than the hens. However, the fact that the cockerels proved ineffective demonstrators in this food-related task immediately suggests that the greater influence of dominant hens as demonstrators was not due to some simple cue such as greater body size or

Table 1. Results of an ANOVA on behaviour in an operant chamber of observer hens from experiment 1: effects of demonstrator social category, observer social rank and experimental replicate

Source of variation	*df*	Total keypecks *F*	Effective pecks to correct key *F*	Ineffective pecks to correct key *F*	Effective pecks to incorrect key *F*	Ineffective pecks to incorrect key *F*	Pecks to feeder door *F*	Pecks elsewhere in chamber *F*
Demonstrator	3,89	3.05*	0.39	3.91*	4.43**	5.24**	1.98	4.41**
Observer	1,89	1.72	6.10*	0.01	1.41	0.10	0.31	0.43
Batch	2,89	6.19**	4.61*	3.58*	2.22	7.36**	6.70**	27.05***
Demonstrator×Batch	6,89	2.64*	1.02	3.90**	2.13	3.19**	2.55*	2.98*

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Table 2. Mean±SE number of pecks made in an operant chamber by hens that had observed different categories of demonstrator

	Total keypecks	Effective pecks to correct key	Ineffective pecks to correct key	Effective pecks to incorrect key	Ineffective pecks to incorrect key	Pecks to feeder door	Pecks elsewhere in chamber
Cockerel	0.90 ± 0.45^{a}	0.55 ± 0.39	0.28 ± 0.16^{b}	0.07 ± 0.05^{b}	0^{a}	1.41 ± 0.81^{a}	3.24 ± 1.27^{a}
Dominant	4.75 ± 1.71^{b}	1.50 ± 0.72	1.79 ± 0.88^{a}	0.58 ± 0.31^{a}	0.88 ± 0.49^{b}	3.21 ± 0.91	10.42 ± 2.60^{b}
Mid-ranking	1.93 ± 0.65	0.63 ± 0.22	0.67 ± 0.29	0.07 ± 0.05^{b}	0.63 ± 0.34	3.53 ± 0.91^{b}	9.80 ± 4.01
Subordinate	2.03 ± 0.84	1.60 ± 0.81	0.17 ± 0.29^{b}	0.17 ± 0.08	0.13 ± 0.43	5.27 ± 1.90^{b}	13.70 ± 3.95^{b}

Different superscript letters indicate significantly different means at $P<0.05$.

force of key pecking. The cockerels were socially dominant to the hens which suggests there may be a gender by dominance interaction in demonstrator salience. Alternatively, the greater influence of dominant hens may be due to some factor associated with their social rank rather than their dominance position per se.

The only significant effect resulting from the classification of the observers as relatively high- or low-ranking birds was that the relatively high-ranked observers performed more effective, correct keypecks. Apart from this there were few general effects of the observer's own social status on social learning. This may be because the most dominant and most subordinate birds in many flocks had already been selected as demonstrators, so that the observers had less extreme dominance positions. Low-ranking birds may be more risk-prone and neophilic, and hence more readily influenced to try a new food source by the ingestive behaviour of a conspecific (Forkman 1996). They are less fearful than dominant birds (Jones & Faure 1982) and a similar prediction might be that subordinate hens are more readily influenced to acquire a new behaviour pattern to obtain food. Our results suggest this was not the case. The high-ranked birds were more successful in their acquisition of new behaviour.

EXPERIMENT 2: PRIOR FORAGING SUCCESS

The ineffectiveness of dominant cockerels as demonstrators in experiment 1 suggested that the social rank of the demonstrator was not the sole determinant of salience. It is possible that male birds are always disregarded as models for new foraging skills. Alternatively, as males do not have to support the nutritional costs of daily egg production they may be disregarded because they spend less time foraging or are less successful foragers. Similarly, it may not be the dominance status of demonstrator hens that is actually the factor that mediates their salience, but some other attribute that is imperfectly correlated with their dominance. In red junglefowl, *Gallus gallus spadiceus*, dominant hens have a greater lifetime reproductive success than subordinates (Collias et al. 1994) and it may be that, either as a cause or an effect of their social position, dominant hens are more successful foragers than subordinates. In this second experiment we manipulated the foraging success of dominant hens prior to using them as demonstrators in the same keypeck task as experiment 1.

Methods

Four flocks, each comprising eight hens, were used in this experiment. In each flock the most dominant and subordinate birds were identified by observation in the home pen as described previously. For the 2-week period before the operant sessions began, these two birds from each flock were placed in adjacent wire cages sited on the wood-shavings floor within the home pen, for 1 h per day. In two flocks the dominant bird was selected as a relatively 'successful' forager and the subordinate bird was selected as relatively 'unsuccessful'. In the other two flocks the dominant bird was selected as relatively 'unsuccessful' whilst the subordinate bird was selected as 'successful'. We manipulated success by simultaneously providing each bird with a food dish filled with wood shavings. The dish of the 'successful' bird contained highly attractive hidden feed items such as mealworms and whole wheat grains. The dish of the 'unsuccessful' bird did not contain these items. These feed dishes were approximately 30 cm from a flock member standing adjacent to the wire cage and were clearly visible. The birds were not food deprived before placement in the wire cages and ad libitum layers' mash was available to the rest of the flock during this procedure. Despite this, the 'successful' bird foraged persistently in her dish throughout the 1-h period, attracting attention from the other birds in the flock which approached, pecked and scratched around the perimeter of the wire cage. The response of the flock members during this time were not quantified so we could not be sure that all flock members had an equal opportunity to observe the behaviour of the successful and unsuccessful bird.

During this 2-week period all the dominant hens were also trained to perform the keypeck response for conventional food using the methods previously described. Thus, we were able to use as demonstrators two dominant 'successful' foragers and two dominant 'unsuccessful' foragers.

Six observer birds were chosen from each flock, excluding the most subordinate hen that had been involved in the foraging success manipulations. Each observer was placed individually in the observation chamber of the operant box for four 5-min observation sessions held on 4 consecutive days. Observers watched their demonstrator perform the same discriminatory operant response used in experiment 1. Observers were not food deprived during observation sessions.

On the fifth consecutive day observers were placed individually in the demonstration chamber after a 16-h period of food deprivation. Their behaviour was monitored continuously for 5 min via an overhead video camera, and any pecks directed to the operant keys were recorded automatically by the computer. Measures derived from the video and computer recordings and used in subsequent analysis were the number of effective pecks made to the correct key, the number of ineffective pecks made to the correct key, the number of effective pecks made to the incorrect key, the number of ineffective pecks made to the incorrect key, the total number of keypecks (effective and ineffective summed), the number of pecks made to the feeder door and the number of pecks directed elsewhere within the demonstration chamber.

Results

The manipulations of foraging success in the home pens did not result in any changes in the social hierarchies of the four flocks studied or any changes in demonstrator behaviour in the operant chamber. In the operant tests there were no significant effects of the prior foraging success of the demonstrator or of the relative social status of the observer on any of the behavioural

Table 3. Results of an ANOVA on behaviour in an operant chamber of observer hens from experiment 2: effects of demonstrator foraging success and observer social rank

Source of variation	*df*	Total keypecks *F*	Effective pecks to correct key *F*	Ineffective pecks to correct key *F*	Effective pecks to incorrect key *F*	Ineffective pecks to incorrect key *F*	Pecks to feeder door *F*	Pecks elsewhere in chamber *F*
Prior success of demonstrator	1,19	0.42	0.33	0.09	0.33	0.35	0.06	0.18
Observer	1,19	0.50	0.33	0.40	0.33	0.22	0.07	0.02

measures taken (Table 3). The pecking behaviour of observers in this experiment was comparable with that found in the previous experiment, with the exception that the number of general pecks to the chamber appeared low. For hens that observed a previously 'successful' forager the mean $\pm$ SE numbers of pecks made in the 5-min test session were 1.00 ± 0.71 general pecks, 3.73 ± 2.3 pecks to the feeder door, and 0.64 ± 0.34 total keypecks. For birds that observed a previously 'unsuccessful' forager the mean number of pecks made in the test session were 2.50 ± 1.70 general pecks, 4.17 ± 1.67 pecks to the feeder door, and 2.50 ± 1.36 total keypecks. The sample size used in experiment 2 gave a power of detecting a change in keypecking of 3.85 pecks (cf. the difference obtained when cockerels and dominant hens were used in experiment 1) of 0.988. However, the power of detecting a change in keypecking of 2.72 pecks (cf. the difference obtained when subordinate and dominant hens were used in experiment 1) fell to 0.536.

Discussion

We found no effects of manipulating the prior foraging success of dominant birds on their salience as demonstrators in a subsequent operant task, although a larger sample size might have been required to detect subtle changes. The 2-week manipulation period might have been too short to outweigh other information that the flock members had about the foraging success of the dominant hen in their flock. However, the only alternative food source was ad libitum layers' mash provided in a hopper that allowed six birds to feed simultaneously with ease. Agonistic interactions at the feed hopper in the home pen, indicative of possible competition, were rare. There was thus little opportunity for differential foraging success outside the manipulation periods.

GENERAL DISCUSSION

The results confirm that directed social learning occurs in flocks of laying hens. Different social categories of demonstrator stimulated different overall amounts of pecking and different patterns of pecking activity within an operant chamber. Dominant hens appeared to stimulate more task-related key pecking whilst subordinate hens stimulated more general pecking at the feeder door. However, when dominant cockerels were used as demonstrators the occurrence of all types of pecking was low when the observers were tested in the operant chamber. The ineffectiveness of cockerels might have been due to their gender regardless of their behaviour, or to differences in their foraging behaviour in the home pens even though they performed the operant response as effectively as demonstrator hens. In experiment 2, we examined the possibility that prior foraging success might mediate the attention directed to demonstrators but we found no differences when we compared successful and unsuccessful dominant hens as demonstrators. An alternative factor that may be partially correlated with dominance in hens is aggressiveness. Hens may pay more attention to conspecifics that maintain their dominance with frequent aggressive acts rather than those that are passively dominant, as were the cockerels in experiment 1.

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