

Social Influences on Feeding Site Selection by Burmese Fowl (*Gallus gallus*)

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Naive, adolescent Burmese red jungle fowl (*Gallus gallus spadiceus*) observed trained conspecifics feeding in a large enclosure. When tested 48 hr later, observers exhibited significantly enhanced preferences both for the type of foraging site and for the area in the enclosure where they had observed conspecifics foraging successfully. Such delayed influences of observation of foraging success on the orientation of feeding by an observer can be explained as an instance of stimulus enhancement (Spence, 1937) but not as an example of local enhancement (Thorpe, 1963).

There is reason to believe that birds feeding in flocks enjoy two quite different sorts of advantage in relation to birds feeding alone. First, by feeding in groups, birds both reduce the time that they spend looking out for potential predators and lower their risk of predation (Bertram, 1978; Hamilton, 1971; Sullivan 1984a, 1984b). Second, and more relevant to the experiments reported in this article, if food both occurs in patches and is abundant within those patches, then social feeding can facilitate food finding by members of a feeding flock (Crook, 1965; Lack, 1968; Newton, 1967; Ward, 1965). For example, Krebs (1973) and Krebs, MacRoberts, and Cullen (1972) have demonstrated that captive birds (*Parus* spp.) were more likely to find hidden food when foraging in groups of four than when foraging in isolation. As soon as one member of a flock found food, others concentrated their search for food both in the general area and in the type of foraging site where food had been discovered.

Krebs et al.'s (1972) and Krebs's (1973) investigations of the social enhancement of foraging efficiency, like almost all other such studies reported in the literature, have demonstrated only immediate effects of social interaction on foraging by group members. Such short-term, social effects on behavior can be interpreted easily as examples of "local enhancement" ("apparent imitation resulting from directing an animal's attention to a particular object or to a particular part of the environment," Thorpe, 1963, p. 134).

In the experiments reported below, we looked for longer term effects of social interaction on foraging by members of bird flocks. Such delayed effects cannot be interpreted easily as results of local enhancement.

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Although there is evidence of rather lasting effects of prior social feeding on the later orientation of pecking by very young chickens (Bartashunas & Suboski, 1984), it is not known whether, as Hess's (1964, 1973) data suggest, such longer term influences on foraging occur only during the first few days of life. If, in general, the experience of feeding in a flock has the potential to facilitate later foraging by flock members, then long-term social effects on feeding ought to be observable in flock-feeding birds of all ages.

These studies were undertaken to determine whether naive adolescent fowl would exhibit durable modifications in the orientation of their foraging behavior as a consequence of simple observation of conspecifics feeding either in specific locations or from specific types of feeding site. Presumably, ground feeding birds such as fowl, while foraging in flocks, have ample opportunity to observe both the foraging site selection and foraging success of fellow flock members. Our goal was to determine whether such observations would orient future foraging behavior of observers toward promising feeding sites.

Experiment 1

Experiment 1 was undertaken to determine whether naive adolescent fowl would tend to exploit a particular type of feeding site 48 hr after observing conspecifics foraging successfully at sites of that type.

Method

Subjects and Maintenance

Forty, 21- to 28-day old, experimentally naive, Burmese red junglefowl (*Gallus gallus spadiceus*) served as subjects. All were descended from a flock of junglefowl maintained in the Department of Psychology of the University of Toronto (Toronto, Ontario, Canada), and all were offspring of birds raised in the vivarium of the McMaster University (Hamilton, Ontario, Canada) Psychology Department.

Eggs were set and incubated in batches of 20 to 40. From hatching until the start of experimental procedures, chicks were maintained on ad lib chick starter (Purina Startina, Ralston-Purina Canada, Woodstock, Ontario, Canada) and water enriched with a vitamin supplement (Vitadol, Tuco Products, Orangeville, Ontario, Canada).

Pilot experiments revealed that it was necessary to keep subjects in pairs during all stages of experiments. Social isolation resulted in both prolonged periods of distress vocalization and total inhibition of foraging by adolescent fowl.

Apparatus

Rearing enclosure. Each group of hatchlings was housed in a rearing cage (1.0 m wide \times 0.3 m high \times 1.0 m deep) constructed of hardware cloth and angle iron with a floor of galvanized sheet metal covered with a thin layer of wood-chip bedding. A 250-W brooder lamp suspended over one corner provided supplementary heat.

Experimental enclosure. Chicks were trained and tested in the experimental enclosure (3.0 \times 0.3 \times 1.0 m) illustrated in overhead schematic in Figure 1. The experimental enclosure was similar in construction to the rearing cage but was divided into an ancillary enclosure (1.0 \times 0.3 \times 1.0 m), a main enclosure (1.5 \times 0.3 \times 1.0 m), and an observation enclosure (0.5 \times 0.3 \times 1.0 m). The main and ancillary enclosures were separated by an opaque, sliding door, and the main and observation enclosures were separated by a screen (1/2-in. [1.27-cm] mesh) partition.

Four circular Pyrex dishes (10 cm in diameter \times 5 cm high), painted white, were present in the main enclosure in a 2 \times 2 array, as illustrated in Figure 1. At any given time during Experiment 1, there were present in the experimental enclosure either (a) a single marked dish and three unmarked dishes or (b) a single unmarked dish and three marked dishes. The outside of each marked dish was decorated with eight circular, red, adhesive labels (1.9 cm in diameter) evenly spaced 1 cm below the rim of the dish. Locations of marked and unmarked dishes were interchanged randomly between each of the training and testing trials.

Procedure

Training demonstrators. Four pairs of demonstrators were each trained to find food in the main enclosure. To begin, a pair of experimentally naive fowl was placed in the ancillary enclosure and food deprived for 4 hr. At the end of the 4-hr deprivation period, 2 g of chick starter were placed in either the marked dish (for 2 pairs of demonstrators) or in the unmarked dish (for 2 pairs of demonstrators). Next, the sliding door separating the ancillary enclosure from the main enclosure was opened briefly to allow the pair of demonstrators to enter the main enclosure. Each pair of demonstrators was then given 5 min to explore and feed in the main enclosure.

On each day of demonstrator training, demonstrators received 5 training trials at 3-min intervals. Trials when one or both birds

remained in the ancillary enclosure for 2 min after the sliding door was opened were repeated 3 min later.

During the training period, strips of newsprint were placed in all four dishes in gradually increasing amounts, until the bottoms of all dishes were totally obscured. Also, the time allowed for demonstrators to feed once they had found food was gradually reduced to 1 min per trial.

Demonstrator training was continued until both birds in a pair directed their first bout of pecking toward the dish that contained food on 4 of the 5 trials on a single day.

Training observers. Sixteen pairs of naive observers were placed, one pair at a time, in the observation cage and food deprived for 24 hr. After a pair of observers had been in their enclosure for 20 hr, a pair of trained demonstrators was placed in the ancillary enclosure and food deprived for 4 hr. Training of observer pairs was begun at the simultaneous conclusion of the periods of deprivation of both demonstrators and observers.

On each of 5 trials separated by 3-min intertrial intervals, a demonstrator pair was released into the main enclosure. During each trial all four dishes were filled with shredded newsprint, and either the single marked or the single unmarked dish contained food. During the training of observers, food was placed in the marked dish of those demonstrator pairs that had been trained to feed from the marked dish and in the unmarked dish of those demonstrator pairs that had been trained to feed from the unmarked dish. On each observer-training trial, demonstrators were allowed to feed for 1 min after finding food. The training procedure was repeated for a second time 24 hr after completion of the first training session.

During the 24-hr period between the end of the first observer training session and placement of each observer pair in the observation enclosure to begin their second training session, both observers and demonstrators were returned to their respective home flocks to feed ad lib.

Testing observers. Immediately after its second training session, each observer pair and each demonstrator pair were returned to their home flocks for 24 hr of ad lib access to food. At the end of this feeding period, each pair of observers was placed in the ancillary enclosure and again food deprived for 24 hr.

Immediately following food deprivation (and 48 hr after the last observer training trial), each pair of observers was released together into the main enclosure for six 5-min test trials, with 3-min intertrial intervals. During each test trial the main enclosure contained four dishes, one of the same type from which the demonstrators of a given pair of observers had been trained to feed and three of the other type. None of the four dishes available in the experimental enclosure contained food, though each was filled with strips of newsprint.

We recorded both the location and duration of bouts of pecking by all subjects throughout both training and test trials. A bout of pecking was defined as a peck or series of pecks directed inside a Pyrex dish; each bout ended when 2 s passed without any pecking occurring.

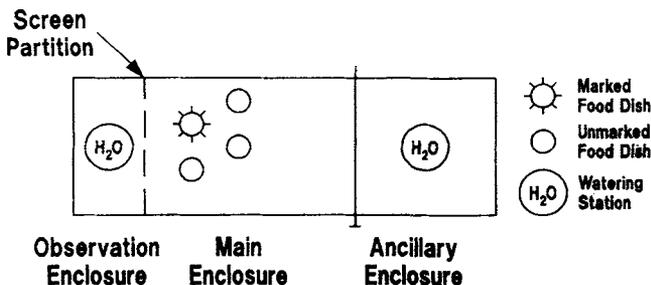


Figure 1. Overhead schematic drawing of the experimental enclosure. (Food dishes and watering stations are shown twice relative size.)

Results

Training Demonstrators

Demonstrator pairs required an average of 9.0 trials \pm 1.5 to achieve criterion performance during training.

Training Observers

Demonstrator pairs spent an average of 9.9 \pm 0.1 of the 10 min of observer training (five 1-min feeding sessions on each

of 2 days) pecking in the type of dish (marked or unmarked) from which they had been trained to feed. Each demonstrator directed its initial bout of pecking toward the appropriate type of food dish on each of the observer training trials in which it participated.

During training, observers approached the screen separating them from the main enclosure and appeared to watch their respective demonstrators closely. While demonstrators were feeding, observers frequently paced back and forth along the screen directly across from demonstrators, rubbed their beaks across the screen, vocalized, and directed bursts of pecking toward the floor of the observation enclosure, though no food was present there.

Testing Observers

Observers in 10 of the 16 observer pairs pecked in a dish during testing. The members of 9 of these 10 observer pairs directed their initial bout of pecking toward the type of bowl from which their respective demonstrators had fed during training of observers (binomial test [Siegel, 1956], $P = 0.25$, $x = 1$, $p = .00003$). On average, these 10 observer pairs pecked in the type of bowl into which their demonstrators had been trained to peck for $90.0\% \pm 10.0$ of the $0.09 \text{ min} \pm 0.03$ that they spent pecking. Nine of these 10 observer pairs pecked for more than 25% of the time at the type of dish into which their respective demonstrators had been trained to peck (sign test, $P = 0.50$, $x = 1$, $p < .03$).

Discussion

The results of this experiment indicate that Burmese fowl can learn to direct their pecking toward a particular type of feeding site (and will retain such information for at least 48 hr) as the result of observing the behavior of conspecifics foraging successfully. The observation of trained conspecifics feeding from a particular type of site was sufficient in itself to orient the feeding behavior of naive observers tested 2 days after they observed the feeding site selection of their respective demonstrators.

Experiment 2

Experiment 2 was undertaken to determine whether naive adolescent fowl could learn from observing the successful feeding behavior of fellow flock members to peck in a particular area in which others had found food. The procedure of Experiment 2 was similar to that of Experiment 1 except that naive fowl were required to learn a particular location, rather than a particular type of feeding site, in which to forage.

Method

Subjects

Thirty-eight, 21- to 28-day-old, experimentally naive, Burmese red junglefowl from the McMaster University vivarium served as subjects. Eight of these subjects served as demonstrators, 30 as observers.

Apparatus

The apparatus was that used in Experiment 1 except that none of the dishes in the experimental enclosure during training of demonstrators or training and testing of observers were marked.

Procedure

Training demonstrators. With the same procedure as in Experiment 1, 2 pairs of demonstrators were trained to find food in each of the four locations where dishes were placed.

Training observers. Fifteen pairs of naive observers were trained with the same procedure described in Experiment 1. In this experiment, either 3 or 4 pairs of observers were trained with demonstrators feeding from each of the four locations where dishes were placed.

Testing observers. Observers were tested in pairs with the same procedure as in Experiment 1. During the testing of observers, none of the dishes were marked, and none contained food.

Results

Training Demonstrators

Demonstrators required an average of $11.8 \text{ trials} \pm 0.8$ to achieve criterion performance.

Training Observers

During the training of observers, the 4 demonstrator pairs spent an average of 9.6 ± 0.2 of the 10 min of observer training (two 5-min sessions) pecking in the location that contained food. They did not peck in alternative locations.

Testing Observers

One or both members of 10 of the 15 pairs of observers pecked in a dish during testing. In one observer pair whose members pecked during testing, one pair member directed a single pecking bout toward the dish in the location where its demonstrators had been trained to feed and the other observer in the pair directed its sole pecking bout toward a dish in another location. Because it was not clear how to treat such an outcome statistically, for purposes of statistical analysis, we considered this pair to have directed its initial bout of pecking at a location other than that exploited by its demonstrators.

Of the 10 pairs of observers that pecked in dishes during testing, 8 directed their initial bout of pecking toward the dish in the location where their respective demonstrators had been trained to feed (binomial test, $P = 0.25$, $x = 2$, $p < .0004$). On average, the 10 pairs of observers pecked in the location where their respective demonstrators had been trained to peck for $86.2\% \pm 10.3$ of the $0.05 \text{ min} \pm 0.01$ that they spent pecking. Nine of the 10 observer pairs pecked for more than 25% of the time that they spent pecking in the location where their respective demonstrators had been trained to peck (sign test, $P = 0.50$, $x = 1$, $p < .03$).

Discussion

The results of the present experiment indicate that observation of trained conspecifics feeding in a particular location can influence the choice of foraging location by observers 48 hr after observation occurred.

Experiment 3

It might be argued that although the results of Experiments 1 and 2 provide statistically reliable evidence of social influence on feeding site selection by fowl, they do not show that this influence is of any ecological relevance. Many of the observer birds did not peck in the test situation and those that did peck did so for only a few seconds.

It must be noted, however, that Experiments 1 and 2 were conducted so as to ensure that pecking in food dishes by observer birds was not rewarded with food. Observers had no prior experience feeding either from food dishes or in the test situation and observers were tested without food in food dishes. It is reasonable to suppose that in natural situations, fowl often receive food rewards for pecking in the types of feeding sites or in the same locations where they have seen conspecifics forage successfully.

In this experiment, we introduced food rewards into the test situation with the expectation that the presence of food in feeding dishes would enhance the amount of pecking subjects exhibited during testing and in the hope that increased pecking might reveal the ecological relevance of the social influences on feeding site selection observed in Experiments 1 and 2.

Method

Subjects

Thirty-four, 21- to 28-day-old, experimentally naive, Burmese red junglefowl from the McMaster University vivarium served as subjects. Eight fowl served as demonstrators and 26 as observers.

Apparatus and Procedures

The apparatus and procedures of this experiment were identical to those used in Experiment 2 except during testing of observers. Each of the four food dishes presented to observers during their testing contained 2 g of the subjects' normal diet, enough food to cover the bottom of a food dish. The food in each dish was concealed beneath strips of torn newsprint.

Results

Training Demonstrators

Demonstrators required an average of $12.5 \text{ trials} \pm 1.5$ to achieve criterion performance.

Training Observers

Demonstrator pairs spent an average of 9.70 ± 0.09 of the 10 min of observer training pecking in food dishes. They

pecked only in the food dishes from which they had been trained to feed.

Testing Observers

One or both members of each of 11 of the 13 pairs of observers pecked in one or more food dishes during testing. Eight of the eleven pairs directed their first bout of pecking toward the dish in the location where their respective demonstrators had fed (binomial test, $P = 0.25$, $x = 3$, $p < .001$).

On average, the 11 pairs of observers pecked in the food bowl from which their respective demonstrators had fed for $79.9\% \pm 3.3$ of the $14.8 \text{ min} \pm 0.7$ that they spent pecking. Members of 9 of the 11 observer pairs directed more than 25% of their total pecking time toward the location from which their demonstrators had fed (binomial test, $P = 0.50$, $x = 2$, $p < .03$, one-tailed).

Discussion

The results of the present experiment indicate that the apparently minor socially induced biases in pecking orientation demonstrated in Experiments 1 and 2 can have profound effects on the foraging behavior of fowl. When, as may be expected to occur in natural foraging situations, reinforcement was available to foraging observer fowl, they not only oriented their first exploratory pecks toward feeding sites where they had seen conspecifics feed 48 hr earlier, they also exhibited sustained feeding from those sites even though equally rewarding alternative feeding sites were available in the immediate vicinity.

General Discussion

The results of this series of experiments indicate that feeding in flocks provides birds with longer term benefits in addition to the immediate increase in efficiency of food finding of the sort reported by Krebs and his coworkers (Krebs, 1973; Krebs et al., 1972).

As a result of observation of the feeding behavior of successful flock members, less successful birds can acquire information as to both types of feeding sites (Experiment 1) and locations (Experiment 2) where food may be found. Such information can be used on later occasions by observers of successful foragers to direct their own foraging behavior toward potentially fruitful sites, even if the initial exploiter of those sites is no longer present. The ability to use information acquired from a successful forager in the absence of that forager may be particularly important to animals of low social rank that are not allowed to share feeding sites with dominants (Baker, 1978; Baker, Belcher, Deutsch, Sherman, & Thompson, 1981).

Although socially induced biases on exploratory pecking are small in themselves, when food is available, these minor biases in pecking orientation can profoundly influence orientation of feeding behavior. Fowl tend to feed in locations where they have observed conspecifics feed and, consequently, tend to ignore alternative potential sources of nutriment.

Both the longer term effects on foraging behavior induced by interaction within feeding flocks described here and the other examples of long-term effects of observation on subsequent foraging reported in the literature (Bartashunas & Suboski, 1984; Mason & Reidinger, 1981) indicate that processes other than local enhancement or social facilitation can play a role in enhancing the probability of food finding by flock-feeding birds. Both social facilitation (Zajonc, 1965, 1969) and local enhancement (Thorpe, 1963) are restricted in their direct effects on behavior to the time that animals are actually interacting (see Galef, 1988, p. 17, for a discussion of longer term, indirect effects of social facilitation and local enhancement).

Spence (1937, p. 821) used the term *stimulus enhancement* to refer to "the enhancement [by the actions of a conspecific] of the particular limited aspect of the total stimulus situation to which the response is to be made." Although Spence did not discuss the duration of the effects of stimulus enhancement on behavior, there is nothing in his definition to preclude long-term changes in the valence of objects as a result of observation of their manipulation by others. Suboski (1990) used the term *releaser-induced recognition learning* to describe a process similar to Spence's stimulus enhancement, again without indicating any temporal restriction on the duration of socially induced alterations in stimulus valence. Taken together, the results of our experiments indicate that in fowl, observation of conspecifics pecking either at an object or in a location results in long-lasting stimulus enhancement and increases the probability that an observer's later feeding behavior will be directed toward the enhanced object or location.

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