SOCIAL FEEDING

IN

BURMESE JUNGLEFOWL

(*Gallus gallus spadiceus*)

By

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Abstract

There is reason to believe that birds feeding in flocks enjoy several different types of advantage relative to birds that feed alone. Most relevant to this thesis, flocking can facilitate individual birds' discovery of potential foraging sites. In the present research, both the long-term consequences of social feeding and the importance of auditory and visual stimuli provided by conspecifics while feeding socially were examined in Burmese junglefowl (*Gallus gallus spadiceus*). The results of experiments presented in Chapter 2 indicated that junglefowl can learn to select either a type of feeding site or a location in which to feed simply by observing feeding companions. Social interaction biased the foraging behaviour of fowl for at least two days after interaction occurred.

In experiments described in Chapter 3, junglefowl used information acquired during their exposure to videotaped companions to orient their own subsequent feeding behaviour. Different aspects of the feeding behaviours of video-taped tutor fowl influenced different aspects of their observers' feeding behaviour. For example, during testing, observer birds' latencies to initiate pecking were reduced by previous exposure to the sight of conspecifics feeding, while the orientation of observers' pecking was influenced only when observers had both seen and heard feeding companions. The final study, presented in Chapter 4, indicated that observer fowl, even while feeding, were themselves able to learn about foraging sites where videotaped companions fed.

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Chapter 1

Introduction

One benefit an individual bird can gain by foraging as a member of a flock is facilitation of its discovery of potential sources of food. Researchers have examined the immediate effects of social feeding on individual birds. However, subsequent modifications in birds' feeding behaviour following their interaction with feeding conspecifics have been largely unexamined. Additionally, few experiments have been performed to determine which of the stimuli provided by feeding conspecifics during flock foraging are sufficient to produce changes in individual birds' subsequent foraging behaviour.

The intent of the present research was to establish whether Burmese junglefowl (*Gallus gallus spadiceus*) demonstrate modifications in their foraging behaviour following their interaction with feeding conspecifics, and to explore whether such changes are maintained for at least two days. The importance of both auditory and visual stimuli in producing changes in the subsequent foraging behaviour of junglefowl following their exposure to video-recordings of conspecifics was also investigated. Finally, the question of whether junglefowl, while they are feeding, are able to acquire foraging information from video-recordings of feeding conspecifics was studied.

A review of the literature relevant to this research is presented with emphasis on the functions of flock foraging and the effects of conspecifics' behaviour on individual

birds' feeding behaviour. An overview of the results of social learning experiments using birds and the function of visual and auditory stimuli in social feeding situations is provided. The duration of the effects of social feeding on individual birds' subsequent foraging behaviour is also discussed. Finally, a brief summary of the social life of Burmese junglefowl in their natural environment is presented.

Functions of Foraging in Flocks

There is reason to believe that birds feeding in flocks enjoy at least three different types of advantage relative to birds that feed alone. First, feeding in groups may reduce an individual bird's risk of predation. Second, birds in a flock may not need to maintain as high a level of vigilance for predators as do solitary birds. Finally, and most relevant to the present experiments, flocking may facilitate individual birds' discovery of foraging sites.

Decreased Risk of Predation

Results of field and laboratory studies are consistent with the hypothesis that birds in a flock are less vulnerable to predation than are solitary foragers (Caraco, Martindale and Pulliam, 1980; Hamilton, 1971; Kenward 1978; Powell 1974; Siegfried and Underhill, 1975). For example, Kenward (1978) used a trained goshawk (*Accipiter gentilis*) to attack feeding flocks of woodpigeons (*Columba palumbus*) and found that the predator's attacks on the pigeons became less successful as the number of birds in an attacked flock increased. Also, the distance of the hawk from the pigeons when the pigeons took flight increased as flock size increased.

Powell (1974) conducted a laboratory investigation of effects of flocking on predation in starlings (*Sturnus vulgaris*). He compared the response times of solitary starlings with those of starlings in groups of 10 when both were presented with an aerial model of a Cooper's hawk (*Accipiter cooperi*). Powell reported that starlings in groups responded more quickly to the hawk model than did solitary starlings.

Decrease in Demand for Vigilance for Predators

A direct effect of increasing flock size on individual birds' levels of vigilance for predators has been demonstrated in several avian species (e.g. house sparrows, Elgar and Catterall, 1981; Elgar, Burren and Posen, 1984; Gluck, 1987; Lima, 1987; doves, Lendrem, 1984; dark-bellied brent geese, Inglis and Isaacson, 1978; pinkfooted geese, Lazarus and Inglis, 1978; Lazarus, 1979; Lindstrom, 1989; Jennings and Evans, 1980; chickadees, Sullivan, 1984a, 1984b; ostriches, Bertram, 1980; see Elgar, 1989 for review). For example, Elcavage and Caraco (1983) determined whether individual house sparrows (*Passer domesticus*) spent less time visually scanning for predators as flock size increased from one to six birds. House sparrows, trained to feed from a baited grid, were filmed for several feeding sessions. Elcavage and Caraco later viewed each session and recorded the frequency and duration of each bird's scanning behaviour. They found that: (1) the probability that a bird was scanning at any time during filming decreased with increasing flock size, and (2) the mean time between a bird's completion of one scan and initiation of its next scan increased with flock size. Feeding in flocks clearly reduced the time that birds

spent looking out for predators, presumably resulting in adaptive allocation of time away from such vigilance and toward other profitable activities such as foraging.

Facilitation of Discovery of Foraging Sites

If foods that members of an avian species are exploiting occur in rich patches, each containing more food than a single individual can eat, then social feeding can facilitate food finding by flock members. Such beneficial effects of flocking on foraging success have been repeatedly demonstrated (Benkman, 1988; Crook, 1965; Elgar, 1987; Ekman and Hake, 1988; Krebs, 1973; Krebs, MacRoberts and Cullen, 1972; Lack, 1968; Newton, 1967; Szekely, Sozou and Houston, 1991; Ward, 1965). For example, Benkman (1988) looked at the foraging behaviour of solitary, captive crossbills (*Loxia curvirostra*), and of crossbills foraging in flocks of either two or four, when the birds were feeding on seeds that were uniformly distributed, moderately clumped, or very clumped in distribution. Benkman reported that crossbills in the very clumped condition, foraging in groups of two, or four, required less time to locate a patch of dense food than did solitary foragers. He concluded that individual crossbills were able to recognize when others had located a patch and would use such social information to facilitate their own location of food.

In sum, birds in flocks experience several advantages relative to solitary birds. Not only are birds in flocks less vulnerable to predation, but they also spend less time looking for predators, and can learn from one another about the location of potential feeding sites.

Social Influences on Feeding Behaviour in Birds

While field studies are most appropriate for analyzing functions of flock feeding, laboratory studies are better suited to determining the ways in which social interaction can affect the foraging behaviour of birds feeding in flocks (Bartashunas and Suboski, 1984; Clayton, 1976; Franchina, Dyer, Zaccaro and Schulman, 1986; Hale, 1977; Klopfer, 1959; Rajecki, Kidd, Wilder and Jaeger, 1975; Rajecki, Wilder, Kidd and Jaeger, 1976; Tolman, 1967a, 1967b; Tolman and Wilson, 1965; Tolman and Wellman, 1968; Turner, 1964). The results of such laboratory studies have led to identification at least of three distinct ways in which birds can affect the feeding behaviours of their fellows.

Presence of a Companion

It has been repeatedly found that isolated birds eat less than do birds that are in the presence of a companion, even if that companion is not itself feeding (e.g. sparrows, *P. domesticus*, and chaffinches, *Fringilla coelebs*, Turner, 1964; domestic chickens, *Gallus domesticus*, Hale, 1977; Rajecki et al., 1975; Tolman and Wellman, 1968). Tolman (1965), for example, compared the number of pecks that isolated chicks (*G. domesticus*) directed toward food on the floor of their cages with the number of pecks produced by chicks that were separated by a transparent barrier from a conspecific that was not feeding. Tolman found that chicks feeding in isolation pecked significantly less often than did chicks feeding in the presence of a companion, even if that companion was not pecking.

Isolated chicks in the Tolman study may have experienced isolation-induced inhibition of feeding mediated by fear, as suggested by Clayton (1978). On this view, the greater frequency of pecking behaviour observed in chicks accompanied by companions, relative to the amount of pecking exhibited by chicks held in isolation, is the result of companions disinhibiting subjects' pecking behaviour by reducing their fear.

Behaviour of a Companion

The behaviour of a companion, as well as a companion's mere presence, can affect feeding by subject birds (e.g. domestic chicks, *G. domesticus*, Rajecki et al., 1976; Tolman, 1967a, 1967b, 1968; Tolman and Wilson, 1965; ducklings, *Anas platyrhychos*, Clayton, 1976; house sparrows, *P. domesticus,* and chaffinches, *F. coelebs*, Turner, 1964). For example, Tolman (1968) reported that a chick separated by a transparent barrier from a feeding companion pecked at food significantly more often than did a chick exposed to a non-feeding companion.

Furthermore, the rate of pecking exhibited by a chick is positively correlated with that exhibited by its companion. For example, Tolman and Wilson (1965) paired a chick (*G. domesticus*) with a companion, and measured the number of food pecks that each of the pair exhibited during testing. Tolman and Wilson varied the level of food deprivation of each companion bird (0, 6 or 24 h), while maintaining the food deprivation of each subject bird at a constant level (6 h). They found that the amount of food consumed by a chick was correlated with the number of hours that its companion chick had been food deprived. The greater the deprivation state of a companion chick, the more it pecked, and

the more its partner, the subject chick, pecked. Thus, a food-deprived companion evoked more pecking in a conspecific than did a less hungry companion.

Orientation of Companion's Behaviour

In a number of species, behaviour of companions can not only affect the rate of pecking exhibited by subject birds, it can also bias the orientation of their feeding behaviour (domestic chickens, *G. domesticus*, Bartashunas and Suboski, 1984; Franchina, Dyer, Zaccaro and Schulman, 1986; greenfinches, *Chloris chloris*, Klopfer, 1959). For example, Suboski and Bartashunas (1984) found that four-day-old chicks (*G. domesticus*) directed their pecking behaviour toward pins of the same colour as those at which a mechanical model was simultaneously pecking. In a more natural, though less well controlled study, Klopfer (1959) found that naïve greenfinches who watched trained conspecifics discriminate between palatable and unpalatable foods (provided in visually distinctive food dishes) more readily learned the discrimination task than did naïve greenfinches that had not observed conspecifics in the situation (Klopfer, 1959).

Social modification of the orientation of drinking, similar to that of feeding, has also been reported in domestic chickens (Franchina et al. 1986). During the preparatory stage of Franchina et al.'s study, tutor chicks were trained to drink from either clear or coloured drinking tubes. During testing, a subject and tutor were placed in adjacent compartments separated by a screen partition. Tutors drank from the type of tube from which they had been trained to drink, and subjects were found to take most of their water from the same type of tube from which their respective tutors drank.

Social Learning in Birds

The attention that birds focus on feeding flockmates has the potential to facilitate acquisition of behaviours required to obtain food as well as to orient feeding toward particular objects. A variety of studies have found that birds demonstrate enhanced acquisition of novel foraging behaviours both during and following their exposure to conspecifics engaged in those novel behaviours (greenfinches, *C. chloris*, Klopfer, 1959; northern blue jays, *Cyanocitta cristata*, Jones and Kamil, 1973; domestic chicks, *G. domesticus*, Johnson, Hamm and Leakey, 1986; pigeons, *Columba livia*, Beiderman et al., 1986; Palametta and Lefebvre, 1985; black-capped chickadees, *Parus atricapillus*, Sherry and Galef, 1984).

Socially learned behaviours that have been studied experimentally have not, typically, been truly novel motor patterns. Rather, research has focused on social learning of variants of motor patterns already present in birds' repertoires (e.g. pecking a keylight, Zentall and Hogan, 1976; Johnson et al., 1986, pecking through paper to obtain food, Palameta and Lefebvre, 1985). The typical protocol of such studies involves, first, exposing a naïve observer bird to a conspecific tutor engaged in whatever behaviour the observer is to acquire, and then assessing the observer's acquisition of its tutor's behaviour relative to that of control subjects that did not have the opportunity for social learning.

Effects of Social Variables On Learning of Operant Responses Associated with Feeding

Zentall and Hogan (1976) used an instrumental conditioning task to investigate social learning in pigeons, *C. livia*, (see also Biederman et al., 1986). Observer and tutor were both placed in an experimental cage that was divided into two chambers by a transparent partition. A grain feeder was located in the center of the front wall of each of the two chambers and there was a response key above each feeder.

During training, observer pigeons were placed on one side of the experimental cage and exposed to one of the following four conditions: (1) a demonstrator that pecked the illuminated key and subsequently fed from the grain feeder, (2) a demonstrator that fed from the grain feeder but did not peck at the response key, (3) a demonstrator that was neither exposed to an illuminated key nor allowed to feed, or (4) a demonstrator that did not gain access to the grain feeder when it pecked the illuminated key.

Zentall and Hogan (1976) reported that the sight of another pigeon pecking a response key for grain (condition 1) resulted in keypecking by a greater number of pigeons than did the sight of another pigeon eating (condition 2), the sight of another pigeon neither pecking nor eating (condition 3), or the sight of a pigeon that pecked but was not rewarded for doing so (condition 4). Similar social facilitation of the acquisition of keypecking behaviour has also been reported in chickens (*G. domesticus*, Johnson et al., 1986).

Effects of Social Variables on Learning of Classically Conditioned Responses Associated with Feeding

Birds' ability to socially learn classically conditioned responses has also been studied (Klopfer, 1959; Mason and Reidinger, 1981, 1982; Mason, Arzt and Reidinger, 1984). For example, Mason et al. (1984) looked at acquisition of food preferences and aversions by red-winged blackbirds (*Agelaius phoeniceus*) that observed conspecific demonstrators that both ate at visually distinctive feeding sites and experienced experimentally manipulated consequences of doing so.

In the Mason et al. study, demonstrator blackbirds were fed their normal rations from yellow food dishes. After the demonstrators assigned to the food aversion condition had eaten roughly 1 g of food, their food cups were removed from their cages and each bird was intubated with methiocarb, a substance that causes retching and vomiting in birds (Mason and Reideinger, 1982). Demonstrators in the preference-learning condition were allowed to continue eating undisturbed. On each of the 12 days immediately following training, each observer blackbird was presented with both yellow and green food dishes containing the observers' normal rations.

Mason et al. reported that observers assigned to the preference-learning condition ate considerably more from the yellow cup than from the green cup, while observers in the aversion-learning condition avoided eating from the yellow cup that had been paired with methiocarb during training, and ate predominantly from the green cup. Food preferences and aversions were acquired by blackbirds as a consequence of observation of the experiences of their demonstrators.

Absence of Social Learning of Feeding Behaviours in Birds

Success in demonstrations of social influence on learning in birds has not been universal. Several researchers have reported no evidence of social learning in birds following their exposure to performances by knowledgeable conspecifics (black-capped chickadees, *P. atricapillus*, Baker, Stone et al., 1988; pigeons, *C. livia*, Giraldeau and Lefebvre, 1987; Lefebvre, 1986; Robertson, Vanayan and Biederman, 1985; Vanayan, Robertson and Biederman, 1985; jackdaws, *Corvus monedula*, Wechsler, 1988).

Positive and negative demonstrations of social learning have often used similar experimental designs. For example, Wechsler (1988), using a design like that employed successfully by Zentall and Hogan (1976), looked at acquisition of a new food-producing technique (manipulation of a food dispenser that led to the release of oats) by jackdaws (*C. monedula*). Over forty-four days of exposure, each observer was separated by a transparent wall from a conspecific demonstrator who manipulated a dispenser and then ate oats. The observer had access to its normal diet during this time. Following exposure, Wechsler determined whether observer birds would approach a dispenser and successfully manipulate it to acquire food. He reported that jackdaws exposed to trained conspecifics did not acquire the foraging behaviour necessary to get oats any faster than did jackdaws that had not watched conspecifics perform the necessary behaviour. It is not clear why Wechsler failed to find social learning in his jackdaws, while Zentall and his colleagues, some of whose work is described above, had great success in similar studies with pigeons.

In some cases, presence or absence of evidence of social influences on learning has depended on how the effect of exposure to the behaviour of conspecifics on observer birds was assessed. For example, Dawson and Foss (1965) exposed naïve budgerigars to conspecific demonstrators who were required to remove a cardboard lid from a dish to gain access to food. On the day following the last of eight exposure trials, each observer bird was presented with the same task that it had watched its demonstrator perform. Dawson and Foss compared the numbers of trials that observers and demonstrators required to learn to remove the lid from the dish. They did not find any support for the hypothesis that budgerigars exposed to conspecifics performing a food-producing skill could acquire that skill more rapidly than could birds lacking such exposure, and yet, Dawson and Foss did find that observers tended to use the same method of acquiring food that had been employed by their respective demonstrators. Those observers whose demonstrators had used their feet to remove the cover from the food dish tended to do so, while those observers whose demonstrators had pecked at the lid or pulled the lid off the dish with their beaks tended to do the same. Thus, when social learning was measured in terms of observers' latencies to acquire the necessary skill, the experiment did not produce evidence for social learning. Still, the statistically reliable finding that observer budgerigars' used the same food-producing method used by their respective demonstrators to open the lid did suggest that observer birds learned how to obtain food while watching their demonstrators.

Analyses of the Effects of Social Feeding on Birds

As described above, the literature provides evidence that, in a variety of species of flocking birds, individuals will both match their feeding behaviours to those of feeding conspecifics and bias the orientation of their feeding towards sites where companions are feeding. However, neither the nature of the stimuli mediating such social effects on feeding nor the duration of such social effects on the feeding behaviours of individuals within a flock have been much studied.

Auditory Cues in Social Feeding in Birds

The role of auditory cues in social learning about feeding sites and food by birds has been examined in several laboratories (Cowan, 1974; Elgar, 1986; Gyger, Karakashian and Marler, 1986; Gyger and Marler, 1988; Marler, Dufty and Pickert, 1986a, 1986b; Sherry, 1977). The usual procedure in such research is to record auditory cues in a normal flock situation, to present the recording to a solitary bird, and then to assess the effects of the recording on the subject's behaviour. Alternatively, experimenters have used, as auditory stimuli, vocalizations of live animals hidden from a conspecific. For example, in the presence of food, domestic male chickens (*G. domesticus*) call and attract females to a food site (Marler et al., 1986b). Marler et al. (1986b) conducted an experiment to determine whether cockerels' food calls varied with the quality of the food that they had discovered. A food-deprived cockerel was tethered behind an opaque barrier and presented with either a preferred or non-preferred food. A hen was placed on the other side of the barrier and could walk around it and approach the cockerel. Marler et al.

reported that the probability of a hen approaching a cockerel was greater when the male was eating a preferred food than when it was eating a non-preferred food. They argued that hens were able to acquire information about the quality of their respective cockerels' food from the cockerels' food calls.

Visual Cues in Social Feeding in Birds

There is a long history of study of the role of visual cues in eliciting and directing feeding by birds. In a classic study of visual mediation of feeding interactions between adult herring gulls (*Larus argentatus*) and their chicks, Tinbergen and Perdick (1951) used cardboard models of adult gulls' heads with bills of various colours to test the importance of bill colour in releasing begging responses in chicks. A red-coloured bill was found to release more begging responses than did any of the other colours studied. Subsequent researchers have used two-dimensional models to study the role of visual stimuli in directing feeding behaviour by birds (Bartashunas and Suboski, 1984). For example, Turner (1967) reported that a mechanical model of a pecking hen could be used to induce a pecking preference in chicks for one of two equally palatable foods.

More recently, researchers have begun to use videorecorded images of birds, instead of mechanical models, to study visual mediation of birds' social behaviour. Evans and Marler (1991) presented evidence that the 'audience effect' on the alarm calling of domestic chickens can be produced using video images rather than live conspecifics to provide the audience.[1]

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[1] The 'audience effect' refers to the finding (Gyger et al., 1986) that cockerels modulate their alarm calling in response to their social environments: Following appearance of an avian predator, cockerels give more aerial alarm calls in the presence of hens do than cockerels in isolation.

Evans and Marler (1991) recorded the number of alarm calls a cockerel, presented with an aerial model of a hawk, made when in the presence of either: (1) an unfamiliar hen, (2) a videotape of an unfamiliar hen, (3) an empty cage, or (4) a videotape of an empty cage. Evans and Marler reported that there was "no hint of a difference between the effects of videotaped or live audiences on cockerels' alarm calling" (Evans and Marler, 1991, p.22). The cockerels called more when in the presence of hens, either live or videotaped, than when alone.

The effectiveness of video images in producing audience effects provides an interesting approach to analyzing the role of visual stimuli in directing social feeding in birds. For example, having established that a videorecording of feeding conspecifics has a facilitatory effect on birds' foraging, an experimenter could now examine the effects of the same recording presented in the absence of auditory cues. Application of more sophisticated editing techniques, including computer-aided editing of video images, provides the opportunity to investigate analyses of visual signals that were previously impossible.

Duration of the Effects of Social Feeding in Birds

Effects of social feeding on the behaviour of flock members have typically been examined by investigating the consequences of social feeding either while, or immediately after, an observer and tutor fed together. Such short-term social effects on foraging can be discussed as instances of: (1) "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), (2) "stimulus enhancement" ("the enhancement of the particular limited aspect of the total stimulus situation to which the response is to be made," Spence, 1937, p.821), or (3) "social facilitation", ("the presence of others enhances the emission of dominant and well-developed responses", Zajonc, 1965, p. 271).

Few studies have examined whether the effects of social feeding on the feeding behaviour of individual birds last for days, hours or even minutes after social interaction is completed. Indeed, there is only one instance where measurement of the effects of social learning on feeding behaviours of birds has been delayed for more then a few minutes after demonstration was completed. Bartashunas and Suboski (1984) reported that 72 h after observing a crude model of a hen "pecking" at a visually distinctive, food-like object (a coloured pin head), 4-day-old domestic chicks (*G. domesticus*) still pecked preferentially at similarly coloured objects.

Whether the social induction of durable preferences for pecking at particular types of objects demonstrated in the Bartashunas and Suboski study occurs only during the first days of life of a chick is not clear. Hess has stated that "there is a definite 'critical period' during which food reinforcement is most effective in modifying innate preferences for pecking at certain objects" (Hess, 1964, p.1136). Hess (1973) presented groups of chicks of varying ages with food reward for pecking at a stimulus at which chicks ordinarily show little tendency to peck (Target A). During testing (6 days later), in the absence of food reward, Hess presented chicks with both Target A and a stimulus that normally elicits a high frequency of spontaneous pecking in naïve chicks (Target B). Hess reported that

food reward associated with Target A was effective in producing long-term modifications of congenital pecking preferences only when chicks were 3 or 4 days old. The long-term target preference of chicks 1, 2 or 5 days old or older was totally unaffected by pairing targets with food reward.

Partial support for the notion of a critical period for food imprinting in birds has been provided by Hogan (1973a, 1973b) who demonstrated that equivalent experience with pecking at food has different effects on chicks of different ages. Hogan reported that when 3-day-old Burmese junglefowl chicks (*Gallus gallus spadiceus*) ingested a given amount of food, they exhibited a greater number of pecks directed toward food than did younger chicks that had eaten the same amount of food. Hogan did not, however, continue his experiments with chickens older than three days of age to provide evidence concerning the end of such a sensitive period.

If there is a sensitive period during which food reinforcement is most effective in modifying innate preferences, then the results of studies of social learning in hatchlings can not be extrapolated to adult chickens. Learning in hatchlings may be dependent upon "stimulus imprinting" (Hess, 1964, 1973), a process acting during early development and not available later in life.

The duration of the effects of social feeding on the behaviour of individual adult birds has not been systematically explored, though it is of some importance that such exploration be undertaken. The duration of effects of social interaction on behaviour can provide insight into the processes supporting social learning. Both social facilitation

(Zajonc, 1965, 1969) and local enhancement (Thorpe, 1963) are restricted to direct effects on behaviour during the time when animals are actually interacting. Consequently, demonstrations that observation of conspecifics' feeding behaviour has effects lasting many hours or days would indicate that such social learning rests on processes other than social facilitation or local enhancement. Similarly, demonstrations that fowl exhibit long-term effects of social interactions on their feeding behaviour after the sensitive period for food imprinting has passed would demonstrate that processes other than food imprinting can support such effects.

Burmese Junglefowl

Flock Structure

The social behaviour of both free-living and captive junglefowl has been described by several researchers (Collias, 1952; Collias, Collias, Hunsaker and Minning, 1965; Kruijt, 1964; McBride, Parer and Foenander, 1969; Stokes, 1971). The birds live in harem flocks, each consisting of a dominant male, four to twelve females and as many as six subordinate males. In general, the dominant male is found at the center of his flock, and dominant females usually remain close to him, while younger, subordinate females are typically at the edge of the flock, as are subordinate males.

Foraging Behaviour

While feeding, junglefowl move as a group, with three to six meters separating flockmates. Thus junglefowl can usually see and hear fellow flockmates (McBride et al, 1969, p. 139). When walking about between feeding bouts, junglefowl hold their tails

upright and closed. The tail is lowered and opened by an individual as soon as it stops to feed (McBride et al., 1969, p.137), and the sight of an opened tail attracts fowl to the displaying individual. Foraging fowl are also attracted to a food source by a variety of vocalizations that have been described as "food twitters" (Breed, 1911, p.14; Stokes, 1971) or "twitter calls" (Kruijt, 1964). In sum, a combination of visual and auditory signals are available which might permit discovery of food to be quickly transmitted through a flock of junglefowl, and flock members rapidly join flockmates that have discovered food (McBride et al., 1969, p.171).

Feeding Behaviour in Hatchlings

The young of junglefowl, like those of other gallinaceous birds, are precocial and, within a few minutes of hatching, chicks begin to peck at small objects (Wood-Gush, 1955). Young can also take advantage of interactions with adults to learn to identify and obtain food. Typically, when a hen locates food, she behaves in such a way that the young will eventually eat that food. For example, a hen may let a chick take a morsel from her beak (Kruijt, 1964, p.117), she may drop the food in front of a chick (tidbitting, Kruijt, 1964, p. 117), or she may use specific calls to alert chicks to the availability of food (Stokes, 1971). Thus, in the period immediately following hatching, chicks can begin learning what to eat through interactions with their mother hen.

Diet

Outside the laboratory, junglefowl forage for patchily distributed foods. McBride et al. (1969) described in detail the diet of junglefowl introduced onto an island in

Queensland, Australia. They reported that junglefowl drank from numerous rain-filled hollows in fig and pisonia trees. All of these hollows contained organic matter and, when they dried, junglefowl returned to eat the insects living under damp leaves. Junglefowl also ate pisonia leaves and figs and were observed chasing and catching flying insects. Analyses of their crop contents revealed that the birds ate slugs, several types of insects, isopods and numerous berries and seeds. A similar diet of insects and fallen fruit has been reported for junglefowl in Samoa (Muse and Muse, 1982).

Suitability of Burmese Junglefowl for Studies of Social Learning

Free-living junglefowl (*Gallus gallus spadiceus*) are highly social birds that are known to forage in flocks. Ground-feeding birds, such as fowl, should have ample opportunity to observe both the foraging site selection and foraging success of fellow flock members. They are, therefore, reasonable subjects for laboratory studies of social feeding. Additionally, Burmese junglefowl are the ancestors of domestic chickens (Zeunner, 1963), and the close phylogenetic relationship of domestic chickens and Burmese fowl permits integration of work on Burmese fowl into the extensive, existing literature describing the feeding behaviour of chickens.

Outline of Research

In Chapter 2, a simple laboratory analogue of natural social feeding is established and the long-term consequences of social feeding for adolescent Burmese junglefowl (*G. spadiceus*) are examined. The importance of both auditory and visual stimuli present

during social feeding in producing modifications in the feeding behaviour of junglefowl is examined in experiments described in Chapter 3. In these experiments, naïve fowl were exposed to video images of feeding conspecifics. Finally, in Chapter 4, the question of whether junglefowl, while feeding, are able to acquire foraging information from feeding conspecifics is studied.

Chapter 2

Investigation of Longer-Term Effects of
Social Feeding in Burmese Junglefowl

The purpose of the first series of experiments was to determine whether social interactions between naïve, adolescent Burmese junglefowl and their more knowledgeable fellows would influence the naïve to feed from the type of foraging site or location that knowledgeable conspecifics were exploiting. The experimental procedure was designed as a laboratory analogue of a natural situation in which a naïve bird was feeding with a flockmate that had learned that food was present either at a specific type of feeding site (Experiment 1) or at a particular location (Experiment 2). The question of interest was whether, as the result of feeding with a knowledgeable conspecific, a naïve bird would learn in which type of feeding site or location food could be found and whether the naïve bird would use that information when subsequently foraging alone. Whether similar effects of social interaction on feeding orientation could be established in junglefowl that were spatially separated from feeding flockmates during their social interaction was explored in Experiment 3.

Experiment 1

Study A

This experiment was undertaken to investigate one type of effect of social interaction on feeding in Burmese junglefowl. Specifically, I wished to know whether the type of feeding site fowl chose to exploit two days after interaction with feeding flockmates was influenced by prior social interaction in the feeding situation.

Methods

Subjects and maintenance

One hundred and two, 21- to 28-day-old, experimentally naïve, Burmese junglefowl (*Gallus gallus spadiceus*) participated in Experiment 1: 26 fowl served as demonstrators, 26 as observers and 26 as naïve companions of observers in the experimental group. Twenty-four additional fowl were assigned to a control group: 8 as demonstrators, 8 as observers and 8 as naïve companions of observers.

The use of companion birds for observers was required because social isolation of adolescent fowl resulted in prolonged periods of total inhibition of their foraging.

All subjects were descended from a flock maintained in the Department of Psychology at the University of Toronto, and all were offspring of birds raised in the vivarium of the McMaster University Department of Psychology.

All birds were maintained on ad libitum food (Purina Chicken Breeder, Ralston-Purina, Woodstock, Ontario) and water to which a vitamin supplement (Vitadol, Tuco Products, Orangeville, Ontario) was added. Food and water were provided in plastic

feeding troughs and watering stations (Porkmaster waterers, W. Murray Clark Ltd., Caledonia, Ontario). Cages were cleaned weekly.

Each flock consisted of one rooster and six or seven hens. The ages of the birds when placed in each flock were staggered so that, at any time, two of the flocks were producing fertilized eggs while the third flock was growing to sexual maturity. To maintain optimal egg production, flocks were replaced when they had been producing fertilized eggs for 12 months (Stromberg, 1975).

The junglefowl breeding colony at McMaster University was maintained on a 14:10 h day:night cycle in a temperature- and humidity-controlled colony room. The colony consisted of three flocks, each housed in a wood-frame breeding cage (1.8 m deep × 1.3 m wide × 1.8 m high) covered with chicken wire. The floor of each breeding cage was covered to a depth of 2 to 3 cm with wood-chip bedding, and the back wall of each breeding cage was equipped with a 2-tier, 10-hole commercial nest box made of galvanized steel (Model 49423, Cyclone International Incorporated, F. Murray Clark Limited, Caledonia, Ontario).

Eggs were collected daily and individually numbered and labelled with cage of origin and date. The eggs were placed for as long as one week on trays in a refrigerated holding tank so that groups of chicks would hatch simultaneously. While in the holding tank, the eggs were maintained at a temperature of between 7 and 12°C with a relative humidity of between 70 and 90 per cent (measured by a hygrometer in the holding tank).

The trays holding eggs were 'tipped' daily to alternately raise the left or right edge of the tray 45° from the horizontal.

At the end of the holding period, eggs were removed from the holding tank and placed in an incubator (Model 20, Humidaire Incubator Co., New Madison, Ohio) for the first 19 days of incubation. During this stage of incubation, eggs were maintained at 37.0°C with a relative humidity of 70 to 80 per cent. For the final two days of incubation, eggs were moved to a hatching incubator (Model 1202, G.Q.F. Manufacturing Co., Savannah, Georgia) and maintained at 37.5°C with a relative humidity of 80 to 90 per cent. The origin of any eggs that did not hatch was recorded. Records of egg production and hatching rate provided information required to identify potential problems in flocks.

For 3 to 4 weeks after hatching, each group of 5 to 20 young fowl was housed in a rearing cage (1 m deep × 1 m wide × 0.3 m high) constructed of angle iron and hardware cloth. Each cage had a floor of galvanized sheet metal which was covered to a depth of 2 to 3 cm with wood-chip bedding. A 250 W brooder lamp suspended over one corner of each rearing enclosure provided supplementary heat. Food (Purina Chick Starter, Ralston-Purina, Woodstock, Ontario) and water were available to chicks in 1-liter. Mason jar "chick feeders" and "chick waterers" (Berry Hill Ltd., St. Thomas, Ontario).

Apparatus

Chicks were trained and tested in an experimental enclosure (3 m deep × 1 m wide × 0.3 m high) like that illustrated in overhead schematic in Figure 1. The experimental enclosure was similar in construction to the rearing cage described in the

preceding section, but was divided into an ancillary enclosure (1 m deep × 1 m wide × 0.3 m high) and a main enclosure (2 m deep × 1 m wide × 0.3 m high) separated by an opaque, sliding door.

As illustrated in Figure 1, eight, 10 cm diam., 5 cm deep, circular, Pyrex dishes, painted white, were present in the main enclosure in a 2 × 4 array. The outside of each of four of the dishes was marked with eight, 1.9 cm diam., circular, red adhesive decals that were evenly spaced 1 cm below the rim of the dish. The other four dishes were unmarked. The positions of marked and unmarked dishes in the main enclosure were interchanged randomly between trials in both the training and testing phases, as described below.

Procedure

Training Demonstrators. Each of 13 pairs of demonstrator fowl was trained to find food in the main enclosure. To begin training demonstrators, a pair of experimentally naïve fowl was placed in the ancillary enclosure and food deprived for 4 h. At the end of the 4 h deprivation period, 2 g of the birds' usual food (Purina Chick Starter) was placed either in each of the marked dishes (7 pairs of demonstrators) or in each of the unmarked dishes (6
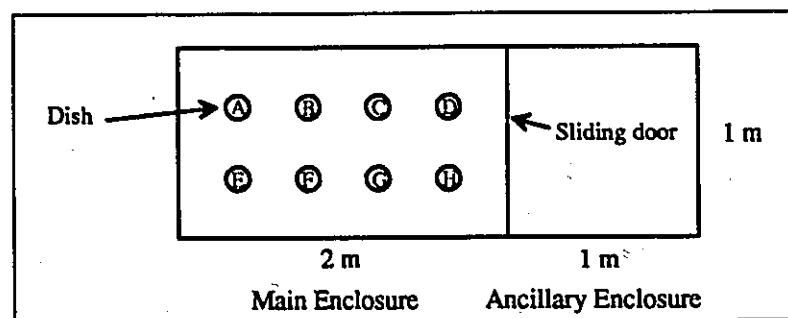

Figure 1. Overhead Schematic Diagram of Apparatus used in Experiments 1 and 2. Dishes were marked as indicated in the text. (Bowl lettering is pertinent to Study B.)

pairs of demonstrators). Next, the sliding door separating the ancillary enclosure from the main enclosure was opened, and each pair of birds was given 5 min to explore and feed in the main enclosure.

On each day of demonstrator training, each pair of demonstrators received 5 such training trials at 3-min intervals. Any trial in which both birds did not leave the ancillary enclosure within 2 min after the sliding door was opened was repeated 3 min later.

Across the 3 to 6 days of demonstrator training, strips of newsprint were placed in all eight food dishes in gradually increasing amounts, until the bottoms of the dishes were totally obscured. Also, the time during which demonstrators were allowed to feed, once they had found food, was gradually reduced to 1 min/trial.

Demonstrator training was continued until both birds in a pair directed their initial bout of feeding toward a dish containing food on 4 of the 5 trials carried out during a single day of training.

Training Observers. Twenty-four h after each of the 13 demonstrator pairs achieved criterion performance, one of its members was placed in the ancillary enclosure together with one of 26 naïve "observer" fowl. Both demonstrator and observer were then food deprived for 4 h. Following deprivation, on five occasions separated by 3 min, each of the 26 demonstrator-observer pairs was released into the main enclosure.

On each of these five observer training trials, all food dishes were filled with shredded newsprint and either all four marked or all four unmarked dishes contained food.

Food was placed in the marked dishes of those 14 demonstrator-observer pairs whose demonstrators had been trained to feed from marked dishes and in the unmarked dishes of those 12 demonstrator-observer pairs whose demonstrators had been trained to feed from unmarked dishes.

On each of the training trials in which each demonstrator-observer pair participated, the pair was left undisturbed in the main enclosure until 1 min after one of the pair members began to feed. At the end of the fifth observer training trial, each observer was returned to its home flock for 24 h ad libitum access to food and water.

During observer training, the experimenter recorded the location and duration of each bout of feeding exhibited by both demonstrator and observer. A bout of feeding was defined as a peck (or series of pecks) directed inside a Pyrex dish by a bird. A bout was considered to have ended when a bird did not peck for 2 s.

Testing Observers. Twenty-four h after completion of observer training, each of the 26 observers was paired with a naïve 21-day-old "companion" junglefowl and each observer-companion pair was placed in the ancillary enclosure and food deprived for 24 h.

Following the 24 h period of food deprivation, each observer and its companion were 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 two food dishes, one marked and one unmarked, both filled with strips of newsprint. Only one dish contained food. For each observer, the type of dish containing food (marked or unmarked)

was the same type as that from which its demonstrator had been trained to feed. Positions

of marked and unmarked dishes were reversed on a random schedule between trials.

The experimenter recorded the location and duration of feeding bouts exhibited by

both the observer and its naïve companion during each test trial.

Control Group. Additional observers ($\underline{n}$=8), assigned to a control group, were

treated identically to observers assigned to the experimental group (treatment of which is

described above) except that the "demonstrator" ($\underline{n}$=8) with which each observer in the

control group was paired during observer training was an experimentally naïve, 21-day-old

conspecific that had not been trained to find food in the main enclosure. As was the case

with members of the experimental group, during testing, observers in the control group

were each paired with a naïve companion fowl ($\underline{n}$=8).

Results

Training Demonstrators. Demonstrator pairs in the experimental condition

required an average (mean±standard error of the mean) of 20.4±2.4 trials to achieve

criterion performance during training.

Training Observers. The 26 demonstrators spent an average of 3.6±0.2 min of the

5.0 min training period pecking in dishes containing food and an average of only

0.6±0.5 min pecking in empty dishes. Each demonstrator pair directed its first pecking

bout toward the type of dish from which it had been trained to feed on an average of

85.2±2.4 per cent of the 5 trials in which each demonstrator participated.

The orientation of pecking behaviour exhibited by observers in the experimental condition during their training was influenced markedly by the behaviour of their respective demonstrators. Twenty-one of the 26 observers pecked at one or both of the two types of food dishes during training and, on an average of 92.1±3.9 per cent of training trials, these 21 observers directed their first pecking bout into a dish while their demonstrator was actively feeding there. Further, the 21 observers that fed during training directed their first pecking bout of each trial into a dish containing food on an average of 75.4±7.9 per cent of trials. They spent an average of 94.9±5.0 per cent of the 1.2±0.3 min that they spent pecking in dishes, pecking in the type of dish from which their respective demonstrators had been trained to feed.

Testing Observers. Twenty of the 21 observers that fed during observer training also fed during observer testing, and 19 of the 20 (Binomial test, $\underline{P}$=0.50, $\underline{x}$=1, $\underline{p}$<.001) directed their first pecking bout during testing toward the type of food dish from which their respective demonstrators had been trained to feed.

On average, the 20 observers in the experimental condition spent 85.8±5.2 per cent of the 2.8±0.4 min that they spent pecking, pecking in the type of dish from which their respective demonstrators had been trained to feed. Eighteen of the 20 observers that fed during testing directed the majority of their pecking toward the type of food dish from which their demonstrators had previously fed (Sign test, $\underline{P}$=0.50, $\underline{x}$=2, $\underline{p}$<.002).

Control Group. Subjects assigned to the control group were something of a disappointment. During training of observers in the control group, only 2 of 8 demonstrators and 2 of 8 observers pecked in a food dish during any of the 5 training trials. The 2 observers that pecked during training were the only observers to peck in food dishes during observer testing.

Discussion

The main results of Study A of Experiment 1 provide evidence consistent with the view that naïve junglefowl can learn to feed at a type of feeding site exploited by more knowledgeable conspecifics. During testing, 48 h after training, 19 of 20 observers directed their first bout of pecking toward the type of food dish (marked or unmarked) from which their respective demonstrators had been trained to feed. Unfortunately, the failure of subjects in the control group to exhibit much feeding behaviour in either the training or test situation resulted in this first experiment providing relatively little insight into behavioural processes that might have resulted in acquisition of such food-dish preferences by observers.

Obviously, those chickens exposed to a knowledgeable conspecific in a feeding situation learned more about where food was to be found in that situation than did those birds that were not exposed to a knowledgeable individual during training. The presence of knowledgeable demonstrators during observer training both elicited feeding (21 of 26 observers in the experimental group fed during observer training while only 2 of 8 observers in the control group did so) and directed feeding toward the same type of food

dish from which demonstrators were feeding (90.8 per cent of observers' first feeding bouts on each trial of their training were directed toward a dish from which a demonstrator was already feeding).

Experience gained while feeding with a knowledgeable bird also facilitated food finding in the subsequent test (20 of 26 birds in the experimental group and only 2 of 8 in the control group found food during testing).

Study B

The intent of the present study was to determine whether, as the result of interaction with trained demonstrators, naïve junglefowl could learn to forage from a particular area, rather than from a particular type of feeding site. The methods used in Study B were similar to those used in Study A, but were modified to examine the effects of demonstrators' behaviour on observers' choices of locations in which to feed rather than effects of demonstrators' behaviour on observers' choices of particular types of feeding sites.

Methods

Subjects

Seventy-five experimentally naïve, 21- to 28-day-old Burmese junglefowl from the Psychology Department vivarium served as subjects. Sixteen subjects served as demonstrators, 16 as observers and 16 as observers' naïve companions. An additional 9 subjects served as demonstrators, 9 as observers and 9 as naïve companions of observers in a control group.

Apparatus

The apparatus used in Study B was identical to that used in Study A except that all food dishes in the 2×4 matrix in the main enclosure were without decals, and, therefore, were identical in appearance.

Procedure

Training Demonstrators. Four pairs of demonstrators were trained, using the procedures described in Study A, to feed from whatever food dish was present in location C in Figure 1, and four additional pairs of demonstrators were trained to feed from whatever food dish was present in location F in Figure 1. Training was continued until both birds in a pair directed their initial bout of feeding toward the dish containing food on 4 of the 5 trials performed on each day of training.

Training Observers. Observers were trained by their demonstrators to feed either from location C or from location F using procedures identical to those used in Study A.

Testing Observers. Observers were tested as in Study A, except that during observer testing all eight food dishes remained in the main enclosure and only the food dish in the location at which each observer's respective demonstrator had been trained to feed contained food.

Results

Training Demonstrators. Demonstrators required an average of 13.8±0.9 trials to achieve criterion performance (see page 27) during demonstrator training.

Training Observers. As in Study A, during training of observers, demonstrators reliably fed at the location where they had been trained to feed; the 16 demonstrators spent an average of 4.0±0.2 of the 5 min of observer training pecking in the rewarded food dish, and an average 0.3±0.2 min pecking in the seven nonrewarded dishes. On an average of 88.4±3.2 per cent of observer training trials, each demonstrator directed its first bout of pecking toward the food dish from which it had been previously trained to feed.

All 16 observers in the present experiment fed during training and their pecking was clearly influenced by the behaviour of their respective demonstrators. The 16 observers directed their first pecking bouts toward the location where their demonstrators were feeding on an average of 98.8±1.3 per cent of training trials. They spent an average of 99.9±0.04 per cent of the 1.8±0.4 min that they spent pecking in the 5 min of training pecking in the food dish where their respective demonstrators had been trained to feed.

Testing Observers. All 16 observers fed during one or more test trials and 12 of the 16 observers directed their first bout of pecking in testing into the food dish located where their respective demonstrators had been trained to peck (Binomial test, $P=0.125$, $x=4$, $p<.001$). The 16 feeding observers spent an average of 90.7±0.2 per cent of the average 3.4±0.5 min each spent pecking in dishes, pecking at the site where their demonstrators had been trained to peck. Fifteen of the 16 observers directed more than 1/8 of their pecking bouts toward the dish in the location where their respective demonstrators had been trained to feed (Sign test, $P=0.50$, $x=1$, $p<.001$).

Control Group. Demonstrators and observers in the control group of the present experiment, like those in the control group of Study A, did not exhibit much pecking behaviour during either their training or their testing. Only 2 of the 9 demonstrators and 2 of the 9 observers pecked in any food dish during observer training, and only 1 of the 9 observers pecked in a food dish during observer testing.

Discussion

The results of Study B were essentially the same as those of Study A; naïve observer fowl that had fed with a knowledgeable demonstrator learned the location of the feeding site that they and their demonstrators had exploited together. Forty-eight h later, the observers returned to the location where they had fed with their respective demonstrators to feed again. Observers in the control group, that lacked opportunity to interact with knowledgeable flockmates during training, learned nothing about the presence of food in the test situation and failed to find food there when given the opportunity to do so during testing, 48 h after training occurred.

Discussion of Experiment 1

The results of Experiment 1 revealed the presence of long-term modifications of adolescent fowl's foraging behaviour as a result of interaction with feeding flockmates. Two days after social feeding occurred, observer fowl biased their pecking toward either the type of food dish or the location that their flockmates and they had previously exploited (Studies A and B, respectively).

An important question is how the pattern of foraging, exhibited by birds that had interacted with knowledgeable conspecifics, developed. Since food was present during testing only in the type of dish or at the location where demonstrators had fed, it may well be that the feeding site preferences exhibited by observer fowl during testing were the result of observers learning where to locate food during the test procedure itself, regardless of their previous interactions with knowledgeable flockmates. This is unlikely. The finding that observers in the control group (i.e. observers that were paired with naïve demonstrators) did not peck in a dish during training suggests that, during training, fowl in the experimental group were attracted to a feeding site by the presence there of a feeding demonstrator and learned where to find food while at the site.

Experiment 2

Study A

To explore whether the bias in feeding behaviour observed in junglefowl in the previous experiment was the result of their finding food during testing, in the present experiment, Study A of Experiment 1 was repeated, but without the presence of food during testing.

Methods

Subjects

Sixty experimentally naïve junglefowl from the Psychology Department vivarium served as subjects: 20 as demonstrators, 20 as observers and 20 as observers' naïve companions.

Apparatus and procedure

The apparatus and method of the present experiment were identical to those described in Experiment 1, Study A except that food was not present in any dish during testing of observers.

Results

Training Demonstrators. Demonstrators required an average of 14.2±0.6 trials to achieve criterion performance during their training.

Training Observers. The 20 demonstrators spent an average of 4.42±0.3 min of the 5.0 min of observer training pecking in the dish containing food, and an average of 0.06±0.2 min pecking in nonrewarded dishes. On an average of 97.0±2.2 per cent of trials, each demonstrator directed its first bouts of pecking toward the rewarded dish.

Nineteen of the 20 observers pecked in a dish during training. An average of 90.8±3.9 per cent of first pecks by observers on each training trial was directed toward a dish from which its demonstrator was actively feeding at that time. An average of 99.9±0.1 per cent of the 2.21±0.3 min that observers spent pecking during the 5 min of training was directed toward the food dish from which their respective demonstrators had been trained to feed.

Testing Observers. Eighteen of the 20 observers fed during one or more test trials, and 14 of these 18 observers directed their first peck during testing into the type of food dish from which their respective demonstrators had been trained to feed (Binomial test,

$\underline{P}$=0.50, $\underline{x}$=4, $\underline{p}$<.03). On average, the 18 observers that fed during testing spent 74.96±7.6 per cent of the 0.57±0.16 min that they spent pecking, pecking in the type of dish from which their respective demonstrators had been trained to feed. Fourteen of these 18 observers directed the majority of their pecks toward the type of foraging site to which their respective demonstrators had been trained to feed (Sign test, $\underline{P}$=0.50, $\underline{x}$=4, $\underline{p}$<.03).

Discussion

The results of the present experiment were similar to those of Experiment 1, Study A; naïve junglefowl exhibited long-term modification of their pecking behaviour following interaction with knowledgeable conspecifics. However, the change in observer fowl's pecking behaviour reported in the present experiment cannot be attributed to individual observers learning about the location of food during testing, because food was not available to them during testing.

Relative to observers in the experimental group of Experiment 1, Study A (observers tested with food present during testing) observers in the present experiment (that had no food present during testing) spent significantly less time pecking into dishes during testing than did subjects in Study A of Experiment 1 (Mann-Whitney U=65.5, $\underline{p}$<.01). This finding suggests that, although observers' interactions with demonstrators may influence where they subsequently choose to feed, the presence of food is important in maintaining pecking at that site.

Study B

The purpose of the present study was to explore the possibility that the findings of

Experiment 1, Study B were the result of junglefowl learning where to locate food during

testing independent of their previous interaction with knowledgeable flockmates. Study B

of Experiment 1 was repeated, but without food being available to observers during

testing.

Methods

Subjects

Forty-eight naïve Burmese junglefowl from the Psychology Department vivarium

participated in the present study; 16 as demonstrators, 16 as observers and 16 as

observers' naïve companions.

Apparatus and procedure

The apparatus and methods used in the present experiment were identical to those

described in Experiment 1, Study B except that, as in Study A of Experiment 2, food was

not present in any dishes during testing of observers.

Results

Training Demonstrators. The 16 demonstrators required an average of 13.8±0.9

trials to achieve criterion performance during their training.

Training Observers. The 16 demonstrators spent 3.6±0.3 of the 5 min of observer

training pecking in the location containing food and 0.01±0.01 min pecking in

nonrewarded locations. On an average of 92.0±2.6 per cent of trials, each demonstrator directed its first bout of pecking toward the rewarded dish.

Thirteen of the 16 observers pecked in a dish during training. On an average of 96.5±2.4 per cent of training trials, these 13 observers directed their first pecking bouts toward the location where their demonstrators were actively feeding. An average of 99.9±0.03 per cent of the 2.4±0.4 min that the 13 observers spent pecking during the 5 min of training was directed in the food dish from which their respective demonstrators had been trained to feed.

Testing Observers. Fourteen of the 16 observers fed during one or more test trials, and 9 of these 14 observers directed their first peck in testing into the food dish located where their respective demonstrators had been trained to peck (Binomial test, $P=0.125$, $x=4$, $p<.001$). On average, 62.8±9.4 per cent of the 0.3±0.1 min that observers spent pecking was spent pecking in the location where their respective demonstrators had been trained to feed. Twelve of the 14 observers that pecked in dishes during testing directed more than 1/8 of their pecking bouts toward the dish located where their respective demonstrators had been trained to feed (Sign test, $P=0.50$, $x=6$, $p<.01$).

Discussion

As in Experiment 1, Study B, in the present experiment junglefowl biased their subsequent pecking behaviour toward the location in the main enclosure where they had previously fed with knowledgeable conspecifics. Again, because food was not available

during testing, this modification in orientation of behaviour could not have been due to junglefowl learning about the location of food during testing.

The results of the present experiment suggest, as do those of Experiment 2, Study A, that the amount of time that observers spent pecking into a dish during testing depended on the presence of food in testing. Observers tested in the presence of food (Experiment 1, Study B) pecked into dishes for a greater amount of time than did observers tested in the absence of food (Mann-Whitney $U=14.5$, $p<.01$).

Discussion of Experiment 2

The results of Experiment 2 were similar to those of Experiment 1; naïve junglefowl that had fed with knowledgeable demonstrators learned the type of dish or the location of the feeding site that they and their respective demonstrators had exploited together. Forty-eight h later, the observers returned to feed in the type of dish or at the site where they had fed two days before with their respective demonstrators even when no food was available in those sites. Thus, effects on the foraging behaviour of junglefowl observed in Experiment 1 were not due to observers learning where to find food during the test period itself.

Experiment 3

The results of Experiments 1 and 2 indicate that naïve fowl that have eaten with more knowledgeable fellows can learn about a potential feeding site more rapidly than can naïve fowl lacking the opportunity to eat with knowledgeable flockmates. Moreover, such social feeding was found to modify the foraging behaviour of fowl for at least two days.

It is, of course, possible that the presence of a feeding flockmate during training in Experiments 1 and 2 served only to release feeding behaviour in naïve observers and to bias naïve observers to orient their feeding toward the same type of dish that their respective demonstrators were exploiting. Once observers had started to feed with their respective demonstrators, the food reward contingent on pecking in the type of feeding dish that a demonstrator was exploiting could have resulted in trial-and-error learning (Church, 1957) by observers about the type of dish in which food was to be found.

Thus, naïve birds may have learned to feed from the same site as their more knowledgeable fellows as the result of a concatenation of social influence and individual learning; social influence both triggered feeding and oriented its initial direction. Individual learning maintained discriminative feeding behaviour. Such a role for social influence in development and maintenance of feeding behaviour is similar to that previously described by Galef (1977) and by Church (1957) in studies of social learning about feeding sites by Norway rats.

Alternatively, it is possible that naïve birds are able to learn about a potential feeding site from observation of the feeding behaviour of their more knowledgeable fellows. In Experiment 3, I examined the possibility that naïve adolescent fowl would learn to forage at the same type of feeding site or location as their respective demonstrators in the absence of any primary reward for doing so.

Study A

The present study was undertaken to determine whether naïve adolescent fowl would exhibit durable modifications in the orientation of their foraging behaviour as a consequence of simple observation of conspecifics feeding in specific types of feeding sites.

Methods

Subjects

Subjects were trained and tested in the experimental cage (3 m deep × 1 m wide × 0.3 m high) illustrated in overhead schematic in Figure 2. This cage was similar in construction to that described in the Methods of Experiment 1, but was divided into ancillary (1 × 1 × 0.3 m), main (1.7 × 1 × 0.3 m) and observation (0.3 × 1 × 0.3 m) enclosures. The experimental and ancillary enclosures were separated by an opaque, sliding door and the experimental and observation enclosures by a screen partition (1.25 cm mesh).
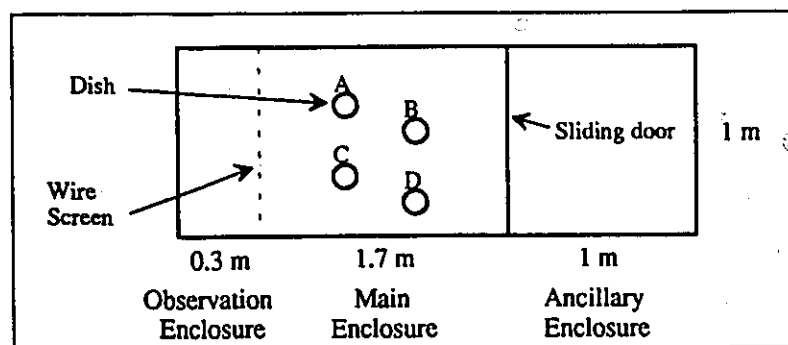

Figure 2. Overhead Schematic Diagram of Apparatus used in Experiment 3. Dishes were marked as indicated in the text.

Forty 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served as subjects. Eight of these subjects served as demonstrators and 32 as observers.

Apparatus

Four Pyrex dishes (described in Experiment 1) were present in a 2×2 array as illustrated in Figure 2. At any one time, during the present experiment, there were present in the main 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 red adhesive decals evenly spaced 1 cm below the rim of the dish. Positions of marked and unmarked dishes were changed randomly between training and testing trials.

Procedure

Demonstrator fowl were first trained to preferentially feed from a visually distinct foraging site. Observer fowl were then exposed to a pair of demonstrators feeding at the site from which the demonstrators had been trained to feed during 10 trials performed over 2 training days. The effect of such exposure on observer fowl's feeding behaviour was examined two days after each observer's final training session. Details of the procedure are presented below.

Training Demonstrators. Each of four pairs of demonstrators were trained to find food in the main cage using the procedure described in Methods of Experiment 1. Two

pairs of demonstrators were trained to feed from an unmarked dish and two pairs of demonstrators were trained to feed from a marked dish.

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

On each of five 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 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 h after completion of the first training session.

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

Testing Observers. Immediately following its second training session, each observer pair and each demonstrator pair was returned to its home flock for 24 h of ad libitum 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 h.

Immediately following food deprivation (48 h after the second observer training trial), each pair of observers was released together into the main enclosure for six 5-min 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 main enclosure contained food, though each was filled with strips of newsprint. Positions of the marked and unmarked dishes were randomly manipulated between trials.

The location and duration of bouts of pecking by all subjects throughout both training and test trials were recorded.

Results

Training Demonstrators. Demonstrators required an average of 9.0±1.5 trials to achieve criterion performance during training. Criterion was defined as both birds in a pair directing their initial bouts of pecking toward the dish containing food on 4 of the 5 trials carried out during a single day of training.

Training Observers. Demonstrator pairs spent an average of 9.9±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 on each of the 10 observer training trials in which it participated toward the type of dish from which it had been trained to feed.

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 their demonstrators, rubbing their beaks across the screen, vocalizing, and directing bursts of pecking toward the floor of the observation enclosure, although no food was present there.

Testing Observers. Observers in 10 of the 16 observer pairs pecked in a dish during testing. The members of nine of these 10 observer pairs directed their initial bout of pecking toward the type of dish from which their respective demonstrators had been trained to feed (Binomial test, $\underline{P}$=0.25, $\underline{x}$=1, p<.001). On average, these 10 observer pairs spent 90.0±10.0 per cent of the 0.09±0.03 min that they spent pecking, pecking in the type of dish from which their respective demonstrator pairs had been trained to feed. Nine of these 10 observer pairs spent more than 25 per cent of the time that they spent pecking, pecking in the type of dish into which their respective demonstrators had been trained to peck (Sign test, $\underline{P}$=0.50, $\underline{x}$=1, $\underline{p}$<0.01).

Discussion

The results of the present experiment indicate that, as a consequence of observing the behaviour of conspecifics foraging successfully, Burmese junglefowl can learn to direct their pecking towards a particular type of feeding site and will retain such information for at least 48 h. Observation of trained conspecifics feeding from a particular type of site was sufficient in itself to orient the feeding behaviour of naïve observers tested 2 days after they had observed trained demonstrators feeding from a particular type of feeding site.

It should be noted that during testing, observers in the present experiment, like those in Experiment 2, exhibited only a small amount of pecking ($\bar{X}$=0.09 min) in comparison with observers in Experiment 1, Study A ($\bar{X}$=2.8 min). This difference in amount of time that observers spent pecking during testing suggests that, although observation of demonstrators' choice of feeding site can orient the pecking behaviour of observers, reward contingent on pecking is required for maintenance of pecking in potential foraging situations. This is an issue to which we shall return in Experiment 4.

In pilot studies for Experiment 3, Study A, a control group was included in which observers were exposed to the main enclosure in the absence of feeding demonstrators. None of the observers pecked in a bowl during testing. Thus, in the present experiment, observers' exposure to feeding demonstratrators affected both the initiation and orientation of observers' subsequent pecking behaviour in testing. However, it could be argued that the bias exhibited by observers in testing represents a preference in naïve fowl to peck an odd stimulus. The results of the following experiment obviate this concern to some extent.

Study B

Study B of Experiment 3 was undertaken to determine whether naïve adolescent fowl could learn, from observing the feeding behaviour of conspecifics, the particular area in which food was to be found. The procedure of the present experiment was similar to that of Experiment 3, Study A except that observers were required to learn a particular location rather than the particular type of feeding site in which to forage.

Methods

Subjects

Thirty-eight 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served as subjects. Eight of these subjects served as demonstrators and 30 as observers.

Apparatus

The apparatus was the same as that used in Experiment 3, Study A except that none of the four dishes in the main cage was marked during demonstrator training and observer training and testing.

Procedure

Training Demonstrators. Using the methods described in the procedure of Experiment 3, Study A, two pairs of demonstrators were trained to find food in each of the four locations where dishes were placed.

Training Observers. Fifteen pairs of naïve observers were trained using the procedure described in Experiment 3, Study A. In the present experiment, either three or

four 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 using the procedure described in Experiment 3, Study A. During testing of observers, none of the food dishes was marked and none contained food.

Results

Training Demonstrators. Demonstrators required an average of 11.8±0.8 trials to achieve criterion performance.

Training Observers. During the training of observers, the four demonstrator pairs spent an average of 9.6±0.2 min of the 10 min of observer training (two 5-min sessions) pecking in the location containing food. They did not peck in alternative locations. On each of the 10 training trials in which each observer pair participated, its demonstrator directed its first bout of pecking toward the food dish in the location at which it had been trained to feed.

Testing Observers. One or both members of 10 of the 15 pairs of observers pecked in a food 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 from which its demonstrator had been trained to feed and the other observer in the pair directed its sole pecking bout toward a dish in another location. To be as conservative as possible in analyzing the results of the experiment, this pair of observers was considered to have

directed its initial bout of pecking to a location other than that exploited by its demonstrators.

Of the 10 pairs of observers that pecked in food dishes during testing, each member of 8 observer pairs directed its initial bout of pecking toward the food dish in the location from which its respective demonstrators had been trained to feed (Binomial test, $P=0.25$, $x=2$, $p<.004$). On average, these 10 pairs of observers spent 86.2 ± 10.4 per cent of the 0.05 ± 0.01 min that they spent pecking, pecking in the food dish in the location where their respective demonstrators had been trained to feed. Nine of the 10 observer pairs that pecked in a dish during testing directed more than 25 per cent of their pecking bouts toward the location from which their demonstrators had been trained to feed (Sign test, $P=0.50$, $x=1$, $p<.02$).

Discussion

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

Study C

It might be argued that although the results of Studies A and B in the present experiment provide statistically reliable evidence of social influence on feeding site selection by fowl, the results 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

during testing did so for only a few seconds. However, it should be kept in mind that in Studies A and B, observers were tested in the extinction condition (i.e. there was no food available during testing). In natural situations, fowl would often receive rewards for pecking in the types of feeding sites or in the locations where they had seen conspecifics forage successfully.

In the present study, primary reward was introduced 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 that such increased pecking would reveal the ecological relevance of the social influences on feeding site selection observed in Studies A and B of the present experiment.

Methods

Subjects

Thirty-four 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served as subjects. Eight of these subjects served as demonstrators and 26 as observers.

Apparatus and procedure

The apparatus and procedures of the present study were identical to those used in Experiment 3, Study B except during testing of observers. In the present experiment, each of the four food dishes presented to observers during their testing contained 2 g of the subjects' normal diet (Purina Chick Starter) concealed beneath strips of newsprint.

Results

Training Demonstrators. Demonstrators required an average of 12.5±1.5 trials to achieve criterion performance.

Training Observers. Demonstrator pairs spent an average of 9.71±0.09 min of the 10 min of observer training feeding from dishes in the location in which they had been trained to feed. They pecked only in the food dish from which they had been trained to feed.

Testing Observers. One or both members of 11 of the 13 pairs of observers pecked in one or more food dishes during testing. Each member of 8 of the 11 pairs directed its first bout of pecking toward the dish in the location where its respective demonstrators had been trained to feed (Binomial test, $P=0.25$, $x=3$, $p<.001$).

On average, the 11 pairs of observers spent 79.9±3.3 per cent of the 14.7±0.7 min that they spent pecking, pecking in the food dish from which their respective demonstrators had been trained to feed. Members of 10 of the 11 observer pairs directed more than 25 per cent of their total pecking time toward the location from which their demonstrators had been trained to feed (Sign test, $P=0.50$, $x=2$, $p<.02$).

Discussion

The results of the present study indicate that the apparently minor, socially induced biases in pecking orientation demonstrated in the first two studies in Experiment 3 can have profound effects on the foraging behaviour of fowl. When, as might be expected to

occur in natural foraging situations, reward was available to foraging observer fowl during testing, they not only oriented their first exploratory pecks toward feeding sites where they had seen conspecifics feed 48 h earlier, they also exhibited sustained feeding from those sites, even though equally potentially rewarding alternative feeding sites were available in the immediate vicinity.

Discussion of Experiment 3

The intent of this series of experiments was to determine whether, in the absence of receiving primary rewards, junglefowl could learn to forage in feeding sites of a particular location or type that they had observed companions previously exploit. The results of Experiment 3 indicated that fowl are able to acquire foraging information by simply observing feeding conspecifics and that such observation produced durable modifications in the orientation of fowl's subsequent foraging behaviours.

General Discussion

The results of Experiments 1 and 2 demonstrated that the interaction of naïve adolescent Burmese junglefowl with knowledgeable conspecifics in a foraging situation could facilitate acquisition of adaptive foraging patterns by the naïve. While foraging with knowledgeable individuals, naïve fowl learned both in what type of location (Experiment 1A and Experiment 2A) and where (Experiment 1B and Experiment 2B) food was to be found. Control subjects in Experiment 1, lacking experience of foraging with knowledgeable conspecifics, failed to learn about food availability.

The finding in both Experiments 1 and 2 of social enhancement of foraging efficiency could be explained as the result of social facilitation (Zajonc, 1965, 1969), local enhancement (Thorpe, 1963) and differential reinforcement. However, both social facilitation (Zajonc, 1965, 1969) and local enhancement (Thorpe, 1963) by definition describe effects on an animal's behaviour during the time it is actually interacting with others (see Galef, 1988, p.17 for discussion of long-term, indirect effects of social facilitation and local enhancement). In the present experiments, modification in foraging behaviour of observer junglefowl was observed two days after their interaction with demonstrators. Further, as the results of Experiment 3 indicated, neither simultaneous presence of observers and demonstrators in the foraging arena nor receipt of reward by observers during either training or testing was necessary to produce the longer-term effects of social interaction on the orientation of foraging behaviour exhibited by naïve observers in Experiments 1 and 2. Adolescent fowl that simply observed trained conspecifics feeding either from one type of potential feeding site (Experiment 3, Study A) or from a particular location (Experiment 3, Studies B and C) exhibited enhancement of their own probability of feeding from such sites two days later. Thus, learning about where to eat took place in the absence of any opportunity for social facilitation, local enhancement or incidental learning.

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 behaviour, 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) has 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.

The conservative view of the results of the present experiments is that, in fowl, observation of conspecifics pecking either at an object or in a location results in long-lasting stimulus enhancement, increasing the probability that an observer's later behaviour will be directed toward the enhanced object or location. Thorpe (1964) reserved the term 'imitation' to describe "the copying of a novel or otherwise improbable act or utterance" (Thorpe, 1964, p.135), and while the present results are also consistent with the view that chickens can learn where to forage by imitation, there is no aspect of the present data compelling such an interpretation.

The present results also indicate that feeding in flocks provides birds with long-term benefits in addition to the immediate increase in efficiency of food finding reported by Krebs and his coworkers (Krebs, 1973; Krebs et al., 1972). As a result of observation of the feeding behaviour of successful flock members, less successful individuals can acquire information as to the identity of likely feeding sites. Such information can be used on later occasions by observers of successful foragers to direct their own foraging behaviour 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 might be particularly important to individuals of low social rank that might not be allowed to share feeding sites with dominants (Baker, 1978; Baker, Belcher, Deutsch, Sherman and Thompson, 1981).

Chapter 3

Analyses of Stimuli Underlying Social Learning in Burmese Junglefowl using Video-recordings

It was shown in Chapter 2 that, after watching conspecifics feed from a visually distinctive foraging site, adolescent Burmese junglefowl preferred to direct their foraging toward the type of site that conspecifics had previously exploited. For example, when offered a choice between marked and unmarked feeding dishes, those observer fowl that previously had watched conspecifics feed from a marked food dish (and ignore unmarked food dishes) preferred to feed from a marked dish. Conversely, those observer fowl that had watched conspecifics feed from an unmarked dish (and ignore marked dishes) preferred to feed from an unmarked dish. Additional data collected in the course of these experiments indicated that, during testing, fowl that had viewed conspecifics feeding in an enclosure exhibited shorter latencies to begin feeding in that enclosure than did fowl that had not observed conspecifics feeding there.

The studies reported below were undertaken to determine which aspects of the behaviour of demonstrator fowl were responsible for the observed social induction of feeding site preference and social facilitation of feeding initiation.

The goal in the present research was similar to that of earlier researchers who used mechanical models to determine which aspects of the total stimulus complex provided by a

feeding hen sufficed to release and orient concurrent pecking by newly hatched chicks (Subsoski and Bartashunas, 1984; Tolman, 1967a; Tolman and Wilson, 1965; Turner, 1964). In the present research, the methods and specific interests differed from those of earlier workers in three ways. First, rather than study the influences of concurrent interaction with feeding fowl on the feeding behaviours of their observers, longer-term effects of such experience on observers' foraging behaviour were examined. Deferred changes in an animal's behaviour following its exposure to the behaviour of another may provide evidence of underlying processes both different from and more sophisticated than those supporting concurrent influence of the behaviour of one animal on another (Galef, 1988; Spiedel and Nelson, 1989).

Second, Evans and Marler (1991) have recently noted that digital procedures for modifying video images allow more sophisticated analyses of visual social stimuli than is possible using mechanical models. Therefore, in the present experiments, rather than using mechanical models to determine which of the visual and auditory signals emitted by feeding fowl would influence initiation and orientation of pecking by their observers, I used audiotaped or videotaped recordings of behaviour as stimuli. The response of fowl to audio- and video-recordings was not found to differ from that exhibited in the presence of live companions, and the use of audio- and video-recordings provided greater control over the stimuli presented to observers during training and also decreased both the number of subjects and the time required to train demonstrators.

Finally, earlier researchers (e.g. Suboski, 1984; Suboski and Bartashunas, 1984; Tolman, 1967a, 1967b; Tolman and Wilson, 1965; Turner, 1964) examined hens' behaviours specialized to elicit and orient pecking by newly hatched chicks. Here interest was in the effects of social influence on foraging efficiency in flock-foraging birds. Therefore, adolescent fowl were used as subjects rather than recently hatched chicks and tidbitting hens.

In the first experiment of Chapter 3 (Experiment 4), effects of visual and auditory stimuli emitted by feeding demonstrators on their observers' subsequent pecking behaviour were examined. The results indicated that both the sight and sound of feeding fowl played a role in elicitating and orienting observers' subsequent pecking behaviour. A second study (Experiment 5) examined whether the modification in observers' pecking behaviour was due to the simple presence of other junglefowl or to the pecking activity in which flockmates were engaged. The final experiments (Experiments 6 and 7) examined the long-term consequences on observers' pecking behaviour following their exposure to feeding demonstrators, active, non-feeding demonstrators or motionless demonstrators.

Experiment 4

The first experiment was undertaken to determine the ability of television images and of tape-recorded feeding sounds to initiate and orient later feeding by Burmese junglefowl. Each of 164 subjects was randomly assigned to one of four experimental groups that differed in the visual and auditory content of the video-recordings to which group members were exposed during training. After training, subjects were tested to

determine their latencies to begin feeding and their preferences when choosing between an unfamiliar type of food dish and the type of food dish from which they had seen and heard videotaped conspecifics feed during training.

Methods

Subjects

One-hundred and sixty-four 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served in the present experiment: eight as demonstrators in video-recordings and the remainder as observers.

Apparatus

Fowl were trained and tested in an experimental enclosure similar in construction to that described in Chapter 2. The present experimental enclosure (2.0 m deep × 1 m wide × 0.3 m high) was divided into ancillary (1 m × 1 m × 0.3 m) and main enclosures (1.5 m × 1 m × 0.3 m), separated by an opaque sliding door. A 33-cm colour video monitor (Panasonic LT 1331YC) was centered in the side of the main enclosure opposite the sliding partition (See Figure 3).
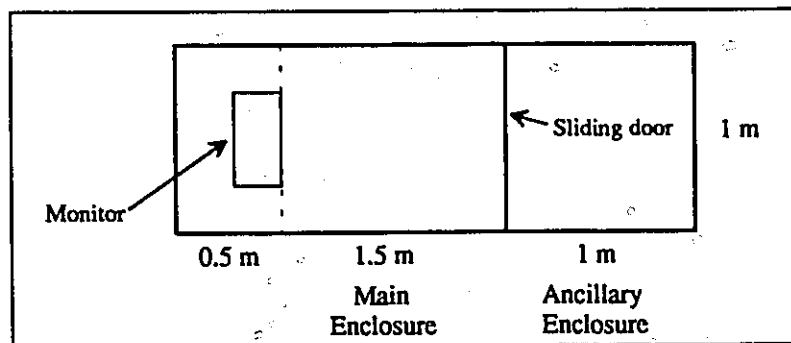

Figure 3. Overhead Schematic Diagram of Apparatus used in Experiment 4, Observer Training.

During testing, two Pyrex dishes (described in Methods of Experiment 1) were presented in the main enclosure in the positions indicated in Figure 4. The exterior of one of these dishes was decorated with eight red adhesive decals evenly spaced 1 cm below the rim of the dish. The other dish was similarly decorated with eight blue adhesive decals as described in Methods of Experiment 1.

Preparing videotapes   Four different 32-min long training videotapes were prepared by editing several hours of videotape showing fowl feeding. The video images had been recorded on closed-circuit television equipment (Panasonic, WV C1110 colour video camera, Panasonic AG 1240 videocassette recorder and Panasonic LT 1331YC 33-cm colour video monitor with a horizontal resolution of 420 lines). Sound was recorded using a dynamic omnidirectional microphone (Model 625 A, Electrovoice Inc., Buchanan, Michigan).

Each training videotape began with a 2-min presentation of an actual-size image of either a red- or blue-marked food dish. This image was followed by a series of fifteen 1-min scenes in which the same type of food dish played a central role.
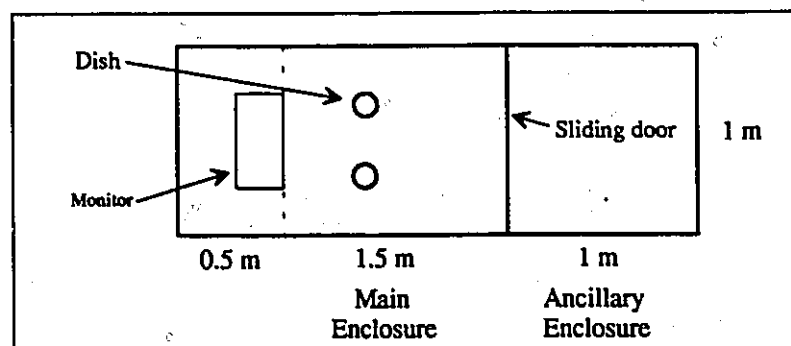

Figure 4. Overhead Schematic Diagram of Apparatus used in Experiment 4, Observer Testing. Dishes were marked as indicated in the text.

Each of the 15 scenes in any one of the four 32-min videotapes were similar. When viewed on a 33-cm video monitor, the four video-recordings each showed a life-size image of one of the following: (1) a red-marked food dish, (2) a blue-marked food dish, (3) a pair of 21- to 28-day-old Burmese fowl feeding continuously from a red-marked food dish, or (4) a pair of 21- to 28-day-old Burmese fowl feeding continuously from a blue-marked food dish. In the latter two video-recordings, the fifteen 1-min scenes of conspecifics feeding were separated by 1-min recordings of the marked dish alone. In recording scenes for all four tapes, camera placement was such that, although a food dish or a food dish and fowl were clearly visible in each scene, any food present in a food dish was not visible.

Tapes were played to subjects in one or two versions: either silent or containing audio recordings of the sound of Burmese fowl pecking vigorously in a food dish (90-110 pecks/min) and uttering "twitter calls" (Kruijt, 1964).

Procedure

Training Observers. To begin training, a pair of 21- to 28-day-old fowl was removed from their rearing enclosure and placed together in the ancillary portion of the main cage, where they were first fed their standard diet (Purina Chick Starter) for 24 h from an unmarked, white dish, and then food deprived for 24 h.

At the end of the 24 h period of food deprivation, the sliding partition separating the ancillary enclosure from the main enclosure was opened, and a training videotape was played through the video monitor.

Each pair of subjects had been assigned to one of four groups differing in the type

of training videotape group members observed: 15 pairs of subjects saw a food dish and

heard no sound (group dish/no sound); 18 pairs of subjects saw a food dish and heard the

sound of fowl feeding (group dish/sound); 22 pairs of subjects watched a pair of fowl

feeding and heard no sound (group fowl/no sound), and 23 pairs of subjects both saw a

pair of fowl feeding from a food dish and heard the sound of fowl feeding (group

fowl/sound). Within each group, approximately half of the subject pairs saw a red-marked

food dish in each 1-min scene; the remainder of subject pairs in that group saw a

blue-marked food dish in each 1-min scene.

When a training videotape ended, each pair of fowl was returned to the ancillary

enclosure, the sliding partition was closed and the video monitor was turned off.

Testing Observers. Pairs of subjects were held in the ancillary enclosure for

10 min between training and testing. During the 10-min interval, two food dishes, one

marked with red decals and one marked with blue decals, were placed in the main

enclosure in the positions indicated in Figure 4. Each of the two marked food dishes

contained 5 g of the birds' standard rations (Purina Chick Starter) covered with sufficient

strips of torn newsprint to conceal the food in the bottom of the dish. The positions of the

red- and blue-marked dishes were counterbalanced across subjects within training

conditions.

To begin testing, the experimenter opened the sliding partition separating the

ancillary enclosure from the main enclosure. During the subsequent 10-min test period, the

birds were left free to feed in the main enclosure. The experimenter recorded: (1) the latency with which a pair of fowl began feeding, (2) the food dish in which each pair of subjects first pecked, and (3) the location and duration of each pecking bout exhibited by each member of a pair of fowl. As in Experiment 1, a bout of pecking was defined as a series of pecks directed inside a feeding dish by a bird; a bout of pecking was considered to have ended when 2 s passed without further pecking.

Results

The main results of Experiment 4 are presented in Table 1, which provides an overview of the behaviour exhibited, during testing, by observers in each of the four training conditions.

Percentage of pairs feeding during testing. As seen in Chapter 2, not all pairs of adolescent fowl that are food deprived for 24 h before being given the opportunity to feed will do so during a 10-min test period. In the present experiment, neither member of 20 of the 78 pairs of observers (26%) ate during the 10-min test. In Experiment 3, pairs of adolescent fowl watched live rather than videotaped conspecifics feed during training and neither member of 13 of 44 pairs of subjects (29%) ate during testing sessions. Exposure to video recordings seems to have been as effective in eliciting feeding in the test situation as was exposure to live conspecifics in earlier experiments. Although a greater percentage of observer pairs in the fowl/sound condition than of observer pairs in other conditions fed during testing, this difference was not statistically significant (χ^2-test for k independent samples, χ^2=2.12, df=3, p=n.s.).

	Training Condition			
	Dish/Sound	Dish/No Sound	Fowl/Sound	Fowl/No Sound
Number of Pairs Trained	18	15	23	22
Per cent of Pairs Feeding During Testing	66.7^A	73.3^A	82.6^A	72.7^A
Per cent Pairs 1st Peck to Trained Dish	50.0^B	54.5^B	89.5^C	43.8^B
Per cent Pairs Feeding More From Trained Dish	50.0^D	54.5^D	89.5^E	43.8^D
Latency to First Peck Mean Min (±SE)	7.1±0.5^F	6.2±0.9^F	3.5±0.7^G	3.8±0.8^G

Cells in the same row that contain different letters differed statistically as indicated in text.

Table 1. Behaviour during testing of subjects in Experiment 4.

Percentage of pairs delivering first peck to the dish presented in training. A χ^2 test revealed a significant effect of training condition on the probability that observers would direct their first peck during testing into the type of dish where they had seen demonstrators feed during training (χ^2-test for k independent samples, χ^2=9.34, df=3, p<.05). Post-hoc Fisher's exact probability tests revealed that observer pairs in the fowl/sound group were significantly more likely than were observer pairs in each of the other three training conditions to direct their first pecking bout toward the type of dish that they had observed during training (all three p<.05).

Percentage of pairs preferring to peck in the dish presented in training. Examination of the percentage of the total time that pairs of observers spent pecking in the type of dish that they had observed during training revealed again that only observers in the fowl/sound group exhibited a consistent bias in the orientation of their pecking. There was a significant effect of training condition on preference for the type of food dish viewed during training, (χ^2=9.34, df=3, p<.05), (where "preference" is defined as an observer pair pecking longer in one type of food dish than in the other). Observers in the fowl/sound group were more likely than were observers in each of the other three groups to prefer to peck during testing in the type of food dish that they had been exposed to during training (Fisher exact probability tests, all three p<.05).

Latency to first peck (min). A 2×2 ANOVA revealed significant effects of training condition on latency to first peck in the 58 pairs of fowl that did peck during testing. Presence of a demonstrator during training ($F_{(1,54)}$=14.6, p<.003), but not the presence of sounds of feeding during training ($F_{(1,54)}$=3.67, p=n.s.), significantly affected latency to first peck during testing. Neuman-Keul's tests revealed that subjects in both the fowl/sound and fowl/no sound groups exhibited significantly shorter latencies to first peck than did observers in either the dish/sound or dish/no sound groups (all four p<.05).

Discussion

To summarize, under the conditions of the present experiment, latency to first peck was reduced by seeing videotaped conspecifics peck during training (regardless of whether

auditory cues were present or absent), while orientation of pecking was modified only following exposure to both the sight and sound of fowl pecking during training.

The results of the present study clearly show that exposure to the videotaped sight and sound of conspecifics feeding, like exposure to the sight and sound of live conspecifics feeding (Experiment 3), can influence the subsequent feeding behaviour of observer fowl. Exposure to videotapes of conspecifics feeding both decreased the feeding latencies of observer fowl and oriented their feeding behaviour toward the type of feeding site that they had watched conspecifics exploit during training.

These results demonstrate the usefulness of videotapes as sources of stimuli to be employed in analyses of social stimuli influencing behaviour in fowl. However, no simple answer to the question of which aspects of the feeding behaviour of one bird influences the feeding behaviour of its companions is available. In the present experiment, latency to begin feeding during testing was affected by visual cues alone; orientation of pecking was influenced by both visual and auditory cues experienced in concert.

Of course, it is possible that increasing either the number or duration of training trials experienced by observers might cause stimuli, which in the present experiment had no effect on the behaviour of observer fowl during testing, to become effective in altering observers' behaviour. Consequently, the results of this experiment indicate only that, for example, the orientation of pecking by fowl is more readily influenced by the combination of the sight and sound of conspecifics feeding than by exposure to just visual or just auditory stimuli emitted by conspecifics.

Experiment 5

In Experiment 4: (1) exposure to the sight and sound of conspecifics feeding at a particular type of foraging site increased the probability that an observing fowl would direct its subsequent feeding behaviour toward sites of that type, and (2) exposure to the sight of conspecifics feeding reduced observers' latencies to begin feeding in the test situation. In Experiment 5, those features of the visual signal provided by feeding fowl that influenced both feeding site preferences and feeding latencies were examined in greater detail.

Methods

Subjects

Seventy 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium participated in the experiment.

Apparatus

The apparatus used in the present experiment was that described in Experiment 4.

Procedure

Training and testing procedures used in Experiment 5 were identical to those used in Experiment 4, except with respect to the materials videorecorded. In the present experiment, both of the videotapes used provided the sounds of fowl feeding vigorously in a food dish. Twenty pairs of observers were exposed to a training videotape containing fifteen 1-min scenes, each of which showed a pair of demonstrator fowl active in the vicinity of either a red- or blue-marked food dish, but not feeding from it. Another fifteen pairs of observers were exposed to a training videotape showing a series of fifteen 1-min

freeze frames taken from the first videotape. These freeze frames each showed pairs of

fowl standing close to food dishes in natural postures.

As in Experiment 4, observer pairs were tested for their food-dish preferences

10 min after viewing a 32-min training videotape.

Results and Discussion

The main results of Experiment 5 are presented in Table 2 which provides an

overview of the behaviour exhibited during testing by observer pairs in each of the two

training conditions. Data from observers in the fowl/sound condition of Experiment 4

(labelled "feeding/sound" in Table 2) are provided for comparison. As can be seen in

Table 2, in comparison with observers in the feeding/sound group, subjects in the

active/sound and still/sound groups exhibited relatively long latencies to initiate pecking in

the test situation, ($F_{a,43}$=4.22, p=.02). Observers' exposure to video images of conspecifics

near a food dish, but not feeding from it while hearing pecking sounds, failed to shorten

observers' latencies to initiate pecking during testing (Neuman-Keul's test both p<.05).

On the other hand, as can also be seen in Table 2, during testing, fowl that had

viewed videotapes of active fowl and heard sounds of feeding during training were more

likely than were fowl that had viewed videotapes of still fowl and heard pecking sounds: to

(1) peck for the first time in the type of food dish that they observed on training

videotapes (χ^2=4.20, df=1, p<.05), and (2) prefer to feed from the type of dish that they

had observed on training tapes (χ^2=4.20, df=1, p<.05). These data indicate that the sight

of conspecifics moving in the vicinity of a feeding site (in combination with the sound of pecking) is more effective than is the sight of still conspecifics (in combination with the sound of pecking) in enhancing preference for a particular type of feeding site. Once again, the stimuli facilitating initiation of pecking and those biasing the direction of pecking differed.

	Training Condition		
	Feeding/Sound	Active/Sound	Still/Sound
Number of Pairs Trained	23	20	15
Per cent of Pairs Feeding During Testing	82.6^A	75.0^A	80.0^A
Per cent Pairs 1st Peck to Trained Dish	89.5^B	80.0^B	41.7^C
Per cent Pairs Feeding More From Trained Dish	89.5^D	80.0^D	41.7^E
Latency to First Peck Mean Min (±SE)	3.5±0.7^F	6.1±0.8^G	5.7±0.9^G

Cells in the same row that contain different letters differed statistically as indicated in the text.

Table 2. Behaviour during testing of subjects in Experiment 5.

Experiment 6

The results of Experiments 4 and 5 indicated that both visual and auditory components of the behaviour of conspecifics can play an important role in enhancing the short-term attractiveness of particular types of feeding sites to adolescent fowl. Experiment 6 was undertaken to determine whether videotapes of the same social stimuli that enhanced the relatively short-term attractiveness of feeding sites to observer fowl would also enhance the longer-term attractiveness of feeding sites to observers. The methods used were basically the same as those that were used with the fowl/sound group of Experiment 4, except that the delay between training and testing observers was 48 h rather 10 min in length.

Methods

Subjects

Thirty-six 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served as subjects.

Apparatus

The apparatus used in the present experiment was that described in Experiment 4.

Procedure

The procedure used in the present experiment was the same as that used with the fowl/sound group of Experiment 4 (i.e. each pair of observer fowl viewed fifteen 1-min scenes of demonstrators pecking in marked food dishes and heard the sound of fowl pecking throughout each scene), except that the interval between the end of training and the beginning of testing was 48 h rather than 10 min in length. During the first 24 h of this

48 h interval, observers were left in the ancillary portion of the experimental enclosure with ad libitum access to their regular diet (Purina Chick Starter) in a Mason-bottle chick feeder. During the second 24 h of the 48 h interval, observers remained in the ancillary portion of the apparatus and were food deprived.

Results

Thirteen of the 18 pairs of subjects (72%) that participated in Experiment 6 fed during the testing phase of the procedure. The mean latency to first peck by these 13 pairs of subjects was 3.54 ± 0.96 min, and 7 of the 13 pairs of observers directed their first bout of pecking during testing toward the type of food dish that they had observed on videotape during training (Binomial test, $P=0.50$, $x=6$, $p=.50$). Eight of the 13 pairs of observers directed the majority of the time that they spent pecking toward the type of dish from which their respective demonstrators had previously fed (Sign test, $P=0.5$, $x=5$, $p=.24$).

Discussion

Although the relatively short mean latency to initiation of pecking suggested that the feeding behaviour of observers may have been influenced by hearing and seeing videotapes of feeding conspecifics during training, when testing was delayed by 48 h there was no sign of an influence of training on observers' preferences for a particular type of food dish during testing.

Experiment 7

Following the failure to find effects of viewing videotapes on the food-dish preferences of observing fowl after a 48 h delay in Experiment 6, a series of pilot studies was performed in which the duration of the exposure of fowl to videotapes during training was gradually increased. It was found that doubling the number of 1-min scenes to which pairs of observers were exposed during training resulted in reliable alterations in food-dish preferences during testing 48 h later. In the present experiment, those aspects of video scenes sufficient to affect feeding site preference and feeding latencies during a test session 48 h after training were determined.

Methods

Subjects

Ninety-six 21- to 28-day-old, experimentally naïve, Burmese junglefowl from the Psychology Department vivarium served as subjects. Each subject was randomly assigned to one of three groups that varied in the visual content of the videotape that group members viewed during training.

Apparatus

The apparatus used in the present experiment was that used in the preceding experiment.

Procedure

The procedure of Experiment 7 was similar to that of Experiment 6, except that during training of the present study: (1) Each pair of observer fowl was exposed to a 32-min long videotape composed of a 2-min exposure to a marked food dish followed by

30 consecutive 1-min scenes each showing both a pair of demonstrator fowl and a food dish (there were no interscene intervals in the tapes), and (2) Observers in each of the three groups viewed scenes that contained recorded sound of fowl feeding and showed one of the following: (a) fowl feeding (group feeding/sound), (b) fowl active but not feeding (group active/sound), or (c) freeze frames of fowl in natural postures taken from videotape showing fowl near a food dish and active, but not feeding (group still/sound). As in Experiment 6, there was a 48 h delay between training and testing.

Results

The main results of Experiment 7 are presented in Table 3, which provides a summary of the behaviour exhibited during testing by observer pairs in each of the three training conditions. As can be seen in Table 3, there was a significant effect of training condition on two of the behavioural indices. First, the orientation of initial pecking by pair members varied significantly as a function of training condition ($\chi^2=7.53$, $df=2$, $p<.05$), with a greater percentage of observers in the feeding/sound group than of observers in either the active/sound or still/sound groups exhibiting a tendency to peck first in the dish observed 48 h earlier during training (Fisher's exact probability tests, both $p<.02$).

Second, and similarly, the percentage of observers preferring to peck in the type of food dish which they had viewed during training (where "preference" is indicated by an observer pair pecking longer in one type of food dish than in the other) varied significantly as a function of training condition ($\chi^2=6.17$, $df=2$, $p<.05$). A greater percentage of observers in the feeding/sound group than of observers in either the active/sound or

still/sound group preferred to peck in the type of food dish that they had observed during

training (Fisher's exact probability tests, both p<.04).

	Training Condition		
	Feeding/Sound	Active/Sound	Still/Sound
Number of Pairs Trained	18	15	15
Per cent of Pairs Feeding During Testing	83.3[A]	86.7[A]	93.3[A]
Per cent Pairs 1st Peck to Trained Dish	93.3[B]	46.2[C]	50.0[C]
Per cent Pairs Feeding More From Trained Dish	85.7[D]	46.2[E]	50.0[E]
Latency to First Peck Mean Min (±SE)	3.2±0.7[F]	5.6±1.3[F]	5.0±1.0[F]

Cells in the same row that contain different letters differed
statistically as indicated in the text.

Table 3. Behaviour during testing of subjects in Experiment 7.

Although the mean latency of first peck was somewhat affected by training condition, the difference among groups in latency to first peck was not statistically reliable ($F_{(2,40)}=2.18$, $p=.13$).

Discussion

The results of Experiment 7 indicate that, under the present training and testing conditions, social influence on feeding site preference resulted from exposure to videotapes providing both the sight and sound of fowl feeding, but not from exposure to videotapes providing views of either active or still fowl near a food dish and the sound of fowl feeding. This result contrasts with the results of Experiment 5 (where testing for the effects of exposure to videotapes occurred 10 min, rather than 48 h, after completion of training). In Experiment 5, exposure to videotapes providing the sound of feeding fowl and the sight of conspecific demonstrators simply active in the vicinity of a food dish biased the orientation of feeding by observer fowl during testing.

General Discussion

The results of the experiments described in Chapter 3 support and extend Evans and Marler's (1991) demonstration of the use of video-recordings to analyze social stimuli eliciting behaviour in fowl. In the present case, video-recordings were found not only to release the behaviour of fowl, but also to orient that behaviour in specific directions. Adolescent fowl were able to use information they acquired by observing videotaped conspecifics, as they used information acquired by observing live conspecifics (Chapter 2), to orient their own subsequent feeding behaviour.

Taken together, the results of the present series of studies indicate that determination of the social stimuli eliciting and orienting future feeding in Burmese fowl is a fairly complex matter. Different aspects of the feeding behaviour of observer fowl were influenced by different aspects of the behaviour of videotaped conspecifics. For example, latency to initiate pecking was reduced by exposure to the sight of conspecifics feeding, while orientation of pecking was influenced only by exposure to the combination of visual and auditory stimuli emitted by feeding conspecifics (Experiment 4). Furthermore, general activity in the vicinity of a food dish (in combination with feeding sounds) oriented pecking toward that food dish but did not shorten the latency of observer fowl to begin feeding (Experiment 5). The efficacy of particular audiovideo stimuli in modifying the later feeding behaviour of observer fowl depended not only on the nature of the stimuli the fowl were exposed to, but also on: (1) the duration of exposure that observers received to those stimuli, (2) the delay observers experienced between stimulus exposure and testing, and (3) the criteria used to identify social influences on the behaviour of observers.

The present results clearly demonstrate both: (1) the adequacy of video images as sources of stimuli sufficient to support social learning about foraging sites in fowl, and (2) the sensitivity of fowl to the quantity and nature of the video images to which they are exposed. However, the present results do not provide a simple answer to the question of the sufficiency of various aspects of social stimuli to support social enhancement of either feeding or feeding-site preference. Indeed, the results of the present experiment suggest that there may be no simple answer to the question of which aspects of the behaviour of

feeding fowl affect the later feeding behaviour of their observers. Feeding behaviour of

fowl can be influenced by both auditory and visual stimuli received from conspecifics, but

the particular stimuli causing social modifications of foraging behaviour will depend on the

details of the situation in which both foraging and social learning occur.

Chapter 4

Investigations of Inhibition of Social Learning

In most social learning studies, a naïve bird is exposed to a tutor engaged in some feeding behaviour to be acquired by the naïve bird. Shortly thereafter, the naïve bird's performance of its tutor's behaviour is assessed. Such experiments may fail to reflect social learning as it occurs outside the laboratory because birds in flocks are often feeding themselves while they see conspecifics feed.

Giraldeau and Lefebvre (1987) have studied the effects on observers of feeding during social learning in pigeons (*C. livia*). Naïve observer pigeons were exposed to a conspecific tutor trained to peck at a stick protruding from a rubber stopper fitted loosely into the opening of a seed-filled test-tube. Pecking by a tutor on a stick caused the stopper and seeds to fall from the tube. During training of observers in Giraldeau and Lefebvre's experiment, tutors and observers were placed in cages facing one another and both tutors and observers were presented with a tube identical to the one from which tutors had been trained to feed. For one group of pigeons, a tray passing under the cages of both observer and tutor was horizontal and food released by a tutor's pecking could not be eaten by its observer. For another group of birds, the tray under tutors' cages was tilted so that the seeds each tutor produced by opening the test-tube rolled toward its observer and the observer could eat the seeds. The frequencies with which observers in each of the two

groups were successful in opening their own tubes were recorded on each of 10 trials on each of 2 consecutive days.

Giraldeau and Lefebvre found that observers that were not allowed to feed on seeds released by their tutors opened their own tubes more frequently than did observers that were allowed to feed on seeds released by their tutors. Giraldeau and Lefebvre proposed that inhibition of observers' acquisition of tube-opening behaviour occurred when observers shared in their tutors' food discoveries.

Given the findings of Giraldeau and Lefebvre, it may be inappropriate to interpret the results of Chapters 2 and 3 as suggesting that, in natural environments, junglefowl foraging in flocks acquire information by observing conspecifics feeding and use this information to enhance their own subsequent foraging success. In the experiments described in Chapters 2 and 3 (excluding Experiments 1 and 2), observer junglefowl were not allowed to eat during their exposure to conspecifics. However, as noted above, there is every reason to expect that, in natural circumstances, junglefowl feed while observing flockmates feeding.

Experiment 8

In Experiment 7, it was established that non-feeding observers' exposure to video-recordings of feeding demonstrators biased observers' subsequent pecking toward the type of site from which their demonstrators had previously fed. The purpose of the present study was to expand on these findings by modifying the procedure of Experiment 7 as follows: Observer fowl were able to feed during their exposure to video images of

feeding demonstrators. The experimental question of interest was whether feeding by observer junglefowl during their exposure to foraging conspecifics interfered with the observers' ability to learn to feed at sites of the type from which conspecifics were feeding.

Methods

Subjects

One hundred and fifty-eight 21- to 28-day-old, experimentally naïve Burmese junglefowl from the Psychology Department vivarium served as subjects in the present experiment. In the No Food in Testing condition, 58 junglefowl served as subjects in the experimental group and 36 served as subjects in the control group. In the Food in Testing condition, 34 junglefowl served as subjects in the experimental group and 30 served as subjects in the control group.

Apparatus

The apparatus was identical to that described for the fowl/sound group in Methods of Experiment 7 except that, during the training period of all observers, an unmarked white dish, filled with the birds' standard diet (Purina Chick Starter) was placed in the main cage, directly in front of and 0.5 m from the video monitor.

During testing, all observers were presented with a red- and a blue-marked dish centered in the main enclosure. In the No Food in Testing condition, the dishes were filled with strips of newsprint. In the Food in Testing condition, both dishes were filled with

observers' regular food (Purina Chick Starter) completely covered with strips of newsprint.

Videotape Preparation. The videotapes presented to observers in experimental groups of both the No Food in Testing and Food in Testing conditions were those presented to subjects in the fowl/sound group of Experiment 7. Each videotape contained the sight and sound of a pair of demonstrators pecking in either a red- or blue-marked dish for 30 min. Observer fowl assigned to control groups in both the No Food in Testing and Food in Testing conditions were exposed to a 32-min video-recording showing either a red- or a blue-marked dish.

Procedure

Training and Testing Observers. All observer pairs were trained and tested using the same procedures employed with members of the fowl/sound group of Experiment 7, except that all subjects in the present experiment had access to a white dish containing their regular diet (Purina Chick Starter) during the period of observer training.

No Food in Testing Condition. In the experimental group, 15 pairs of observer fowl were exposed to a video-recording of demonstrators feeding from a blue-marked dish and 14 observer pairs were exposed to a video-recording of demonstrators feeding from a red-marked dish. In the control group, 9 observer pairs were exposed to a video-recording of a blue-marked dish and 9 observer pairs were exposed to a video-recording of a red-marked dish.

Food in Testing Condition. In the experimental group, 9 pairs of observer fowl were exposed to a video-recording of demonstrators feeding from a blue-marked dish and 8 observer pairs were exposed to a video-recording of demonstrators feeding from a red-marked dish. In the control group, 8 pairs of observers were exposed to a video-recording of demonstrators feeding from a blue-marked dish and 7 observer pairs were exposed to a video-recording of demonstrators feeding from a red-marked dish.

Results

The main results of Experiment 8 are presented in Table 4, which provides data describing the behaviour exhibited during training and testing, by observer pairs in experimental and control groups of both the No Food in Testing and Food in Testing conditions.

Training

Time feeding in training (min). Since this study was undertaken to look at effects on observers' feeding behaviour subsequent to their exposure to feeding demonstrators, the data from junglefowl that did not feed during training were excluded from the study. The total time spent feeding during training by those observers that did feed during training did not differ across observers in the No Food in Testing and Food in Testing conditions ($F_{(1,72)}=3.64$, $p>0.05$).

Testing

Orientation of pecking. Compared to observers in the control group, observer fowl in the experimental group biased both their initial pecking bouts and the majority of the

total time that they spent pecking toward the type of foraging site at which their videotaped companions had fed during training in both the No Food in Testing (Fisher's exact probability tests, both $p<.03$) and Food in Testing (Fisher exact probability tests, both $p<.02$) conditions.

	No Food in Testing		Food in Testing	
Training	Experimental Group	Control Group	Experimental Group	Control Group
Number of Pairs Trained	29/29[A]	18/18[A]	15/17[A]	13/15[A]
Mean Total Time Feeding Min (±SE)†	10.6±0.9[B]	11.8±1.09[B]	10.6±1.4[B]	14.7±1.3[B]
Testing	Experimental Group	Control Group	Experimental Group	Control Group
Number of Pairs Peck in a Dish	25/29[C]	16/18[C]	15/15[C]	13/13[C]
Per cent of Pairs 1st Peck in Videotaped Dish	80.0[D]	37.5[E]	80.0[D]	38.0[E]
Per cent Pairs Pecking More From Videotaped Dish	72.0[F]	37.5[G]	80.0[F]	30.8[G]
Mean Latency to 1st Peck Min (±SE)	1.7±0.3[H]	2.4±0.8[I]	1.9±0.5[H]	2.6±0.9[I]
Mean Total Time Pecking Min (±SE)	0.8±0.2[J]	0.7±0.04[J]	13.4±1.8[K]	12.1±1.2[K]

Cells in the same row that contain different letters differed statistically.
†Data for those subjects that did feed during training.

Table 4. Behaviour during training and testing of subjects in Experiment 8.

<u>Latency to first peck and total time spent pecking</u>. In both the No Food in Testing and Food in Testing conditions, observers in experimental groups began pecking into dishes more quickly in testing than did observers in the control groups ($F_{(1,65)}$=5.83, p<.05, both Neuman-Keul's tests, p<0.05).

The presence of food was found to significantly affect the total amount of time that observers spent pecking in a food dish in testing. Relative to observers in the No Food in Testing condition, when food was present during testing, observers spent more time pecking into food dishes ($F_{(1,65)}$=324.16, p<.00001, Neuman-Keul's test, p<.01).

Discussion

Feeding by observers during their exposure to video images of feeding conspecifics did not significantly affect the observers' subsequent foraging behaviour compared to that of observers that did not feed during their exposure to feeding fowl in the feeding/sound group of Experiment 7. Furthermore, as in Experiment 3, when food was available in the type of site where videotaped conspecifics fed, as might be expected in a natural situation, fowl not only oriented their first pecks toward this site but also remained feeding from this site although an equally rewarding site was available. These results suggest that while feeding near their fellows, junglefowl are able to learn about alternative foraging sites at which neighboring flockmates are feeding and to use this information to enhance their subsequent foraging success.

In the months since the present experiment was completed, Giraldeau and Templeton (1991) have published an extension of the Giraldeau and Lefebvre (1987)

experiments described in the introduction to the present chapter. In their original studies of effects on social learning (Giraldeau and Lefebvre, 1987), when observer pigeons where able to eat seeds released by their respective tutors, tutors received no reward for opening test-tubes. Giraldeau and Templeton (1991) included conditions in which both observer pigeons and their tutors were rewarded after the tutors released seeds by pulling a stopper from a test tube, thus removing a confound present in the Giraldeau and Lefebvre studies. Giraldeau and Templeton reported that observers did not experience an inhibition in learning their respective tutors' food producing behaviours.

Thus, the apparent critical event that inhibited social learning by observers in the Giraldeau and Lefebvre (1987) study was not the provision of food to observers, but rather the lack of provision of reward to tutors. The results of Experiment 8 are consistent with those reported by Giraldeau and Templeton (1991).

Chapter 5

Conclusion

The results of the present research are consistent with the notion that feeding in flocks can facilitate birds' later foraging success (e.g. Crook, 1965; Krebs, 1973; Krebs, MacRoberts and Cullen, 1972). Naïve fowl that were allowed to interact with conspecifics that had been trained to feed from a novel foraging site biased their subsequent feeding toward the novel foraging site that their trained fellows were exploiting. In comparison, naïve fowl that lacked the opportunity to interact with companions feeding from a novel feeding-site were unlikely to feed at all. Thus, interaction with knowledgeable conspecifics influenced both the initiation and the orientation of naïve junglefowl's subsequent feeding.

The results of the experiments described in the body of this thesis also showed that junglefowl need not actually feed with trained conspecifics to experience a subsequent increase in foraging efficiency; junglefowl allowed only to watch conspecifics eating from distinctive foraging sites oriented their own subsequent foraging behaviour toward the sites from which fellow junglefowl had fed. Furthermore, fowl exposed to video images of feeding conspecifics exhibited modifications in foraging behaviour similar to those exhibited by fowl exposed to live, feeding conspecifics. Thus, junglefowl were able to use information acquired during exposure to live or videotaped conspecifics to enhance their own subsequent foraging success.

Previously, effects of social feeding on the behaviour of flock members have been examined either when or immediately after birds have fed together (e.g. Franchina et al., 1986; Tolman and Wilson, 1965). The present research, representing one of the first studies to investigate longer-term effects of social feeding in birds, revealed that facilitatory effects of social feeding on the foraging behaviour of fowl were sustained for at least two days following birds' interaction with either live or videorecorded conspecifics.

Experiments examining the duration of effects of social interaction on individual birds' foraging behaviour provided information concerning the behavioural processes underlying social learning in birds. Since, in the present studies, long-term changes in foraging behaviour of fowl due to social feeding were demonstrated using animals that were considerably older than the age associated with food imprinting (Hess, 1964, 1973), observed effects of social feeding on the subsequent foraging behaviour of observer fowl were not dependent upon processes, like food imprinting, that act solely early in life. The acquisition of foraging information that occurred during social feeding probably involved stimulus enhancement (Spence, 1937). The presence of social facilitation (Zajonc, 1965, 1969) or local enhancement (Thorpe, 1963) were contraindicated by the occurrence of social learning in the absence of trained conspecifics during testing of observers. Additionally, modifications in fowls' foraging behaviour following their exposure to feeding fellows cannot be attributed to the effects of differential reward; observers were trained and tested in the absence of food.

Experimenters have demonstrated the utility of laboratory studies for determining how members of bird flocks affect one another's foraging behaviour (e.g. Tolman, 1965, 1967a, 1967b; Tolman and Wellman, 1968; Turner, 1964). In the present research, use of audio- and video-recordings permitted further analyses of the stimuli emitted by conspecifics that influence junglefowl foraging. For example, exposure to the image of feeding conspecifics was found to modify the latency with which fowl subsequently initiated feeding in testing. Observer fowl previously exposed to a video-recording of the sight and sound of conspecifics feeding from a novel foraging site initiated feeding in testing more quickly than did observer fowl exposed to video-recordings of a novel foraging site presented together with the sound of fowl feeding, but without images of fowl feeding.

The behaviour of companions, as well as their presence at a feeding site, was shown to be important in affecting the later behaviour of their observers. Observer fowl exposed to video-recordings of either feeding or active non-feeding conspecifics were more likely to bias their later pecking toward the type of feeding site presented with their demonstrators than were observers shown video-recordings of still fowl.

Taken together the results described above suggest that exposure to video-recordings of feeding fowl and of active but non-feeding fowl affected the foraging behaviour of observer fowl similarly. However, other measures of effects of social feeding on the foraging behaviour of fowl indicated that exposure to feeding conspecifics had different effects on observers' foraging behaviour than did exposure to active conspecifics

that were not feeding. Exposure to active, non-feeding conspecifics was insufficient to establish long-term modifications in either the orientation or initiation of foraging behaviour of their observers. When assessed two days after a training session with video-recordings of feeding companions, fowl biased their foraging behaviour toward the type of feeding-site from which their respective conspecifics had fed, and began feeding more quickly than did fowl trained with video-recordings of active, non-feeding conspecifics. Thus, while exposure to active junglefowl may bias the orientation of fowl's feeding behaviour, long-term modifications of both orientation and initiation of feeding were found only in fowl exposed to feeding conspecifics.

The importance of the behaviour of conspecifics in social learning of foraging information in junglefowl would not have been apparent if the duration of the effects of social feeding on the orientation and latency of fowl's foraging behaviour had not been examined. For example, looking only at the immediate consequences of social feeding on orientation of fowl's subsequent foraging suggested that both feeding and active, non-feeding conspecifics affected the feeding behaviour of observer fowl similarly. However, both measures of observers' latencies to initiate feeding and measures of the duration of effects of social feeding on observers' foraging behaviour revealed that feeding conspecifics and active, non-feeding conspecifics affected their observer's foraging behaviour differently. The results of this and other research (Dawson and Foss, 1965) underscore the importance of recording multiple measures when studying effects of social feeding in birds.

The usefulness of video- and audio-recordings in studies of social feeding has been repeatedly demonstrated in the present research. However, it should be noted that exposure to live and videorecorded fowl did not have identical effects on observer fowl. Observers required longer exposure times in experiments using video-recordings of feeding fowl than in experiments using live, feeding fowl to exhibit later alterations in feeding behaviour. For example, fowl demonstrated immediate biases in their foraging behaviour following 5 min of exposure to live, feeding conspecifics (See Appendix A), whereas fowl exposed to video-recordings of feeding companions required 15 min of exposure to produce similar changes in their immediate foraging behaviour.

Investigations of long-term effects of social feeding on fowl's foraging behaviour also revealed a disparity between the exposure time required in studies using live versus videorecorded conspecifics. Two days following 10 min of exposure to live junglefowl feeding, fowl showed significant modifications in their foraging behaviour (Experiment 3). Fowl exposed to video-recordings of feeding conspecifics required 30 min of exposure to video-recordings of junglefowl to exhibit similar changes in their later foraging behaviour (Experiment 7). The increased exposure time required to affect behaviour when using videorecorded conspecifics as stimuli may be understood as the result of exposure to videorecorded conspecifics producing weaker response in fowl than exposure to live conspecifics. In the present body of research, this weaker response was compensated for by increasing the length of time that observers were exposed to videorecorded fowl.

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Appendix A

In a pilot study, shorter-term effects on observer fowl's foraging behaviour following their exposure to feeding conspecifics were studied using the Methods described in Experiment 3, Study A with the following modifications in procedure: (1) Observer fowl were exposed to a pair of feeding demonstrators for five 1-min training trials, and (2) Observers were tested 5 min after the completion of their final training trial.

Observers in 14 of the 18 observer pairs trained, pecked in a dish during testing. The members of 12 of these 14 observer pairs directed their initial bout of pecking toward the type of dish from which their respective demonstrators had been trained to feed (Binomial test, $P=0.25$, $x=2$, $p<0.001$). On average, these 12 observer pairs spent 81.3 ± 7.8 per cent of the 0.11 ± 0.04 min that they spent pecking, pecking in the type of site from which their respective demonstrators had fed during training. All of the 12 observer pairs spent more than 25 per cent of the time that they spent pecking, pecking in the type of site into which their demonstrators had fed previously (Sign test, $P=0.50$, $p<0.01$).