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Food Scrounging and Diffusion of Foraging Skills in Pigeons, *Columba livia:* The Importance of Tutor and Observer Rewards

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Abstract

Naive feral pigeons (*Columba livia*) adopt novel foraging skills after watching tutors demonstrating them. Despite this ability, novel foraging skills do not always spread within pigeon flocks. Two factors are important in determining whether skills will spread or not. 1) Tutor reward: naive observers fail to acquire a novel skill if the tutor is not rewarded for its demonstration. 2) Scrounging: observers also fail to acquire the skill when they obtain rewards from the tutor's demonstrations (i.e. when they scrounge). We examine jointly the relative importance of tutor reward and of scrounging in promoting the diffusion of skills. Moreover, we investigate how magnitude of scrounger reward could affect the diffusion of skills. In Experiment 1 we found that scrounging had a stronger effect than tutor reward, but that the performance of observers was inhibited most strongly when tutors obtained no reward and observers scrounged. In Experiment 2 we found that the magnitude of scrounger reward had no effect on observers' acquisition of skills when tutors were rewarded. These results, taken with those of earlier work, suggest that variables such as tutor reward and scrounging, as well as task complexity and density of tutors in groups, are important factors affecting skill diffusion within groups.

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Introduction

The ability to acquire new foraging skills is of obvious biological importance to opportunistic foragers that exploit a wide diversity of food types. Social learning can promote the acquisition of new skills and lead to their spread within populations (see reviews by ROPER 1986; GALEF 1988; LEFEBVRE & PALAMETA 1988). Experiments on social learning, conducted mostly in birds, rats and primates (GALEF 1988; LEFEBVRE & PALAMETA 1988; WECHSLER 1989; FRAGASZY & VISALBERGHI 1990) have emphasized the subjects' ability to use different mecha-

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nisms of social learning. These mechanisms include local enhancement (the attraction to the site of a feeding animal THORPE 1963); stimulus enhancement (the attraction to the same type of object or patch that is being explored by others SPENCE 1937); and imitation (the acquisition of novel motor patterns following observation of individuals performing them [THORPE 1963; but see DAVIS 1973; GALEF 1976; 1988 for reviews]). Demonstrating the existence of social-learning mechanisms is of pivotal importance in the study of cultural transmission. Equally important, however, is the study of the factors that operate within groups to promote the diffusion of skills (GIRALDEAU & LEFEBVRE 1987).

The number of experimental studies of skill diffusion within groups is small, and several have focused on feral pigeons (*Columba livia*) (LEFEBVRE 1986; GIRALDEAU & LEFEBVRE 1986, 1987). Pigeons are an ideal species for experimental studies of skill diffusion in groups. They have the appropriate ecology, because they are gregarious, generalist, opportunistic foragers that readily adapt to changing environmental conditions (MURTON 1971; MURTON et al. 1972a, b). Much is already known about their conditioning (DELIUS 1983) as well as their ability to use social-learning mechanisms (PALAMETA & LEFEBVRE 1985; PALAMETA 1990). In pigeons, observation of a trained tutor enhances acquisition of novel foraging skills (PALAMETA & LEFEBVRE 1985; GIRALDEAU & LEFEBVRE 1986, 1987), and they are also capable of acquiring new motor patterns by imitation (PALAMETA 1990).

In one study, a food-finding skill spread quickly within two urban flocks of pigeons, and addition of a pre-trained tutor to one of the flocks accelerated the diffusion of the skill in that flock (LEFEBVRE 1986). New foraging skills, however, do not always spread quickly within pigeon flocks. When GIRALDEAU & LEFEBVRE (1987) presented a captive flock with a novel foraging task, the skill only spread to a few individuals. A similar lack of diffusion was also observed in a pigeon flock in two other experiments (LEFEBVRE 1986; GIRALDEAU & LEFEBVRE 1986). Therefore, the spread of innovations within groups may not depend only on the animals' ability to use social-learning mechanisms. Other factors can also influence the diffusion of skills.

Two factors have already been shown to affect rate of skill diffusion within pigeon flocks. Novel skills spread to observers when tutors are rewarded for performing their skill (PALAMETA & LEFEBVRE 1985), and when the tutors' demonstrations do not reward the observers (GIRALDEAU & LEFEBVRE 1987; but see DEL RUSSO 1971 for rodents). Tutors can reward observers in a flock feeding context when the food clumps discovered by tutors can be exploited (scrounged) by observers. Scrounging can inhibit the diffusion of the skill within flocks in two distinct ways. On the one hand it provides naive individuals with feeding opportunities that keep them from investing the time necessary to acquire the skill through conditioning. This effect is known as frequency-dependent learning (GIRALDEAU 1984). GIRALDEAU & LEFEBVRE (1987) suggested that scrounging, in addition, acts to inhibit social learning. They provided evidence for the negative effect of scrounging on social learning through a series of experiments using the duplicate-cage method of training (GIRALDEAU & LEFEBVRE 1987).

In a duplicate-cage system, a tutor pigeon, situated in a cage facing an observer pigeon, is required to perform a task to obtain food presented in a tray between the cages. The observer has the opportunity of performing the same novel task in order to obtain its own reward. Using such a system GIRALDEAU & LEFEBVRE (1987) found that nonperforming "control" tutors failed to transmit the skill to observers. As predicted by PALAMETA & LEFEBVRE (1985), the food-finding skill was learned rapidly by observers when the tutor was rewarded for performing the skill. However, observers failed to learn when the food-receiving tray between the cages was inclined such that most or all of the reward produced by the tutor's performance slid to the observer's side, thus allowing observers to "scrounge" the tutor's food. GIRALDEAU & LEFEBVRE (1987) concluded therefore that the tutor's demonstration enhanced acquisition of the skill but not when the tutor's behaviour provided food to the observer.

Because of the inclined tray in GIRALDEAU & LEFEBVRE's (1987) scrounging condition, all or almost all of the tutor's food slid to the scrounging observers. It follows that not only could observers scrounge but they also observed a tutor that obtained no food reward for its demonstration. In their nonscrounging condition, however, tutors had access to all their food, so observers, in addition to having no scrounging opportunity, saw tutors with food rewards. Because tutors obtained little or no food in the scrounging condition and all their food in the nonscrounging condition, it is uncertain whether the inhibition of learning observed in the scrounging condition was due to the tutor's lacking a reward, as was found by PALAMETA & LEFEBVRE (1985), or to the observers' obtaining a reward.

Situations where tutors provide observers with rewards only make biological sense if they are functionally analogous to flock feeding conditions where individuals scramble for food discovered by others. In those scramble, flock-feeding conditions food patches can be divided in many different ways. Depending on the food-patch defensibility, social rank of foragers, size of the patch and group size, scroungers can get smaller or larger shares of patches. If observer reward inhibits skill acquisition, then it is important to determine how different patch divisions between tutors and observers affects the rate of skill diffusion.

The goal of the present study is to follow up GIRALDEAU & LEFEBVRE's (1987) investigation of the effect of scrounging on the acquisition of food-finding skills. First we ask which of tutor or observer rewards affects the acquisition of the skill. Then we ask how different-sized observer rewards affect skill acquisition by observers.

Experiment 1: Tutor vs. Observer Payoff

Methods

Subjects

28 adult pigeons purchased from a commercial supplier, were used as naive observers. 10 of these had been included earlier in an unrelated seed preference experiment. Two wild-caught birds were used as tutors. All birds were maintained on a 12-h light cycle in individual cages, provided with ad libitum access to water and maintained at 85—90 % of their ad libitum body mass.

Procedure

The foraging task and general testing procedures were similar to those of GIRALDEAU & LEFEBVRE (1987). All individuals were tested while within their respective home cages. A naive observer-bird was placed 23 cm away, facing a pretrained tutor that performed the food-finding skill. The skill consisted of removing the stopper from an inverted test tube held vertically 6 cm above the ground. An acceptable tube opening required that the observer peck, bite, or pull either the stopper or a stick protruding from the stopper. Any other forms of tube opening (i.e. with the neck or the back of the head) were considered accidental.

In a demonstration trial an observer was placed facing a tutor. A stand that held both the observer's and the tutor's tubes was slid into place such that each bird had simultaneous access to a tube. The tutor pecked at its tube and when the stopper fell, seed rewards (depending on condition, see below) were poured by the experimenter into the tray. Each bird only had access to its own reward but could see whether the other bird received seeds. The tubes were withdrawn either 60 s after the tutor's tube opening when observers were unrewarded by the tutor (nonscrounging condition), or 60 s after the observers had stopped eating when the tutor rewarded them (scrounging condition). Therefore, in both conditions observers had at least 60 uninterrupted s to peck at their tube. The next demonstration occurred 30 s later if the observer had not opened its tube or 5 s later if it had. Observers were always rewarded with 10 millet seeds whenever they opened their own tube. Observers were presented with 10 demonstrations per day for 2 consecutive days.

In the conditions where tutors never obtained rewards, modifications were introduced to avoid extinction effects in the tutor. The tutor was allowed a rewarded tube-opening once before the observer was placed in the experimental set-up and again after the observer was removed following the day's 10 demonstrations. In addition, the tutor was given a rewarded tube opening between the 5th and 6th demonstration while the observer's view was blocked.

Experimental Design

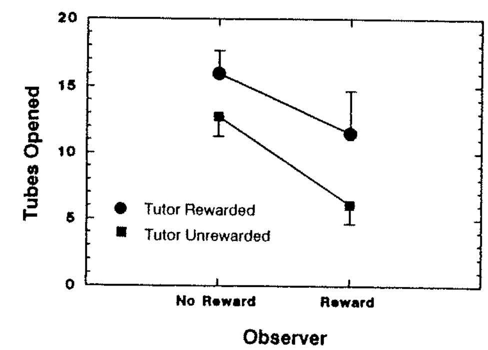
28 subjects were arbitrarily assigned to one of four tutor and observer reward combinations. Not all combinations were run concurrently. We first tested 6 birds in each of three reward combinations: 1. rewarded tutor with rewarded observer; 2. rewarded tutor with unrewarded observer; 3. unrewarded tutor with rewarded observer. Then, we ran two reward combinations: 4. unrewarded tutor with unrewarded observer; and 5. unrewarded tutor with rewarded observer. The last combination (5) served as a replicate of combination 3 that was run earlier. The combinations rewarded tutor with unrewarded observer (2) and unrewarded tutor with rewarded observer (3) are analogous to GIRALDEAU & LEFEBVRE's (1987) "no scrounging" and "scrounging" treatments respectively. Like GIRALDEAU & LEFEBVRE (1987) we measured the effectiveness of transmission, and hence learning, as the total number of tubes opened by observers in the course of 20 demonstrations; the sooner the skill transmission the greater the number of tubes opened.

Results

All but 2 of the observers opened at least one test tube. One subject was dropped from the -/- group because of a technical problem during the experiment. The mean number of tubes opened by observers in the two replicate tutor-unrewarded-with-observer-rewarded combinations (combinations 3 and 5 above) did not differ significantly ($\bar{x}$, SD, 5.8, 6.1; 6.4, 3.5 respectively; $t = 0.192$, $df = 9$, ns). Therefore, the subjects of each replicate were pooled and results for all reward combinations analysed with 2 × 2 analysis of variance using two levels of tutor reward and two levels of observer reward.

Rewarding the tutor enhanced transmission of the skill both when the observer was rewarded and when it was unrewarded, but the effect was short of statistical significance ($F = 3.94$, $df = 1$, $p = 0.059$; Fig. 1). Rewarding the observer, on the other hand, significantly inhibited transmission both when tutor

Fig. 1: Mean number of tubes opened by naive subjects in each reward combination of Exp. 1. Vertical bars indicate one SE



was rewarded and when it was unrewarded (Fig. 1; $F = 6.54$; $df = 1$, $p = 0.018$). There was no significant interaction between observer and tutor reward ($F = 0.25$, $df = 1$, ns). We cannot conclude with certainty, therefore, that tutor reward has no effect on observer performance. However, the statistical significance of the inhibitory effect of scrounging on transmission of the skill was contingent upon tutors being unrewarded.

Experiment 2: Magnitude of Scrounger Payoff

Methods

Subjects

A new group of 39 wild-caught, adult feral pigeons was used as naive observers. The two tutors were the same individuals as in Exp. 1. All subjects were housed and maintained as in Exp. 1 except for the body mass that was held slightly higher, at 90—95 % of their ad libitum mass.

Procedure

The procedure was similar to that of Exp. 1 except for some minor differences. During a demonstration the observer's tube was available for slightly shorter periods because the experimenter counted 60 s from the time the tutor started pecking its tube rather than from the time the tutor opened its tube. The inter-demonstration interval was longer and kept at 60 s in all cases. Not all birds were given a total of 20 demonstrations because we stopped testing birds once they opened 5 tubes consecutively. In Exp. 1 all subjects that opened 5 consecutive tubes continued to do so as long as tubes were presented to them. This time accidental tube openings produced seeds as they did in GIRALDEAU & LEFEBVRE (1987).

Experimental Design

To determine the effect of magnitude of observer reward, the subjects were arbitrarily assigned to one of three reward levels: 13 in small-reward, 12 in large-reward and 14 in a control, no-reward treatment. In the no-reward treatment the observer was never rewarded by the tutor's tube opening. In the small and large treatments the observer always received rewards of 5 and 30 seeds respectively once the tutor opened its tube. In all three treatments the tutor always obtained 10 seeds when it opened its tube. Similarly, the observer received a 10-seed reward for opening its own tube. The number of tubes opened by observers were analysed with a one-way analysis of variance.

Results

The magnitude of observer reward had no significant effect on the acquisition of tube-opening behaviour ($F = 1.6$, $df = 2$, $p = 0.2$; Fig. 2). As in Exp. 1, the presence of tutor reward canceled any inhibition induced by observer reward. When tutors were rewarded, observer reward, even when it was three times larger than the tutor's, still failed markedly to inhibit transmission of the foraging skill.

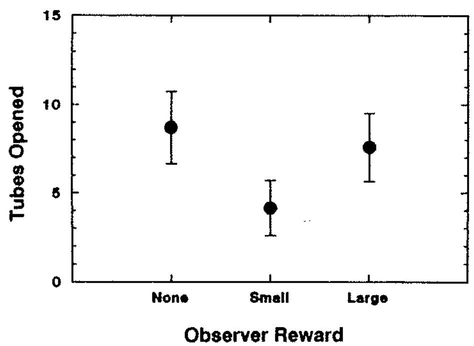


Fig. 2: Mean (± SE) number of tubes opened by naive observers in the three reward combinations of Exp. 2

The overall performance of observers in all three conditions, however, is lower than levels recorded in Exp. 1. As many as 13/39 subjects never opened any tubes. The difference between the two experiments could result from two important differences between the subjects used in each experiment. Subjects in Exp. 1 were commercially obtained from a pigeon farm while those in 2 were wild-caught. The pigeons in Exp. 2 were obviously more disturbed by their captivity and never habituated to the presence of experimenters to the extent of those of Exp. 1. Moreover, the birds of Exp. 2 were maintained at a higher relative body mass (90—95 %) than those of Exp. 1 (85—90 %), thus possibly reducing the rewarding effects of food. These differences, combined with the longer inter-demonstration intervals of Exp. 2, may have reduced the transmission of tube-opening behaviour in Exp. 2 but are unlikely to affect our conclusions concerning the absence of an observer-reward effect.

Discussion

Our experiments confirm GIRALDEAU & LEFEBVRE's (1987) earlier report that observer scrounging, obtaining a food reward from the tutor's behaviour, in a duplicate-cage set-up, inhibits the acquisition of a food-finding skill. However, our results go one step further by suggesting that the inhibition due to scrounging may be contingent upon the tutor receiving no reward for performing the task. Providing food to tutors appears to reduce the inhibitory effect of scrounging on observer performance, even when scroungers receive rewards of up to 3 times the amount provided to tutors.

Our results may initially appear to be at odds with two earlier findings. First, we found that, statistically, tutor reward had little effect on observer performance while PALAMETA & LEFEBVRE (1985) found that tutor reward was required to promote skill acquisition in pigeon observers. Second, we found that when tutors were rewarded, even large observer rewards failed to inhibit learning while GIRALDEAU & LEFEBVRE (1987) concluded that scrounging in a flock context (where tutors likely were rewarded) accounted for the weak skill diffusion in their flock. We deal with each of these apparent contradictions in turn.

Tutor Reward Important?

The contradiction between our study and past studies (PALAMETA & LEFEBVRE 1987) on the effect of tutor reward may not be as strong as it initially appears. It would be difficult for us to argue that tutor reward has absolutely no effect on observer performance when the main effect of tutor reward just fails to reach accepted levels of statistical significance ($p = 0.059$). Moreover, tutor reward must have some effect on observers because scrounging inhibits learning in observers only when tutors are unrewarded.

The lack of a statistically significant main effect of tutor reward we observed is due, for the most part, to the relatively high performance levels of the 4 subjects in the tutor-unrewarded with observer-unrewarded condition (Fig. 1). Under similar reward conditions PALAMETA & LEFEBVRE's (1985) observers failed to learn while ours learned almost as well as unrewarded observers given rewarded tutors. The difference between these studies may be due to dissimilarity in the behaviour required to learn the foraging task. Our tube-opening task was relatively simple, requiring only a single response directed to the stopper to achieve success. PALAMETA & LEFEBVRE's (1985) pigeons, on the other hand, had to learn to peck persistently at a paper barrier in order to reach the food behind it. Tutor reward, therefore, may enhance transmission, but the effect could be most obvious when tasks require persistence on the part of observers. We tentatively conclude, therefore, that tutor reward may have a reduced effect on the transmission of simple, one-step tasks.

Scrounging in Flocks

GIRALDEAU & LEFEBVRE (1987) and LEFEBVRE (1986) noted that under some conditions, pigeons in flocks showed little evidence of social transmission of skills. A similar absence of learning was also observed in pairs of zebra finches (BEAUCHAMP & KACELNIK 1991). GIRALDEAU & LEFEBVRE (1987) proposed that scrounging inhibited skill diffusion in their flock. Our results suggest that this explanation would be correct only if flock tutors (patch finders) received no food reward when they discovered a food patch (i.e. that scroungers obtained all the food). It is unlikely, however, that flock tutors obtained no food when they discovered patches. Although GIRALDEAU & LEFEBVRE (1987) did not measure the rewards obtained by finders and joiners in their flock, rewards were measured in flocks of grass finches (Estrildidae) that, much like pigeons, scramble for food discovered by others (GIRALDEAU et al. 1990). Individual finches that found patches obtained significantly more food per patch than those that scrounged

(GIRALDEAU et al. 1990). Pigeon food-finders in flocks likely also obtained a sizable share of the reward. Thus, scrounging itself may no longer account for the lack of transmission in the flock.

The reduced inhibitory effect of scrounging on skill transmission in flocks depends, of course, on the extent to which results obtained with the duplicate-cage method can be transposed directly to flock situations. The duplicate-cage method is designed specifically to simplify and therefore to allow control of conditions under which naive observers are influenced by the behaviour of tutors. Observers within flocks, however, are likely confronted with a much wider range of potentially relevant stimuli than observers in the duplicate-cage situation. For instance, in flocks, not all individuals are useful tutors. Flock observers are faced with the problem of determining which individuals are demonstrating a relevant or rewarding response, a difficulty that was incorporated into BOYD & RICHERSON's (1988) models of cultural transmission but that is absent in duplicate-cage designs. In addition, flock-feeding individuals, unlike caged birds, have the opportunity of learning to follow food finders, a response that can also interfere with social learning (GIRALDEAU & LEFEBVRE 1987; BEAUCHAMP & KACELNIK 1991).

By its simplicity, therefore, the duplicate-cage design might enhance the effect of useful tutors on observers. If flocking conditions in some way reduce the effect of tutors, then scrounging under flock conditions might inhibit skill acquisition even when tutors are rewarded. In effect, rewarded tutors in flock conditions could be as inefficient at promoting skill use in scrounging observers as unrewarded tutors in the duplicate-cage set-up.

Conclusions

Pigeons are capable of social learning (PALAMETA & LEFEBVRE 1985; GIRALDEAU & LEFEBVRE 1987; PALAMETA 1990) and attention should now be directed to the factors that likely govern whether such learning will occur or not under flocking conditions. Our results suggest that unrewarded-tutor demonstration acts as a sufficient promoter of skill use for simple, one-step tasks. Multiple-step skills, however, could require the additional incentive of tutor reward.

If these duplicate-cage results are to be transposed to group feeding conditions, studies should now examine the factors that alter the influence of tutors within flocks. Tutor reward might have weaker effects on observers in groups because of the complexity and richness of the potential information available in such conditions. Future research should take two complementary directions. On the one hand, the duplicate-cage system should be modified to investigate some of the potential factors affecting skill transmission. For example, what would be the effect of tutor and observer rewards when several tutors are provided to observers in a cage experiment? Further studies should also be conducted with foraging groups. In jackdaw flocks, for instance, WECHSLER (1989) found that a novel skill spread at a constant rate, suggesting that tutor density does not affect diffusion rate. It would be important, therefore, to know more about the effect of group conditions on skill acquisition. For example, what is the effect of group size and

the density of tutors? Our study illustrates that understanding the process of skill diffusion within groups requires examination of the promoters and inhibitors of transmission as well as the specific mechanisms involved.

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