Anim. Behav., 1987, **35**, 387–394

Scrounging prevents cultural transmission of food-finding behaviour in pigeons

LUC-ALAIN GIRALDEAU* & LOUIS LEFEBVRE†
**Department of Psychology, University of Toronto, Toronto, Ontario, M5S 1A1, Canada*
†Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montréal, Québec, H3A 1B1, Canada

Abstract. Living in groups should promote the cultural transmission of a novel behaviour because opportunities for observing knowledgeable individuals are likely to be more numerous in this condition. However, in this study pigeons who shared the food discoveries of others (scroungers) did not learn the food-finding technique used by the discoverers (producers). Individually-caged pigeons prevented from scrounging easily learned the technique from a conspecific tutor. When caged pigeons obtained food from the tutor's performance, most naïve observers failed to learn. In a flock, scroungers selectively followed producers. In individual cages, scrounging during the tutor's demonstration was equivalent to getting no demonstration at all. This effect of scrounging did not interfere with subsequent acquisition of the food-finding behaviour when scrounging was no longer possible.

Many animals are known to adopt a novel behaviour as a result of observing others performing it (see Galef 1976; Bonner 1980; Mainardi 1981 for reviews). This type of learning has been variously labelled cultural transmission, social learning, imitation, observational learning, etc. One consequence of such learning is the potentially rapid spread of behavioural innovations within populations. All other things being equal, cultural transmission should be very rapid in group-living animals, since the rate of diffusion of the innovation increases with the frequency of contact between knowledgeable and naïve individuals (Cavalli-Sforza & Feldman 1981).

When animals forage in groups, however, occasions arise in which some individuals (scroungers) may parasitize the food discoveries of other individuals (producers; Barnard & Sibly 1981; Barnard 1984). Pigeons, *Columba livia*, exhibit these producer and scrounger behaviours (Giraldeau & Lefebvre 1986), but they do so in a flexible way: different individuals become producers in different contexts, leading to what Giraldeau (1984) calls a skill pool, a system of exchangeable producer–scrounger roles.

Feral pigeons are highly opportunistic flock feeders (Murton & Westwood 1966; Murton et al. 1972) and are thus prime candidates for cultural learning. Palameta & Lefebvre (1985) have shown that individually-caged pigeons can adopt a novel food-finding behaviour via observational learning and local enhancement. Yet when pigeons are tested in a group, the same behaviour that is easily learned by caged individuals spreads to only a few birds within the flock (Giraldeau & Lefebvre 1986; Lefebvre, in press). The scrounging that occurs in a group thus appears to be associated with a blockage of learning.

In this paper, we test the hypothesis that scrounging blocks cultural learning. We first examine producing and scrounging in a group context and determine whether dominance and competition for opportunities to produce can account for the producer–scrounger relationship. We then test whether scrounging is sufficient to block observational learning in individually-caged birds. Finally, we investigate whether scrounging blocks learning (1) by interfering with the reception of information during observation of the producing skill, (2) by blocking only performance, despite acquisition of information about the producing skill, or (3) by long-term interference with learning of the skill.

FLOCK EXPERIMENTS

General Methods

Subjects

The flock experiments were done on a group of 16 feral pigeons maintained in a 6 × 4 × 3 m indoor aviary. Each bird could be identified individually either by conspicuous plumage or by plastic wing tags. Outside experimental periods, the birds had free access to food, water and grit. During the experiments, the birds were maintained at 90–95% of their ad libitum body weights.

Procedure

The setup in the aviary consisted of a row of 48 opaque inverted test-tubes 5 cm apart, 15 cm above the floor. To discover the food (2 g of millet seed) placed in five test-tubes selected at random, a pigeon had to peck downward on a small wooden stick protruding from a rubber stopper fitted loosely into the tube's aperture. Pecking caused the stopper and the food to fall to the ground, where it covered an area of approximately 60 cm^2. We chose tube-opening as a task because dispersal of seed from the tubes allowed us to manipulate the opportunity of scrounging easily.

Diffusion Through the Flock

Methods

The tubes were available to the flock for 27 2-h sessions in which 0–13 trials were performed. A trial normally consisted of the opening of all five tubes containing food; birds ceased to search on a few occasions at the end of a session, thus leaving some trials with fewer than five discoveries. All sessions were recorded on a videocassette system. From these recordings, the identity of each individual opening a seed-filled tube was noted; these individuals were called producers.

Results

During these experiments, pigeons approached the test-tubes and usually one or two individuals pecked at the stoppers. When food fell to the floor, 10–12 individuals (scroungers) rushed to the site and began feeding. In all, we analysed 108 trials in which 365 food discoveries were made. The distribution of discoveries was aggregated (Fig. 1A) and significantly different from the uniform distribution we would expect had the discoveries been equally distributed within the flock ($G_{adj}=1431{\cdot}39$, $df=14$, $P<0{\cdot}0001$; Sokal & Rohlf 1981). Two individuals were responsible for 97% of the discoveries. A clear producer–scrounger relationship developed in the aviary, and the skill required to produce failed to spread.

Competition for Performance?

Methods

To determine whether the aggregation of discoveries was the result of competition for performance of discoveries, we removed the two best producers from the flock (birds 15 and 16) for another 26 sessions. We again noted from videocassette recordings the identity of individuals that discovered food. If scroungers in the previous experiments knew how to open tubes, but were being outcompeted by the more efficient birds, the replacement of producers by ex-scroungers should be very rapid.

Results

We analysed 153 food discoveries occurring in 63 trials. Again, the distribution of discoveries was aggregated, with a single bird accounting for 150 of the 153 discoveries (Fig. 1B; H_o = uniform distribution, $G_{adj}=708{\cdot}50$, $df=12$, $P<0{\cdot}001$). This individual required 15 sessions before producing the first discovery. The clumped distribution of discoveries in the first experiment therefore cannot be the result of competition for performance.

Effects of Dominance

In some producer–scrounger systems, dominance hierarchies determine which individuals produce and which individuals scrounge (Baker et al. 1981; Rohwer & Ewald 1981; Czikeli 1983). Although this does not seem to be the case in pigeons (Giraldeau & Lefebvre 1986), we tested whether the producer–scrounger relationship observed in the aviary sessions could have been due to social dominance.

Methods

We assumed that the most relevant expression of

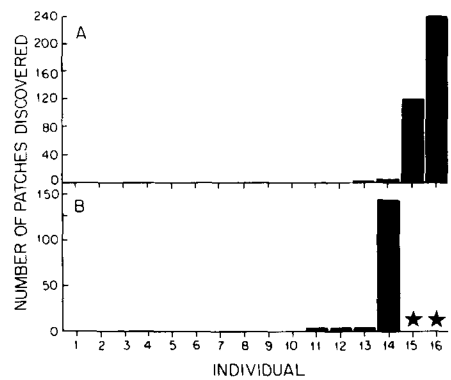

Figure 1. The number of discoveries made by each individual in the experiments of the aviary series. A. Experiment 1. B. Experiment 2; the stars indicate the individuals which were removed.

dominance in our experiments was the priority of access to food (Richards 1974). We measured this in the complete flock during four 2-h sessions distributed over a 4-week period following the removal sessions. Each session was preceded by 24 h of food deprivation. From videocassette recordings of each session we determined the time required by each individual to reach a total of 60 s of feeding from a small non-depleting 5 × 5 × 30 cm column feeder placed on the floor in the middle of the aviary. High-ranking animals reach this criterion sooner than lower ranking ones.

Results

An individual's rank of priority of access to the feeder remained fairly consistent over the 4 weeks of the test (Table I). We summed the times to reach the criterion feeding time for each individual over the four sessions to establish an overall priority of access ranking. The ranks in this hierarchy were correlated with discovery performance ranks based on the total number of discoveries made by each individual during both sets of aviary sessions. There was no significant correlation between priority of access and discovery performance (tau = +0·291, df = 14, P = 0·12).

Table I. Kendall rank correlation matrix of priority of access to food over 4 weeks (significance level in parentheses)

	Week 2	Week 3	Week 4
Week 1	0·407 (0·006)	0·108 (NS)	0·406 (0·028)
Week 2	—	0·471 (0·010)	0·514 (0·006)
Week 3		—	0·251 (NS)

Do Scroungers Follow Producers?

Since not all flock members can feed from any one food discovery, it should benefit scroungers to follow producers. Proximity to sites of food discovery should maximize a scrounger's chances of having access to a discovery, as well as the time it can spend eating from it.

Methods

We observed whether scroungers remain close to producers. To do this, we used the videocassette recordings of the last 12 sessions of the experiment described above on competition for performance. The floor directly below the tubes was divided into six rectangular zones of equal surface (eight tubes wide). We noted the position of each pigeon at 5-s intervals only when the discoverer was present in one of the zones and no feeding was occurring or had occurred in the previous 5 s. An index of association was established as the difference between the proportion of producer–scrounger and scrounger–scrounger co-occurrences.

Results

The degrees of association between scroungers and producers was obtained from a total of 1894 scans. Over all sessions, scroungers tended to be found more frequently in zones containing the producer than in zones that contained only scroungers. The extent to which scroungers associated with producers was a function of the producer's rate of discovery (tau = +0·571, df = 9, P = 0·01). Because the food-containing tubes were randomly positioned, the rate of discovery must have been a function of the rate of tube opening. Thus, the positive correlation suggests that scroungers cued specifically on the tube-opening behaviour of the producer.

EXPERIMENTS ON INDIVIDUALLY-CAGED PIGEONS

General Methods

Subjects

In the next three experiments, we used 46 individually-caged adult pigeons, different from the ones used in the previous experiments. As was the case for the aviary experiments, the birds were given free access to food, water and grit outside experimental periods. During the experimental periods, the birds were maintained at 90–95% of their ad libitum body weight.

Procedure

We designed the cage experiments to provide naïve observer pigeons with individual tube-opening demonstrations from a pre-trained conspecific tutor. To do this, the tutor and the observer were each placed in cages of 30 × 20 × 30 cm facing each other 30 cm apart, separated by a tray. Each bird was presented simultaneously with a test-tube, identical to those used in the aviary experiments, 1 cm in front of their cage. The birds could peck at the tube's stopper through a 19 × 5·3 cm opening in the front of their cages. The tubes were available for 1 min and then removed briefly to mark the end of a presentation. When tube opening by a bird produced food, a small quantity of millet seed (0·5 g) fell into the tray placed directly under the tube. We ran three experiments using this setup, each differing in the type of information and reward provided by the tutor.

Diffusion of Tube-opening Behaviour in Caged Birds

Methods

The extreme aggregation in patch production obtained in the aviary experiment could have been the result of marked variation in the pigeons' learning ability. In order to determine whether this could be the case, we presented 14 individually-caged naïve birds with 10 daily tube-opening demonstrations by a tutor for 4 consecutive days. To mimic an intermittent reinforcement schedule of the type used in the aviary sessions, the tubes contained food on every fifth opening. Thus, each day the naïve birds observed two successful and eight unsuccessful tube-openings by the tutor. If the oberservers had started opening tubes during the demonstrations, they were allowed to continue responding past the demonstration period until they accumulated 10 tube-openings. This was done to standardize the daily experience gained by each observer. In this experiment, food released by the tutor was available only to the tutor.

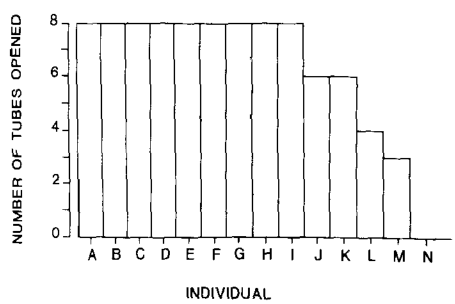

Figure 2. The number of food-containing tubes opened by each observer during 40 presentations of intermittently successful non-scrounging demonstrations.

Results

A total of 13 out of 14 previously naïve birds performed tube-opening behaviour within eight successful tube-opening demonstrations (40 total presentations). The distribution of tube-openings was not different from uniform (Fig. 2; $G_{adj}=18{\cdot}93$, $df=12$, NS). This contrasts sharply with the results obtained in both series of aviary sessions where three of the six individuals which had discovered at least one food source were responsible for over 98% (511/518) of all discoveries. The aggregation of discoveries in the aviary thus cannot be due to strong individual variation in the potential for adopting tube-opening behaviour. The same innovation which failed to spread within the flock was learned rapidly by individually-caged birds.

Scrounging and the Acquisition of Tube-opening

We hypothesized that the crucial difference between the aviary birds and the caged observers of the previous experiment was the scrounging opportunity provided in the aviary. The following experiment was designed to test this hypothesis.

Methods

Sixteen naïve birds were randomly assigned to one of two groups. Both groups received 10 daily demonstrations by a tutor for 2 consecutive days. In one group, the non-scrounging demonstration group (NSD), the tray between the birds was kept horizontal and divided into separate compartments so that the tutor's food discoveries could not be shared by the observers. In the other group, the scrounging demonstration group (SD), the tray was tilted towards the observer so that the seeds the tutor discovered rolled to the observers' side. Because the observers could eat in this condition, the presentations were extended for 1 min after the observer had stopped eating. This ensured that the SD observers had at least as much time to open their tube as NSD observers.

Results

Pigeons given the opportunity of scrounging during a demonstration showed very little tube-opening behaviour (Fig. 3). Only two of eight previously naïve SD birds, compared to eight of eight in the NSD condition, performed the behaviour (Fisher's exact test = 0·0007). The SD birds also opened significantly fewer tubes than the NSD birds (Wilcoxon rank sum test, $R1=39{\cdot}5$, $N1=N2=8$, $P<0{\cdot}01$; Ferguson 1971).

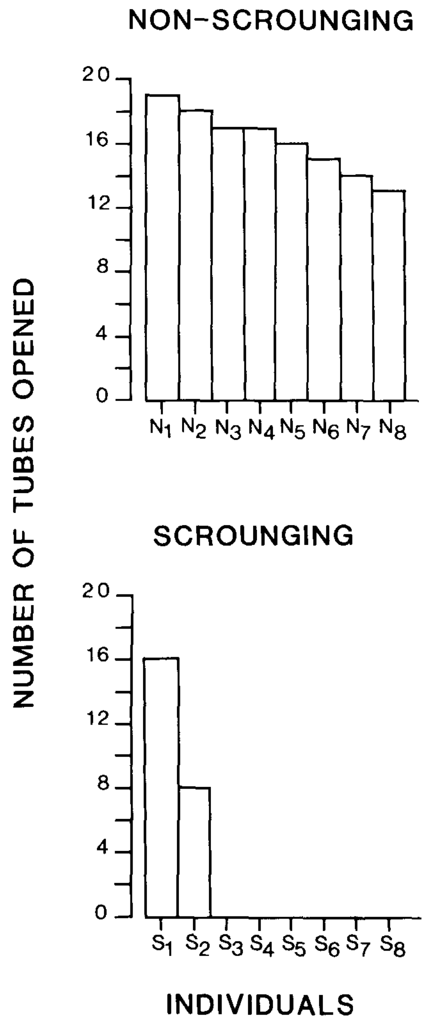

Figure 3. The number of tubes opened by pigeons provided with non-scrounging demonstrations compared to pigeons provided with scrounging demonstrations.

Effect of Scrounging on Observational Learning

Scrounging may interact with cultural learning in several ways. It could interfere with the reception of information transmitted by the tutor, so that scrounging during a demonstration is equivalent to getting no demonstration at all. Alternatively, scroungers may acquire some information about the producing skill despite the fact that they do not perform it. Finally, scrounging may exert a long-term effect, interfering with subsequent learning of the skill when opportunities for scrounging do not occur anymore. The goal of the following experiment is to distinguish between these possibilities.

Methods

Another group of 16 naïve pigeons was randomly divided into two groups. One group was first given 10 daily scrounging demonstrations for 2 consecutive days (SD1), followed by 10 daily non-scrounging demonstrations for another 2 consecutive days (SD2). The other group was given 10 daily non-demonstrations for 2 consecutive days (ND1), followed by 10 daily non-scrounging demonstrations for 2 consecutive days (ND2).

The non-demonstration condition consisted of presentations similar to those of the NSD group of the previous experiment, except that the tutor's tube had no stopper. The tutor therefore could not demonstrate tube-opening behaviour. The tutor was given a small quantity of food at the start of each presentation so that observers in both conditions had tutors which were feeding.

If scrounging blocks the reception of information conveyed by the tutor, the SD1 observers should perform no better than birds that obtain no tube-opening information, the ND1 birds. If scrounging also interferes with subsequent learning of the producing skill, the SD2 observers should perform more poorly than the ND2 observers. If, on the other hand, scroungers acquire information about the producing technique, the SD2 birds should outperform the ND2 birds, even if SD1 and ND1 birds do not differ.

Results

SD1 birds did not perform any differently from ND1 birds (Fig. 4), whether measured in terms of the number of birds that learned (one of eight in both cases) or the number of tubes opened (three in ND1 compared to one in SD1). More SD2 birds (eight/eight) learned the innovation than ND2 birds (three/eight, Fisher's exact test = 0·0128; Fig. 4). However, the difference in the total number of tubes opened by each group did not quite reach statistical significance (Wilcoxon rank sum test, $R1 = 50{\cdot}5$, $N1 = N2 = 8$, $P < 0{\cdot}10$).

DISCUSSION

Pigeons in experiment 1 of the cage series readily learned the food-finding skill required to obtain seed. Since observers that were given no demon-

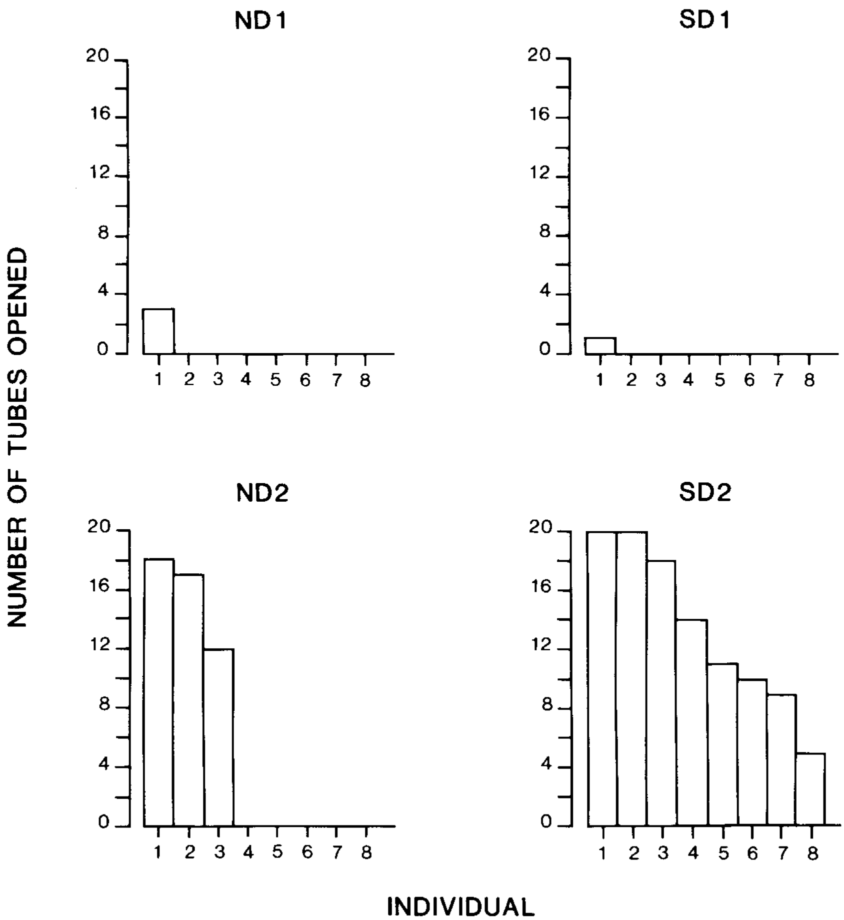

Figure 4. The number of tubes opened by pigeons provided with non-demonstrations (ND1) followed by non-scrounging demonstrations (ND2), compared to birds provided with scrounging demonstration (SD1) followed by non-scrounging demonstrations (SD2).

strations failed to learn (experiment 3), we can infer that the learning mechanism for tube-opening was probably observational learning. Thus, contrary to the results of Sherry & Galef (1984) on chickadees opening cream tubs, pigeons require a demonstrator to learn the task used in the present study. Different food-finding problems may vary in their level of difficulty for different species, and it appears that the task employed here was difficult enough for pigeons to require a tutor.

When pigeons were allowed to scrounge, however, whether in a group or in individual cages, tube-opening was performed by only a few birds. In the aviary, neither dominance nor competition for opportunities to produce could account for differences in the frequency of opening. Both of these results confirm those of Giraldeau & Lefebvre (1986) using different food-finding tasks. Results from experiment 2 of the cage series suggest that scrounging itself is responsible for the fact that opening failed to spread in the aviary tests. The inhibition caused by scrounging provides a plausible mechanism for one component of the frequency-dependent learning that Giraldeau (1984) proposes as a basis for the skill-pool effect. In a skill pool, initial differences in food-searching skills between individuals are magnified by frequency-dependent learning: individuals that find food get better and better at producing, while individuals that start scrounging remain scroungers. The present study suggests two reasons for the latter effect: (1) scroungers do not learn, even when tutors repeatedly perform the producing skill in front of them (experiment 2 of the cage series), and (2) scroungers selectively follow producers (experiment 4 of the aviary series).

These two factors are probably additive. In a flock, following a producer might interfere with the learning of the producing technique. When scroungers are caged, however, following is precluded, but scroungers still do not learn. Experiment 3 of the cage series suggests that scrounging interferes with the reception of information conveyed by the tutor, since scroungers perform as poorly as birds that get no demonstrations. This interference does not seem to exert a long-term inhibition on learning to open. When ex-scroungers are put in a situation where they cannot scrounge (group SD2), they learn at least as easily as birds that had no prior scrounging experience (group ND2). Moreover, our results seem to suggest that scroungers acquire some information about the producing skill even when they do not perform it, since more birds learn in group SD2 than in group ND2. Caution is needed here, however, since group ND2 seems to be unusually poor at learning to open if compared to the birds in experiment 1 of the cage series: only two of the seven birds that had not opened in ND1 eventually learned in group ND2, while 13 of 14 birds learned in experiment 1 (Fisher's exact probability $=0.005$). In contrast, all seven birds that failed to open in SD1, learned in SD2. The question of whether some information about producing is transmitted during scrounging demonstrations thus cannot be answered clearly.

One potential explanation for the low transmission of tube-opening in the aviary is the greater stimulus complexity of demonstrations performed in a group context. Aviary birds must extract information about the producing skill from a high level of background noise. In the removal experiment, for instance, each observer has to cope with 12 other scroungers, moving around constantly, before cueing in on the producer. In cages, by contrast, only one target bird is available and its behaviour is considerably constrained by the apparatus. However, we think this explanation is unlikely. If stimulus complexity is a possible factor, its importance is probably outweighed by the 100-fold difference in the number of demonstrations available in the aviary compared to the individual cages. Despite more than 4500 tube-opening demonstrations in the aviary (500 of them with seed), only six of 16 birds discovered at least one food source. In the cage experiments, 13 of 14 birds had opened tubes after only 40 demonstrations (eight with seed). In addition, evidence showing that scroungers follow producers suggests that birds can extract information from the aviary context, but that this information deals with the identity of the producer and his level of efficiency, not with the nature of the food-finding technique.

Opportunities for scrounging thus clearly appear to limit cultural learning. Such opportunities are frequency-dependent: payoffs for a scrounger depend on the number of discoveries made by producers, as well as the number of scroungers competing to join these discoveries (Barnard & Sibly 1981). The latter effect is, among other things, a function of patch size and defensibility. When the food discovered by a producer is distributed over a small area, a reduced number of scroungers would have access to it. If producing and scrounging are learned equivalents of evolutionarily stable strategies (Dawkins 1980; Harley 1981), a reduction in the payoffs associated with scrounging should induce some individuals to switch to producing. More animals should learn the producing skill when opportunities for scrounging are restricted. This is a prediction that follows both from the frequency-dependent nature of the producer–scrounger system and from the results of the present study. Experiments manipulating the size and defensibility of discoveries may help us to understand in greater detail the effect of scrounging payoffs on learning of the producing skill.

Our experiments suggest that group-living may not necessarily lead to higher rates of cultural transmission when scrounging occurs. In urban pigeon populations, frequent movement of individuals to and from feeding sites may constantly disrupt any potential producer–scrounger equilibrium (Lefebvre 1985). In these conditions, cultural learning may occur at a higher rate than in the closed population studied here, as naïve scroungers arrive and experienced producers depart (Lefebvre, in press). In many cases, however, frequency-dependent blockage of learning, whether acting alone or in conjunction with factors such as instability of group membership, may exert a strong effect on rates of cultural transmission. Factors such as social tolerance and food source defensibility, which determine the opportunities for scrounging, may affect the frequency of occurrence of this inhibitory effect.

ACKNOWLEDGMENTS

This study was supported by N.S.E.R.C. Operating Grants to L.L. and Jerry Hogan, as well as by F.C.A.C. and McGill University graduate fellowships to L.-A.G. We thank Sara Shettleworth and Jerry Hogan for kindly reading and commenting on an earlier draft of this manuscript. Two anonymous reviewers provided suggestions which considerably improved the presentation of our results.

REFERENCES

Baker, M. C., Belcher, C. S., Deutsch, L. C., Sherman, G. L. & Thompson, D. B. 1981. Foraging success in junco flocks and the effects of social hierarchy. *Anim. Behav.*, **29**, 137–142.

Barnard, C. J. 1984. The evolution of food-scrounging strategies within and between species. In: *Producers and Scroungers: Strategies of Exploitation and Parasitism* (Ed. by C.J. Barnard), pp. 95–126. New York: Chapman & Hall.

Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.*, **29**, 543–550.

Bonner, J. T. 1980. *The Evolution of Culture in Animals.* Princeton: Princeton University Press.

Cavalli-Sforza, L. L. & Feldman, M. W. 1981. *Cultural Transmission and Evolution: A Quantitative Approach.* Princeton: Princeton University Press.

Czikeli, H. 1983. Agonistic interactions within a winter flock of slate-coloured juncos (*Junco hyemalis*): evidence for dominants' strategy. *Z. Tierpsychol.*, **61**, 61–66.

Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? In: *Sociobiology: Beyond Nature/Nurture?* (Ed. by G.W. Barlow & J. Silverberg), pp. 331–367. Boulder: Westview Press.

Ferguson, G. A. 1971. *Statistical Analysis in Psychology and Education.* 3rd edn. New York: McGraw-Hill.

Galef, B. G., Jr. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In: *Advances in the Study of Behavior* (Ed. by J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Beer), pp. 77–100. London: Academic Press.

Giraldeau, L.-A. 1984. Group foraging: the skill pool effect and frequency-dependent learning. *Am. Nat.*, **124**, 72–79.

Giraldeau, L.-A. & Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim. Behav.*, **34**, 797–803.

Harley, C. B. 1981. Learning the evolutionarily stable strategy. *J. theor. Biol.*, **89**, 611–633.

Lefebvre, L. 1985. Stability of flock composition in urban pigeons. *Auk*, **102**, 886–888.

Lefebvre, L. In press. Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. *Ethology*.

Mainardi, D. 1981. Tradition and the social transmission of behavior in animals. In: *Sociobiology: Beyond Nature/Nurture?* (Ed. by G.W. Barlow & J. Silverberg), pp. 227–255. Boulder: Westview Press.

Murton, R. K., Coombs, C. F. B. & Thearle, R. J. P. 1972. Ecological studies of the feral pigeon *Columba livia* var. II: Flock behaviour and social organization. *J. appl. Ecol.*, **9**, 875–899.

Murton, R. K. & Westwood, N. J. 1966. The foods of the rock dove and feral pigeon. *Bird Study*, **13**, 130–146.

Palameta, B. & Lefebvre, L. 1985. Social transmission of a food-finding technique in pigeons: what is learned? *Anim. Behav.*, **33**, 892–896.

Richards, S. M. 1974. The concept of dominance and methods of assessment. *Anim. Behav.*, **22**, 914–930.

Rohwer, S. & Ewald, P. W. 1981. The cost of dominance and advantage of subordination in a badge signaling system. *Evolution*, **35**, 441–454.

Sherry, D. F. & Galef, B. G., Jr. 1984. Cultural transmission without imitation: milk bottle opening by birds. *Anim. Behav.*, **32**, 937–938.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry: the Principles and Practice of Statistics in Biological Research.* 2nd edn. New York: W.H. Freeman.

(Received 27 December 1985; revised 6 March 1986; MS. number: A4590)