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INFORMATION TRANSFER IN PIGEON COLONIES

Summary: The hypothesis that communal roosts and breeding colonies of birds act as information centres for food-finding was tested using pigeons, *Columba livia,* in Hawke's Bay, New Zealand. The birds roosted and bred in lofts, but were free each day to search for food in the surrounding fields. Two of three experiments showed that naive pigeons could learn the location of a patch of food when with experienced birds. A fourth experiment showed that naive birds learned by following experienced ones to a good feeding area. Pigeons returning from a successful foraging trip did not transfer information on the distance and direction of the food to other members of the colony.

Keywords: Columbidae; Columba livia; pigeon; communal nesting; communal roosting; information transfer; food intake; food location.

Introduction

The hypothesis that communal roosts and breeding colonies of birds act as information centres for food-finding (Ward, 1965; Ward and Zahavi, 1973) has been tested directly by De Groot (1980), Loman and Tamm (1980), Anderson *et al*., (1981) and Fleming (1981). De Groot (1980) demonstrated in the laboratory that weaverbirds *(Quelea quelea)* could learn from knowledgeable roostmates where to find food and water. Loman and Tamm (1980) provided carcasses of pigs and chickens in the field, and measured how frequently they were visited by hooded crows *(Corvus cornix)* and ravens *(C. corax)*. Their results were equivocal. In a minority of experiments, visits to a carcass increased markedly on the day after it was discovered, suggesting that the bird that found it might have been followed by others when it returned from the roost.

The experiments of Anderson *et al*., (1981) on wild black-headed gulls *(Larus ridibundus)* and of Fleming (1981) on pied wagtails *(Motacilla alba)* did not support the hypothesis. Their results must be interpreted cautiously because their experiments may have coincided with periods when food was abundant and there was no advantage to the birds in transferring information.

Alternatively, the food that they supplied may have been inferior in some way to that occurring naturally. In this event the colony as a whole would be unlikely to switch to the experimental food after its discovery, even if the information was transferred. Anderson *et al*., and Fleming considered these possibilities unlikely.

Clearly, tests on free-ranging birds have failed to demonstrate that their roosts and breeding colonies act as information centres for food-finding. The experiments described here on semi-feral pigeons *(Columba livia)* living in lofts were designed to test this hypothesis directly. The following questions were addressed: is information transferred from knowledgeable to naive birds; if so, does this transfer increase the recipient's food intake; do the return rates differ for pigeons that have fed successfully or unsuccessfully in the same field; and if information is transferred, what mechanism is involved?

Methods

Study Area

The study was carried out in fields near Havelock North (176º 53'E; 39º 41'S). The district has a temperate climate and fertile soils used for orchards, market gardens, grazing and mixed crops. It contains several thousand feral pigeons roosting and breeding mainly on coastal cliffs; eggs are laid in all months of the year. The birds commute daily to fields to feed on both weed seeds and commercial crops, especially maize and peas gleaned mainly from stubbles. Dilks (1975a, b) has described the diet and breeding biology of feral pigeons in Hawke's Bay.

Birds

Forty-four pigeons of mixed age were obtained in December 1980 from three lofts in agricultural areas of Hawke's Bay. These birds were semi-feral and accustomed to obtaining grit, water and some food by foraging in fields. They were marked individually with coloured leg bands, and housed for three months in a large loft (Loft A). Maize, peas and water were supplied *ad libitum* in the loft. In March 1981, the colony was split into two flocks of similar size and composition. One of the flocks remained confined in Loft A; the other was moved and confined in another loft (Loft B) of similar size and internal design 200 m . away. Loft A was opened in May 1981, and Loft B one month later.

The birds continued to be fed *ad libitum* on the

ground near their lofts for the first month following release, but thereafter their ration was reduced and given irregularly, so that for several days each week the birds had to forage entirely for themselves. Some birds disappeared shortly after the food supply was reduced, and others returned to their natal colonies. Losses were higher from Loft B than Loft A. More chicks fledged from Loft A than B during 1981 and early 1982, which further accentuated the difference in the size of the two colonies. When the first experiment started in May 1982, a year after the birds were first released, Loft A contained 42 pigeons and Loft B 19.

The reproductive success of pigeons in each loft was determined from weekly visits. The identity of pigeons incubating eggs or feeding young was recorded, and all chicks were individually banded when they fledged.

General Procedures

The following procedures were common to the first three experiments:

1. The colony was manipulated while the other was left undisturbed as a control. The colonies were sometimes reversed for successive experiments.
2. At the start, a rich patch of food was created out of sight of. both lofts. The food consisted of maize, sprinkled over about 25 m^2 of bare ground, at a density of 100-400 grains/m^2. It was replenished when necessary, so that there was always sufficient for many pigeons. At each site, there were few naturally occurring surface seeds so there was a marked gradient in profitability between the artificial food patch and its surroundings. A different site was used for each experiment.
3. Supplementary feeding near the lofts ceased when an experiment started and resumed when it finished.
4. The identity and number of pigeons that fed each day at the patch of food were recorded. Most pigeons were recognizable at a distance, and it was always possible to determine which colony they belonged to. However, on two occasions when large flocks landed for just a few minutes, it was not possible to read the bands on every bird.
5. Both lofts were closed after the birds returned at dusk, and opened again each morning. This enabled birds to be caught whenever necessary, but it also synchronized departures.

Experiment 1

This experiment tested whether information on the whereabouts of food was transferred from knowledgeable to naive birds. In May 1982, at a site 400 m from Loft A and 300 m from Loft B, food was supplied at dawn on day 1, before the birds were released. For the remainder of day 1 and all of day 2, the birds from both lofts were allowed to range freely to determine if any discovered the food.

Shortly after sunrise on day 3, five of the 42 pigeons in Loft A were selected at random and carried in a small wire cage to the food. The cage was positioned so that the birds could feed through the bars, then opened remotely about 2 minutes later. The pigeons then fed near the cage for another 2 or 3 minutes before flying back to their loft. The remaining birds in Loft A and the 19 control birds in Loft B were released after the five 'food-finders' returned. Thereafter until the experiment terminated at dusk on day 7, the birds from both lofts were free to forage each day.

Experiment 2

This experiment tested the same prediction as Experiment 1. It was carried out in June 1982, at a site 1.6 km north of the lofts. Five randomly selected birds from Loft A were taken to the food on day 1 and released, as in Experiment 1. Birds used as food-finders in Experiment 1 were not selected. The remaining 43 birds in Loft A and the 18 control birds in Loft B were released immediately after the food-finders had been removed. Two of the five food-finders returned to Loft A and were then taken back to the food in the afternoon of day 2 (three were outside the loft and could not be caught); all five were again taken back in the morning of day 3. The naive birds from both lofts were free to forage throughout both of these days. From day 4 onwards, the five food-finders were released with the naive birds. The experiment terminated in the evening of day 7.

Experiment 3

This experiment again tested whether information was transferred from knowledgeable to naive birds, but its main aims were (1) to determine if this increased the recipient's food intake and (2) to compare the return rates of pigeons that had fed either successfully or unsuccessfully in the same field.

The experiment was undertaken in October 1982 in a cultivated field 1.4 km south of the lofts. One day 1, five randomly chosen birds from Loft B were taken to the patch of maize and released, as in Experiment. 1. When they departed, five randomly chosen birds from Loft A were taken to the same field and released at another site about 60 m from the

food. The remaining birds in both lofts were free to forage throughout day 1. The same procedure was adopted on day 2, except that the order of releasing the birds from each loft at the experimental site was reversed. From day 2 onwards, both the food-finders and naive birds from each loft had to forage entirely for themselves. The experiment ended prematurely at dawn on day 5 when people began working in the field near the maize. Throughout this experiment, birds in both lofts, including nestlings, were weighed each night in the first three hours of darkness.

Experiment 4

This experiment aimed to distinguish between two possible mechanisms of information transfer: (1) whether naive birds followed knowledgeable ones to food, or (2) whether knowledgeable birds communicated the location of food on their return to the colony.

The experiment was undertaken in November 1982, in a small cultivated field 2.7 km west of the lofts. Five randomly selected birds from each loft were taken to the site each morning for three days and fed and released there, as in Experiment 2. Birds remaining in the lofts were free to range throughout the first three days. When Loft B was opened on day 4, the five food-finders were removed until all naive birds had departed. They were then returned to the loft and confined there for 1.5 hours before being released. Thus, naive birds from Loft B were with knowledgeable birds during the night, but had no knowledgeable birds to follow for the first 1.5 hours of the day. All of the birds in Loft A were released together on day 4, except for five randomly selected naive individuals, which were confined for 1.5 hours in a small cage 80 m from their loft. These birds were released at the same time as the food-finders from Loft B. This release procedure was repeated on days 5 and 6.

From day 7 onwards, all birds in Loft A were released together. It was no longer necessary to hold five naive birds back for the first 1.5 hours of the day, because it was obvious by then that removing birds from a colony did not impair the behaviour of those that were free to forage. The food-finders in Loft B, however, continued to be released 1.5 hours after the naive birds in their loft. Any naive birds in Loft B that found the food at the experimental site were from the next day onwards treated in the same way as the five original food-finders. The first mechanism of information transfer predicts a significant difference between lofts in the proportion of naive birds finding the food in the first 1.5 hours; the second mechanism does not. The birds in both lofts were again weighed each night throughout the experiment, which terminated on day 11.

Results

Experiment 1

For the first three days, no pigeons from Loft A discovered the maize at the experimental site, other than the five taken there at sunrise on day 3 (Fig. 1). . None of these birds returned to the site on day 3. Three small flocks from Loft A, comprising two 'food-finders' and six naive birds, fed at the site on day 4. On day 5 eight flocks from Loft A landed at various times at the experimental site. The first and largest of these comprised 34 birds, but they fed briefly and departed before all of them could be identified. However, of these, a minimum of 23 had to be naive birds visiting the site for the first time.

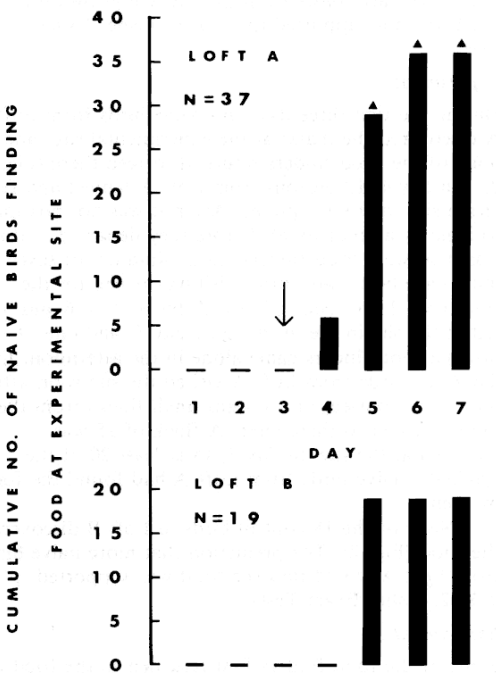

Figure 1: *Number of naive pigeons from treatment (A) and control lofts (B) finding the food at the experiment site during each day of Experiment 1. N. refers to the number of . naive birds in each loft at the start. Arrow indicates the day(s) on which the food-finders were taken to the maize.* ▲= *minimum estimate.*

Birds from Loft A continued to feed on the maize until the experiment finished on day 7. A flock of 41 landed at the site on day 6, so at least 36 of the 37 naive birds in the loft had discovered the food by then. At no time did all birds from Loft A arrive at the site together.

None of the 19 control birds found the food during the first four days of the experiment (Fig. 1). On day 5, however, the entire colony landed 30 m from the maize, and discovered it about 15 minutes later. There were no Loft A pigeons on the food at this time, but their movements to and from the site earlier in the day may have indicated the general whereabouts of the maize to the Loft B birds. On days 6 and 7, the birds from the two colonies sometimes fed together.

At least 36 out of 37 naive birds from Loft A and all 19 from Loft B found the maize. The prediction that more naive birds from Loft A would find the food was not supported (p = 0.66; Fisher Exact Test).

Experiment 2

During the first three days, no naive birds from Loft A discovered the maize at the experimental site, and none of the food-finders returned to feed there (Fig. 2). On day 4, 12 pigeons from Loft A landed and fed at the site for four minutes. Again it was not possible to identify all individuals before they departed, but at least two were food-finders, so a minimum of seven must have been naive birds visiting the site for the first time. Two flocks of Loft A birds (n = 6 and 4) fed at the site in the morning of day 5, and one of the original food-finders came alone in the afternoon. On day 6, 24 birds from Loft A visited the site soon after they were released, and several small flocks from the same loft landed there later. A flock of 25 was recorded at the site on day 7, so at least 20 of the originally naive birds from Loft A had found the food by then.

None of the 18 control birds in Loft B discovered the food (Fig. 2). The prediction that more naive birds from Loft A would find the food was supported (p = 0.0002; Fisher Exact Test).

Experiment 3

Some of the food-finders first returned to the food on day 2; a single bird from Loft B fed there for 10 minutes early in the afternoon, and two others landed briefly 1.5 hours later. They were not accompanied by naive birds (Fig. 3). Eight flocks of Loft B pigeons fed at the site on day 3. Two of these contained naive birds (three in a flock of six, and one in a flock of

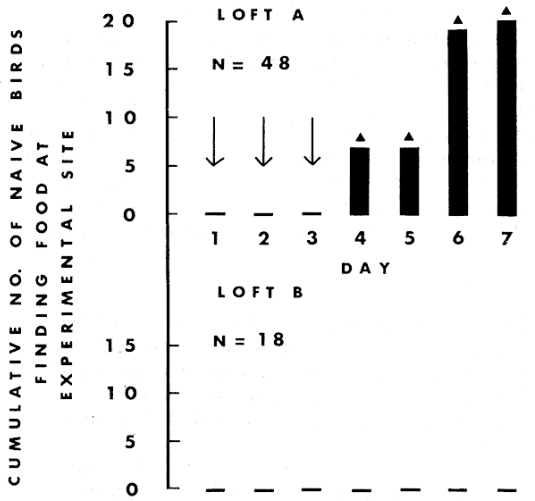

Figure 2: *Number of naive pigeons from the treatment (A) and control lofts (B) finding the food at the experimental site during each day of Experiment* 2. *Convention as in Fig*. 1.

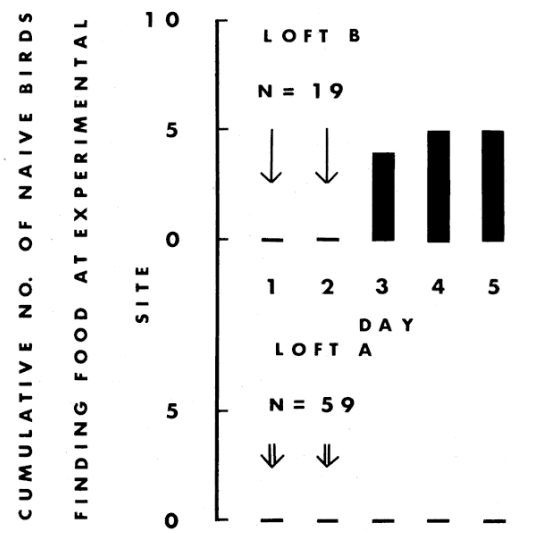

Figure 3: *Number of naive pigeons from the treatment (B) and control lofts (A) finding the food at the experiment site during each day of Experiment* 3. *Open arrows indicate days on which pigeons were taken to the experimental site and released in an area where no maize had been provided. Other conventions as in Fig. 1.*

two), and six comprised food-finders only.

The fifth naive bird to find the maize arrived with two food-finders in the morning of day 4. This flock was preceded by two others comprising both food-finders and naive birds which had fed at the site the previous day. Several flocks of Loft B pigeons circled over the maize in the afternoon of day 4, but were frightened away by people and tractors working in the field.

None of the 59 control birds from Loft A discovered the maize, and the five birds which were taken twice to the field and released in an area without maize did not return. By comparison, the five birds from Loft B which experienced good feeding at the site all returned there at least twice in the following three days. The difference between lofts in the proportion of naive birds finding the food, and the difference in the return rates of successful and unsuccessful foragers, were both significant ($p = 0.0004$ and 0.004 respectively; Fisher Exact Test). The results of this experiment therefore support the hypothesis that birds learn from each other where to find food, and confirm the assumption that succesful foragers return to good feeding areas while unsuccessful ones do not.

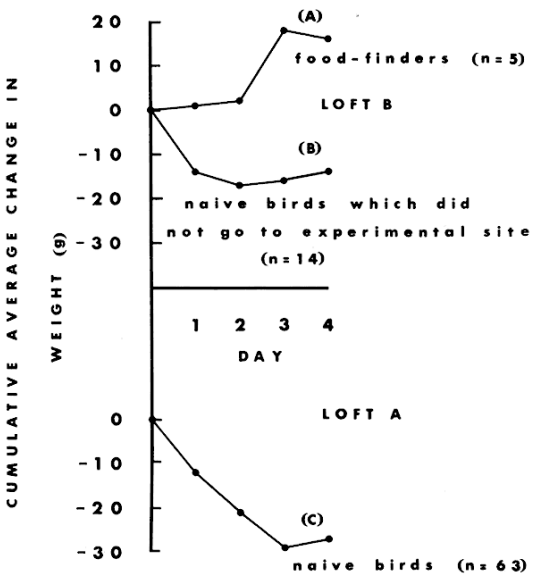

Figure 4: *Changes in weight of pigeons in the two lofts during Experiment* 3.

During this experiment, the five food-finders from Loft B increased in weight by an average of 18 g (Fig. 4a). The five birds that followed them to the maize enhanced their food intake by doing this; all increased in weight by an average of 12 g on the day that they discovered the food, whereas four of them had shown weight losses of 1-5 g on the day preceding their discovery. Of the 14 birds in Loft B that did not find the maize, 11 lost an average of 27 g, one showed no change throughout the experiment, and two increased by an average of 28 g (Fig. 4b). The birds which increased were chicks of food-finders, which had left the nest but were still being fed by their parents. Two chicks whose parents did not find the maize lost 60 g and 70 g.

The 63 control pigeons in Loft A lost an average of 27 g during Experiment 3 (Fig. 4c). Six of these birds, however, increased by 5-10 g, and two showed no change. The greatest losses of 40-95 g were again shown by chicks which had fledged but were still dependent on their parents for food.

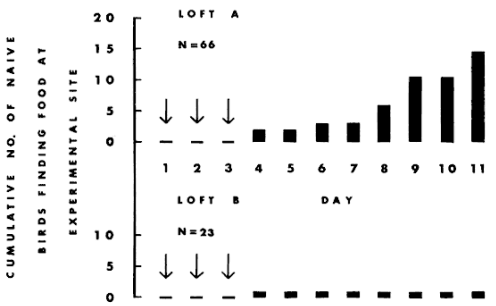

Figure 5: *Number of naive pigeons from Loft A and Loft B finding the food at the experimental site during each day of Experiment 4. Conventions as in Fig.* 1.

Experiment 4

Relatively few naive birds discovered the maize in this experiment (Fig. 5), although food-finders from both lofts commuted regularly to the site from day 4 onwards. No flocks from Loft B landed at the site during the first 1.5 hours of each day, whereas 8 did from Loft A. There were, however, no significant differences between lofts in the proportion of naive birds visiting the food in the first 1.5 hours of each day, or throughout the experiment (Table 1).

In this experiment, the identity of every bird that landed at the experimental site was established. Whenever a naive bird arrived at the site for the first

Table 1: *Number of naive birds from Lofts A and B that found maize during Experiment 4. Knowledgeable birds in Loft B were confined for the first 1.5 hours of each day; those in Loft A were not.*

	NAIVE BIRDS		
	No. finding maize		No. not finding maize
	First 1.5 h	Remainder of day	
Loft B	0	1	22
Loft A	2	12	52

(total numbers finding maize vs total not finding maize)
$X^2 = 3.5$, 1 df, n.s.

time, it was always in a flock containing at least one bird that had been there previously. If naive birds were discovering the food by chance, or had learned of its whereabouts in the colony, they should have sometimes arrived alone or in flocks comprising only naive birds. Simulations based on Loft A estimated that the probability of all 14 naive birds arriving at the food with at least one knowledgeable bird was 1.5×10^{-5} or 1 in 67,000 (Appendix 1). This result suggests strongly that information was transferred by following, rather than by communication in the colony.

There was some evidence that information was exchanged more freely between members of family groups than between distantly related individuals. On eight occasions in the fourth experiment the follower was unrelated to the food-finder, but on seven other occasions the follower was either its mate (4), offspring (1), or sibling (2). Mates and relatives followed knowledgeable birds significantly more often than would be expected by chance ($X^2 = 16.5$, 1 df, $p = 0.001$).

Once a naive bird had discovered the food, its next visit to the site was sometimes made alone, which showed that some birds needed to make only one trip to a patch of food in order to learn where it was. Others apparently made navigational errors when they first returned, either circling for several minutes over neighbouring fields before giving up and flying back to their loft, or landing in the right field but not finding the maize.

In the fourth experiment, the five food-finders from Loft B lost weight initially, then started to regain it from day 4 onwards. They finished the experiment with an average net loss of 28 g (A, Fig. 6), but nevertheless fared better than 12 adults in the loft which did not find the maize (B, Fig. 6). Nine chicks in Loft B, which were about to fledge or had recently done so, showed no net change in weight (C, Fig. 6). None of these chicks had food-finders as parents, but they were fed regularly by a young unmated male, which in the 11 days of the experiment made 48 trips to the maize.

In Loft A, one of the original food-finders did not return to the maize, and another did so only once; these birds lost on average 52 g. The remaining three food-finders visited the site regularly and maintained weight (D, Fig. 6). The 14 birds that followed them to the maize increased by a mean of 14.7 g on the day that they discovered it. The same birds increased by a mean of only 1.1 g on the day preceding their discovery.

Of the 49 birds in Loft A that fed elsewhere throughout the experiment, 39 lost 10-80 g, 2 disappeared, and 8 (7 adults and one chick) showed no net change or increased by 5-45 g (C, Fig. 6). The chick's parents discovered the maize midway through the experiment.

To summarize, the pigeons varied considerably in their daily intake of food. A few birds managed to maintain or increase weight by finding natural sources of food near their lofts; most in the same situation lost up to 80 g or 20-35% of their body weight. Birds that were taken to the experimental food source, or followed others there, generally had the highest weight gain within the colony.

Discussion

The results of Experiments 2 and 3 support Ward and Zahavi's (1973) hypothesis that roosts and breeding assemblies of birds can serve as information centres, wherein knowledge of the location of food may be obtained by birds which have been unsuccessful in their own searches. Experiment 1 did not support the hypothesis, because birds from the control loft also found the food. But they may not have discovered it by chance. The opening of their loft faced directly towards the food, and its inhabitants had an unobstructed view of pigeons from the other loft circling above the food and dropping down to feed. Local enhancement, where birds find food by observing where others are feeding, is known in many species (Krebs *et al.,* 1972). Experiment I probably did not provide a fair test of the hypothesis, therefore. In subsequent experiments the food was placed at a much greater distance from the lofts, to prevent the possibility of learning by local enhancement.

In pigeons, information was apparently

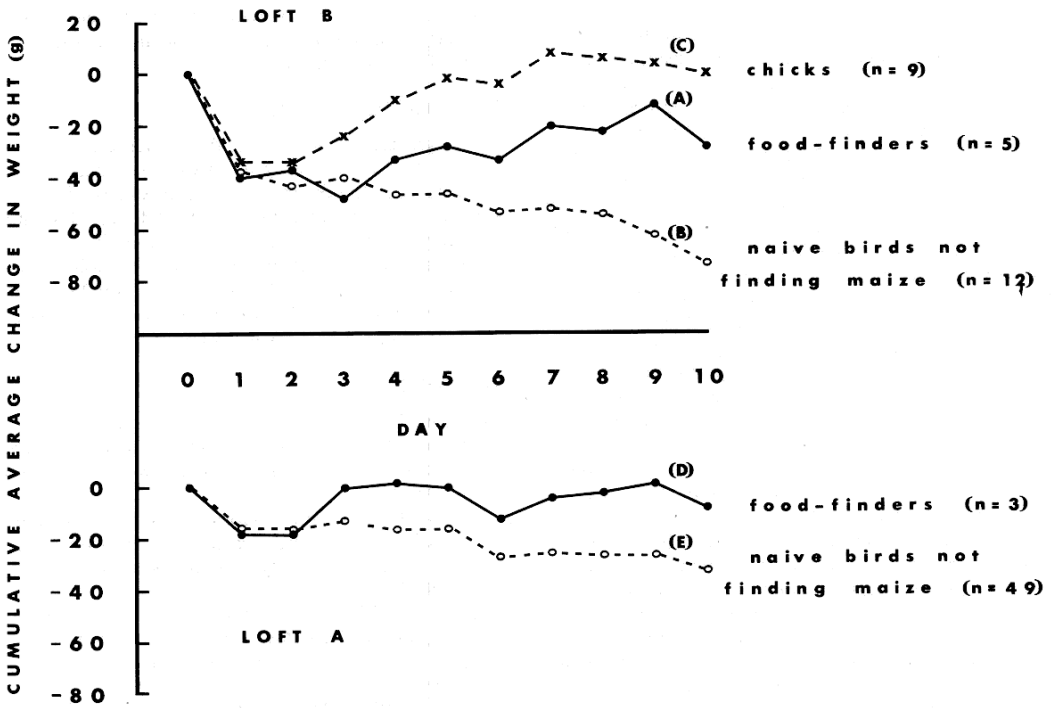

Figure 6: *Changes in weight of pigeons in the two lofts during Experiment 4.*

transferred by following. Our casual observations suggest that knowledgeable birds were generally the first to leave each morning, and their purposeful flight may have provided the cue for others to follow. Before departure their behaviour and physical appearance did not differ noticeably from that of naive birds. Later in the day, however, successful foragers may have been identified by their distended crops.

On the other hand, the association between knowledgeable and naive birds at the time of departure from the loft may have been entirely fortuitous. It is not a critical assumption of Ward and Zahavi's hypothesis that unsuccessful foragers can recognize successful ones. An unsuccessful forager would, on average, increase its chances of finding food by following any bird leaving the colony, even if it has no information on that bird's recent foraging success.

The experiments demonstrated that one return trip to a patch of food was sufficient for most pigeons to learn of its location; from then on they could return to the site alone, or with others. Their ability to learn quickly has several advantages: the food is unlikely to germinate, rot, or be eaten by competitors before its location is known precisely; and navigational errors made whilst learning of its whereabouts are reduced.

In the first two experiments, the majority of the colony switched rapidly to the maize soon after some of its members discovered it. In the last two, however, where food was supplied at a greater distance from the loft, changeover was gradual and incomplete. In the 11 days of the fourth experiment, for example, only 17% of the 89 naive birds in the two colonies flew to the maize.

Feral pigeons living on coastal cliffs in Hawke's Bay frequently fly more than 10 km to feed (pers.

obs.), so the maize provided in the last two experiments should have been well within the birds' foraging range. Indeed, the maximum distance used was 2.7 km - a flying time of less than 3 minutes. Despite this, it appeared to be further than some birds would travel. On one occasion, in the fourth experiment, 24 out of a flock of 27 turned back when they were about 300 m from the maize and several other times individuals and small groups left the flock after travelling about 1 km. These birds did not drop out en route because they knew of better or equally good sources of food closer to the loft, since the birds' that did complete the journey weighed significantly more after the experiment than those that did not. Their reluctance to complete the trip suggests that our intermittent feeding between the experiments may have conditioned some birds to remain near the lofts.

Pigeons that lead others to good feeding areas presumably incur a cost by doing this; they have to share food that they otherwise might have preserved for their own use. For some foods, such as spring-sown peas, the cost would be minimal because they would germinate quickly, irrespective of how many birds fed on them. With more persistent foods, however, such as grain in stubbles, finders could conceivably increase their own intake by keeping its whereabouts a secret. They apparently did not attempt to do this, possibly for two reasons. Firstly, all of the mechanisms for withholding information or deceiving others that we can imagine, such as knowledgeable birds taking a false bearing whenever they are followed, would waste time and energy, or incur other penalties such as an increased risk of being preyed upon. These costs may well be greater than those associated with sharing food. Secondly the costs of sharing may be offset by benefits resulting from feeding in a flock, such as protection from predators (Page and Whitacre, 1975; Kenward, 1978), increased feeding rate (Murton, 1971) or feeding time (Jennings and Evans, 1980) and fine-scale learning of the whereabouts of food (Krebs *et al.,* 1972).

Trivers (1971) has suggested that altruism towards unrelated individuals can evolve, provided there is reciprocation, discrimination against cheaters, and the benefit to the recipient is greater than the cost to the actor. These provisos might be fulfilled in small, stable colonies, such as those used in this study. We induced reciprocation experimentally and observed it once naturally, but did not determine if it occurred as a rule. Clearly, individual recognition and reciprocal altruism cannot be possible in winter roosts of, for example, starlings *(Sturn us vulgaris)* or rooks *(Corvus frugeligus),* which may comprise several thousand or even millions of birds. It remains to be tested whether these large concentrations also act as information centres for food-finding.

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Appendix .1

Computer simulations were designed to estimate the probability of naive birds always arriving at the experimental food source in a flock containing at least one knowledgeable bird. They assume that naive and mixed flocks have an equal chance of finding the food, an assumption that holds if information is exchanged at the colony, but not if information is exchanged by following.

The choice of flock size and frequency was based on data recorded during the founh experiment. The knowledgeable birds were assigned randomly to flocks and the number of flocks containing (I) knowledgeable birds only, (2) knowledgeable and naive birds, and (3) naive birds only, were noted for each simulation. One hundred simulations were carried out for each number of knowledgeable birds (5 on day 1 to 19 on day 11). By summing the number of flocks of each kind and dividing by the total number of flocks in 100 simulations (3000), the probabilities that the next flock to arrive at the site will be knowledgeable, mixed or naive, were estimated to be:

For each simulation the 71 birds in Loft A were split into flocks as follows:

Flock Size	Number of Flocks	Number of Birds
1	7	7
2	12	24
3	8	4
4	1	4
5	1	5
7	1	7
	30	71

No. of knowledgeable birds	Probability whole flock is naive	Probability flock is mixed	Probability whole flock is knowledgeable	Probability flock is mixed (given that it does not comprise knowledgeable birds only)
5	0.84	0.14	0.01	0.15.
6	0.81	0.17	0.02	0.17.
7	0.79	0.19	0.02	0.20.
8	0.76	0.22	0.02	0.22
9	0.73	0.23	0.04	0.24
10	0.71	0.26	0.04	0.27.
11	0.68	0.28	0.04	0.29
12	0.66	0.30	0.04	0.31
13	0.64	0.31	0.05	0.33
14	0.62	0.33	0.05	0.35
15	0.59	0.35	0.06	0.37.
16	0.57	0.37	0.07	0.39.
17	0.55	0.38	0.07	0.41.
18	0.53	0.40	0.07	0.43.
19	0.51	0.40	0.09	0.44.

Column 5 lists the probabilities of the next naive bird arriving in a mixed as opposed to naive flock, calculated from the equation

$$\text{probability of next bird arriving in mixed flock} = \frac{\text{probability (flock is mixed)}}{\text{probability (flock is naive)} + \text{probability (flock is mixed)}}$$

(Flocks comprising knowledgeable birds only can be ignored, since naive birds must come to the site in either a naive or mixed flock). The numbers with asterisks correspond to the sequence of increasing numbers of knowledgeable birds observed in Loft A during the fourth experiment. The probability that all the naive birds arrive in mixed flocks by chance is the product of these asterisked numbers, i.e. 1.5×10^{-5} or 1 in 67 000.