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The Use of Personal and Public Information in Foraging Flocks of European Starlings

Jennifer J. Templeton

A Thesis

in

The Special Individual Program

Presented in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy at
Concordia University
Montréal, Québec, Canada

March 1993

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ABSTRACT

The Use of Personal and Public Information in Foraging Flocks of European Starlings

Jennifer J. Templeton, Ph.D.
Concordia University, 1993

Recent models have considered the problem of how a solitary animal should make efficient foraging decisions when it must acquire information while it forages. However, the presence of others likely has important consequences for this information-gathering (sampling) process. This thesis tests the hypothesis that when foraging socially, European starlings (*Sturnus vulgaris*) use both "personal information" (gathered from their own foraging activities) and "public information" (obtained from observing the foraging activities of neighbouring conspecifics) to direct their foraging decisions in a profitable manner. In an aviary experiment, the ability of captive starlings to use environmental cues discovered via their own patch exploitations and via those of others was examined to evaluate the contribution of each source of information to individual feeding efficiency in groups. The ability to recognize "public" cues correctly enabled starlings to take advantage of the foraging activities of others both by arriving at their profitable discoveries more quickly and by actively avoiding their unprofitable discoveries, thus saving valuable foraging time. In a series of aviary experiments, starlings were found to assess poor patches more rapidly by combining information obtained from their own unsuccessful sampling efforts with information obtained from observing the unsuccessful sampling efforts of another individual foraging in the same patch. The degree to which public information was used, however, depended on the cost of patch assessment; when this cost was high, personal sampling declined and the use of public information increased. Finally, in a field experiment, the ease with which personal and public information could be acquired simultaneously and the variability in patch quality were manipulated in order to determine what sources of information free-living starlings were using to monitor patch depletion. When both personal and public information were available simultaneously, starlings were sensitive both to their own foraging rates and to those of other flock members, and used this information to estimate patch quality and direct their patch departure decisions.

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PREFACE

A large component of an animal's behaviour is devoted to acquiring food resources. These food resources are ultimately transformed into survival and offspring; thus we assume that over evolutionary time, natural selection has promoted efficient foraging decisions, given certain physiological, psychological, and ecological constraints (Krebs & Kacelnik 1991). This fundamental assumption about foraging behaviour has given rise to a large body of research known as foraging theory, which comprises a number of economic models and tests of these models (Stephens & Krebs 1986). Foraging behaviour has been most commonly divided into two main categories: exploiting prey items and exploiting patches of prey items (MacArthur & Pianka 1966). Foraging research, in turn, has tended to focus on two decisions which have developed out of these categories: "prey choice", what prey or patch types a forager should choose to exploit; and "patch departure", how long a forager should continue to exploit a patch before moving on to potentially more profitable patches (Pyke 1984).

Early foraging models assumed that foragers had complete information concerning the relevant parameters of their foraging decisions (reviewed by Stephens & Krebs 1986). It was assumed, for example, that a hypothetical forager was capable of perfectly recognizing the quality (resource density) of all patch types upon encounter with them and that this recognition was independent of its foraging experience within each patch (e.g. Charnov 1976). However, although these early models have been extremely useful for developing testable predictions and for shaping the field as a whole, in reality, the information possessed by a forager is more likely to be incomplete (Stephens & Krebs

1986, Valone & Brown 1989). More recent models and experimental tests of these models, therefore, have been concerned with the problem of how an animal should make efficient foraging decisions when it must acquire information while it forages (Oaten 1977, Krebs et al. 1978, McNamara & Houston 1980, 1985, Green 1980, Iwasa et al. 1981, Lima 1985, Kamil et al. 1988, Shettleworth et al. 1988, Valone & Brown 1989, Valone 1992).

Until recently, studies of the process of information acquisition have focused on the decisions of solitary foragers. However, because a large number of animal species forages socially, and because the acquisition of information can be time-consuming and costly (Stephens & Krebs 1986), the presence of others likely has important consequences for the information-gathering (sampling) process. For this reason, recent theoretical models (Clark & Mangel 1984, 1986, Valone 1989, Krebs & Inman 1992) and empirical tests of these models (Krebs & Inman 1992, Valone & Giraldeau In press) have begun to consider the possibility that foragers may be paying attention to the sampling activities of conspecifics and using this supplementary, "public" information (Valone 1989) in combination with their own "personal" information (Valone 1989) to help them direct their foraging decisions in a profitable manner.

In this thesis, I present four experimental studies in which I investigate how European starlings (*Sturnus vulgaris*) use different sources of information to make various types of foraging decisions, both when alone and when in groups. The starling is an excellent species with which to examine this foraging question. Starlings forage in flocks of varying sizes throughout the year (Feare 1984, Williamson & Gray 1975, Fischl & Caccamise 1985); and as well as reducing the hazards of predation (Powell 1974, Jennings & Evans 1980), this flocking behaviour is believed to increase the ability to discover and exploit localized and transient patches of food, as illustrated by the tendency for starlings to approach other starlings in feeding postures (Feare 1984). In addition, their apparent tendency to imitate the foraging behaviour of neighbouring birds whether in single- or mixed-species flocks (Williamson & Gray 1975, Feare & Inglis 1979) implies that starlings pay attention to the foraging activities of others. Sharing of food sources is not without conflict, however; males are dominant to females and can restrict access of subordinate birds to feeding sites when space is limited (Feare & Inglis 1979).

Starlings often probe for prey items hidden below the soil surface (Feare 1984); thus they must rely on information obtained from their sampling activities and from environmental cues to estimate the quality of a potential foraging site (Alcock 1973, Tinbergen 1981, Draulins 1988, Mitchell 1989). Indeed, it has even been suggested that obtaining information about short-term changes in profitability may be so important for starlings that they prefer to search for their food rather than take freely-available identical food (Inglis & Ferguson 1986). In addition, results of field experiments examining the foraging decisions of individual starlings (Tinbergen 1976, 1981) have led researchers to speculate that starlings may be able to minimize their sampling time on poor patches by obtaining at least some of their sampling information from others (Tinbergen & Drent 1980). The starling has been used successfully as an experimental animal in a variety of laboratory studies (Powell 1974, Feare & Inglis 1979, Lejeune 1980, Draulins 1988, Wenger et al. 1991) and recently, they have also been used in experiments dealing specifically with information-acquisition and foraging decisions in solitary individuals (Lima 1985, Kacelnik et al. 1986, Cuthill et al. 1990, Brunner et al. 1992).

In Chapter 1 of this thesis, I examine how the use of personal and public information influences an individual starling's decisions to exploit or ignore its own patch discoveries and to approach or avoid the patch discoveries of others. By manipulating both the type of information (environmental cues) a starling is able to recognize and the point at which this information becomes available during the patch exploitation process, I show how the information to which a forager has access can influence its ability to make profitable foraging decisions.

In Chapter 2, I investigate the patch sampling behaviour of starlings foraging alone and in pairs. I first examine how solitary starlings use the personal information acquired from their past foraging experience and current sampling activities to estimate patch quality, and then compare solitary patch departure decisions with the departure decisions made when birds are given access to different amounts of public sampling information. I continue this investigation in Chapter 3, where I manipulate the cost of acquiring personal information and determine how this cost of patch assessment influences not only an individual's use of personal sampling information to direct its patch departure decisions, but its reliance on public sampling information as well.

Finally, in Chapter 4, I present a field experiment on patch assessment in foraging flocks of starlings in which I manipulate both the ease with which personal and public sampling information can be acquired simultaneously and the degree of variability in patch quality. By examining how individual foraging success influences the order of patch departure by flock members under differing foraging conditions, I determine what source of information, or combination of information sources the birds may be using to direct their patch departure decisions in a group-foraging context.

Chapter 1

Public Information and Scrounging Decisions in Starlings: The Value of Recognizing Different Foraging Cues

Group living is considered to provide both reduced predation hazards and increased foraging benefits (see reviews by Caraco & Pulliam 1984, Clark & Mangel 1986). The foraging benefits of group membership are generally thought to arise from the group's ability to share information concerning each individual's foraging success (Clark & Mangel 1984); an individual that can recognize when another group member has discovered food can decide to move towards the successful individual and compete or "scrounge" (Barnard 1984) for the food. When animals do this, they can reduce both variance in searching time (Caraco 1981, Pulliam and Millikan 1982, Caraco & Giraldeau 1991) and the chance of obtaining no food within a given time period (Thompson et al. 1974, Baker et al. 1981, Hake and Ekman 1988). As well, when food patches offer more food than can be eaten by the group or are extremely ephemeral, scrounging may increase individual foraging rates (Pulliam & Millikan 1982, Clark & Mangel 1984).

In addition to providing foraging benefits, the use of information in foraging groups can potentially compensate for the costs of having to share food with others. In a simple game theoretical model, Clark and Mangel (1984) demonstrate that individuals which scrounge from the discoveries of other group members obtain higher feeding rates than those that forage independently within the group; an individual that forages independently ignores the successes of others, but still has to share its own discoveries with them. Thus, each group member must constantly monitor the activities of others and share their food simply to avoid the cost of being the only individual that does not do so (Clark and Mangel 1984, Vickery et al. 1991).

Individuals that forage in groups for patchily-distributed prey thus are faced with numerous foraging decisions. Not only must they use "personal information" (Valone 1989) to decide whether to exploit or to continue exploiting patches encountered via their own foraging activities; but they must also decide how to respond to the "public information" (Valone 1989) provided by the foraging activities of others in order to compete effectively within the group. In the present study, I examine individual decision-making in foraging groups by focusing on these two key characteristics of group foraging behaviour: the use of public information, and the competitive nature of foraging within a group.

The use of information by foraging groups has been studied in two main contexts. In the case of information centers (Ward and Zahavi 1973), information pertaining to another group member's foraging success can potentially be obtained at a site remote from the actual discovery of food, such as a communal roost or a breeding colony. An observing individual can then either depart in the direction from which the successful individual returned or follow the successful member back to the foraging site later (Krebs 1974, Galef & Wigmore 1983, Greene 1987, Wilkinson 1992). More commonly, however, information is exchanged at the site where food discoveries are occurring. In this paper, I am concerned with the latter situation.

Previous studies have provided evidence for the use of public information at a foraging site by documenting the phenomenon of "local enhancement" (Thorpe 1963) or "area copying" (Barnard and Sibly 1981), where individuals approach the discoveries of others and either share their food, or forage nearby (Krebs et al. 1972, Waite 1981, Giraldeau and Lefebvre 1986). Although these studies indicate that information is being used, they say little about the kinds of information a forager is able to use; public information appears to be obtained either from simply seeing the discovered prey items or from observing the eating motions of the discoverer (Drent & Swierstra 1977, Feare 1984). However, several other forms of public information may indicate the profitability of a patch; this information could become available at several stages during the patch exploitation process and an observing individual could respond to this information in a variety of different ways. For example, upon discovery of food, a forager may change its behaviour slightly (e.g. Metz et al. 1991) such that an alert observer can use this change as a cue indicating the presence of prey. Behavioural cues may also indicate the size and profitability of prey items as was suggested in a field study of interspecific kleptoparasitism in black-headed gulls (*Larus ridibundus*) and lapwings (*Vanellus vanellus*), where gulls apparently used the duration of the crouch posture of a plover (which predicts the size of the worm it is about to capture) in order to select which plover to attack (Barnard & Stephens 1981, Thompson 1983). Similarly, certain physical patch characteristics that are exposed by another forager's exploitation of a patch could potentially be used by an observing individual as environmental cues indicating the presence or absence of prey, again enabling it to decide whether to approach, or even avoid the patch.

Under the competitive conditions in which group foragers search for food, it is likely that the ability to detect and even predict the imminent discovery of food by another would provide a significant foraging advantage. For instance, in a laboratory study of producing and scrounging in two species of socially-foraging finches (*Lonchura punctulata* and *Taenopygia guttata*), Giraldeau et al. (1991) suggested that food finders (producers) were consistently observed to obtain more food than scroungers simply as a result of the small temporal delay between the discovery of food and the arrival of scroungers. The ability to recognize the foraging success of another individual as quickly as possible, therefore, should allow a scrounger to arrive at a profitable patch sooner and hence obtain a larger share of the discovery than one lacking this ability. Likewise, recognizing a lack of foraging success in another individual should be just as important, because avoiding an unprofitable or empty patch could save valuable foraging time (Benkman 1988, Templeton, Chap. 3).

In the following experiment, I examine how the use of public information by European starlings (*Sturnus vulgaris*) foraging in pairs influences individual scrounging decisions and foraging returns. I do this by manipulating both the type of public information a starling can recognize and the point at which this information becomes available during the patch exploitation process. In my experimental foraging task, information concerning the quality of a patch is potentially available either in the form of a concealed colour cue or from the behaviour of an exploiting individual. The foraging environment is also manipulated such that colour cues are either present or not, and provide either correct or incorrect information concerning the presence of food.

If the ability to use different forms of public information effectively within a foraging group is advantageous, then those individuals that correctly recognize the colour cues exposed by another's patch exploitation activities should be able to respond more quickly to discoveries of profitable patches, and hence obtain a greater share of the available food. In addition, the ability to use colour cues should enable an individual to recognize when another bird is exploiting an unprofitable patch and thus to avoid that patch. Recognizing and responding selectively to public information, therefore, should allow an individual to improve its foraging efficiency and hence compete more effectively with other group members. In the following experiment I document whether starlings use public cue information and determine the extent to which the use of such information provides foraging benefits.

METHODS

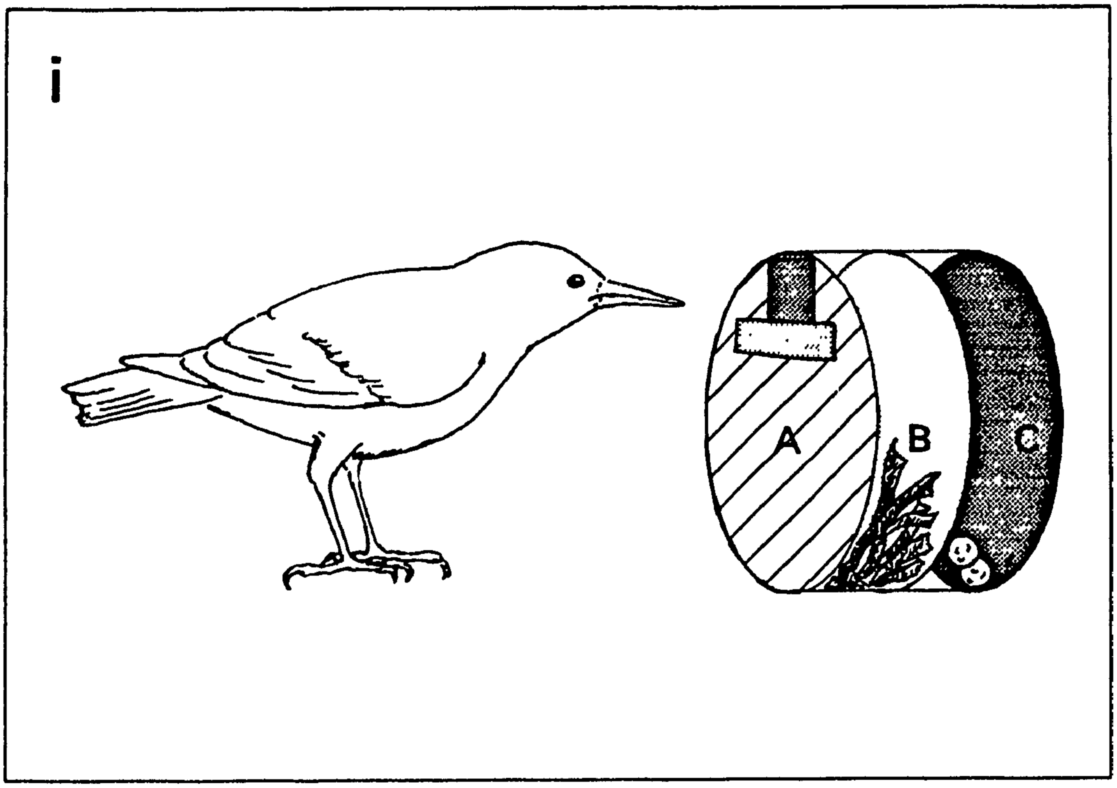
Subjects

Subjects were 18 wild-caught, adult starlings of known sex that had been in captivity for six months prior to the start of the experiment. These birds were randomly selected from a population of 25 starlings housed in groups of five in large (107 x 62 x 92 cm) holding cages. One additional bird, a female with whom the subjects had no previous contact, served as a foraging partner to each subject in the testing sessions. When not being used in an experiment, all birds were maintained on an *ad libitum* diet of insectivorous bird food and moistened mynah pellets ("8-in-1 Tasty Dinner with Fruit"). Water was always available and lighting was set on a 12 h day/night cycle.

Experimental Task

The experimental patches were horizontal, open-ended cardboard cylinders 9 cm in diameter and 6.5 cm deep (Fig. 1.1.i). Each patch contained two compartments: an "information" and a "food" compartment, arranged in such a way that the information compartment was always accessed before the food compartment. Exploiting the patch consisted of accessing both compartments. To "open" the information compartment, a bird

Figure 1.1.i. The experimental foraging task: A) lid with seal; B) outer "information" compartment with tissue paper; C) inner "food" compartment with pellets. (ii) Top view of the experimental arena showing the 18 patches, three of which are open: D) support frame; E) patches.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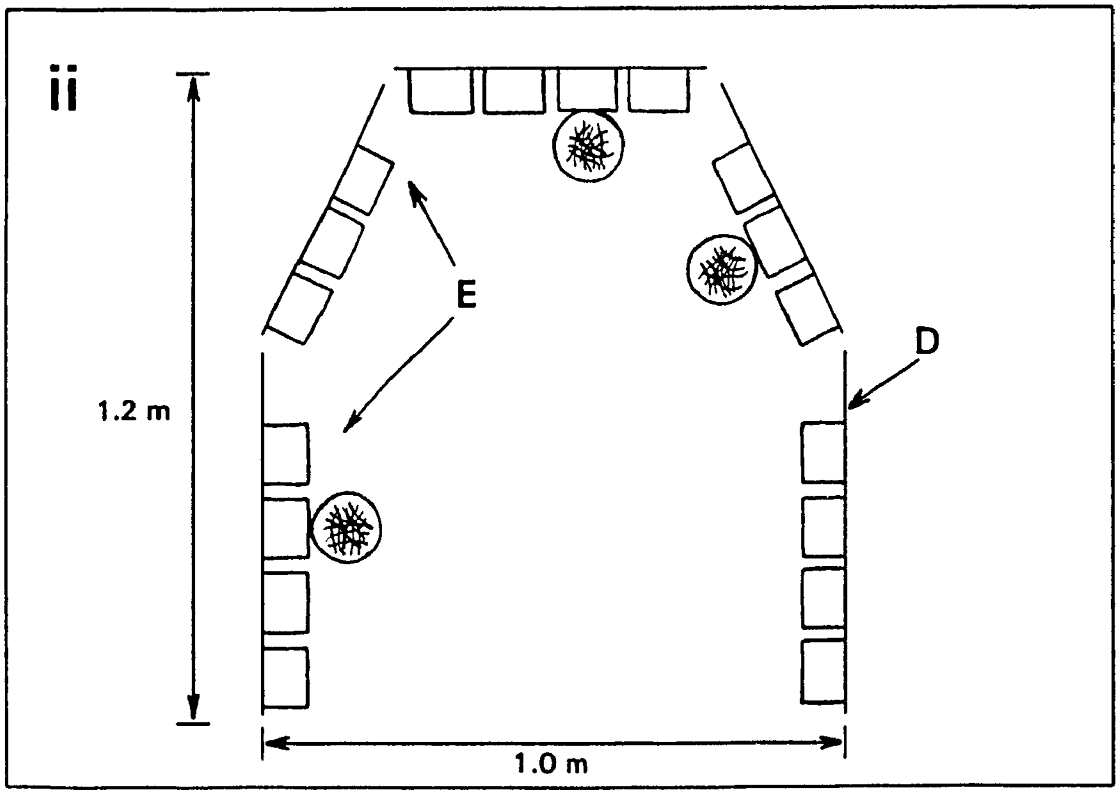
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had to break a paper seal which usually required a single peck. A lid covering the face of the cylinder would then fall open, revealing coloured tissue paper on the inside of the lid and within the information compartment. At this point, the bird could either "check" the food compartment of the patch by piercing through an inner barrier of heavy paper with its beak, or ignore the food compartment and move on to the next patch.

Training I: Learning to Use Patches and Colour Cues

The 18 subjects were randomly assigned to one of three treatments, with the constraint that each group was composed of four males and two females. There were two treatment groups in which subjects were trained to recognize and respond to specific colour cues. In one of these groups, birds learned that black tissue paper always predicted the presence of food and that yellow always predicted its absence; I called this the black "recognizer" group. In the yellow "recognizer" group, the opposite association was learned. In a third group, birds learned that black and yellow did not provide any information on the presence or absence of food; I called this the control group.

Starlings were first trained individually in small cages (62 x 62 x 62 cm) to exploit single patches. This was accomplished through a programme of "shaping" whereby successive approximations of the foraging task were presented to the subjects. The birds readily learned the task, usually becoming proficient within ten presentations. At this stage, shredded tissue paper was added to the information compartment. For recognizer birds, patches with the rewarded colour always contained two mynah pellets, whereas patches with the non-rewarded colour contained none. For the control birds, each colour was associated with food 50% of the time. All birds received ten presentations of single patches (five of each colour), after which patches were presented in pairs. Birds were only allowed to access the food compartment of one patch before both patches were removed. Thus, for recognizer birds, if the colour cue in the first patch indicated the absence of food, the subject had to halt its exploitation of that patch and open the other one. If the second patch also contained an unrewarded colour, it too had to be ignored rather than exploited. If it was exploited, both patches were removed and no further presentations were made for five minutes. If the bird (correctly) ignored the empty food compartment, another presentation followed within 30 s. Recognizer birds were required to meet a criterion of ten successive decisions to ignore the food compartment following the discovery of unrewarded colours. It took the two recognizer groups an average of 59.2 ± 5.2 (N=12) presentations over a two to three day period to meet this criterion. Control birds were not required to meet a criterion, but were given two days of presentations with paired patches with food present 50% of the time in order to keep the amount of training equivalent. Two birds of the same treatment group were trained at the same time in adjacent cages.

Training II: Learning to Use the Foraging Arena with a Partner

The second phase of training was designed to accustom the birds both to the experimental arena and to foraging in pairs. Pair foraging took place in an indoor aviary (2.4 x 2.4 x 2.7 m). Eighteen experimental patches were attached with Velcro^{tm} to vertical wooden supports (90 x 17 cm) and arranged on the floor in a "U"-shaped arena (Fig. 1.1.ii). This arrangement meant that whenever a patch was opened, the colour in its information compartment would be visible from any point within the arena. Birds of the same treatment group were trained in the arena in pairs for five training trials. The pair to be trained was transferred to the aviary the day before arena training began. The five training sessions took place over three days: one session on the first day and two sessions on each of the following two days, starting at 13:00 h. I prepared patches outside of the aviary; birds remained on a perch while I attached these patches onto the sides of the arena.

For arena training, food was distributed in a clumped fashion; only two of the 18 patches contained food (six pellets each). The positioning of the two food patches was random, subject to the requirements that they were never adjacent to each other and they were never in the same position from one training trial to the next. The food was distributed non-randomly with respect to colour cue; for recognizer birds, two patches with the rewarded colour cue contained food; for the control birds, one black patch and one yellow patch each contained food. This meant that for pairs of birds from all three treatments, food was equally clumped, thus the tendency to scrounge was promoted equally.

During all stages of training, subjects were deprived of food from the time the lights came on at 09:00 h until the start of daily training sessions. From 18:00 h until lights went out at 21:00 h, each bird received 10 g of regular food mixture in a small dish. At the end of the training period, the birds weighed approximately 80-85% of their initial free-feeding body weight.

Testing

Individual birds from each treatment were tested in the arena while paired with the same partner bird. The partner's function was to provide a subject with two types of public information: colour cues and behavioural cues. In order to measure the subjects' payoffs when scrounging, it was necessary to use a partner bird that would allow scrounging from the experimental patches. Preliminary tests indicated that a small female (LPW) was unlikely to prevent subjects from scrounging at the patches she discovered. Like the control subjects, LPW was trained to respond to both colours indiscriminately, thus she checked the food compartments of patches regardless of which colour cues were present. In addition, LPW had initially been trained on a uniform distribution where half of the patches contained food, thus reducing the likelihood of her attempting to scrounge from subjects (sensu Benkman 1988). To allow me to distinguish between the two birds on the videotapes, the partner bird had a small dot of white paint on the top of her head. A test started when the first bird of the pair landed in the arena and lasted until all 18 patches had been exploited.

Recognizer and control subjects were tested with the same partner bird once in each of three experimental environments at 1.5 h intervals in the order: 1) "informing", 2) "uninforming", and 3) "misinforming". In the informing environment, the concealed colour cues were in accord with a recognizer bird's past training experience, and thus provided recognizers with correct information concerning the presence or absence of food within a patch. In the uninforming environment, colour cues were absent, thus there was no additional information for recognizer birds concerning the quality of a patch. Finally, in the misinforming environment, the colour cues were in conflict with a recognizer bird's past training experience, and thus recognizer birds had incorrect information concerning the quality of a patch. Colour cues were meaningless to control birds in all three environments. In each environment, food distribution was identical; nine patches contained food (two pellets each) and nine were empty. Positioning of patches was random; however, there were never more than two patches of the same colour or food type in a row.

Data Collection

From colour videotapes of each test session, I recorded all patch exploitations by both the subject and partner bird, and noted the colour cue and the amount of food obtained at each of these events. I used four different measures of individual responses to public information. The first of these was "joining efficiency", the proportion of total patches joined that contained food, a joining event being defined as the subject arriving at a patch either while it was being exploited by the partner or within 1 s of the partner's departure from that patch. Secondly, for each food patch joined, I recorded "joining latency", which was the time between the partner first starting to check a patch and the subject's arrival at that patch. The third measure was the amount of food a subject obtained from joining the partner at a food patch. A subject received a score of 0 if it arrived after the partner had eaten both food pellets; 1 if it ate one pellet; and 2 if it ate both food pellets. Finally, I also recorded the proportion of food and empty patches at which joining was avoided. "Avoiding" occurred when a subject either approached the partner as it exploited a patch, but interrupted its approach before joining; or when the subject watched the partner, but did not approach. A subject was only considered to be watching the partner if it paused for at least 1 s and turned its head towards the partner. In order to estimate the mean temporal cost of joining at an empty patch, I recorded the time it took for a bird to check the food compartment of a patch, from the first piercing of the inner barrier to departure. This was measured three times for each of the subjects and the partner bird.

I predicted that if recognizer birds responded selectively to public information, then they should do better in the informing environment than in the uninforming environment, and better in the uninforming environment than in the misinforming environment. Thus, in the informing environment, I expected recognizer birds to: 1) have a higher mean joining efficiency; 2) have a lower mean joining latency; 3) obtain a greater share of the food at joined patches; and 4) avoid a higher percentage of empty patches than in either of the other two environments. The control birds, on the other hand, were expected to have intermediate scores in all three environments.

Unless otherwise noted, data were analyzed with SYSTAT (Wilkinson 1990), using two- and three-way repeated measures analyses of variance (ANOVAR) to compare the performance between recognizer and control groups among informing, uninforming, and misinforming environments, and with one-way ANOVARs to compare performance within each of the two groups among the three environments. Where necessary, appropriate transformations were carried out on the data before analyses. All values reported are means (± SE).

RESULTS

In all comparisons, data for black and yellow recognizer groups were pooled and presented as the recognizer group because there were no significant differences between these two treatments in any of the three environments. In virtually all trials, the subject and partner birds landed within 1 to 2 s of each other, and remained in the foraging arena until all patches had been exploited. Mean trial duration was 138.6 ± 14.7 s (N=54).

The partner bird exploited an equivalent number of patches in the presence of recognizer and control birds in each of the three test environments, thus providing subjects with a comparable number of opportunities to respond to public information (Table 1.1). Some of these opportunities were missed by both recognizers and controls due to the

Table 1.1: The mean (± SE) number of opportunities for public information use (patches exploited by the partner) in each of the test environments, as well as the significance levels of comparisons (Kolmogorov-Smirnov tests) among environments and between recognizer and control birds.

	Informing	Uninforming	Misinforming	Environment Comparison
Recognizers	9.3(0.6)	10.0(1.0)	9.4(0.5)	NS
Controls	9.7(1.1)	7.7(0.7)	8.2(1.1)	NS
Group Comparison	NS	NS	NS	

subjects' being occupied with their own patch exploitation activities; however, when subjects were paying attention to the partner's exploiting activities, they responded either by joining it or by avoiding it (Table 1.2). Because these three types of responses were not independent, the data were first analyzed with a three-way ANOVAR, comparing the responses of the two groups over the three test environments. A significant three-way interaction between group, test environment, and response type (square-root transformed data, F=3.730, df=4,64, p=0.009) suggested that the manner in which birds responded to public information varied depending on both the environment and the ability to recognize environmental cues. Subsequent two-way ANOVARs were run for each type of response to public information. There were no significant differences in the number of missed opportunities either between the two groups or over the three environments, indicating that birds in both groups still had a comparable number of opportunities to respond more directly to public information (Table 1.2). I will consider these two more direct responses to public information below.

Joining

When a subject joined the partner, it displaced her from the patch either physically or by vocalizing as it approached. Not all birds joined the partner bird in all three environments; in fact, one of the 12 recognizer birds and two of the six control birds never joined. However, the mean number of joins per trial in Table 1.2 include the data of these non-joining individuals. The two groups did not differ in the degree to which they joined the partner bird (two-way ANOVAR, F=1.007, df=1,16, p=0.331); but the joining tendency appeared to be affected more in the recognizer group than in the control group, (group x test interaction; F=3.138, df=2,32, p=0.057). Recognizer birds showed

Table 1.2: The breakdown of responses to public information into the mean (± SE) number of missed, joined, and avoided opportunities for each of the test environments.

	Informing	Uninforming	Misinforming
Missed			
Recognizers	5.5(0.8)	6.3(0.8)	5.5(0.5)
Controls	7.8(2.0)	5.7(1.4)	5.0(1.9)
Joined			
Recognizers	1.3(0.4)	2.9(0.8)	2.7(0.5)
Controls	1.3(0.6)	1.2(0.7)	2.2(1.1)
Avoided			
Recognizers	2.4(0.3)	0.6(0.2)	1.3(0.3)
Controls	1.0(0.4)	0.8(0.4)	0.8(0.3)

a significant change in the mean number of joining events over the three environments (one-way ANOVAR, F=5.325, df=2,22, p=0.013, Table 1.2). The change in joining tendency over the three environments exhibited by the control birds, however, was not significant (F=0.818, df=2,10, p=0.469, Table 1.2).

The mean proportion of total patches joined that contained food represents the degree to which subjects responded correctly to public information, and this is presented in Figure 1.2. Due to missing values and insufficient variation, data in each group were analyzed with a Friedman two-way ANOVA, the non-parametric equivalent of ANOVAR (Wilkinson 1990). As predicted, recognizers experienced a reduction in the proportion of joins that were correct over the three environments (Friedman $\chi^2 = 10.889$, df=2, p=0.004, Fig. 1.2). Controls, on the other hand, experienced no significant change in the proportion of joins that were correct over the three environments (Friedman $\chi^2 = 1.750$, df=2, p=0.417, Fig. 1.2). All the patches at which recognizer birds joined contained food in the informing environment, and this was a significantly higher proportion of correct responses than was achieved by control birds in the same environment (Mann-Whitney U test: U=22.5, df=1, p=0.010, Fig. 1.2).

Joining latencies were a measure of how quickly subjects were able to recognize and respond to public information (Fig. 1.3). As predicted, a two-way ANOVAR found a significant interaction between group and test environment (log-transformed data, F=7.0, df=2,14, p<0.001). This was a direct result of recognizer birds showing a significant change in their joining latencies over the three test environments (one-way ANOVAR, F=11.521, df=2,10, p=0.003), an effect that was absent in control birds (F=0.949, df=2,4, p=0.460, Fig. 1.3). The ability to use the colour cues in the informing

Figure 1.2. Mean (+SE) proportion of the total number of patches joined that contained food, for recognizer and control birds in each of the three test environments. Filled bars: informing; hatched bars: uninforming; open bars: misinforming. Sample sizes are given above each bar; numbers differ due to some individuals joining in some environments, but not in others.

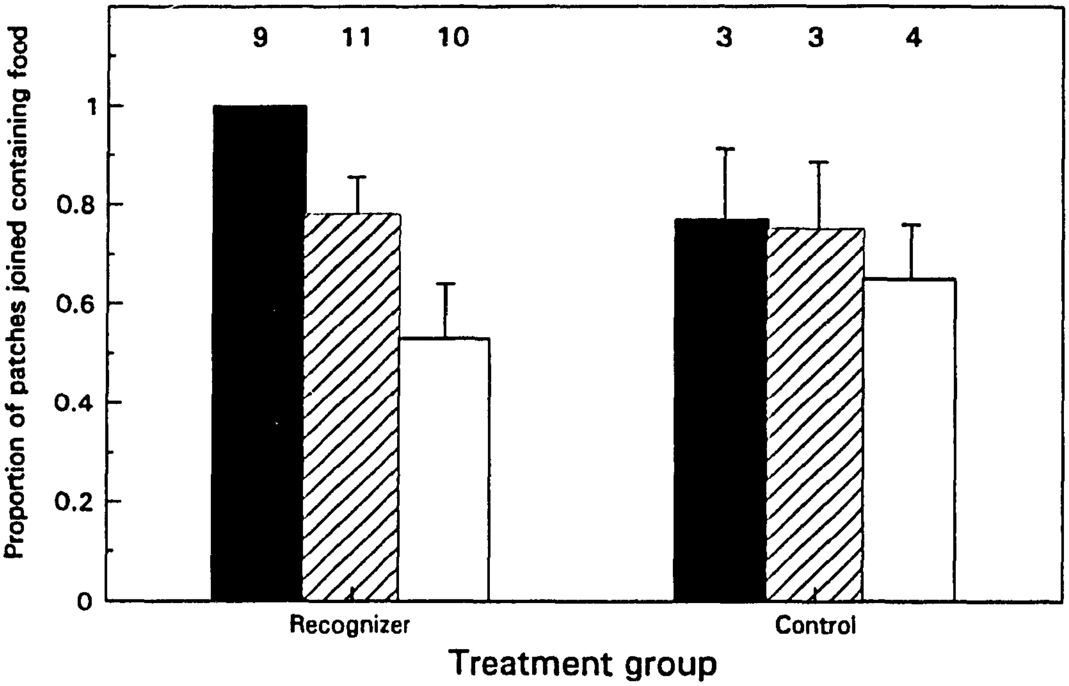
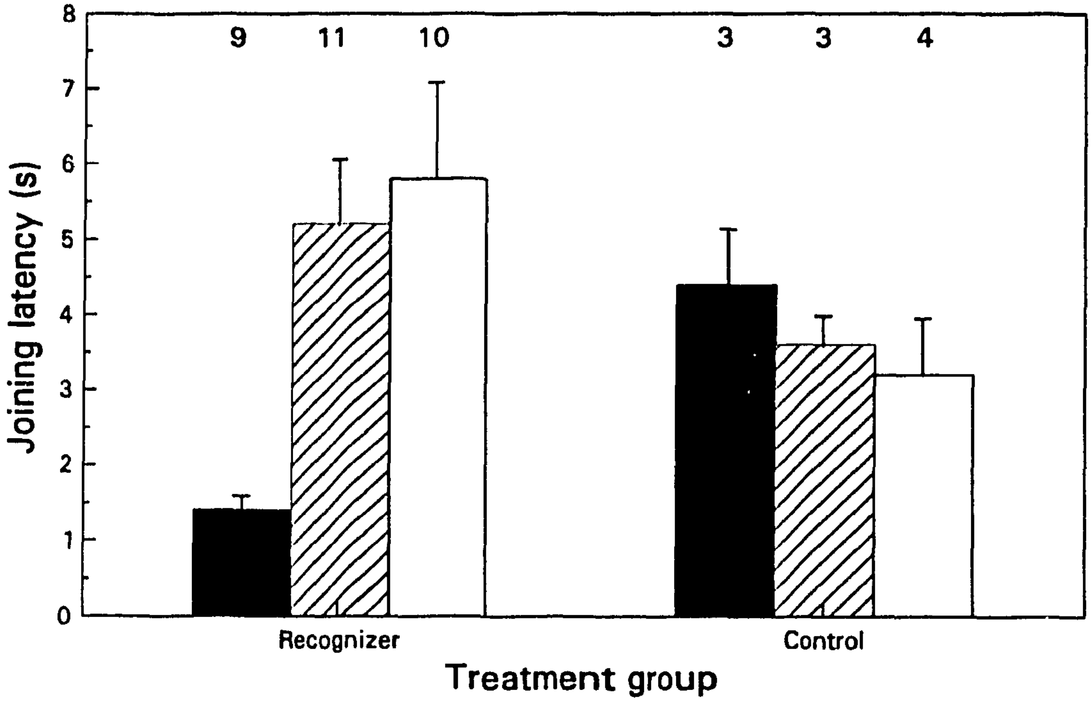

9
11
10
3
3
4
Proportion of patches joined containing food
1
0.8
0.6
0.4
0.2
0
Recognizer
Control
Treatment group

Figure 1.3. Mean (+SE) latency for recognizer and control birds to join the partner after it started to check a patch in each of the three test environments. Filled bars: informing; hatched bars: uninforming; open bars: misinforming. Sample sizes are given above each bar; numbers differ due to some individuals joining in some environments, but not in others.

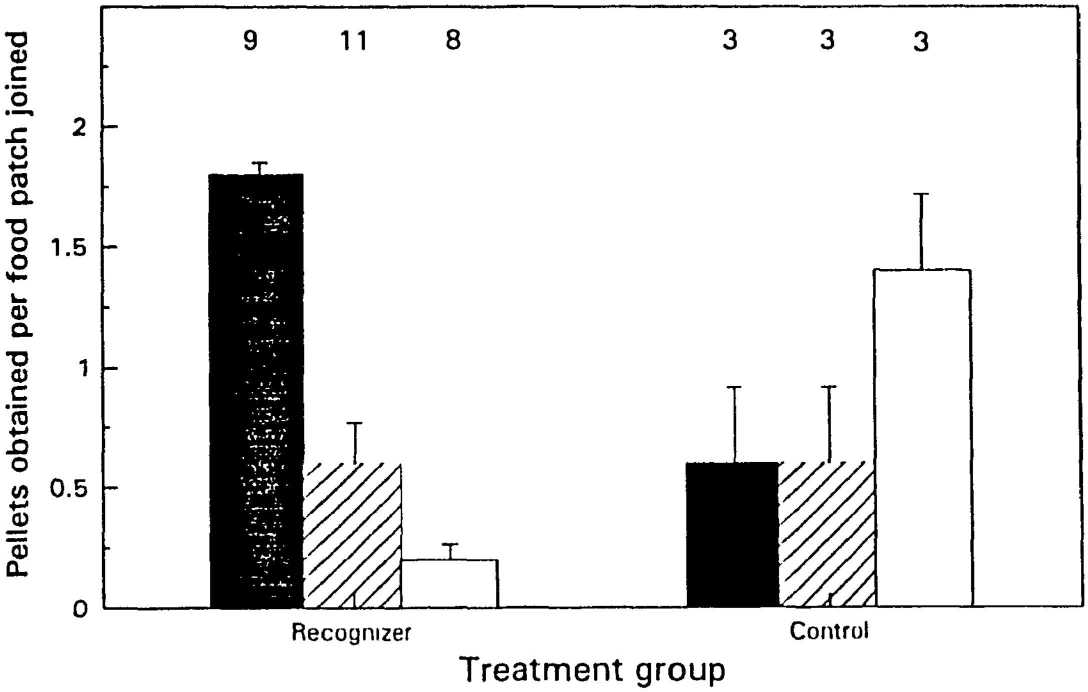


9
11
10
3
3
4
8
7
6
5
4
3
2
1
0
Joining latency (s)
Recognizer
Control
Treatment group

environment reduced the joining latencies of recognizer birds and hence allowed them to join at the partner's patch more quickly than control birds (log-transformed data, t=-5.690, df=13, P<0.001, Fig. 1.3). However, the mean joining latencies of recognizers were significantly higher in both the uninforming and misinforming environments than in the informing environment (contrasts subsequent to one-way ANOVAR, F=22.461, df=1, p=0.005; F=22.552, df=1, p=0.005, respectively, Boneferroni-adjusted level of significance set at p=0.02). In the uninforming environment, recognizer birds would have had to rely exclusively on the relatively delayed feeding behaviour of the partner bird as their only source of public information; thus their arrival was also delayed. In the misinforming environment, the conflicting information between the colour cue and feeding behaviour of the partner bird may have acted to reduce the speed at which a recognizer approached a patch, relative to that in the informing environment.

The mean number of pellets that recognizer birds obtained at each food patch joined was a reflection of the change in joining latencies over the three environments. As predicted, a two-way ANOVAR showed a significant interaction between group and test environment (square-root transformed data, F=16.029, df=2,14, p<0.001), resulting from the highly significant change in the number of pellets that recognizers scrounged from correct patches over the three environments (F=48.059, df=2,12, P<0.001, Fig. 1.4). Unlike recognizers, the three control birds that scrounged from food patches did not exhibit a significant change in the mean number of pellets obtained over the three environments (F=1.3, df=2,4, p=0.4). Due to their short joining latencies in the informing environment, recognizers were able to obtain significantly more pellets at each correct joining event in this environment than were control birds (t=3.912, df=10, p=0.003, Fig.

Figure 1.4. Mean (+SE) number of pellets obtained per food patch joined by recognizer and control birds in each of the three test environments. Filled bars:informing; hatched bars: uninforming; open bars: misinforming. Sample sizes are given above each bar; numbers differ due to some individuals joining food patches in some environments, but not in others.


Pellets obtained per food patch joined
0
0.5
1
1.5
2
9
11
8
3
3
3
Recognizer
Control
Treatment group

1.4).

Avoiding

In addition to joining the partner bird, subjects could also respond to the public information it provided by avoiding the patch the partner was exploiting. There were two types of avoiding behaviour: a subject either approached the partner as it exploited a patch, but interrupted its approach before joining; or the subject watched the partner, but did not approach. The latter type comprised 39% of the total avoids made by recognizer birds; and 32% of the total avoids made by control birds.

Subjects rarely showed either type of avoidance behaviour when colour cue information was lacking, as was indicated by the low mean number of avoids per trial shown both by recognizer birds in the uninforming environment, and by control birds in all three environments (Table 1.2). This change in avoidance behaviour according to the availability of colour cues produced the significant interaction between group and test environment (two-way ANOVAR on square-root transformed data: F=6.849, df=2,32, p=0.003).

When birds avoided the partner, they could avoid it as it exploited food patches (incorrect response) or as it exploited empty patches (correct response). Because of missing values, my analysis of correct avoidance behaviour is limited to comparing the behaviour of recognizer birds in the two environments in which colour cue information was available: the informing and misinforming environments. In those individuals that did avoid, a significantly higher mean proportion of their total avoids was from empty patches (correct responses) in the informing environment (0.9 ± 0.1, N=11) than in the misinforming environment (0.2 ± 0.1, N=8, Wilcoxon paired-sample test, used due to insufficient variation: Z=-2.64, N=8, p=0.008). The recognizers, therefore, were actively avoiding joining at those patches containing the colour which they associated with a lack of food. In the informing environment, the advantage of this decision was considerable given that the temporal cost of checking patches was 6.4 ± 1.1 s (N=19). Since recognizers avoided joining 2.4 times on average in the informing environment (Table 1.2), this meant a savings in search time of over 12 s, more than 10% of the mean trial time.

Foraging Intake

Table 1.3 presents the mean total intake per trial of recognizer and control birds in each of the three test environments. An individual's total intake consisted of the number of pellets obtained from its own patch exploitations ("exploiting intake") plus the number of pellets obtained from joining the partner ("joining intake", Table 1.4). A highly significant interaction between group and test environment (two-way ANOVAR on square-root transformed data: F=78.904, df=2,32, p<0.001) illustrates how the intake of recognizer birds depended on the cues available in the foraging environment. Overall, recognizers experienced a highly significant change in their mean total intake per trial over the three tests (one-way ANOVAR: F=173.274, df=2,22, p<0.001), an effect which was absent in control birds.

The ability to use colour cue information correctly gave recognizer birds a clear foraging advantage in the informing environment. Recognizers obtained over twice as many pellets per trial in the informing environment as in the uninforming environment (F=90.020, df=1, P<0.001); and almost twice as many pellets as control birds in the informing environment (t=4.083, df=16, P<0.001, Table 1.3). Using colour cue information incorrectly, however, was costly for recognizer birds; they obtained

Table 1.3: The mean (± SE) total number of pellets obtained per trial by recognizer and control birds in each test environment.

	Informing	Uninforming	Misinforming
Recognizers	12.4(0.6)	5.4(0.6)	0.8(0.3)
Controls	7.3(1.3)	9.8(1.1)	9.3(1.3)

Table 1.4: The mean (± SE) number of pellets obtained from patches exploited and joined and the percent of total pellets contributed by joining for recognizer and control birds in each test environment.

	Informing	Uninforming	Misinforming
Exploited			
Recognizers	10.2(0.8)	3.9(0.7)	0.3(0.2)
Controls	6.7(1.0)	9.0(1.1)	7.8(0.6)
Joined			
Recognizers	2.3(0.7)	1.5(0.5)	0.4(0.2)
Controls	0.7(0.5)	0.8(0.7)	1.5(0.7)
% Joined			
Recognizers	17.8(5.5)	33.7(11.2)	33.3(14.2)
Controls	6.1(4.5)	7.9(6.0)	12.6(5.7)

significantly fewer pellets per trial in the misinforming environment than in the uninforming environment (F=70.84, df=1, P<0.001, Table 1.3).

The mean number of pellets obtained from patches exploited and joined by recognizer and control birds is presented in Table 1.4. There was a significant interaction between group and test environment for each of exploiting intake (two-way ANOVAR on square-root transformed data: F=37.343, df=2,32, p<0.001) and joining intake (F=6.853, df=2,32, p=0.003). These interactions reflect the significant changes in exploiting intake (one-way ANOVAR, F=75.552, df=2,22, p<0.001) and joining intake (F=7.775, df=2,22, p=0.003) experienced by recognizer birds over the three tests (Table 1.4). When the percent of total intake contributed by joining was compared between recognizers and controls over the three environments, there was a marginally non-significant interaction between group and test environment (F=2.860, df=2,32, p=0.072). This interaction was likely due to the fact that recognizers showed a significant change in the proportion of their total intake contributed by joining when the ability to use colour cue information was constrained in the uninforming and misinforming environments (F=18.996, df=2,22, P<0.001, Table 1.4). In contrast, there was no significant change in the proportion of total intake contributed by joining in the control birds (F=1.994, df=2,10, p=0.187, Table 1.4).

DISCUSSION

My study has demonstrated that the ability to use different forms of information in a group-foraging context can have a significant influence on an individual's foraging decisions and its foraging payoffs. The ability to recognize colour cues allowed recognizer individuals to respond selectively to the patch exploitations of the partner bird; and in an informing environment, these selective foraging decisions were clearly profitable. A higher proportion of the patches joined by recognizer birds contained food than did those joined by control birds, and since recognizers could recognize and respond more quickly to successful public information than could control birds, they were able to obtain more food with each correct joining event. By also recognizing when the partner bird was exploiting empty patches, recognizer individuals were able to avoid joining and consequently saved a considerable amount of foraging time. These findings lend solid experimental support to suggestions made in previous field studies that group foraging animals may be capable of using a variety of different types of public foraging information to make profitable foraging decisions (Rabenold & Christensen 1979; Barnard & Stephens 1981; Greene 1987), and in addition, they show how the information available to an individual can influence its ability to compete effectively for resources within a foraging group.

Joining

The enhanced payoffs enjoyed by early joiners have important implications for information use in producer-scrounger (finder/joiner) systems (Barnard & Sibly 1981; Giraldeau et al. 1990; Vickery et al. 1991). Previous studies have assumed or demonstrated either that producer and scrounger individuals share discovered food equally (e.g. Clark & Mangel 1984) or that a larger share of a discovery is obtained by the producer in the form of a "producer's advantage" (Ward & Enders 1985; Caraco 1987; Giraldeau et al. 1990; Vickery et al. 1991). However, my findings suggest that a producer's advantage may only occur when informational cues indicating the success of the producer to a potential scrounger are reduced or absent. When such cues are available, a "scrounger's advantage" could also be possible. In fact, it might be predicted that if such a disproportionate share of the patch were regularly obtained by early joiners, the frequency of scrounging behaviour observed in a population would be expected to increase.

Dominant individuals in particular might be most likely to become proficient at learning to recognize cues related to the profitable discoveries of others, especially in environments with a clumped food dispersion where dominance confers a foraging advantage (e.g. Feare & Inglis 1979, Theimer 1987). This, in turn, could lead them to begin specializing at joining (Baker et al. 1981; Rohwer & Ewald 1981), especially if there are costs to using both personal and public information concurrently (Vickery et al. 1991). The advantages of learning to recognize foraging cues for dominant individuals should not rule out the advantages for subordinates also learning to do so however. The ability to use cues produced by their own foraging activities to recognize profitable and unprofitable sites, and to use cues produced by the activities of others to recognize and depart from unprofitable feeding sites more quickly (Benkman 1988, Templeton, Chap. 3) should still provide sufficient foraging advantages for the acquisition of such information to be worthwhile.

Avoiding

The ability to respond selectively and profitably to public information meant not only that the recognizer starlings were able to join their partner at a higher proportion of patches containing food than were control birds, but that they also were able to avoid joining the partner at empty patches. This is the first clear evidence that animals may be just as likely to use public information about unsuccessful foraging when directing their foraging decisions, rather than simply not noticing it. This finding contrasts with two of the first experimental studies which examined information use in groups. Krebs et al. (1972) and Krebs (1973a) found that great tits (*Parus major*), black-capped chickadees (*P. atricapillus*) and chestnut-backed chickadees (*P. rufescens*) were just as likely to join an unsuccessful bird as they were to join a successful one, perhaps because the birds had not yet learned how to discriminate between successful and unsuccessful foraging on the novel tasks or because the time wasted on such errors was low. Until recently, the only indication that animals may be capable of using public information about unsuccessful foraging has been Benkman's (1988) intriguing, but nevertheless indirect evidence that red crossbills (*Loxia curvirostra*) could be recognizing a lack of foraging success in others and using this information to avoid poor patches.

By recognizing when the partner was at an empty patch and directing their foraging efforts elsewhere, recognizer starlings were able to avoid wasting valuable foraging time. In natural group-foraging situations, where there usually are more than two individuals present, the advantage of recognizing a lack of foraging success should be even greater. The time saved could be spent not only in an individual's own search for food, but in monitoring the potentially successful discoveries of the rest of the group members. The advantage of recognizing unsuccessful behaviour would be most marked, however, in environments where food patches of the same type and quality are found together in the same locations, for example, pine cones on the same tree. Here, recognizing unsuccessful information would allow a forager both to avoid exploiting similar patch types and to depart from such unprofitable areas more quickly (Benkman 1988).

Foraging Intake and The Value of Information

The foraging intake obtained by recognizer and control starlings provides us with a means of evaluating the consequences of different types of responses to personal and public information. Although the control birds were trained on an equivalent proportion of empty and food patches as recognizer birds, they had no further knowledge of the quality of different patch types. The only way control birds could maximize their average payoffs, therefore, was by making the same decision with each patch type, that is, by exploiting every patch they opened. In contrast, recognizer birds were able to recognize patch quality perfectly, at least in the informing environment. Hence, by responding selectively to the information produced by their own and the partner bird's foraging activities, recognizer starlings were able to enjoy an overall mean foraging intake in the informing environment that was almost double that of control starlings (Table 1.3). This difference in average pay-off between foragers with perfect recognition and foragers lacking such prior knowledge is referred to as the "value of recognition" (Gould 1974; Stephens & Krebs 1986).

Knowing how much a given type of information is worth to a forager can give us an indication of how willing that forager should be to pay the costs of acquiring such information, and hence, the likelihood that it will be used in the future. Of course, the foraging payoffs enjoyed by my recognizer birds in the informing environment do not include the costs that would normally be involved in the learning of foraging cues (one of the "costs of recognition"; Stephens & Krebs 1986). Because I trained these subjects specifically to recognize the colour cues, they "paid" this cost before the exploitation of the patches rather than during. Under natural foraging conditions, however, the cost of such information acquisition should be a function of environmental conditions. As the number of potential cues in an environment increased, for example, so would the memory costs of learning these cues (e.g. Draulins 1988). In such a situation, one might expect that individuals would begin to specialize on a limited selection of cues, perhaps even differing from one another in the cues that they learned as a consequence of frequency-dependent learning (Giraldeau 1984).

How an individual values both personal and public sources of information should also vary according to environmental conditions; and this will likely be reflected in the degree to which each source of information is used. For instance, the highest incidence of joining was shown by recognizer starlings in the uninforming and misinforming environments (Table 1.2). In the former environment, the sudden decline in the ability to use personal information due to the removal of the coloured tissue paper, and the concomitant decline in personal exploiting intake (Table 1.4) appeared to favour joining, despite the absence of colour cues. Similarly, in the misinforming environment, the direct conflict between the recognizer birds' knowledge of colour cues and the incorrect colour information in the patches caused a further drop in their exploiting intake (Table 1.4) and was again associated with a higher level of joining than in the informing environment (Table 1.2). These changes in joining tendency could not be explained simply by learning since control birds showed no significant changes in joining behaviour over the three test environments.

In the past, the study of information acquisition and decision-making has focused almost exclusively on solitary foragers (reviewed by Stephens and Krebs 1986), and only recently have both theoretical and empirical studies begun to consider common foraging problems such as sampling, patch assessment, and patch departure decisions from a group-foraging perspective (Clark and Mangel 1984, 1986, Valone 1989, Krebs & Inman 1992, Valone and Giraldeau In press, Templeton, Chapters 2, 3 and 4). My study adds to our knowledge of the use of information in foraging groups by showing that in order to understand both how individuals make decisions in foraging groups and what the consequences of their foraging decisions will be, we need to understand the different kinds of information they have available to them.

Chapter 2

Optimal Sampling Behaviour in Solitary and Group-foraging Starlings

It is increasingly acknowledged that the ability of animals to make profitable foraging decisions is constrained by incomplete foraging information (Stephens & Krebs 1986), and this is particularly true for patch departure decisions (Valone & Brown 1989). Rather than perfectly recognizing the quality of a resource patch upon encounter with it (e.g. Charnov 1976), a forager often has to rely on the sampling information it acquires while exploiting a patch in order to estimate the patch quality and thus decide whether to continue exploiting the patch or to depart (Oaten 1977, Green 1980, 1984, McNamara 1982). How foragers should acquire different types of sampling information and use it to make optimal patch departure decisions has been the subject of much theoretical (Oaten 1977, Green 1980, 1984, McNamara & Houston 1980, Iwasa et al. 1981, McNamara 1982, Valone 1991) and empirical (Lima 1984, 1985, Kamil et al. 1988, Valone & Brown 1989, Cuthill et al. 1990, Valone 1991, 1992) research.

Most patch departure research has focused on the decisions of solitary foragers. But for many animals, foraging takes place in groups; so it is worth considering whether an animal will alter its foraging decisions depending upon the information it acquires from observing the activities of conspecifics foraging in the same patch. The use of social foraging information in a patch assessment context has only recently been considered theoretically (Clark & Mangel 1984, 1986, Valone 1989). Like the models of solitary patch estimation, these social patch estimation models assume that individual group members are able to form an estimate of patch quality by combining their prior knowledge of the distribution of resources among patches in the environment with their current patch sampling information (Green 1980, Iwasa et al. 1981, McNamara 1982). In addition to these two forms of "personal" information (Valone 1989), however, social patch assessment models assume that each individual's patch sampling activities can be observed by other group members and used as a third, supplementary source of sampling information, known as "public" information (Valone 1989). Theoretically, a forager that has access to such public information should be able to assess the quality of a resource patch more quickly and more accurately than one relying on personal information alone (Clark & Mangel 1986), thereby preventing the underutilization of resource patches in a foraging group (Valone 1989).

To date there has been only one experimental study of patch estimation in foraging groups. In this study, Valone and Giraldeau (In press) considered which of the above three kinds of information were being used by pairs of foraging budgerigars (*Melopsittacus undulatus*) to estimate the quality of food patches containing hidden seeds. By examining how individual foraging success influenced patch persistence and order of patch departure in uniform and variable environments, Valone and Giraldeau were able to conclude that the birds' foraging decisions were influenced both by their current foraging success within a patch and by the type of environment in which they were foraging. However, they found no evidence for the use of public information, perhaps as a result of a possible incompatibility between obtaining personal and public information simultaneously (Valone & Giraldeau, pers. comm.).

Valone and Giraldeau (In press) tested for evidence of public information use in patches where subjects were assumed to base their estimate of patch quality at least in part on their current seed intake rate. But an alternative method of testing for the use of public information is simply to examine the departure decisions of animals attempting to recognize empty patches. This method has the advantage of avoiding both the problem of controlling the amount of food each individual acquires, and the potentially confounding effects of satiation. If public information is used in such a situation, it would clearly be advantageous; the resulting increase in the rate of patch estimation (Clark & Mangel 1986) would allow foragers to depart more quickly, and thus waste less time sampling unprofitable sites.

In empty patches, sampling information would have to be acquired from a *lack* of foraging success, an ability that has been demonstrated in two experimental studies of patch assessment by solitary foragers (Lima 1984, 1985). In these experiments, Lima allowed free-ranging downy woodpeckers (*Picoides pubescens*, 1984) and captive European starlings (*Sturnus vulgaris*, 1985) to forage singly in patchy environments where the experimental patches were either empty or contained a fixed number of hidden food items randomly distributed among the holes of a patch. The problem for Lima's birds was to determine how many holes to sample unsuccessfully before giving the patch up as empty and to do this in a way which maximized their long-term energy intake rate. Based on the work of Oaten (1977) and Green (1980), Lima developed a simple mathematical model to predict the optimal number of empty holes to sample before departure from a patch, and found that his birds' actual sampling behaviour was in qualitative agreement with this optimum. Thus, unlike Valone and Giraldeau's study, where foragers were using their foraging success to estimate the number of food items remaining in a patch (Valone 1989), Lima's (1984, 1985) birds were using their lack of foraging success to estimate the probability that a patch was empty.

To investigate whether a group forager could make use of another individual's lack of success as a source of public information in the assessment of empty patches, I compared the sampling behaviour of starlings foraging alone and in pairs. This required two main modifications to Lima's (1985) original experimental design. First, I had to create a situation where two birds would consistently sample the same patch at the same time. For this reason, there were only two patches present per trial, to which I could control access. Although Lima's model (1985) makes no explicit assumptions concerning the number of patches available in an environment, Lima did test his model in a multi-patch system, with 25 patches available per trial. Secondly, unlike Lima's patches where the starlings had to peck covers off holes to check them, the holes in my patches were designed in such a way that they provided no visual cue that they had been checked. This was done to ensure that birds would not sample fewer holes when in pairs simply because there would be fewer unchecked holes left to sample. However, Lima's model assumes systematic search where each hole is checked no more than once by an individual; an assumption that must be verified due to the novel hole design used in the current study. In order to ensure that any behavioural differences observed between solitary and paired starlings were related to changes in their sampling behaviour, therefore, it was first necessary for me to show that solitary starlings could assess patch quality in a two-patch system and do so by sampling systematically. Accordingly, the first part of my experiment was devoted to establishing whether the starlings were indeed sampling systematically and whether their patch departure decisions could be predicted by Lima's model. Starlings were given solitary foraging trials on the experimental patches, allowing them to learn the distribution of food and assess the patches. The data collected from these trials were then used to determine what the optimal sampling behaviour should be.

In the second part of my experiment, I tested for the use of public information. I hypothesized that a starling would be able to assess an empty patch more quickly by combining the personal information it obtained from its own unsuccessful sampling efforts, with the public information it obtained from observing the unsuccessful sampling efforts of a conspecific foraging in the same patch. However, because it was possible that a bird might automatically leave a patch earlier if another bird was foraging on the same patch, it was necessary to test subjects when paired with one of two types of partner bird. One partner sampled very few holes and thus provided a low amount of sampling information; the other partner sampled numerous holes and thus provided a high amount of sampling information. I predicted that if my starlings used public information, they would sample fewer holes when with the low information partner than when alone; and even fewer holes when with the high information partner.

GENERAL METHODS

Subjects

Experimental subjects were six wild-caught, experimentally naive, adult starlings (four males and two females) that had been in captivity for one year. These birds were selected from a population of 30 starlings housed in groups of six in large (107 x 62 x 92 cm) holding cages. Two additional birds, both female, were selected to act as partner birds during the testing phase; these two starlings were housed individually in smaller cages (61 x 60 x 62 cm) in visual contact with one another. When not being used in an experiment, all birds were maintained on an ad libitum diet consisting of a mixture of bread, dog food, and turkey starter crumbs, supplemented with cheese, mealworms, and moistened mynah pellets ("8-in-1 Tasty Dinner with Fruit"). During an experiment, subjects were maintained at 85% of their initial free-feeding body weights. Water was always available, and lighting was set on a 12 h day/night cycle.

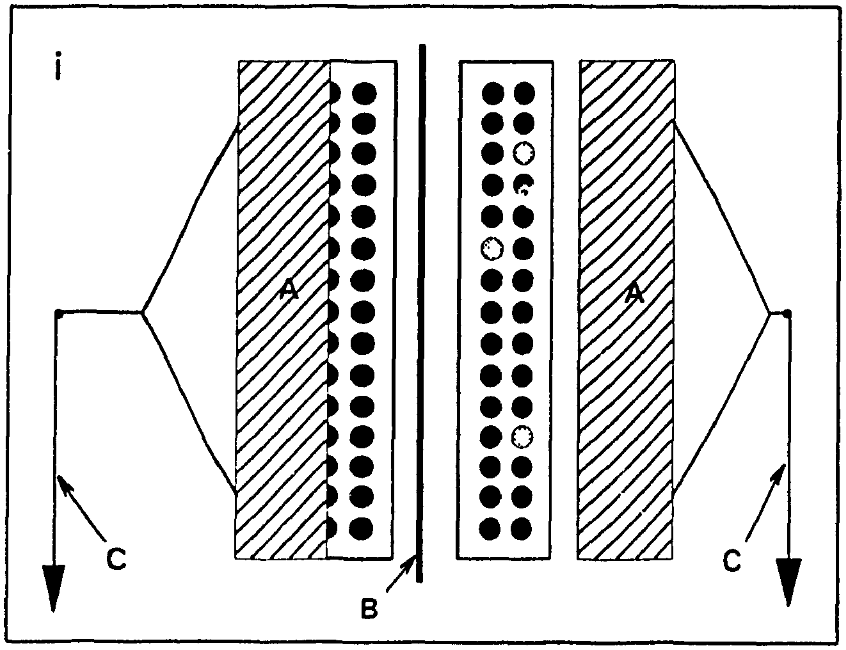
Foraging Environment

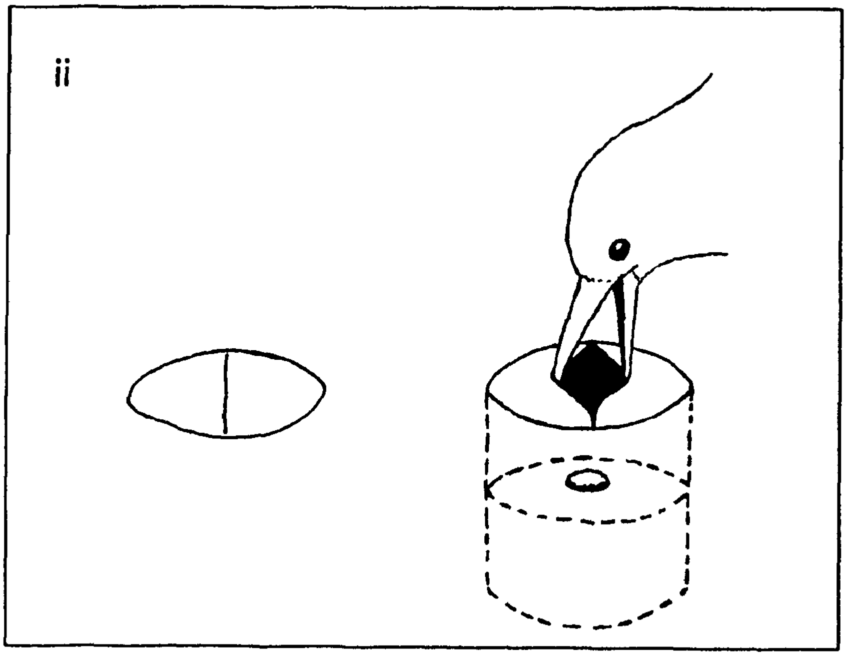
The foraging environment was located in an experimental aviary (2.4 x 2.7 x 3.0 m). Two patches were present per trial (Fig. 2.1.i); these were long, rectangular pieces of foam (133 x 21 x 5 cm), separated by a vertical wooden barrier (84 x 135 cm). Each patch consisted of 30 numbered holes in a 2 x 15 array, with 4 cm separating each of the 15 pairs of holes and 2 cm between each member of a pair (Fig. 2.1.i). Within each hole was a section of cardboard tubing 4 cm in diameter and 2.5 cm deep. Over the top of the tube was stretched a piece of opaque grey latex into which had been cut a 3.5 cm slit. Thus, a starling could only check a hole by probing its beak into the slit and opening its mouth (Fig. 2.1.ii). When the bird removed its beak, the cover returned to its original position, leaving little or no visual cues to indicate it had been checked.

Training

A new subject was released into the experimental arena with the two partner birds and given ad libitum food in a dish for an acclimation period of one day. The partner birds and food were then removed, and after a 15 h food deprivation period, training began. The subject was first provided with a small, eight-hole training patch (30 x 21 x 5 cm) onto which was sprinkled 5 g of the regular food mixture. Once this food had been consumed (usually within 1 h), mynah pellets were suspended in the slits of the rubber hole covers;

Figure 2.1.i. Schematic top view of the two 30-hole experimental patches. A) patch covers; B) vertical barrier; C) pulley system controlling cover removal. (ii) Detail of a starling sampling an experimental hole by probing its beak into a slit in the opaque latex cover.


i
A
A
B
C
C


ii

the pellets would fall into the hole when pecked, prompting the starlings to pry apart the covers to obtain the pellets. When these pellets had been consumed (again within 1 h), the patch was replenished with one pellet hidden in each hole. Once these pellets were consumed, this was repeated twice and then the subject was again food-deprived overnight for 15 h.

On the second day of training the two longer experimental patches, stocked with three pellets each, were placed in the arena on either side of the barrier and covered with a strip of cardboard. One cover was removed and once the bird had obtained the three pellets, the other cover was removed and the bird allowed to forage on the second patch (Fig. 2.1.i). This procedure was repeated, with the second cover being removed earlier and earlier until the bird would remain foraging on the first patch without being disturbed by the sound of the moving cover. This required a mean of 5.7 ± 0.9 trials ($\bar{X}$ ± SE, N=6).

Part I: Sampling behaviour of solitary starlings in a two-patch system

Methods

Procedure

Following training, a subject received a total of 100 trials over a four day period. In any given trial, each patch had a 0.5 probability of being uncovered first and a 0.5 probability of containing food (over the 100 trials, 51.3 ± 0.7% of the patches were empty), with the constraint that a patch could not contain food or be empty more than three trials in a row. When a patch did contain food, only three randomly-selected holes contained one mynah pellet (0.12 ± 0.01 g) each; the same hole could not contain food from one trial to the next.

A trial started as soon as the subject stepped onto the first patch and ended once it had stepped off the second patch, at which point I entered the aviary and removed the patches. I then removed any remaining pellets from the patches and stocked the next set of pre-selected random holes with fresh pellets as necessary. I waited for slightly less than five minutes from the end of the previous trial to return the patches to the aviary. At the sound of a five minute signal from the camera, the patches were uncovered. A mean of 28.3 ± 2.7 trials were run per day for the first three days.

During the last 15 trials on the fourth day, a second, naive starling was released into the aviary 15 min prior to the start of the trials. This was done in preparation for the public information testing phase (Part II of this chapter); the purpose was to allow the subject to get used to another bird being in the arena during the presentation of patches and to prevent the subject from associating the presence of another bird with empty patches (since patches were always empty during testing). The naive bird, which was fed to satiation prior to its introduction to the aviary, tended to sit on top of the barrier during trials and occasionally landed beside the patch on which the subject was foraging.

To maintain each subject's weight at approximately 85 % of its initial free-feeding weight during the experimental period, supplemental food was provided 30 min after the last trial of the day. This food consisted of additional pellets such that the total pellets for the day was 100 (12 g). If the bird's weight had dropped below 85 %, it received an extra 15 g of the regular food mixture; if its weight was above 85 %, it received only an extra 10 g of food mixture. The amount of food provided thus was either 90 % or 73 %, respectively, of a captive starling's average free-feeding intake of 30 g/day (Koops and

Giraldeau, unpublished data). The mean initial free-feeding weight of the subjects was 86.0 ± 2.2 g, and they were tested at a mean of 83.3 ± 1.0 % of this free-feeding weight.

Data Collection and Analyses

Solitary sampling data were collected from videotapes of the 100 trials. Unless otherwise stated, data were collected from only the first patch visited in each trial. These data were considered to be more relevant than second patch data since the birds still had "somewhere to go" after exploiting the first patch, but nowhere to go after the second. Data included the number of holes sampled before departure from both empty and food patches, the number of holes probed more than once ("reprobes") on empty patches, and the number of pellets obtained from food patches. Food patch data included only those patches where one or more pellets were found; data from patches where all pellets were missed were included with empty patch data.

Optimal sampling solutions were determined for each individual using Lima's patch assessment model (Lima 1985), which includes both fixed and individually-measured time parameters. The fixed parameters were: the probability that a patch contained food, in this case, 0.5; and the number of pellets in a food patch, in this case, 3. I obtained estimates of the time parameters for each individual bird, which were: the time to check an empty hole (te), the time to check a full hole (tf), and the travel time (tt). The time to check an empty hole was calculated by dividing the total time spent on an empty patch by the number of holes checked (Lima 1985). The mean for each bird, taken over the last 20 empty patches visited, was used as my estimate of its te. An estimate of tf was obtained for each bird from the mean tf over the last 20 food patches visited, using the following formula with each patch (Lima 1985): $tf=[f-(b-m)te]/m$, where f represents the total time spent on the food patch; b represents the total number of holes checked; m represents the number of pellets found (1, 2, or 3); and te is the estimate obtained above.

The operational definition of the travel time parameter in my study was problematical. In Lima's (1985) study, travel time was measured as the mean travel time between patches, but in his study there were multiple patches, and thus multiple inter-patch travel times available per trial. Because only two patches were available per trial in the present experiment, however, it was unclear what the birds would use as their "travel time": the actual time to the next patch; or the imposed five-minute waiting period between trials; or possibly some combination of the two (e.g. Cuthill et al. 1990). For each bird, therefore, I generated three different optimal sampling predictions from Lima's model using each of inter-patch time, inter-trial time, and the average of the two. Inter-patch travel time was defined by Lima as the time between a starling lifting its head from the last hole checked on the first patch until the beak touched the first hole checked on the second patch. Using this definition, I obtained a mean inter-patch time for each subject from the last 20 videotaped trials, the times being determined to the nearest 0.1 s using a stopwatch. Inter-trial times were not measured specifically for each bird (see procedure above); I therefore used 300 s as a reasonable estimate of the mean inter-trial interval.

The birds' sampling activities on empty and food patches were averaged over the 100 trial period in five blocks of 20 trials each. I assumed that each bird's sampling behaviour had stabilized once frequency distributions of the number of holes it sampled on empty patches were not significantly different from one block of trials to the next, using the Kolmogorov-Smirnov ("K-S") two-sample test (Lima 1985, Wilkinson 1990). A two-way repeated measures analysis of variance (ANOVAR) was used to analyze changes in sampling behaviour on empty and food patches over the five blocks of trials.

Before I could compare the final sampling behaviour on empty patches with the three possible optimal sampling solutions predicted by Lima's model, I first had to confirm that each bird was sampling systematically (probing each hole only once) by the last block of trials. I did this by finding the number of reprobes in a given number of total holes probed on each of 10 empty patches in the last block of trials and comparing the mean reprobes with the expected number of reprobes for both random and systematic sampling. By "random", I mean that a given hole within a patch is equally likely to be probed whether or not it has been probed before (Green 1987). For a forager sampling a patch randomly, I calculated the expected number of reprobes (R) in a given number of total holes probed using the following equation:

$$R=A-[B+1-\frac{(B-1)}{(N-1)}]$$

where A is the total number of holes probed (including the current probe), B is the cumulative number of different holes probed prior to the current probe, and N is the number of holes in a patch (in this case, 30).

Following this, the observed mean number of holes sampled by each bird on empty patches in the last block of trials was then compared with each of the three possible optimal sampling solutions predicted by Lima's model, using paired t-tests. In addition, because the starlings sampled a distribution of holes rather than a single number, I compared the estimated payoff for the observed sampling behaviour with the optimal payoff using a modified version of Lima's model (Green 1990) which takes this variability in sampling behaviour into account. Unless otherwise noted, square-root transformations were carried out on all data before analyses with SYSTAT (Wilkinson 1990). All values are reported as $\bar{X} \pm$ SE.

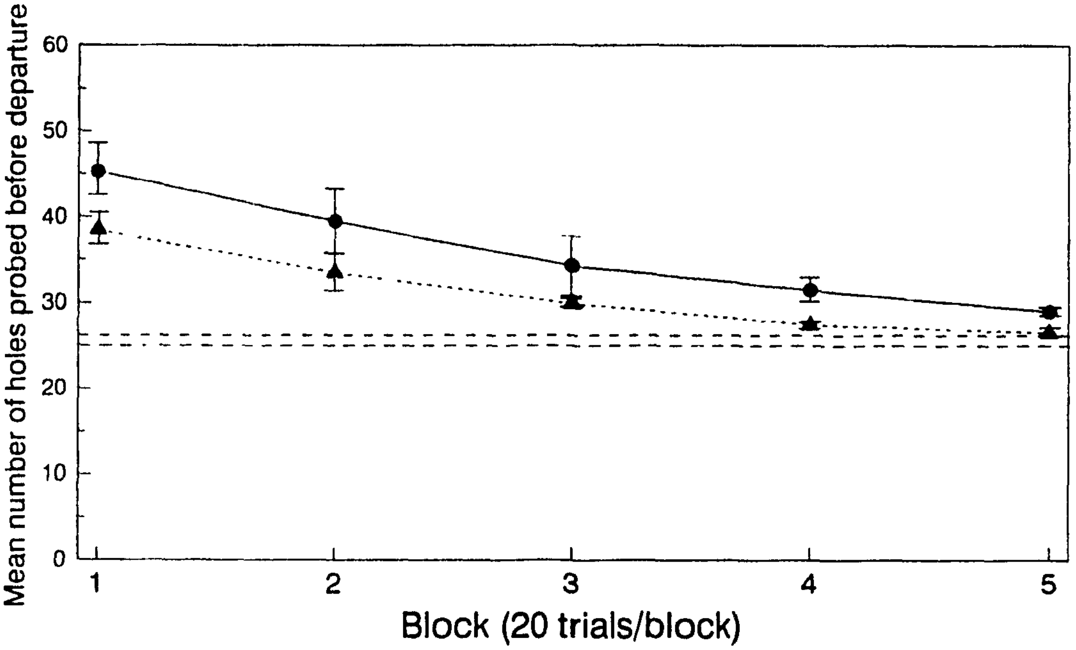
Results

Figure 2.2 shows the mean number of holes sampled before departure from food patches and empty patches in each of five blocks of trials over the 100 trial period. For five of the six subjects, stable sampling behaviour was reached by the last two blocks of trials (K-S tests, $p > 0.05$). The number of holes sampled before departure on both food and empty patches declined significantly over the five blocks (two-way ANOVAR: $F=19.367$, $df=4,40$, $p < 0.001$, Fig. 2.2), suggesting that the subjects were learning the availability and distribution of food and were adjusting their sampling behaviour accordingly. The birds had a tendency to sample more holes on food patches than on empty patches ($F=4.511$, $df=1,10$, $p=0.060$). By the last block of training, significantly fewer holes were sampled on empty patches (26.5 ± 0.4) than on food patches (29.0 ± 0.5); paired t-test, $t=-4.637$, $df=5$, $p=0.006$), indicating that the birds were discriminating between them. Two observations suggested that my starlings did not learn precisely how many prey were in a food patch, however. Once a pellet was discovered, a starling usually checked all the holes of a patch rather than leaving once all three prey had been found. In addition, there were a few occasions where a starling left a food patch after obtaining only one or two pellets (15.6 ± 2.5% of all food patches), though it was rare for food to be missed entirely (0.33 ± 0.20% of all food patches).

Systematic Sampling

For each bird, I determined whether the birds were sampling systematically by recording the mean number of reprobes made in the first 26 probes on each of 10 empty

Figure 2.2. Mean (±SE) number of holes sampled by solitary starlings per trial per block before departure from food (●) and empty (▲) patches in each of five blocks of trials over the 100 trial period. The three horizontal lines represent the mean number of empty holes to sample according to the three optimal sampling solutions predicted by Lima's (1985) model. These were calculated using, from the bottom, the mean inter-patch time; an average of inter-patch and inter-trial times ("averaging"); and mean inter-trial time ("tracking") as the travel time component of the model.



Mean number of holes probed before departure
60
50
40
30
20
10
0
1
2
3
4
5
Block (20 trials/block)

patches in the last block of trials. I chose 26 because this was the mean number of empty holes being probed before departure in the last block of trials. If the birds were sampling systematically, the number of holes reprobed should be zero regardless of the total number of holes sampled. If the birds were randomly sampling holes, however, they would be expected to average 8.1 reprobes in the first 26 probes. The subjects were found to have a mean of 0.17 ± 0.2 reprobes in 26 probes. This was significantly less than expected for random search ($t=18.2$, $df=5$, $p<0.001$), but not significantly different from the zero reprobes expected for systematic search ($t=0.39$, $df=5$, $p>0.5$). Therefore, I concluded that the birds were sampling systematically by the end of the training sessions, and thus the sampling behaviour in the last block of trials could be compared with the optimal sampling solutions predicted using Lima's model.

Observed versus Predicted Sampling

The time parameters required to calculate the optimal sampling solutions were estimated separately for each individual. The mean time to check an empty hole was 0.52 ± 0.01 s and to check a full hole and handle the pellet was 1.91 ± 0.28 s. The inter-patch travel time was 3.06 ± 0.65 s; and as noted above, inter-trial time was 300 s for each bird. Each subject was very consistent in the manner in which it travelled between the first and second patch. Three of the subjects started at the end of a patch closest to the camera, sampled the patch and then walked around the barrier to start at the far end of the second patch. The other three subjects also started at the end of a patch closest to the camera, sampled and then either ran back down the first patch (two birds) or flew over the barrier to start at the end of the second patch closest to the camera.

The three horizontal lines on Figure 2.2 represent mean values of the three possible optimal sampling solutions predicted by Lima's model. These were first calculated separately for each individual using the time-related model parameters te, tf, and the three different "travel times": inter-patch, inter-trial, and the average of inter-patch and inter-trial times. Owing both to the similarity among the individual birds' time parameter scores and to the insensitivity of the model's optimal sampling solution (Lima 1985), all subjects had similar predicted values for each of the three optima. The mean inter-patch sampling solution for the six subjects is shown as the lowest predicted optimum at 15.5 ± 0.5 holes. The other two mean predicted sampling solutions shown are the average and inter-trial optima at 25.0 ± 0.0 and 26.3 ± 0.2 holes, respectively (Fig. 2.2).

The observed sampling behaviour was consistent with only one of the three predicted sampling solutions. The mean number of holes sampled on empty patches in the last block of training (26.5 ± 0.4 holes) was significantly higher than both the mean inter-patch optimum (paired t-test: $t=13.537$, $df=5$, $p<0.001$) and the mean average optimum ($t=3.498$, $df=5$, $p<0.017$). However, there was no significant difference between the observed number of holes sampled and the mean predicted inter-trial optimum ($t=0.480$, $df=5$, $p=0.652$), suggesting that inter-trial time had the strongest influence on the birds' patch departure decisions.

Because each of my starlings exhibited a distribution of the numbers of empty holes sampled, rather than a fixed sampling solution, I used a slightly modified version of Lima's model (Green 1990) to compare the observed payoffs my starlings achieved with the payoffs they could have achieved if only the optimal number of empty holes had been sampled. I did this by first determining the different intake rates that my birds would achieve at each number of holes sampled, then I calculated a weighted average of these rates over the frequency distribution of the numbers of holes they actually sampled (Green 1990). In this way, I estimated the mean foraging rates achieved by my starlings using each of the three different "travel time" parameters and compared these three estimated rates to each of the three maximum intake rates that would be achieved if only the optimal number of holes were sampled. When only inter-patch time was considered in the travel time component, the estimated mean foraging rate was 88.8% of that achieved by a hypothetical optimal forager. However, when the inter-trial and average times were each considered, the estimated foraging rates were, respectively, 99.0% and 99.1% of the intake rates that would be achieved by a perfectly optimal forager. The similarity between these two percentages slightly modifies the conclusion I reached above, and suggests that both inter-trial time and inter-patch time were important factors influencing the starlings' foraging decisions and foraging returns.

In summary, the results from the first part of this experiment suggest that my starlings were indeed able to acquire information from their unsuccessful sampling activities and that they used this personal information in an optimal fashion to assess the quality of the experimental patches. These findings should ensure that any behavioural differences observed between solitary and paired starlings in the following part of my experiment will be related both to changes in their sampling behaviour and to the use of public sampling information.

Part II: Testing for the use of public information

Methods

Following the 100 trials examining solitary sampling behaviour, subjects were paired with partner birds and tested for the use of public sampling information.

Information Partners

Each partner bird was trained to provide different amounts of sampling information when it sampled the empty right-hand (test) patch with the subject. The "low information" partner probed only three well-spaced holes (positions 3, 16, and 25), each of which had a small blue dot on the cover (the dots were meaningless to the subject birds). During training, zero to three of these marked holes contained a pellet. The "high information" partner, on the other hand, was trained to learn that out of the 30 holes in the right-hand patch, only one, randomly chosen hole contained food. Thus, this partner probed many holes during a test trial. The left-hand patch never contained food, thus the partners learned never to visit it.

Testing Procedure

Each subject was given three consecutive trials in each of three test conditions: 1) alone; 2) paired with the low information partner; and 3) paired with the high information partner. The order of these testing conditions was arranged in a Latin square design over subjects. During each test trial, both patches were empty, and the cover of the test patch was always removed first. In each test trial, the subject and partner were required to land within three seconds of one another: if this did not occur, I interrupted the trial and a retest followed immediately. Before each set of three test trials, each subject was given a set of three food trials in the presence of a naive starling. The food distribution in these trials was such that three pellets were present in each patch in the first trial, and then in only one of the patches in the other two trials. The purpose of these food trials was to help the subject maintain a relatively constant hunger level over the testing period and also to prevent the extinction of its sampling behaviour that could result from repeated exposures to empty patches during testing. A total of nine food trials and nine test trials were run on a test day. Within each set of food or test trials, there was a five minute inter-trial interval. Sets of trials were run every 30 min.

Data Collection

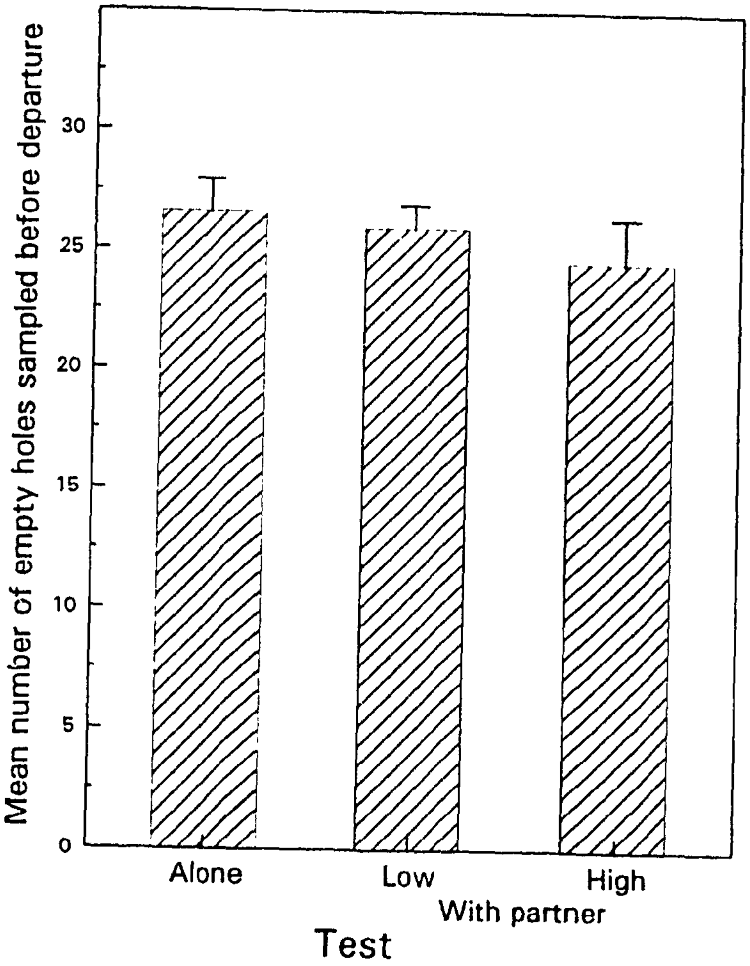
Test trials were videotaped, and the number of empty holes sampled as well as the time spent on the right-hand patch during each trial was recorded for both subject and partner birds. Subject data were summarized as mean scores per test condition and analyzed with a one-way repeated measures analysis of variance (ANOVAR) over the three conditions; high and low information partner data were summarized as mean scores per subject and compared with a paired t-test. Appropriate transformations were carried out before analyses; all data are reported as $\bar{X} \pm$ SE.

Results

In 31 of the 36 (86%) test trials in which subjects were paired with partners, the subject and partner landed within one second of one another. In only two of these test trials did the partner bird not land within the three-second time limit, but retests were successful.

I found no evidence for the use of public information (Fig. 2.3). Subjects sampled a similar number of empty holes before departure when alone as when with the low and high partners (square-root transformed data, $F=0.985$, $df=2,10$, $p=0.407$). In addition, subjects spent a similar amount of time sampling the empty test patch when alone (13.0 ±

Figure 2.3. Mean (+SE) number of empty holes sampled by subjects before departure from the empty test patch under the three test conditions: alone, paired with the low information partner, and paired with the high information partner.


Mean number of empty holes sampled before departure
0
5
10
15
20
25
30
Alone
Low
High
With partner
Test

0.9 s) as when with the low (14.5 ± 1.0 s) and high (13.1 ± 1.4 s) partners (log-transformed data, F=1.060, df=2,10, p=0.382). Subjects had a slightly lower probing rate when with the low (1.9 ± 0.1 probes/s) and high (1.9 ± 0.1 probes/s) partners than when alone (2.1 ± 0.1 probes/s). However, this difference was not significant (log-transformed data, F=2.402, df=2,10, p=0.141).

The lack of public information use was not a consequence of poor partner performance. With each subject, the high partner consistently probed at over twice the rate (1.8 ± 0.1 probes/s) of the low partner (0.8 ± 0.1 probes/s; paired t-test on log-transformed data: t=-11.099, df=5, p<0.001). The high partner also consistently made more probes (17.3 ± 1.9) before departure than did the low partner (5.1 ± 0.8; square-root transformed data, t=-6.672, df=5, p=0.001). In all test trials, both partner birds either left before or, occasionally, at the same time as the subject.

DISCUSSION

This study has clearly shown that solitary starlings were able to use their personal sampling information to assess patch quality and make profitable foraging decisions in an experimental two-patch system. When foraging in pairs however, the starlings made no use of public sampling information and continued to rely on personal information alone to make their patch departure decisions.

Solitary sampling and personal information

Several lines of evidence support the conclusion that the starlings were acquiring information from their own sampling activities. The decline in the number of holes sampled on both food and empty patches over the 100 solitary trials implied that the birds were learning how food was distributed among patches and were adjusting their sampling behaviour in response to it, despite the fact that they did not know precisely how many pellets were in a patch. In addition, the observation that significantly fewer holes were sampled before departure on empty patches than on food patches by the end of the solitary trials indicates that the birds were capable of discriminating between empty and food patches based on their foraging success.

That the birds were using their personal sampling information in an optimal fashion was illustrated by the fact that their sampling behaviour could be accurately predicted by Lima's patch assessment model, at least when the inter-trial interval was included as part of the model's travel time component. Like Lima's (1985) birds, however, the observed sampling behaviour was in qualitative, but not precise quantitative agreement with the predicted behaviour; whereas the model predicts that a single number of holes should always be sampled without success, a distribution of sampled holes was actually observed. Despite this slight deviation from predicted behaviour, the consequences for the birds' foraging payoffs (Green 1990) were negligible; the mean expected intake rate was at least 99% of that which would be achieved by a hypothetical optimal forager. Thus, my starlings were using a sampling strategy which enabled them to forage at close to the predicted optimum intake rate, although exactly how they were able to do this is unclear. Like Lima's birds, my birds appeared to be using a sophisticated sampling rule similar to the type proposed by Green (1984, 1990), that is, "search n holes in each patch; if no prey have been found, leave; otherwise, remain until all holes have been searched". Such a sampling strategy would not necessarily require an ability to count, although it would require an ability to estimate the duration of time intervals, a skill which has recently been demonstrated in starlings (Cuthill et al. 1990, Wenger et al. 1991, Brunner et al. 1992). In this way, as the time a starling spends sampling empty holes increases, its estimate of the probability that the patch is empty should also increase.

The two-patch system used in this experiment raised the question of what would be the best or most reasonable time frame over which to measure intake rate, a common problem in optimal foraging work (Templeton & Lawlor 1981). This issue was particularly relevant to my study because two patches per trial meant that within a daily experimental session there was almost an equal number of inter-patch and inter-trial intervals; whereas in Lima's experiment, there were at least four times as many inter-patch as inter-trial intervals per day. How one incorporates these two different time intervals into the patch assessment model, therefore, will depend at least in part on what the forager itself considers to be part of its foraging time. If, as Lima assumed, the forager becomes satiated during the trial period, the inter-trial interval need not be considered by either the experimenter or the starling as part of its foraging time. Hence, it was probably reasonable for Lima to include only the mean inter-patch interval in his calculation of the optimal sampling solution. However, in my study, the birds were never satiated during the experimental period. Thus, it should not be surprising to find that their sampling behaviour could be most closely predicted when the inter-trial time was incorporated into the model in some way.

There were two possible ways my starlings could have been responding to inter-trial time. First, my comparison of their observed sampling behaviour with the three sampling optima predicted by Lima's model suggested that the starlings might have been responding solely to the most recent "travel time", which in this case was the inter-trial interval.

Cuthill et al. (1990) refer to such responding to short-term experience as "tracking" and report that, at least under conditions of rapidly fluctuating travel times, starlings will track the most recent travel time. Although such behaviour does not maximize the rate of energy intake as determined by the marginal value model (Charnov 1976, Stephen & Krebs 1986), it will maximize intake rates when the chance of being interrupted while foraging is high (Cuthill et al. 1990).

The second way in which the starlings could have been responding to inter-trial time was by incorporating it into an average of inter-patch and inter-trial times, a response which Cuthill et al. (1990) refer to as "averaging". If, as is likely, my unsatiated starlings were considering the entire daily experimental period as their foraging time, such a response would have maximized their expected intake rate over this foraging period. My comparison of the birds' observed sampling payoffs with the three optimal payoffs predicted by Green's (1990) model showed strong support for averaging, which produced an estimated intake rate that was practically indistinguishable from that of an optimal forager. The observation that the birds were sampling slightly but significantly more holes than predicted by Lima's optimal sampling solution for averaging, however, suggests that if my starlings were indeed averaging, then they were also oversampling to a certain extent. Oversampling is a common phenomenon in studies of patch departure and has been reported in numerous laboratory and field experiments (Kämil & Yoerg 1982, Kacelnik 1984, Lima 1984, 1985, Tamm, 1987, Valone 1992). When a forager has some degree of uncertainty about environmental parameters, such as the number of prey per patch as in my experiment, it has been suggested that oversampling may be an appropriate response. If there is a chance that the patch is actually good, it may be worth taking a slight loss in intake rate to gain more information and potentially detect any changes in environmental conditions (Houston et al. 1982, Lima 1985, Valone 1992).

The design of my experiment does not allow me to distinguish between averaging and tracking as possible explanations for my starlings' sampling behaviour. Indeed, it may be that they were doing both to a certain degree. This would provide an alternative explanation for the apparent oversampling observed in my study; if the birds were averaging, but weighting their memory of the most recent time interval (inter-trial time) more heavily (Cuthill et al. 1990), then they should sample more holes than would be expected if all time intervals were weighted equally. It is worth considering such an alternative explanation for other cited cases of oversampling as well. In Lima's (1985) study, for example, two of his four starling subjects were given inter-trial intervals that were twice as long as the intervals of the other two birds, and it was these former birds which exhibited the most oversampling, perhaps because their satiation did not last the full inter-trial interval.

Paired sampling and public information

Despite the fact that my starlings were able to acquire personal information from their unsuccessful sampling activities on the experimental two-patch system, I found no evidence for the use of unsuccessful public sampling information when the subjects sampled an empty patch in the presence of a sampling partner bird. Subjects sampled a similar number of empty holes before departure when with each of the high and low information partner birds as when alone. This lack of public information use is comparable with the finding of the only other empirical study of patch assessment in foraging groups to date. Valone and Giraldeau (In press) showed that although budgerigars foraging in pairs on food patches used their own personal foraging information, they completely disregarded the foraging success of their neighbours when making their patch departure decisions.

One possible explanation for the lack of public information use in both Valone and Giraldeau (In press) and the present study was the potential incompatibility between obtaining personal and public information simultaneously (e.g. Vickery et al. 1991). Valone and Giraldeau, for example, proposed that the millet seeds used were probably too small and thus eaten too quickly for a discovery to be noticed by a neighbouring bird. In my study, two aspects of the birds' behaviour on the long, narrow patch could have produced a similar incompatibility. For instance, it might have been difficult for a subject to observe the partner's sampling activities if it was always either just in front of or just behind the subject. However, the two birds generally tended to start at opposite ends of the patch and moved towards one another, which should have allowed for at least some observation of the partner by the subject. In addition, all subjects sampled the patch in an extremely methodical manner, searching the first pair of holes from right to left, the next pair from left to right and so on. Thus it might have been difficult to observe the partner if the subject had to devote its full selective attention to its own sampling activities.

An alternative, and perhaps more intriguing explanation for the lack of public information use is the possibility that public information may only be used when the information obtained from one's own personal sampling activities is either insufficient or too costly to acquire, or both. Although a high number of empty holes were sampled before departure in the present study, the extremely low frequency of reprobe errors and the fact that food patches were almost never given up as empty suggests that the cost of assessment was actually very low. Thus the subjects were able to rely on their personal information alone to assess the state of a patch, making public information simply unnecessary.

The lack of public information use in my experiment, therefore, could simply have been an artifact of the experimental patches. If this is indeed the case, then to test for the use of public information in the future, it will be necessary to create a new patch condition in which the compatibility between obtaining personal and public information simultaneously and the cost of patch assessment are both increased. This experiment is the subject of my next chapter.

Chapter 3

The Influence of the Cost of Patch Assessment on the Use of Personal and Public Information by Foraging Starlings

In nature, the food supply of an animal is often clumped or patchy in its distribution (Tinbergen & Drent 1980, McNamara 1982, Wilkinson 1992), thus one problem facing a forager attempting to maximize its net rate of energy intake is deciding when to leave one patch and move on to another (Krebs et al. 1974, Charnov 1976). When prey items are hidden and the quality of a resource patch is unknown, a forager's decision to stay or depart must depend at least in part on the personal sampling information that it acquires while exploiting the patch (Green 1980, Lima 1985, Valone & Brown 1989). In an attempt to understand how animals use such sampling information to estimate patch quality, a variety of patch assessment models have taken an economic approach to the study of information acquisition, predicting the optimal quantity of sampling that a forager should perform before its departure from a patch (Oaten 1977, Green 1980, 1984, McNamara & Houston 1980, McNamara 1982). In general, these models assume that individual foragers form an estimate of patch quality by combining their prior knowledge of the distribution of resources among patches in the environment with their current patch sampling information, and then use this estimate to make their patch departure decision (Oaten 1977, Green 1980, McNamara 1982).

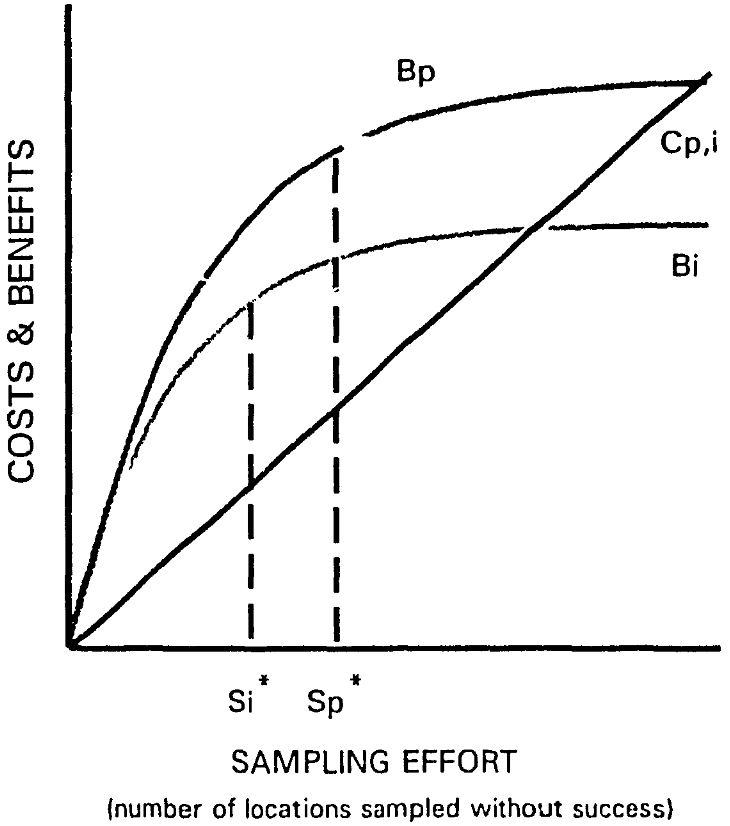
In one of the first empirical tests of a patch assessment model, Lima (1985) allowed captive solitary European starlings (*Sturnus vulgaris*) to forage in a patchy environment where the experimental patches were either empty or contained a fixed number of hidden food items randomly distributed among the holes of a patch. The problem for Lima's starlings was to determine to what extent to sample a patch unsuccessfully before giving it up as empty, and to do this in a way which maximized their long-term energy intake rate. Lima developed a modified version of Oaten's (1977) and Green's (1980) patch assessment models which predicted the optimal number of empty holes to sample before departure from a patch and found that his starlings' actual sampling behaviour was in qualitative agreement with this optimum.

A key assumption of Lima's assessment model is that sampling is systematic; that is, holes previously probed are not reprobed. In this way, a forager is able to increase its estimate of the probability that a patch is empty with each additional empty hole sampled. Lima's assumption of systematic search is not an unreasonable one; starlings (Lima 1985, Templeton Chap. 2), downy woodpeckers (*Picoides pubescens*, Lima 1984), and pigeons (*Columba livia*, Baum 1987) have all been shown to sample experimental patches in a systematic fashion. There is also good field evidence that foragers' movements both within and between patches are non-random (Krebs 1973b). The ability to forage systematically appears to be achieved either by the animal forming a "cognitive map" of locations recently searched, as has been suggested to be the case for rats searching in radial arm mazes (e.g. Olton et al. 1981), or by the animal simply following a sequence of movements which allows it to be an "efficient harvester" (Armstrong et al. 1987) Brown creepers (*Certhia americana*), for example, normally search the bark of a tree by starting at the base and spiralling upwards (Ehrlich et al. 1988); bumblebees, too, tend to start at the lowest flowers of an inflorescence and move up (Pyke 1981).

Whether an animal forages systematically by using a cognitive map or by harvesting efficiently, however, its ability to do so is likely to depend on the foraging environment. Theoretically, the costs of acquiring foraging information will be influenced both by the size and the structural features of a foraging site (Armstrong et al. 1987). For instance, the larger the patch, the more locations within the patch that must be remembered and avoided, and the greater the likelihood of errors. Similarly, the manner in which the potential resource locations are arrayed within a patch and the availability of cues which indicate that a location has already been checked are both likely to influence a forager's ability to sample the patch in systematic fashion. An excellent example of a system which promotes highly systematic exploitation is the linear array of florets on the inflorescences of silvery lupine (*Lupinus argenteus*) plants and the change in the colour of the florets once they are depleted of nectar (Gori 1989).

Lima's (1985) patch assessment model predicts the optimal sampling behaviour given that foragers are able to sample resource locations perfectly systematically. When environmental conditions limit the capacity of a forager to sample systematically, however, it will begin to recheck previously checked locations within a patch. This tendency to recheck locations should increase with the number of locations already sampled, resulting in a lower rate of information gain than would be the case with perfectly systematic search. Figure 3.1 presents a graphical model of optimal sampling effort under conditions of perfectly and imperfectly systematic sampling. The benefit curves represent the increase in information acquired about patch quality as a function of sampling, and this increase in information is assumed to contribute to long-term energy acquisition (Lima 1985). The benefit curves for both perfectly and imperfectly systematic sampling increase at

Figure 3.1. Graphical model of optimal sampling effort for perfectly (p) and imperfectly (i) systematic sampling. B, benefit (increase in information); C, cost of sampling; S^*, optimal sampling effort. When it is not possible to sample in a perfectly systematic fashion, a forager should reduce its sampling effort. This model applies specifically to a foraging environment where patches are either empty or contain a fixed number of hidden food items (e.g. Lima 1985). For more details, see text.


Bp
Cp,i
Bi
COSTS & BENEFITS
Si*
Sp*
SAMPLING EFFORT
(number of locations sampled without success)

monotonically decreasing rates. The costs of sampling (time and energy) are assumed to increase linearly with the number of locations sampled. The optimal amount of sampling effort occurs at the point where the difference between the benefits gained and the costs incurred is maximized. As Figure 3.1 shows, the lower rate of information gain with imperfectly systematic search means that it is more costly to acquire the same amount of information under difficult sampling conditions than under easy sampling conditions. This results in a shift in the optimal amount of sampling effort ($S^{*}i$) relative to the optimum for perfectly systematic sampling ($S^{*}p$) such that fewer holes should be sampled. Thus, when it is difficult to sample a patch systematically, a forager should reduce its sampling effort.

In addition to reducing its personal sampling activities, a forager could also respond to the difficulty of acquiring sampling information by making use of the "public" information (Valone 1989) provided by the activities of conspecifics sampling in the same patch. In this way, the forager could obtain supplementary information about the quality of a patch at a reduced cost. The use of public information in a patch assessment context has only recently been considered theoretically (Clark & Mangel 1984, 1986, Valone 1989), and tested experimentally (Valone & Giraldeau In press, Templeton Chap. 2). Both experimental tests failed to document the use of public information, however. There were two potential reasons for the lack of public information use in the experiment reported by Templeton (Chap. 2). First, it was possible that the linear array of holes in the experimental patches rendered the simultaneous use of personal and public information incompatible by forcing the two starlings to forage one behind the other. Second, I considered the possibility that public information may be used only when the information obtained from one's own personal sampling activities is either insufficient or too costly to acquire, or both. The linear array of holes used in the previous experiment (Chap. 2) promoted systematic sampling, thus enabling the subjects to acquire information at relatively low cost.

In the present study, I examined the influence of the cost of patch assessment on the use of personal and public information by manipulating the ease with which starlings could sample experimental patches systematically. Instead of the linear array of holes used in Templeton (Chap. 2), experimental patches had a square array of holes which I assumed would increase both the difficulty of keeping track of holes already sampled and the compatibility between obtaining personal and public information simultaneously. In the first part of my experiment, there were two experimental conditions. In the "easy" condition, cues were available which indicated whether a hole had already been checked; whereas in the "difficult" condition, these cues were absent. I predicted that, relative to the easy condition, solitary birds in the difficult condition would: 1) make more sampling errors; 2) sample fewer empty holes before departure; and 3) sample fewer empty holes than the optimum number predicted by Lima's (1985) patch assessment model (Chap. 2).

In the second part of my experiment, I tested whether birds in the difficult condition would make use of public information when sampling an empty patch in the presence of a sampling conspecific. I hypothesized that a starling would be able to assess the patch more quickly by combining the personal information it obtained from its own unsuccessful sampling efforts, with the public information it obtained from observing the unsuccessful sampling efforts of a partner bird foraging in the same patch. Subjects were paired with one of two types of partner bird. One partner sampled few holes and thus provided a low amount of sampling information; the other sampled numerous holes and provided a high amount of sampling information. I predicted that if my starlings used public information, they would sample fewer holes when with the low information partner than when alone; and even fewer holes when with the high information partner.

GENERAL METHODS

The methods used in this study are completely analogous to those in the previous chapter and are summarized below.

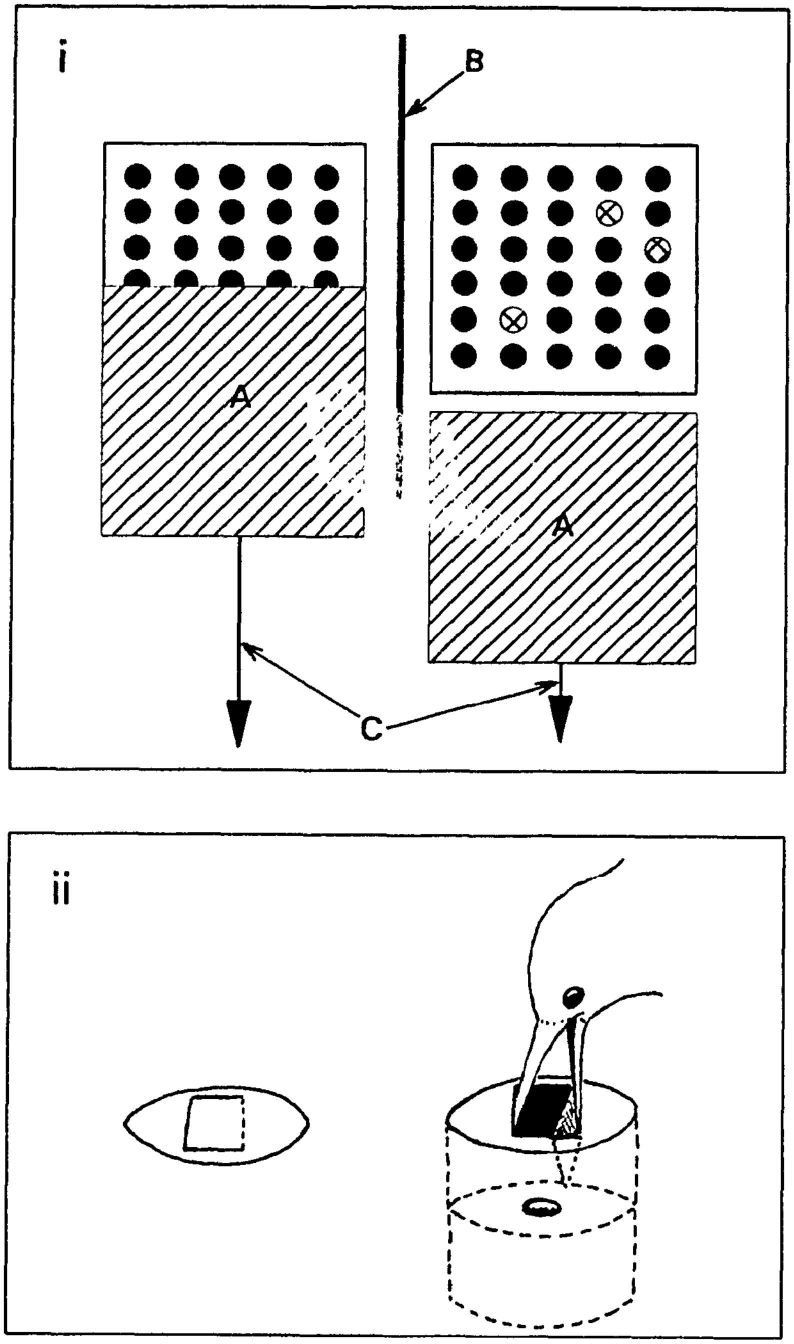
Subjects

Experimental subjects were ten wild-caught adult starlings, with five birds (four males and one female) assigned to each of the easy and difficult experimental conditions. These birds had been in captivity at least three months prior to testing and were selected randomly from a population of 20 experimentally naive starlings. The partner birds used during the public information testing phase were the same as those in Templeton (Chap. 2).

Foraging Environment

The foraging environment was situated in an experimental aviary similar to that used in the previous two chapters. Two patches were present per trial. These patches were square pieces of foam (45 x 45 x 5 cm), separated by a wooden barrier (84 x 135 cm, Fig.3.2.i). Each patch consisted of 30 numbered holes in a 6 x 5 array, with 3 cm separating each hole. Within each hole was a section of cardboard tubing 4 cm in diameter and 2.5 cm deep. In the difficult condition, the top of each cardboard tube was covered with a piece of opaque grey latex into which had been cut a 4 cm slit, as had been used in Chapter 2 (Fig. 2.1.ii). In the easy condition, the top of the tube was covered with a piece

Figure 3.2.i. Schematic top view of the two experimental patches. A) patch covers; B) barrier; C) pulley system controlling cover removal. (ii) Detail of a starling sampling an experimental hole in the easy condition by pecking the flap and probing its beak into the opening in the cardboard cover.


i
B
A
A
C
ii

of thin grey cardboard, into which had been cut a 2.3 cm x 1.2 cm wide flap. This flap opened inwards when probed and remained open (Fig. 3.2.ii). The two experimental conditions were alternated over subjects, starting with the difficult condition.

PART I: Sampling behaviour of solitary starlings on easy and difficult patches.

Methods

Procedure

Following an initial training period in which birds learned how to sample holes (Templeton, Chap. 2), a subject received a total of 100 solitary sampling trials on one of the patch conditions over a four day period. In any given trial, each patch had a 0.5 probability of containing food, with the constraint that the same patch could not contain food or be empty more than three trials in a row. When a patch did contain food, only three randomly-selected holes contained one mynah pellet each; the same hole could not contain food from one trial to the next. Over the 100 trials, 52.9 ± 0.5 % (X ± S.E.) of the patches were empty in the difficult condition; a comparable percentage, 52.3 ± 0.8 %, were empty in the easy condition (including those food patches in which all three pellets were missed).

A trial started as soon as the subject stepped onto the first patch and ended once it had stepped off the second patch, at which point I entered the aviary and removed the patches. During the five minute inter-trial intervals, any remaining pellets were removed from the patches and pre-selected random holes were stocked with fresh pellets as necessary. Between 24 and 36 trials were run per day for the first three days in both conditions. A naive bird was present during the last 15 trials on the fourth day to allow the subject to get used to the presence of another bird in the aviary in preparation for the public information testing phase (Part II).

To maintain a subject's weight at approximately 85% of its initial free-feeding weight during the experimental period, supplemental food was provided 30 min after the last trial of the day, as described in Templeton (Chap. 2). Birds in the difficult and easy conditions were tested at 81.8 ± 1.5% and 84.9 ± 2.1% of their free-feeding weights respectively.

Data Collection and Analyses

Solitary foraging data were collected from videotapes of the 100 trials for each individual in each of the two experimental conditions. Unless otherwise stated, only data from the first patch visited in each trial were used. These data included the number of holes sampled before departure from both empty and food patches, the number of holes probed more than once ("reprobes") on empty patches, the number of pellets eaten and missed, and estimates of the time parameters to be used in the calculation of the optimal sampling solutions by Lima's (1985) patch assessment model. These time parameters were: te, the time to check an empty hole; tf, the time to check a full hole; and tt, travel time. Time parameters were estimated separately for each individual using the data from the last 20 trials (as described in Templeton, Chap. 2). Travel time was estimated by taking the average of a bird's mean inter-patch travel time and the five minute inter-trial interval, which had been shown in the previous chapter to be a better predictor of patch departure decisions than inter-patch travel time alone. Food patch data included only those patches where one or more pellets were found; data from patches where all pellets were missed were included with empty patch data.

In order to confirm that sampling was difficult in the difficult condition and easy in the easy condition, I recorded two types of sampling error that the birds could commit: reprobed holes and missed food items. I expected both types of error to be more frequent in the difficult condition than in the easy condition. For each bird, I counted the number of reprobes per total probes on each of the last 20 empty patches visited. From these data, I calculated the mean percent reprobes for each condition, thus allowing the two conditions to be compared even if they differed in mean total probes. In addition, I examined whether reprobes increased with the total number of holes sampled in a patch; for each condition, a linear regression of percent reprobes against total probes was carried out on the data from the last 20 empty patches visited by each bird. For missed food errors, I determined the total number of patches where one or more of the three pellets were missed, summarized this as a percentage of all food patches visited, and compared percentages between conditions using independent t-tests.

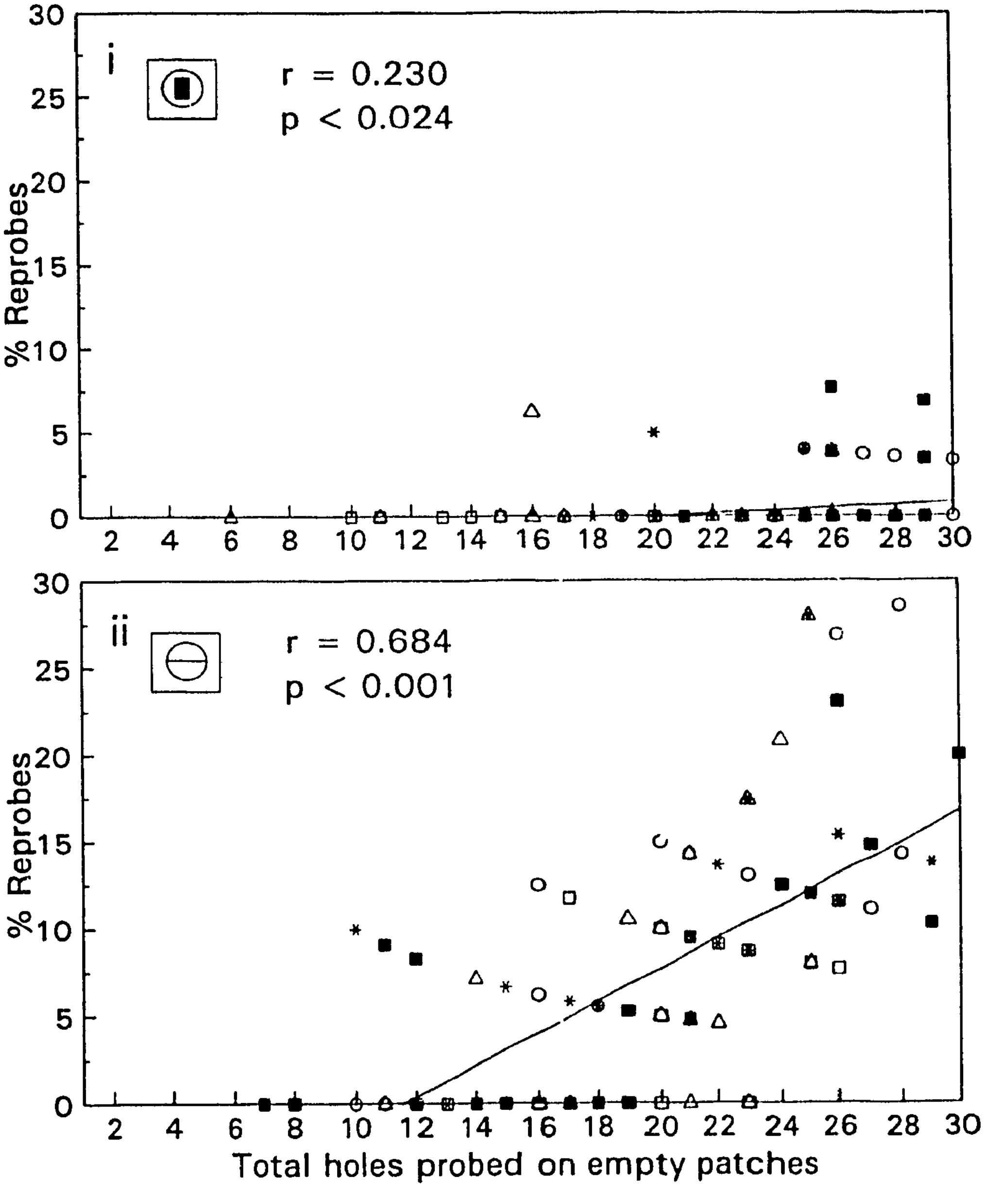
The birds' sampling activities on empty and food patches in the difficult and easy conditions were averaged over the 100 trial period in five blocks of 20 trials each. I assumed that each bird's sampling behaviour had stabilized once the frequency distributions of the numbers of holes it sampled on empty patches were not significantly different from one block of trials to the next, using the Kolmogorov-Smirnov ("K-S") two-sample test (Lima 1985, Wilkinson 1990). A three-way repeated measures analysis of variance (ANOVAR) was used to analyze changes in sampling behaviour on food and empty patches in the two conditions over the five blocks of trials. The number of holes sampled on empty patches during the last block of trials was then compared between the two experimental conditions using an independent t-test to determine whether sampling was lower in the difficult condition than in the easy condition. Finally, the number of holes sampled on empty patches was compared between each condition and its optimal sampling solution as predicted by Lima's (1985) patch assessment model using a paired t-test. All values are reported as $\bar{X} \pm$ S.E., and appropriate transformations were carried out before analyses with SYSTAT (Wilkinson 1990).

Results

Sampling Errors in Easy and Difficult Conditions

An examination of the sampling behaviour of birds in both conditions suggested that they were attempting to sample the patch in a systematic fashion, even in the earlier blocks of trials. Individuals tended to start at the same corner of the patch each time, sampling the edge holes first before spiralling in towards the centre. Despite this pattern of behaviour, however, a comparison of sampling errors between the two conditions indicated that it was indeed more costly to assess patches in the difficult condition than in the easy condition, and this was particularly true for reprobe errors. Although the percent of total holes reprobed on empty patches in the last two blocks of trials was quite low in the difficult condition (8.0 ± 1.2%), this was still markedly higher than the percent reprobes made in the easy condition (0.7 ± 0.2%; t-test, arcsine-square root transformed data: $t=6.984$, $df=8$, $p<0.001$). Following an ANCOVA which confirmed the homogeneity of both slopes and intercepts of each individual's data, the percent reprobes were regressed against the total number of empty holes sampled by each bird on the last 20 empty patches in each condition. I found a slight, but significant increase in percent reprobes with total probes in the easy condition ($Y = -1.011 + 0.075X$, $p=0.024$, Fig. 3.3.i). In the difficult condition, however, the proportion of holes reprobed increased dramatically with the total

Figure 3.3. Percent of total holes reprobed as a function of the total number of holes probed on the last 20 empty patches by each of the five subjects in the (i) easy and (ii) difficult conditions. The data for each subject are represented with different symbols.


i
r = 0.230
p < 0.024
ii
r = 0.684
p < 0.001
% Reprobes
0
5
10
15
20
25
30
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Total holes probed on empty patches

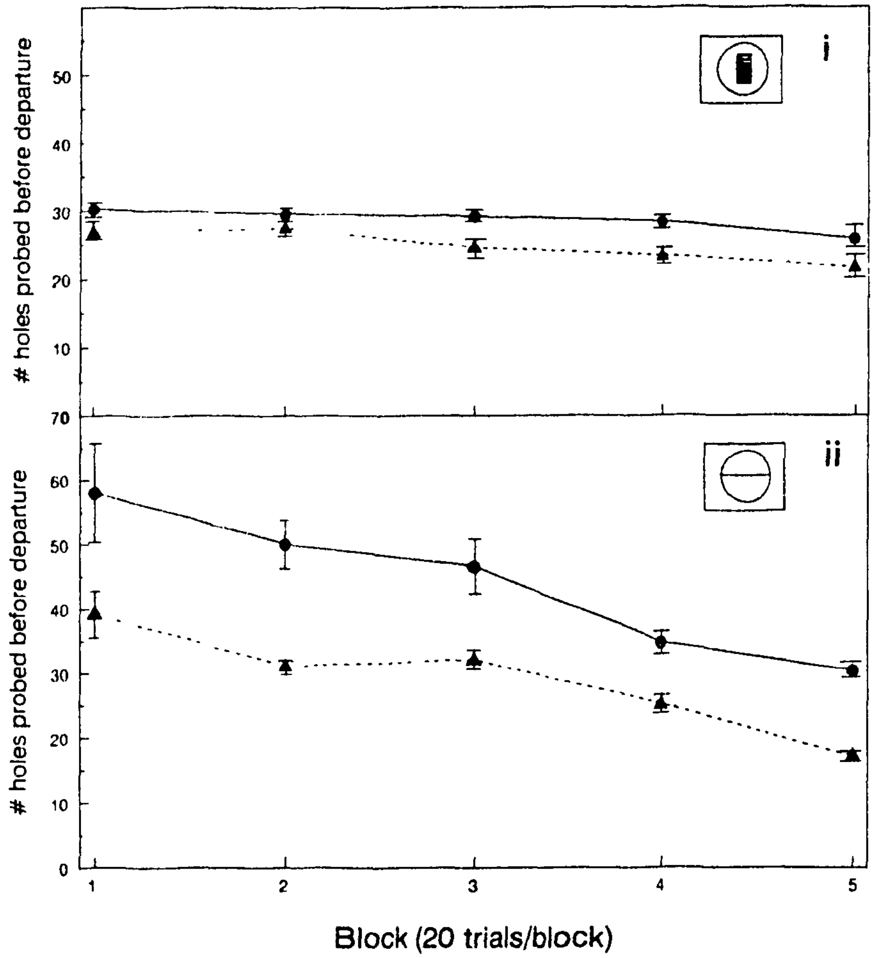
number of holes probed ($Y = -10.753 + 0.935X$, $p<0.001$, Fig. 3.3.ii). This meant that although the difficult condition birds would have been able to acquire accurate information about patch quality for the first 10 to 15 empty holes sampled, further sampling would have improved their estimate of patch quality at a decreasing rate with each additional probe made.

The difficulty the birds had in keeping track of holes already sampled in the difficult condition was also reflected by the number of food items they missed. Over all food patches, birds in the difficult condition had a higher percentage of patches where one or more pellets were missed (29.2 ± 3.3 %) than did birds in the easy condition (15.6 ± 1.0 %; t-test, arcsine-square root transformed data: $t=4.061$, $df=8$, $p<0.004$). However, there was no significant difference in the percent of visited food patches where the pellets were missed entirely between the difficult (2.7 ± 0.9 %) and easy conditions (1.8 ± 0.4 %; t-test, $t=0.978$, $df=8$, $p=0.357$)

Sampling Behaviour in Easy and Difficult Conditions

Birds in both experimental conditions showed a significant decline in the number of holes sampled on food and empty patches over the five blocks of solitary sampling trials (3-way ANOVAR on square-root transformed data; $F=29.462$, $df=4,64$, $p<0.001$, Fig. 3.4.i and ii), indicating that they were learning the availability and distribution of food and were adjusting their sampling behaviour accordingly. When the sampling behaviour on food and empty patches is compared between the two conditions, however, it is apparent that the ability of a starling to keep track of the holes it has already sampled plays a key role in its patch departure decisions. A highly significant effect of experimental condition ($F=78.110$, $df=1,16$, $p<0.001$) and a significant interaction between condition and trial

Figure 3.4. Mean (±S.E.) number of holes sampled before departure from food (●) and empty (▲) patches in each of five blocks of trials over the 100 trial period in the (i) easy and (ii) difficult conditions. The dotted line at 25 holes is the mean predicted number of empty holes to sample (n*) according to Lima's (1985) model.



i
ii
holes probed before departure
50
40
30
20
10
70
60
0
1
2
3
4
5
Block (20 trials/block)

block (F=11.346, df=4,64, p<0.001) reflect the initially much greater sampling activity of the difficult condition birds, and the subsequently steep decline in this sampling activity over trials as compared with the sampling behaviour of the easy condition birds (Fig. 3.4.i and ii).

Birds in both conditions used their lack of foraging success to discriminate between patches of different quality; they sampled more holes on food patches than on empty patches (F=83.195, df=1,16, p<0.001), and this was consistent over trials, as shown by the lack of interaction between patch quality and trial block (F=0.185, df=4,64, p=0.890). There was, however, a greater difference between the number of holes sampled on food and empty patches in the difficult condition than in the easy condition (condition x patch quality interaction: F=22.780, df=1,16 p<0.001), suggesting that when the starlings were limited in their ability to keep track of previously sampled holes, they were willing to increase their sampling only if food was discovered; otherwise, sampling remained low.

As predicted, by the end of the solitary sampling trials, birds in the difficult condition were responding to their reduced ability to keep track of sampled holes by sampling fewer holes on empty patches (17.2 ± 0.7) than birds in the easy condition (21.7 ± 1.6, t-test: t=2.516, df=8, p<0.036). In addition, the fact that four of the five difficult condition birds did not achieve stable sampling behaviour on empty patches by the last block of trials (K-S tests, p<0.03) suggests that this sampling behaviour was continuing to decline. In comparison, all birds in the easy condition reached sampling stability on empty patches by blocks 4 and 5 (K-S tests, p>0.05).

Systematic Sampling

As I described above, reprobe errors on empty patches were more frequent in the difficult condition than in the easy condition during the last two blocks of trials. This implied that the difficult condition birds were not sampling systematically, and therefore were violating a key assumption of Lima's (1985) patch assessment model. Thus, before I could compare the birds' observed sampling behaviour with that predicted by Lima's (1985) model, it was necessary to determine whether these birds had been able to reduce the number of holes reprobed and thus achieve systematic sampling on empty patches at least by the last block of trials. To do this, I compared the number of reprobes observed with the number expected for both systematic and random search. Because the birds in the two conditions were sampling different mean numbers of holes on empty patches by the last block of trials (difficult, 17.2 ± 0.7 holes; easy, 21.7 ± 1.6 holes), I chose to record the mean number of reprobes made in 17 total probes for the difficult condition, and the mean number of reprobes made in 22 total probes for the easy condition.

If the birds were using systematic search, the expected number of holes reprobed should of course be zero regardless of the total number of holes sampled. If the birds were randomly sampling holes, however, they would be expected to average 3.5 reprobes in the first 17 probes and 5.9 reprobes during the first 22 probes. For the difficult condition, the mean number of reprobes in 17 probes was 0.7 ± 0.2. This was significantly less than the number of reprobes expected for random search ($t=5.7$, $df=4$, $p<0.01$), but not significantly higher than zero reprobes ($t=-1.48$, $df=4$, $p>0.1$). For the easy condition, the mean number of reprobes in 22 probes was 0.03 ± 0.02. Again, this was markedly less than expected for random search ($t=89.0$, $df=4$, $p<<0.001$), and not significantly different from zero (t=-0.43, df=4, p>0.5). Therefore, the birds in the two patch conditions were considered to be sampling systematically, at least by the end of the solitary sampling period.

Observed versus Predicted Sampling Behaviour

The dotted lines on Figures 3.4.i and ii represent the mean predicted number of empty holes to sample in order to maximize long-term intake rate, calculated for each condition using Lima's (1985) time-related model parameters te, tf, and tt (Chap.2). There were no significant differences found between the two conditions in any of these parameter scores: the mean time to check an empty hole was 0.59 ± 0.01 s and 0.61 ± 0.03 s for difficult and easy conditions respectively (log-transformed data, t=-0.698, df=8, p=0.505); and the time to check a full hole and eat the pellet was 2.17 ± 0.35 s and 1.81 ± 0.15 s for difficult and easy conditions respectively (t=0.750, df=8, p=0.475). Average travel time was calculated to be 151.3 ± 0.4 s for both conditions.

The optimal number of empty holes to sample was calculated for each bird separately; all birds in both conditions were found to have the same predicted optimum of 25 holes. By the last block of trials, the birds in the difficult condition had reduced the number of holes sampled before departure from empty patches to 17.2 ± 0.7 holes which, as predicted, was significantly lower than their own optimum of 25 holes (paired t-test: t=-11.759, df=4, p<0.001). In contrast, the number of empty holes sampled by birds in the easy condition (21.7 ± 1.6), was not significantly different from their predicted optimum of 25 holes (t=-2.092, df=4, p=0.105).

These data on personal sampling behaviour suggest that the reduced ability to keep track of holes already probed would have indeed made it more costly for a starling to assess patch quality in the difficult patch condition. Compared with the easy condition, birds in the difficult condition made more reprobe errors on empty patches and were more likely to miss pellets in those patches that did contain food. By the last block of trials, birds in the difficult condition had reduced their sampling of empty patches to a level significantly lower than both the sampling of easy condition birds and their predicted optimal sampling level. Although this reduction in sampling was accompanied by a reduction in reprobe errors, less sampling meant that the birds would have departed empty patches earlier with a lower degree of certainty about patch quality. Because of this, the birds in the difficult condition should have been in need of an additional source of sampling information, such as public information.

PART II: Testing for the use of public information

Methods

Following the 100 solitary trials measuring the use of personal sampling information, the subjects from the difficult condition were paired with partner birds and tested for the use of public information on difficult patches. The procedure followed was the same as that used in Chapter 2, and is summarized below.

Information Partners

There were two types of partner bird, each trained to provide different amounts of sampling information when it sampled the right-hand (test) patch with the subject. The "low information" partner was trained to probe only a few holes; the "high information" partner, to probe many holes (Templeton Chap.2). The left-hand patch never contained food, thus the partners learned never to visit it.

Testing Procedure

Each subject was given three consecutive trials in each of three test conditions arranged in a Latin square design over subjects: 1) alone, 2) paired with the low information partner, and 3) paired with the high information partner. Both patches were empty during test trials, and the cover of the right patch was always removed first. The subject and partner were required to land within three seconds of one another; if they did not, the trial was interrupted and a retest followed immediately. Before each set of three test trials, a subject was given a set of three food trials in the presence of a naive starling in order to prevent the subject from associating the presence of a partner bird with empty patches. The food distribution in these trials was as described in Templeton (Chap. 2). A subject received a total of nine food and nine test trials on a test day. Within each set of three trials, there was a five minute inter-trial interval. Sets of trials were run every 30 min.

Data Collection and Analyses

Test trials were videotaped, and the number of empty holes sampled as well as the time spent on the right-hand patch was recorded for both subject and partner birds. Subject data were analyzed with a one-way repeated measures analysis of variance (ANOVAR) over the three test conditions; and with subsequent contrasts between test conditions. Data for the two partners were summarized as mean scores per subject and analyzed with a paired t-test. Appropriate transformations were carried out before analyses with SYSTAT (Wilkinson 1990); all data are presented as $\bar{X} \pm$ S.E.

Results

In 22 of the 30 "partnered" test trials (73%), the subject and partner landed within one second of one another. In only four of the test trials (each time with a different subject), partner birds did not land within the three-second time limit. In these cases, retest attempts were unsuccessful, with the partner bird refusing to land. Therefore, for four of the five subjects, it was necessary to obtain mean test scores from two rather than three successful trials in one of the "partnered" test conditions.

Sampling behaviour of subjects in the three test conditions is presented in Figure 3.5. A significant difference in the number of empty holes sampled over the three test conditions indicates that subjects were indeed using public sampling information to direct their patch departure decisions (square-root transformed data, F=9.082, df=2,8, p=0.01). As predicted, subjects sampled significantly fewer holes before departure from the empty test patch when with the high partner than when alone (F=18.467, df=1, p=0.010, Fig. 3.5). They also sampled marginally fewer holes when with high partner than when with the low partner (F=10.443, df=1, p=0.032, Boneferroni adjusted level of significance, p=0.02, Fig. 3.5). Probing rates of the subjects differed significantly among the three test conditions (log-transformed data, F=10.530, df=2,8, p=0.006, Fig. 3.6). Subjects had significantly lower probing rates when with partner birds than when alone (F=15.926, df=1, p=0.016), which suggests that the subjects were actually paying attention to the partners' sampling activities.

As in the previous study, measures of the two partner birds' sampling behaviour confirmed that they were providing different amounts of sampling information. With each subject, the high partner consistently probed at over twice the rate (1.7 ± 0.1 probes/s) of

Figure 3.5. Mean (+S.E.) number of empty holes sampled by subjects before departure from an empty patch under the three test conditions: alone, paired with the low information partner, and paired with the high information partner.

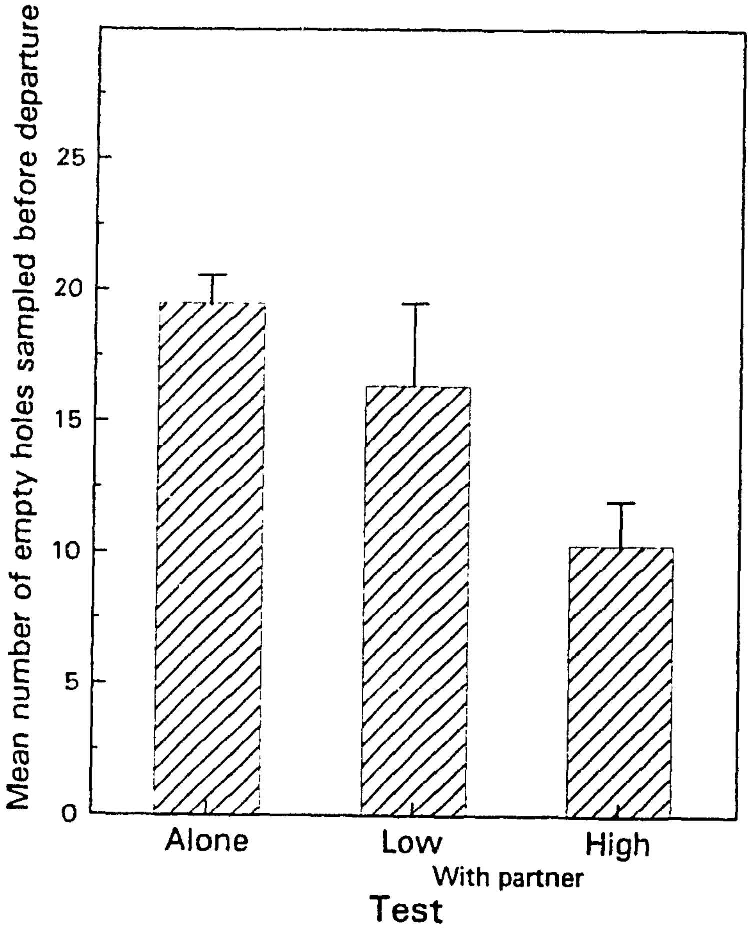
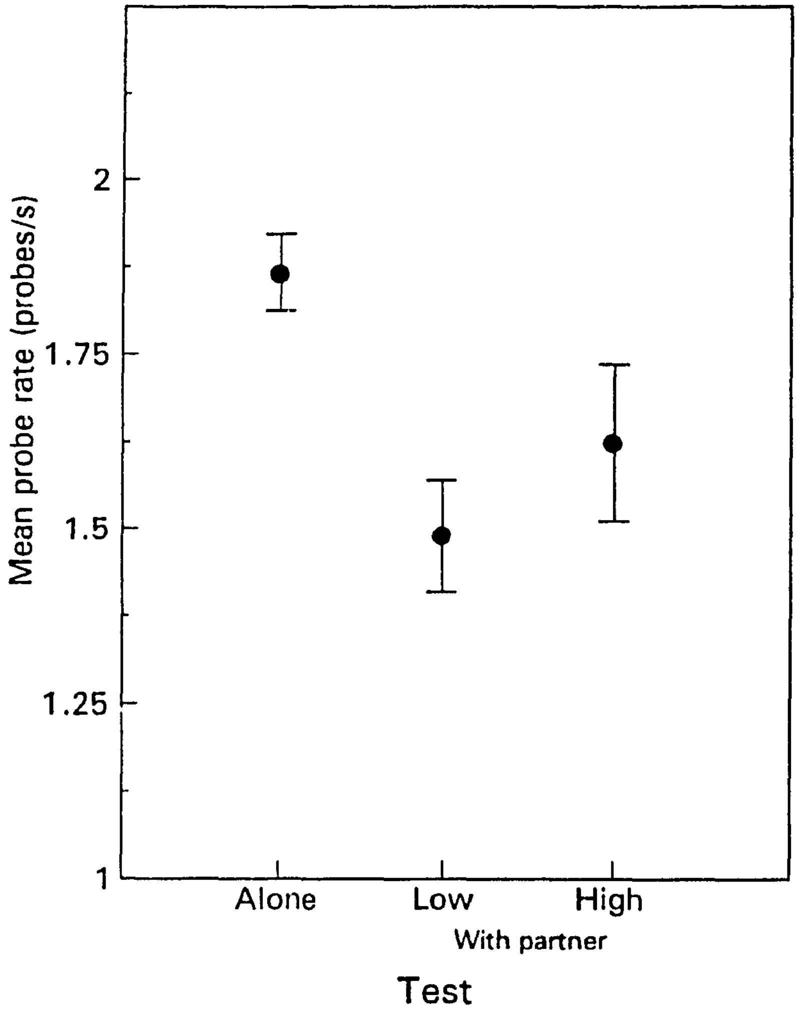

Mean number of empty holes sampled before departure
0
5
10
15
20
25
Alone
Low
High
With partner
Test

Figure 3.6. Mean (±S.E.) rate of sampling (holes probed per second) under the three test conditions: alone, paired with the low information partner, and paired with the high information partner.


Mean probe rate (probes/s)
2
1.75
1.5
1.25
1
Alone
Low
High
With partner
Test

the low partner (0.8 ± 0.1 probes/s; paired t-test, log-transformed data: t=-6.602, df=4, p=0.003). In addition, the high partner consistently made more probes (10.3 ± 2.1) before each subject departed than the low partner did before it departed (4.0 ± 0.5; paired t-test, square-root transformed data: t=-3.382, df=4, p=0.028).

DISCUSSION

The results of my study demonstrate that when the structural features of a foraging patch constrain a starling's ability to sample in a systematic fashion, the starling will respond to this constraint by reducing its acquisition of personal sampling information when alone, and by taking advantage of public sampling information when in the presence of a sampling conspecific. These findings, when combined with the lack of public information use in Templeton (Chap. 2), suggest that the degree to which both personal and public information will be used is likely to depend on the type of environment in which foraging takes place.

Personal Sampling Information

The physical characteristics of the two patch conditions in this experiment had a marked effect on the ability of the birds to sample empty patches systematically. Although most individuals appeared to be attempting to avoid previously sampled holes by sampling around the perimeter of the patch before moving inward (e.g. Bell 1991), the lack of sampling cues in the difficult condition meant that this sampling technique had only limited success. The more holes the birds probed, the greater their probability of making reprobe errors. This reduced ability to sample systematically was accompanied by a higher likelihood of missing pellets, despite the fact that the birds increased their sampling efforts once food was discovered.

The increasing tendency to reprobe holes meant that starlings in the difficult condition would have been acquiring personal information about the state of a patch at a depressed rate relative to birds in the easy condition. Thus, birds in the difficult condition were obtaining less information for the same sampling costs (e.g. Fig. 3.1). It is worth noting that the degree to which constraints on systematic sampling depress the rate at which information is acquired is likely to depend on the distribution of food among patches. For example, if patches are either full (containing one food item per hole) or empty, as was the case in Lima's (1985) environment A, only one hole would have to be sampled without success for a patch to be considered empty, and systematic sampling within such patches would be unnecessary. The less food that is available in food patches, however, the greater will be the depressing effect of systematic sampling constraints on the rate of information acquisition.

In a review on the costs of mate assessment, Gibson and Höglund (1992) suggest that as the costs of assessment increase, the extent of personal sampling should be expected to decrease. This was indeed the case in the present study. As predicted by my graphical model (Fig. 3.1), the starlings in the difficult condition responded to the constraints on their systematic sampling and to the consequently increased cost of information acquisition by sampling fewer empty holes before departure than birds in the easy condition, and fewer holes than the optimum predicted by Lima's (1985) patch assessment model. In contrast, birds in the easy condition showed no significant deviation from the predicted sampling behaviour. These findings illustrate how constraints on the cognitive capabilities of animals can be used to explain and even predict deviations from the optimal behaviour predicted by many models in behavioural ecology, which tend to make untested assumptions about these capabilities (Yoerg 1991). Lima's (1985) model, for example, assumes that the forager is capable of sampling systematically, but it does not consider how easily this is achieved. When systematic sampling is difficult, therefore, Lima's model overestimates the optimal sampling behaviour.

Public Sampling Information

In an evolutionary model of social learning, Boyd and Richerson (1988) show that social learning will be favoured under conditions where personal information is both costly to acquire and of low quality. In the present study, not only was it costly to acquire personal sampling information in the difficult condition, but the increasing probability of reprobes meant that the information obtained was of decreasing quality too. Thus, it might be expected that subjects in the difficult condition would attempt to reduce the costs of assessment either by blindly copying the foraging decisions of the partner birds (Howell 1979, Gibson & Höglund 1992) or by using the partners' foraging activities as a source of additional sampling information (Clark & Mangel 1984, 1986, Valone 1989). If a subject chose to copy the departure decisions of the partner birds (i.e. leave at the same time), it would have been expected to sample fewer holes and depart early with the low information partner, and to sample more holes and depart later with the high information partner, relative to its sampling and departure decisions when alone. On the other hand, if a subject chose to use the partners' sampling activities as a source of public information, it would have been expected to sample fewer holes with the low information partner than when alone and even fewer holes when with the high information partner. The birds in my study exhibited the latter pattern of behaviour, suggesting that they were indeed making use of public sampling information.

A potential alternative explanation for the observed pattern of behaviour, however, is that the subject viewed the high information partner as a "stronger" competitor than the low information partner, and thus departed earlier to avoid this competition. Two key observations argue against this possibility. First, if the subjects had responded to the partner birds as competitors, their probing rates would have been expected to increase, in a variation on Clark and Mangel's (1986) "milkshake effect". Increased probing rates would also have been expected by the "vigilance effect" (Bertram 1978), which predicts a decline in individual vigilance levels and a consequent increase in individual probing rates as the number of foragers in a group increases, an effect which has been noted in starlings foraging on the periphery of small flocks (Jennings and Evans 1980, Keys and Dugatkin 1990). Rather than increasing their probing rates, however, the subjects probed at a significantly lower rate when with partner birds than when alone, implying that they were in fact paying attention to the partners' sampling activities. This observation is compatible with the view that vigilance and foraging are mutally exclusive activities, whether the vigilance is to watch for predators or to watch the foraging activities of others (Lazarus 1979, Pulliam et al. 1982, Lendrem 1984, Vickery et al. 1991).

An additional, anecdotal observation also argues against the early departures of the subjects as being merely a response to increased competition. While being tested with a subject on an "empty" patch, the low information partner appeared to find the remains of a pellet that had mistakenly been left behind from a previous food trial. The subject rushed over to the partner, checked the same now-empty hole, and then proceeded to check more holes than it checked on average when sampling an empty patch alone. This trial was discounted due to the error, but it indicated both that the subject was paying attention to the partner's sampling activities, and that it used the partner's discovery to conclude that the patch apparently did contain food.

This study thus provides the first experimental evidence for the use of public sampling information in a patch assessment context. My findings support the suggestion by Tinbergen & Drent (1980) that starlings in the field may pay attention to the sampling activities of others and in this way are able to waste less time sampling unprofitable sites. Benkman (1988), too, suggested that captive red crossbills (*Loxia curvirostra*) were using the unsuccessful foraging activities of conspecifics both to avoid and to depart more quickly from poor patches, although his evidence for this was indirect. My work also confirms the theoretical work (Clark & Mangel 1984, 1986, Valone 1989) which first proposed the use of public information in a patch assessment context, and provides support for the assumption that the foragers weight personal and public information equally (Clark & Mangel 1984, 1986, Valone & Giraldeau In press).

Previous experiments examining the use of public information have been few. Valone and Giraldeau (In press) tested for the use of public information in pairs of budgerigars (*Melopsittacus undulatus*) foraging for hidden seeds, but found no evidence for it; a fact they attributed to the difficulty the birds may have had in recognizing public foraging success due to the small size of the seeds. The work of the present study and that of Templeton (Chap. 2) is distinctive because subjects were tested on empty patches. Thus the subjects could respond only to the information provided by the sampling activities of the partner birds, and not to their own satiation levels or to patch depletion effects.

The results of my study suggest that public information will be used when patch assessment is costly and additional information is required. However, because the design of the difficult condition increased both the difficulty of assessment and the ease of watching the partner birds, the contribution of the increased compatibility between personal and public information to the use of public information remains unclear and the importance of incompatibility cannot be discounted. To examine specifically how the incompatibility between acquiring personal and public information simultaneously might influence the use of public information, therefore, it will be necessary to manipulate this incompatibility experimentally. This experiment is the subject of my next chapter.

Chapter 4

The Compatibility Between Personal and Public Information: A Field Experiment on Patch Assessment in Foraging Flocks of Starlings

Animals that forage in groups for patchily-distributed prey have been shown to acquire information from others concerning the kinds of places that are likely to contain food (Krebs et al. 1972, Krebs 1973, Palameta 1989), and one consequence of using this information is that foraging individuals are able to locate resource patches more quickly when in groups than when alone (Thompson et al. 1974, Clark & Mangel 1984). Groups of foragers are also less likely to overlook food patches (Baker et al. 1981) such that individuals in groups have a lower variance in feeding rate than those foraging solitarily (Pulliam & Millikan 1982, Caraco 1984, Hake & Ekman 1988). Even if patch locations are known to all group members, however, an additional advantage may arise from the use of information concerning patch quality (Valone 1989). Here, individuals could combine an estimate of patch quality obtained while harvesting resources from the patch with an estimate obtained by paying attention to the success of conspecifics foraging in the same patch. In this way, group foragers may be able to assess patch quality more quickly and more reliably than individuals foraging alone (Clark & Mangel 1984, 1986, Valone 1989).

Group foragers are proposed to have three different sources of patch assessment information available to them (Valone 1989). Two of these sources of information are "personal"; the third is "public". Personal information acquired during the exploitation of the current patch is referred to as "patch-sample" information (e.g. Valone 1991). Patch-sample information can include the number of food items obtained so far and the total time spent in the patch (Iwasa et al. 1981, Green 1987). The second type of personal information comprises any foraging information acquired before the exploitation of the current patch and is referred to as "pre-harvest" information (Valone 1991, Valone & Giraldeau In press). Pre-harvest information includes a knowledge of the distribution of resources in the environment (Oaten 1977, McNamara & Houston 1980, Green 1980) as well as sensory information (environmental cues) or the ability to remember patches that are temporally predictable in quality (Valone 1991). Public information is acquired from monitoring the foraging success of other individuals feeding in the same patch (Valone 1989).

In theoretical investigations of patch estimation in foraging groups, Clark and Mangel (1984, 1986) assume that individuals can obtain public information without any decrement in their own individual foraging rates. Thus, obtaining patch-sample information is considered to be completely compatible with obtaining public information. However, the assumption of complete compatibility between searching for one's own food and watching others is unlikely to be a realistic one. Studies on anti-predator vigilance have demonstrated that scanning for predators and searching for food can often be mutually exclusive activities, depending on the foraging environment and the foraging task (Metcalfe 1984, Lawrence 1985, Lima 1987). In addition, the results of three empirical studies examining the process of patch estimation in foraging groups (Valone & Giraldeau In press, Templeton Chap. 2, Chap. 3) indicate that under certain foraging conditions, some degree of incompatibility between personal and public information may in fact be more likely. Valone and Giraldeau (pers. comm.), for example, suggested that the small size of the hidden millet seeds may have made it difficult for a budgerigar to recognize foraging success in another individual while simultaneously searching for its own seeds. In Templeton (Chap. 2), the linear array of holes in the experimental patches may have forced the starlings to forage one behind the other, making it difficult for the birds to acquire personal and public information simultaneously. When the compatibility between acquiring personal and public information was increased by modifying the experimental patches and allowing pairs of starlings to assess patch quality side by side, starlings paid attention to the sampling activities of their neighbour and altered their patch departure decisions (Templeton Chap. 3). However, these patch modifications also increase the cost of patch assessment by making it more difficult for the starlings to keep track of their own patch-sampling activities. Hence, it remains unclear whether the difference in public information use from Chapters 2 to 3 was due to the increased cost of patch assessment, or to the increased compatibility between the acquisition of patch-sample and public information, or to a combination of the two effects.

The purpose of the present study was to examine how the compatibility between the acquisition of patch-sample and public information might influence the use of the three different kinds of patch assessment information in foraging groups. To do this, I carried out a field experiment with wild starlings in which I experimentally manipulated both the ease with which individual birds could simultaneously acquire patch-sample and public information on the same experimental patch, and the variability in patch quality. Based on the assumption that individuals would decide to leave a patch when their estimate of patch quality fell to some critical threshold level (e.g. Tinbergen & Drent 1980, Brown 1988, Valone 1989, Valone & Giraldeau In press), I predicted how the use of various combinations of pre-harvest, patch-sample, and public information would affect an individual's estimate of patch quality and hence its patch departure decisions. I then compared the birds' actual foraging behaviour with these predictions by monitoring how individual differences in foraging success influenced patch departure decisions under different foraging conditions. The predictions were also based on the assumption of random search, where a given spot within a patch is equally likely to be searched whether or not it has been searched before. This assumption is contrary to the systematic foraging behaviour observed in Templeton (Chapters 2 and 3); however, in those studies, only two birds at most were on an empty patch at the same time. In the present study, the fact that several individuals would be on a food patch at the same time suggested both that it would be difficult for the birds to move around the patch in a systematic fashion (e.g. Hake & Ekman 1988), and that birds would sample the patch more extensively when food was discovered. Thus I assumed their search would at least be non-systematic.

There are only four rational assessment strategies that could be used to estimate the quality of a resource patch, assuming that foragers rely on patch-sample information either alone, or in combination with pre-harvest information, public information or both to estimate patch quality (Valone & Giraldeau In press). These assessment strategies are presented below.

1) Patch-sample information alone:

In this assessment strategy, individual foragers are assumed to base their estimate of patch quality only on their patch-sample information, in this case, their own average intake rate in the patch. This assumption is consistent with the work of Tinbergen and Drent (1980), which reported that solitary starlings do indeed appear to use their own intake rates as a measure of the profitability of a feeding site. For a pair of foragers, one is likely to be less successful than the other at any given point in time and I assume that this individual will have the lower estimate of patch quality and hence will reach the critical departure level first. In addition, when the less successful bird leaves first, the greater the difference in success between the two birds at the time of the less successful individual's departure, the longer the more successful individual will be expected to remain searching in the patch (Valone and Giraldeau In press).

2) Combining patch-sample and pre-harvest information:

In this assessment strategy, an individual's patch estimates are a function of both its current foraging success and its prior information concerning environmental variability (Valone & Giraldeau In press). If patch quality is highly variable (for example, a clumped distribution with no resources in some patches but many in others), patch estimates will increase when resource items are found because this indicates to the forager that the patch is rich. If no resource items are found, however, patch estimates will decline with the time spent searching (Iwasa et al. 1981, Green 1987, Valone 1989). Like the previous assessment strategy, therefore, less successful individuals will be expected to depart first and as the difference in foraging success between the less and more successful individuals increases, so too will the extra patch time of the more successful bird (Valone & Giraldeau In press).

In an environment where the variance in patch quality is low, however, patch assessment models (Iwasa et al. 1981, Green 1987, Valone 1989) have shown that patch estimates will either decrease with each resource item obtained (in what is essentially a patch depletion effect) or will decrease with the time spent in the patch, independent of the number of resource items obtained. In the former case, the more successful forager would be expected to depart first; whereas in the latter case, differences in foraging success will not influence the order of patch departure. If both of these possible outcomes are taken into consideration, therefore, the most conservative prediction for this strategy in a low variance or constant environment is that the less successful forager will not depart first, and that the degree to which individuals differ in foraging success will not influence extra patch time (Valone & Giraldeau In press).

3) Combining patch-sample and public information:

In this assessment strategy, I assume that the foragers will weight patch-sample and public information equally (Clark & Mangel 1986, Valone & Giraldeau In press, Templeton Chap. 3) so that at any point in time, both foragers should have the same estimate of patch quality regardless of their own foraging success. Thus, when the acquisition of personal and public information are compatible, differences in foraging success will not be expected to have an effect on the order of patch departure; nor will differences in foraging success influence extra patch time because birds are expected to depart at approximately the same time (Valone & Giraldeau In press). When the simultaneous use of personal and public information is no longer compatible, however, foragers should rely on patch-sample information alone and consequently the predictions will match those of assessment strategy 1.

4) Combining patch-sample, pre-harvest, and public information:

If all individuals have the same pre-harvest information and weight the three sources of information equally, all group members will possess the same estimate of patch quality (Valone & Giraldeau In press). When the acquisition of personal and public information is compatible, foragers are expected to be ave in the same manner as those using the previous strategy; differences in foraging success will not be expected to have an effect on the order of patch departure, nor will differences in foraging success influence the extra patch time of the more successful individual. In contrast, when the two sources of information are incompatible, foragers will not have easy access to public information and may use only patch-sample and pre-harvest information. In that case the foragers should behave according to the combined patch-sample and pre-harvest assessment strategy 2.

The predictions for each of the four assessment strategies under the combined conditions of compatibility and environmental variability are summarized in Table 4.1. These predictions match those of Valone and Giraldeau (In press) when both sources of information are compatible; compatibility only affects the predictions of those strategies in which public information is used. As can be seen from Table 4.1, the advantage to manipulating the compatibility between personal and public information is that it enables me to distinguish between assessment strategies 3 and 4, which Valone and Giraldeau (In press) could not do.

In this study, I manipulated the compatibility of acquiring patch-sample and public information by varying the height of opaque barriers in the foraging patch, which made it difficult for starlings to observe other flock members while they probed in the food patch. I also manipulated the degree to which the experimental environment varied in patch quality by having either a constant patch quality or a highly variable patch quality. I then compared individual foraging success, patch departure order, and extra patch time of pairs of starlings with the predictions made by each assessment strategy for each environment-compatibility combination (Table 4.1).

Table 4.1: Predictions of how differences in foraging success will influence both the order of patch departure of a focal pair of birds and the extra time spent by the second bird before departure. These predictions apply to groups of individuals using different types of information to assess patch quality, as a function of the environmental variability and the compatibility between acquiring patch-sample and public information.

Information	Environment	Compatibility	
		Compatible	Incompatible
1) Patch Sample	Constant	L, +	L, +
	Variable	L, +	L, +
2) Patch Sample + Pre-harvest	Constant	Not L, 0	Not L, 0
	Variable	L, +	L, +
3) Patch Sample + Public	Constant	N, 0	L, +
	Variable	N, 0	L, +
4) Patch Sample + Pre-harvest + Public	Constant	N, 0	Not L, 0
	Variable	N, 0	L, +

L: less successful bird leaves first.

Not L: either the more successful bird leaves first or N (see below).

N: differences in foraging success will not influence order of departure.

+: the higher the difference in success, the longer the extra time spent on the patch by the second bird.

0: difference in success will not influence extra patch time of second bird.

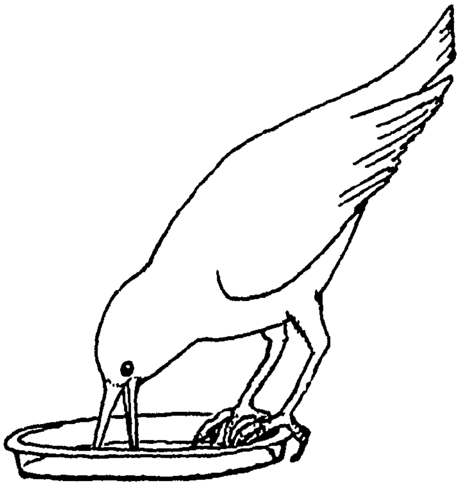
METHODS

This study was conducted during February and March 1992 on a third floor balcony of a small (three-storey) apartment building in Montreal, Quebec. The balcony was situated on the north-east corner of the building and therefore received little to no direct sunlight. During trials, a single experimental patch was placed on a wooden platform (1 m^2) attached to the balcony railing. Trials were videotaped from a window overlooking the balcony.

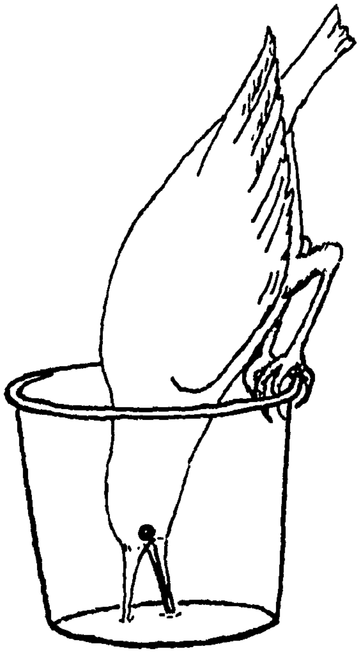
The artificial patch was a shallow plastic tray (68 x 42 x 3.5 cm) filled with sand (3 cm deep) into which were sunk 40 opaque, plastic cups (8 cm diam.) with the bottoms removed. These were arranged in five rows of eight cups attached together with masking tape, and were cut to create either a "compatible" patch with all cups 3.5 cm high (0.5 cm above the sand surface, Fig. 4.1.i) or an "incompatible" patch with all cups 10 cm high (7 cm above the sand, Fig. 4.1.ii). The food items used were small pellets of orange cheddar cheese (0.23 ± 0.04 g). There was a maximum of one cheese pellet per cup; a pellet was hidden below the sand surface by pressing it down with a fingertip. If a cup was empty, I also made a shallow depression with my finger so that a bird had to probe in the sand with its beak to determine whether or not food was present.

Over the two week period prior to setting up the platform, a total of 31 starlings were trapped on the balcony in a pull-string trap. These birds were sexed, weighed, banded with unique colour combinations, and marked on the head with a dot of non-toxic acrylic paint before being released. In order to attract as many different starlings as possible to the experimental patch and to give them experience with foraging under both incompatible and compatible conditions, the patch was made available in the mornings for

Fig. 4.1.i. Starling sampling a single low cup in the "compatible" condition; the bird's eyes remain above the rim of the cup at all times. (ii) Starling sampling a single high cup in the "incompatible" condition; the head of the starling is well below the rim of the cup during sampling.



i



ii

a two-week period prior to the start of the experiment. For the first two days of this period, each cup contained a cheese pellet, clearly visible on the sand surface. Following each visit by starlings, I removed the patch and replenished it indoors. Starlings were observed to fly to a nearby tree (15 m away) or to chimneys on adjacent buildings (25 m away) between patch presentations. After the first two days, the pellets were gradually covered up until the starlings would immediately begin to probe in the sand upon their arrival at the patch. Once the birds were consistently searching in the sand, I varied patch quality such that there were either 40 pellets (with $p=0.4$) or zero pellets (with $p=0.6$), with the constraint that there were no more than three patches in a row of the same quality. This was done in order to give the birds experience with empty patches and thus prevent the extinction of patch visits and cup sampling whenever empty patches were encountered. This specific distribution of pellets, although having a high variance, had the same mean number of cheese pellets per patch (16 pellets) as in the experimental environments described below.

Experimental Environments and Procedure

There were two experimental environments, "variable" and "constant", each with a different distribution of pellets in the patch over trials. Both of these environments offered an average of 16 pellets per patch. In the variable environment, there were three patch types: empty, poor, and rich, each of which occurred randomly in 33% of the trials with the constraint that there were no more than three of each type in a row. An empty patch contained no cheese pellets; a poor patch, eight hidden pellets, randomly distributed among the 40 cups; and a rich patch, 40 hidden pellets. Half of each of the three patch types were presented in the compatible condition; the other half, in the incompatible condition. In the constant environment, the patch always contained 16 hidden pellets per trial, randomly distributed among the 40 cups. Again, in half the trials, the patch was in the compatible condition; in the other half, the patch was in the incompatible condition.

A trial was defined as at least one bird visiting the patch and probing in at least one cup. Daily trials began one half hour after sunrise and continued until approximately 12:30 h which allowed a maximum of 16 trials per day. After the last trial of the day, mixed food (grated cheese, turkey starter crumbs, bread crumbs, and bologna) was spread out on the platform for the afternoon. To give birds extended experience with each type of food distribution, I ran 130 consecutive experimental trials in each environment, with two days in between the two environmental conditions during which time mixed food was available on the balcony in the morning. The variable environment was available first and the constant environment second; time limitations precluded more than one set of trials for each environment.

Data Collection and Analyses

Data were collected from videotapes of the last 60 trials run in each environment. Only data from patches where food was present were used. Pairs of focal birds were selected randomly from among the first four individuals to arrive at a patch, with the constraints that: 1) the second focal bird arrived within four seconds of the first; 2) no pellets had been discovered by another individual prior to the arrival of both members of the focal pair; 3) both members of the pair actively probed cups for pellets; and 4) the second member of the pair to depart did not obtain any pellets after the first bird's departure.

The data collected from each focal pair of birds included: the time at which each member of the pair landed on the patch; the time that each member left the patch; the number of pellets each bird consumed until the time that the first bird left; and the number of birds foraging on the patch at the same time as the focal pair. I also recorded the time to probe in both low and high cups using data from 10 birds in each environment, five birds for each of high and low cups. Because the predictions of the four assessment strategies are based on the assumption of random search (Valone & Giraldeau In press), I determined whether the birds were indeed probing the cups randomly by determining the number of reprobes (cups probed more than once by an individual bird) in the first 30 cups probed, again using data from 10 birds in each environment.

I scored a bird as being the more successful member of the focal pair if it had eaten more pellets than the other bird before one of them departed. Cases where both members of a pair were equally successful were omitted, as were cases of simultaneous departure. To investigate differences in individual foraging success and order of departure from the patch, I compared the observations to the predictions for each of the four assessment strategies under each of the four environment-cup combinations (Table 4.1), using one- and two-tailed binomial tests depending on the predicted order of departure.

Predictions concerning differences in foraging success and extra patch time (Table 4.1) were tested using only those cases where the least successful bird left first. The degree to which members of a pair differed in their foraging success was categorized as "small" or "large" (sensu Valone & Giraldeau In press), using the median difference in success as the cut-off point. These data were analyzed with one-tailed t-tests.

Where necessary, appropriate transformations were carried out on the data before analyses with SYSTAT (Wilkinson 1990). Unless otherwise stated, all values reported in the text are $\bar{X} \pm$ SE.

RESULTS

General Results

I ran a mean of 10.0 (range 5-16) trials per day in the constant environment and a mean of 11.6 (range 6-15) trials per day in the variable environment. Thus, the constant and variable environment's 130 trials were completed after 13 and 11 days respectively. During the last 60-trial period from which data were collected, there was no significant difference in the mean daily temperature between the constant (-12.7 ± 0.5°C) and variable (-10.9 ± 1.4°C) environments (N=20 trials each environment, log-transformed data, t=1.145, df=38, p=0.259).

Of the starlings captured prior to the start of the experiment, 14 were male (89.9 ± 1.1 g), and 17 were female (86.8 ± 1.8 g). Only five of these marked birds were ever seen again, however, and these just occasionally; thus the use of known individuals for data collection was precluded. Starlings generally arrived at the patch within 10-15 min of it being placed out on the platform (constant environment: 6.0 ± 2.5 min; variable environment: 10.9 ± 2.5 min, N=20 trials each). During the trials from which data were collected, there was a slight tendency for more birds to be present on the experimental patch in the variable than in the constant environment (Table 4.2; two-way ANOVA on square-root transformed data, F=3.827, df=1,36, p=0.058). Birds probed a mean of 48.0 ± 7.2 and 40.6 ± 11.1 (N=20 in both cases) cups per trial in the constant and variable environments respectively. Starlings in both environments took significantly longer to probe high cups than low cups (Table 4.2; log-transformed data, F=10.897, df=1,16,

Table 4.2: Mean (± SE) number of birds foraging on the patch as well as the mean time required to probe each cup, the mean latency for the second bird of a focal pair to arrive, and the mean time focal pairs spent together on the patch as a function of the environmental variability and the compatibility between acquiring patch-sample and public information.

	Constant Environment		Variable Environment	
	Compatible	Incompatible	Compatible	Incompatible
Mean number of birds on patch per trial	5.5(0.7)	4.3(1.4)	6.5(1.0)	6.8(1.1)
Mean time to probe each cup (s)	1.3(0.2)	1.7(0.3)	1.2(0.1)	1.8(0.2)
Mean arrival latency of 2nd focal bird (s)	1.5(0.3)	1.6(0.3)	1.4(0.2)	1.7(0.3)
Mean time focal pairs together on patch (s)	60.1(11.6)	84.5(8.9)	57.7(16.5)	59.3(13.7)

p=0.005), presumably as a result of having to bend over further to probe inside the deeper cups. Once the birds located a cheese pellet, handling times were quite short (0.7 ± 0.1 s, N=10).

Due to the poor return rate of marked individuals, it was necessary to use data from pairs of unmarked focal birds: 10 pairs for each of the four environment-cup combinations, one pair per trial. For the variable environment, five pairs of birds were used from each of the poor and rich patch types. Although it is impossible to rule out completely some degree of pseudoreplication, the fact that up to 18 starlings were observed to forage on the patch at one time and that an estimated 30 to 50 starlings were regularly observed to feed on the platform following the last trial of the day suggests that a total of 10 pairs of birds for each environment-compatibility combination was a reasonably conservative sample size.

In over 90% of the focal pairs the second bird arrived within 3 s of the first. The mean arrival latency of second birds did not differ between environments (two-way ANOVA on log-transformed data, F=0.130, df=1,36, p=0.720) or compatibility condition (F=0.914, df=1,36, p=0.345, Table 4.2). Focal pairs foraged together for approximately 1 min before one of the members departed (Table 4.2). Again, the time spent together on the patch was not significantly affected by either the type of environment (log-transformed data, F=2.905, df=1,36, p=0.097) or the compatibility condition (F=1.735, df=1,36, p=0.196).

To determine whether birds in both environments were probing cups randomly, I compared the mean number of reprobes in the first 30 cups probed with the number expected for both random and systematic search. The birds in the constant environment were found to have a mean of 8.2 ± 1.0 reprobes. This was not significantly different from the 8.4 reprobes expected for random search ($t=0.06$, $df=9$, $p>0.2$), and was significantly higher than the zero reprobes expected for systematic search ($t=2.37$, $df=9$, $p<0.05$). Similarly, the birds in the variable environment were found to have a mean of 9.6 ± 0.9 reprobes in the first 30 cups probed. This again was not significantly different from the 8.4 reprobes expected for random search ($t=0.38$, $df=9$, $p>0.2$), and was significantly higher than the zero reprobes expected for systematic search ($t=3.05$, $df=9$, $p<0.02$). Therefore, I concluded that the birds in both environments were probing cups in a random fashion. This random search was likely promoted both by the discovery of food, which would have encouraged a bird to probe more cups and thus increased its probability of reprobes (e.g. Templeton Chap. 3), and by the presence of several other individuals which made it difficult for a bird to follow a set search path (pers. obs.)

Individual Foraging Success and Departure Order

The orders of departure of less and more successful members of focal pairs are presented in Table 4.3. I compared the observed orders of departure to those predicted by each of the assessment strategies, using the binomial test. When the direction was predicted, a one-tailed test was used; when no direction was predicted a priori, a two-tailed test was used. P values reported in Table 4.3 correspond to those comparisons between the observations and the most closely-matching predictions. In compatible foraging conditions, there were no significant relationships between relative foraging success and order of patch departure; in both environments, less successful and more successful individuals left first in an equivalent number of trials (Table 4.3). This finding is consistent with assessment strategies 3 and 4 (Table 4.1). In incompatible foraging conditions, there were significantly more trials where the less successful member of the focal pair left first

Table 4.3: Number of trials in which the bird that departs first is either equally, less, or more successful than the other in each environment-compatibility combination. The p values are based on binomial tests of the predicted orders of departure.

	Constant Environment		Variable Environment	
	Compatible	Incompatible	Compatible	Incompatible
Equally successful	2	1	1	1
Less successful departs first	4	7	4	8
More successful departs first	4	2	5	1
Significance level	$p=1.0^a$	$p=.09^b$	$p=1.0^a$	$p=.02^b$

a: 2-tailed test, b: 1-tailed test.

in the variable environment, and a similar, though non-significant pattern was observed in the constant environment (Table 4.3). These results, therefore, provide support for assessment strategy 4 (Table 4.1).

Difference in Foraging Success and Extra Patch Time

The median difference in foraging success between less and more successful birds was 2.0 pellets in the variable environment, and 1.5 pellets in the constant environment. Therefore, I chose to use 2 pellets as the cut-off point for "large" (>2) and "small" (≤ 2) differences in foraging success when examining the extra patch time spent by the second bird to leave the patch. There was no effect of the magnitude of the difference in foraging success on the second birds' extra patch time in the compatible condition, although the small sample sizes (due to the fact that only cases where the least successful bird left first could strictly be included in the analyses; $N=2$ in each of the large and small differences in success for both environments) weaken this conclusion (Table 4.4). In contrast, when foraging was incompatible, the extra patch time was markedly longer when the birds experienced large differences in foraging success than when they experienced small differences in success, and this was true for both environments (Table 4.4). These results are therefore only consistent with assessment strategy 3. It is worth noting that even if all data are included in the four analyses, the same conclusion would have been reached. There was no relationship between foraging success and extra patch time in the compatible condition in either the constant ($t=-1.179$, $df=8$, $p=0.136$) or variable ($t=1.661$, $df=8$, $p=0.135$) environments; and extra patch time was related to differences in foraging success in incompatible conditions in both the constant ($t=-9.967$, $df=8$, $p<0.001$) and variable ($t=-3.126$, $df=8$, $p=0.007$) environments.

Table 4.4: Mean duration (s) of the more successful focal bird's extra patch time before departure from the test patch as a function of the extent of within-pair difference in foraging success for each environment-compatibility combination. Results of one-tailed t-tests on log-transformed data, testing the prediction that the more successful bird should stay longer when the difference in success is "large" (>2 pellets), are shown below each pair of mean durations.

	Compatible		Incompatible	
Difference:	≤ 2 pellets	> 2 pellets	≤ 2 pellets	> 2 pellets
Constant Env.	6.4 ± 3.8	5.2 ± 3.0	1.6 ± 0.8	37.4 ± 3.7
t-test	t=0.208, df=2, p=0.427		t=-8.361, df=5, p<0.001	
Variable Env.	2.8 ± 2.5	3.4 ± 3.3	7.5 ± 0.8	26.0 ± 9.9
t-test	t=0.027, df=2, p=0.491		t=-3.455, df=6, p=0.007	

DISCUSSION

This study has shown that group foraging starlings do indeed make use of public information to help them assess the quality of a resource patch. However, the results do not allow me to determine which of assessment strategies 3 and 4 the birds may have been using. The results of departure order suggest that the starlings were using a combination of patch-sample, pre-harvest, and public information (assessment strategy 4) to assess the quality of the experimental resource patch. In the variable environment, differences in individual foraging success were only related to the order of patch departure when the acquisition of personal and public information was incompatible; here, less successful members of focal pairs left first significantly more often than more successful birds in both environments. In the constant environment, however, differences in individual foraging success were not significantly related to the order of departure in the incompatible condition. Although this lack of significance was likely an effect of small sample size, it indicates that pre-harvest information was being used. In the compatible condition, foraging differences had no influence on the order of patch departure in either environment, suggesting that all birds had similar estimates of patch quality at their departure as a result of sharing each other's information on foraging success (Clark & Mangel 1986, Valone 1989).

The results of extra patch time, however, suggest that the starlings were using only patch-sample and public information (assessment strategy 3). When acquiring public information was incompatible with acquiring patch-sample information, the degree to which members of focal pairs differed in foraging success was positively associated with the extra time spent on the patch by the more successful individual; and this was true for both environments. This indicates that there was no sharing of information and that only personal patch-sample information was being used. In the compatible condition, on the other hand, the extra time spent by the more successful birds was not related to the degree to which members of focal pairs differed in foraging success. Like the results on departure order, therefore, this finding again implies that the birds were paying attention to the foraging activities of neighbouring birds. Thus, they had similar estimates of patch quality at their departure despite individual differences in personal foraging success.

It is worth considering the possibility that the results of extra patch time obtained under incompatible foraging conditions may have been due to some effect of cup height other than the reduced visibility of one's foraging companions. Both a reduced ability to manoeuvre on the high cups, and a reduced ability to scan for predators when probing in high cups might well be expected to influence a bird's foraging decisions under these conditions. For example, one potential effect might have been an increase in the critical departure threshold (Brown 1988, Valone 1989) such that birds would tend to depart from the patch earlier, at higher estimates of patch quality. However, if this did indeed occur, it should have had the same effect on both more and less successful individuals, such that less successful birds would still be expected to depart first. In fact, I found that focal pairs tended to spend slightly more time together on incompatible than on compatible patches (Table 4.2), which suggests that the critical departure level did not increase under incompatible conditions and that the birds were just as willing to forage in high cups as in low cups.

Compatibility between Personal and Public Information

The lack of public information use in the incompatible condition suggests that although the cost of patch assessment may influence whether public information will be required (Templeton Chaps. 2 and 3), the compatibility between personal and public information will determine the degree to which public information will actually be used. The fact that birds did not depart simultaneously when foraging in the compatible condition implies that there was still some degree of incompatibility between sampling cups and watching others, even in this condition. Ironically, this incompatibility could simply have been an effect of group size. Valone (1989) points out that in pairs or very small groups, it might be possible for a bird to observe all the successes of others while exploiting a patch. In larger groups, however, it would be difficult to keep track of the activities of all other individuals, particularly when the positions of some individuals might block the view of others and interfere with the transfer of public information.

Under natural foraging conditions, there are several possible factors which might limit the transfer of information between individuals. In addition to physical barriers such as tall grasses or boulders, the size of the prey items may make it difficult to recognize the foraging success of a neighbour (e.g. Valone & Giraldeau, pers. comm.). As well, the difficulty of the foraging task could influence the ease with which a forager can pay attention to the activities of others and still forage with a reasonable level of efficiency (e.g. Metcalfe 1984, Lima 1987). In a field study on predator vigilance, for example, Lawrence (1985) allowed European blackbirds (*Turdus merula*) to forage on an experimental patch where the prey were either cryptic (matching the foraging substrate) or conspicuous (contrasting with the substrate). Lawrence (1985) found that during the difficult (cryptic) foraging task, the blackbirds reduced their scanning rates for predators, suggesting that the selective attention required for efficient foraging reduced the compatibility between searching for food and watching for predators in much the same way that the high cups in my experiment reduced the compatibility between searching for food and watching others.

In the field, it might be predicted that the departure decisions of individuals in foraging groups may depend on ecological factors such as the characteristics of the foraging environment or the foraging task. Brownsmith (1977), for example, showed that the rate of movement of foraging starling flocks was more rapid and the length of time spent in given locations was shorter when the birds were foraging in short grass (< 6 cm) than in taller grass. The reasons for this behaviour pattern were not clear in Brownsmith's (1977) study, but it is consistent with the use of public information in compatible conditions (short grass). If visibility is indeed necessary for the use of public information, greater differences in individual departure times should be expected when foraging conditions are incompatible than when they are compatible. If group cohesion is also important, however, (e.g. Cody 1971, Hutto 1988) the simultaneous departure of group members from a patch may occur even when foraging conditions are incompatible. In such cases, individual foragers may have to rely on alternative cues such as auditory signals between group members in order to remain with the group (Valone, pers. comm.).

This field experiment is the first study to provide evidence that foragers use the successful foraging activities of others to assess the quality of a resource patch. It supports the empirical suggestion of Tinbergen and Drent (1980) that starlings may be paying attention to the sampling activities of others when assessing patch quality, and it also confirms the theoretical suggestions of Clark and Mangel (1984, 1986) and Valone (1989) that foragers share information to aid their estimations of patch quality. These results extend the findings of Templeton (Chap. 3), which demonstrated that captive starlings recognized the unsuccessful foraging activities of conspecifics and used this information in combination with both their own patch-sample information and their pre-harvest information to aid in their assessment of experimental patches. Taken together, these studies show that when personal and public information are compatible, group foraging starlings are alert and sensitive to the foraging rates of flock members and will use this information in combination with their own to direct their patch departure decisions.

CONCLUSIONS

This thesis has shown that in order to understand both how individuals make decisions in foraging groups and what the consequences of their foraging decisions will be, we need to understand the various kinds of information they have available to them. The ability to recognize different types of public foraging cues allows starlings to compete more effectively within a foraging group. They respond more quickly to the foraging activities of others, and thus obtain higher scrounging returns from profitable patches than birds lacking this ability. This has important implications for information use in producer-scrounger systems, where either equal sharing of discovered resources or a "producer's advantage" are generally assumed; when informational cues are available, a "scrounger's advantage" may also be possible. The ability to use different foraging cues also allows foragers to respond selectively to public information by avoiding unprofitable sites and thus saving valuable foraging time. This finding questions the implicit assumption of earlier group foraging studies that foragers either cannot recognize or simply do not notice a lack of foraging success in others.

This thesis has provided some of the first detailed examinations of the process of patch assessment in foraging groups. My experimental two-patch system has proven itself to be an effective tool in the study of information acquisition both in solitary and group foragers, at least when the correct time intervals are taken into consideration. I have also illustrated the importance of understanding the various constraints on a forager's ability to acquire information. When the structural features of a foraging patch constrain a starling's ability to sample the patch in a systematic fashion, the cost of patch assessment is increased. The starling responds to this constraint by reducing its acquisition of personal sampling information when alone and by taking advantage of public sampling information when in the presence of a sampling conspecific. This is the first experimental evidence for the use of public sampling information in a patch assessment context, and it opens the way for future studies examining other factors which may influence the use of public information in foraging groups, such as the effect of group size.

Finally, my thesis has demonstrated that the compatibility between personal and public information can also impose a constraint on the ability of a forager to acquire different types of patch assessment information simultaneously. Whether this constraint is due to impeded vision, the size of the prey items, or the difficulty of the foraging task, my findings suggest that the patch departure decisions of individuals in foraging groups will depend at least in part on the characteristics of the foraging environment. I have shown that when the acquisition of personal and public information is compatible, group foraging starlings are alert and sensitive to the foraging rates of flock members and will use this information not only to direct their scrounging decisions, but to direct their patch departure decisions as well.

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