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Are Flocks of Specialists  
More Efficient Foragers Than Flocks of Generalists?  
A Test of the Skill Pool Hypothesis

Nancy R. Ennis

A Thesis  
in  
The Department  
of  
Biology

Presented in Partial Fulfilment of the Requirements  
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## Abstract

### Are Flocks of Specialists More Efficient Foragers Than Flocks of Generalists? A Test of the Skill Pool Hypothesis

Nancy R. Ennis

Group foraging experiments involving 16 captive spice finches (*Lonchura punctulata*) foraging in flocks of four individuals in indoor aviaries were conducted to determine whether groups of complementary specialists will feed more efficiently than groups composed of generalists. Finches were pre-trained either as specialists on one patch type or generalists capable of searching for food in two patch types. Results of flock feeding experiments show that specialist birds fed at a significantly higher rate than generalists. However, specialists neither searched patches more quickly nor did all specialists have greater patch opening ability. Half of the birds trained as generalists exhibited a strong significant bias for one of the two patch types. Nevertheless, consistent with the specialist-generalist flock comparisons, birds trained as generalists but that specialized did not achieve any higher patch opening ability, searching rates, nor overall feeding rates than unspecialized generalists. Evidence suggests that the enhanced feeding rates in skill pools could be due to possession of more efficient joining strategies, not to an enhanced patch searching efficiency as the jack-of-all-trades principle would predict.

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## Introduction

### I. Diet Breadth and Foraging Efficiency

To survive, animals must consume prey without falling prey themselves. Exploitation of prey has given rise to a wide variety of behavioural adaptations. Some animals exploit a diverse range of food items and habitats, while others concentrate their foraging on a narrower range of items and habitats. These foraging strategies are known as generalist and specialist strategies respectively (Schoener 1971).

Ecologists make a basic assumption about the costs and benefits of generalist and specialist foraging strategies. This assumption is known as the jack-of-all-trades principle (MacArthur & Pianka 1966). For any resource exploited by a specialist and a generalist, the jack-of-all-trades principle predicts that the generalist's exploitation of that particular resource will be less efficient than the specialist's. By using only a few foraging skills, specialists can become very efficient at obtaining food using those skills (Pietrewicz & Kamil 1981, Persson 1985). The jack-of-all-trades principle has been invoked for interspecific comparisons (e.g. Drummond 1983, Lavery & Plowright 1988), which assume that selection over generations has allowed increased foraging efficiency via feeding specialization. It has also been used for intraspecific comparisons (e.g. Werner et al. 1981, Werner & Sherry 1987), where specialization is achieved within an individual's lifetime, often as a result of learning. In both cases specialists benefit from a greater foraging efficiency, but at the expense of increased

vulnerability to fluctuations in food supply resulting from their narrower diet range (Boag & Grant 1981, Partridge & Green 1985).

## II. Diet Breadth in Group Foraging

### **A) Social Learning**

Group foraging may provide animals with the opportunity to increase their foraging benefits by learning about potential new food sources from other group members (Krebs et al. 1972). This social learning may occur through several mechanisms (see reviews by Davis 1973, Galef 1976): (1) social facilitation, in which the foraging behaviour of one animal releases identical behaviour in an observing animal (Thorpe 1956), (2) local enhancement, in which the observer's attention is directed towards the area in the environment where an animal is feeding (Thorpe 1956), and (3) observational learning (Klopfer 1961, Lefebvre & Palameta 1988), or true imitation (Thorpe 1956), in which the observer copies precisely a novel technique (see review of imitation by Davis 1973). Whichever mechanism is responsible, social learning implies that an animal exposed to others will increase its repertoire of foraging skills, thereby becoming more of a generalist. In spite of increased foraging generalization and expectations of the jack-of-all-trades principle, social learning can potentially increase foraging efficiency if it allows individuals access to an increased density of food. For instance, Krebs (1973) proposed that individuals in multispecies flocks have a foraging advantage over those in single species flocks due to social learning. In his study, two species of chickadees, *Parus atricapillus* and *P.*

*rufescens*, foraging in the same artificial environment modified their searching behaviour based on information they obtained from watching the foraging activity of individuals of the other species, though the type of social learning that occurred was not investigated. A naive individual of one species was paired with a bird from the other species that had been trained to forage in a novel type of food patch containing a single food item. The naive bird was more likely to discover the patch type when paired in this manner than naive birds paired with another naive bird. Members of different species, which likely feed in different places or on different food types, can therefore learn from one another about novel feeding places in mixed flocks. This may result in increased availability of food and thus increased foraging rates.

#### **B) Food Scrounging**

Several authors have suggested that social learning, primarily social facilitation, would be an important advantage of flocking for birds (e.g. granivores) whose food is heterogeneously distributed such that the food is found in rich clumps or patches (Crook 1965, Lack 1968, Krebs 1973). Social facilitation would more likely lead to social learning if the flock forages in areas where more than one food clump is located. But under this type of patchy food distribution, group foraging may also allow animals to obtain (scrounge) all or a share of the food discoveries of others without having to use the behaviour necessary for its discovery (Barnard & Sibly 1981). In such cases, animals also potentially increase their diet breadth, but by scrounging, not by social learning.

Food scrounging (Barnard & Sibly 1981) may take the form of

kleptoparasitism or joining. Kleptoparasitism (see review by Brockmann & Barnard 1979) occurs when an individual "steals" the food produced (i.e. discovered) by another, while joining occurs when individuals scramble for shares of food patches found by one individual (Giraldeau et al. 1990). Two main factors seem to influence whether kleptoparasitism or joining is likely to occur: characteristics of the food source and phenotypic asymmetries between individuals (Giraldeau 1984, Giraldeau et al. 1990). Kleptoparasitism is more likely to occur if the food item is relatively valuable, that is, rare, indivisible, high-quality, or obvious (Brockmann & Barnard 1979). For example, in winter, black-headed gulls (*Larus ridibundus*) more often take larger, more noticeable worms captured by less agile lapwings (*Vanellus vanellus*) rather than from golden plovers (*Pluvialis apricaria*) (Barnard & Thompson 1985). Large inter-individual differences due to physical factors such as size (e.g. striped parrotfish, *Scarus iserti*, Clifton 1989) or social factors such as a dominance hierarchy (eg. Harris' sparrows, *Zonotrichia querula*, Rohwer & Ewald 1981) can also foster kleptoparasitism and prevent smaller or subordinate individuals from gaining access to food. However, when food patches are divisible and there are no marked inter-individual differences, kleptoparasitism may give way to joining.

Since an individual can rarely hide its feeding activity (Giraldeau 1984), group foraging may provide many joining opportunities. Feeding activity may attract others in the group to the vicinity of the feeding individual. This local enhancement (see Section II.A Social Learning) is commonly reported in birds (Krebs et al. 1972, Rubenstein et al. 1977, Barnard & Sibly 1981, Waite 1981, Pöysä 1987) and, with

the numerous examples of joining both in vertebrate carnivores (Kruuk 1972; Schaller 1972) and birds (Rand 1954, Murton et al. 1972), suggests that joining may be a common group foraging strategy.

### **C) Interaction of Social Learning and Joining**

Joining, as well as social learning, may allow group-foraging animals to feed from a wider diversity of food types. Increased diversity likely leads to a higher density of available food, such that joining may result in higher foraging efficiencies for group foragers than for those foraging solitarily. However, these two mechanisms of increased diet diversity (joining and social learning) may not be compatible.

Recent evidence indicates that, at least in pigeon flocks (*Columba livia*: Giraldeau & Lefebvre 1987, Giraldeau & Templeton 1991), pairs of zebra finches (*Taeniopygia guttata*: Beauchamp & Kacelnik 1991), and groups of capuchin monkeys (*Cebus apella*: Frigaszy & Visalberghi 1990), joining can inhibit an individual from learning a new food-finding skill. Consequently, in groups where joining occurs (i.e. food is clumped), adoption of a new foraging skill by social learning may be less likely to occur. Partridge & Green (1987) also note that their jackdaws, *Corvus monedula*, may have been slow to learn foraging tasks because they often begged food from one another, and thus did not need to learn the task to obtain food.

Social learning and joining will have slightly different consequences on an animal's foraging efficiency. Social learning allows each organism to search for and find a wider range of food items. Each forager generalizes its diet and gains from the increased number of exploitable items, but must contend with a lower generalist

efficiency at exploiting each item. Joining, on the other hand, also provides foragers with an increased diversity of exploitable items, but because the range of searching behaviour remains specialized, Giraldeau (1984) predicts that the specialized foragers can achieve greater foraging efficiency than generalists.

### III. The Skill Pool Hypothesis

Giraldeau (1984) suggested that intraspecific groups contained sufficient inter-individual differences to allow specialized individuals within the group to gain a generalist's diet breadth by joining. He argued that groups would act as "skill pools" whenever: 1) individuals specialize on searching for different food items or looking in different places, and 2) individuals find (produce) food and are able to join food discoveries made by other specialists in the group (Giraldeau 1984). He implied that individuals would tend to join at those types of food patches that they cannot produce themselves. If the specialized searchers form a skill pool, he argued, the jack-of-all-trades principle predicts that they would have higher foraging efficiencies than generalists, but because they join, would end up with the same diet breadth as a group of generalists.

In an earlier section (II.B Food Scrounging), I have shown that joining is a common foraging strategy among group foragers. Formation of a skill pool, therefore, requires only that individuals within groups adopt and maintain strong individual differences in foraging behaviour.



#### IV. Evidence for Skill Pools

##### **A) Evidence for Intraspecific Differences in Foraging Behaviour**

The literature supporting the ubiquity of individual specialization is extensive (see reviews by Partridge & Green 1985, Magurran 1986). Unfortunately, intraspecific variability in behaviour has often been treated as the result of errors due to poor experimental design and an uninteresting problem to be overcome (Magurran 1986, Slater 1981). Optimal foraging theory (Stephens & Krebs 1986) in particular addresses the behaviour of "typical" individuals and ignores individual variability. However, an increasing number of studies focus on individual differences in foraging behaviour (e.g. Giraldeau & Lefebvre 1985, McCleery & Sibly 1986, Templeton 1987, West 1988). Maynard Smith (1982) identifies and discusses seven mechanisms which can give rise to variable behaviour. They are broadly categorized as genetic or non-genetic. However, in practice it is extremely difficult to disentangle the effects of genes from non-genetic effects such as environment and development in behaviour (Magurran 1986). As a result, several authors (Partridge & Green 1985, Magurran 1986) discuss three functional mechanisms as being the most important means by which individual differences in foraging behaviour can develop and be maintained, noting that genetics may affect any or all of them. These mechanisms are: 1) a variable environment, 2) the behaviour of conspecifics, and 3) phenotypic differences (including differences due to genes). I will briefly discuss these mechanisms, noting recent papers which may be appropriate examples of each. I will place most emphasis on the third mechanism, phenotypic differences, and in particular, individual

learning.

### 1. Variable environment

The nature of the food may vary spatially. Spatial variation may be such that individuals encounter only one type of food and thus geographic variation in behaviour may result (e.g. Hedrick & Riechert 1989). Additionally, the characteristics of the food types themselves, such as size or defense capability, within an area at one time may be dissimilar enough to require different feeding behaviour (e.g. Persson 1985). Maximum exploitation of one food type may interfere with the exploitation of other types within that area. For example, the ability of jays (*Cyanocitta cristata*) to detect, on slides, one cryptic moth species does not improve when slides of another cryptic moth species are randomly intermixed (Pietrewicz & Kamil 1981). Jays were more accurate when slides of only one species were presented. As a result of a heterogeneous or variable environment, differences within a foraging group may occur (e.g. Werner & Sherry 1987).

### 2. Behaviour of conspecifics

The profitability of a particular foraging behaviour may be dependent upon the behaviour of others in the group. The more individuals exploiting a food resource, the lower the payoff to each exploiter. At some point it will pay some individuals to exploit other food types. This sort of negative frequency-dependence can lead to evolutionarily stable strategies (Maynard Smith 1982, Parker 1984). In a population of initially identical phenotypes the stable mixture of behavioural strategies could come about by frequency-dependent selection acting to maintain the frequency of

strategies at an equilibrium, where the costs and benefits to each are equal (e.g. Rohwer & Ewald 1981).

### 3. Phenotypic differences

Phenotype differences may cause particular food items or foraging methods to be more profitable than others. Individuals may be constrained by age, size or sex to particular subsets of the species' behavioural foraging methods (e.g. Troyer 1984, Hockey et al. 1989). A skill pool cannot operate if searcher/joiner roles are fixed within individuals, as they might be if foraging differences were due to phenotypic differences such as age or sex. This is because operational skill pools require that animals search patches on some occasions and join at patches on other occasions. Any factor that prevents this, such as a dominance hierarchy based on physical differences that affects priority of access to food (bib and crown colour in Harris' sparrows, Rohwer & Ewald 1981), would make it unlikely for a skill pool to operate. Phenotypic differences due to individual learning may be particularly important for the skill pool hypothesis, since individual learning necessitates a certain degree of behavioural flexibility which might allow animals to respond more readily to the behaviour of others or to changes in the food supply.

Individual learning may magnify initial individual differences or may cause individuals to acquire behaviour simply due to different experiences or to chance. Edwards (1989) has provided evidence of the effect of assorted foraging experience. During the postfledging period, differences in diet choice among young osprey (*Pandion haliaetus*) were strongly related to their first few successful encounters with

fish prey and did not change even though the abundance of each fish species later changed. Further evidence for a strong influence of individual learning on diet choice is provided by the similarity in diet choice exhibited by sibling osprey. The probability that this similarity was due to chance was low. Therefore, Edwards concludes that some form of learning through social contact was probably responsible for the consistent diet choice. The effect of the genetic relatedness between the siblings on this phenomenon is not discussed, though it seems a likely alternative explanation. Foraging experience also has the potential to inhibit learning. As discussed in section II.C, the acquisition of a novel skill by naive pigeons was inhibited to a large extent when they could obtain food from the discoveries of experienced demonstrators and when the experienced demonstrator did not feed from its own food discovery (Giraldeau & Lefebvre 1987, Giraldeau & Templeton 1991).

There is no reason to doubt that these three mechanisms cannot function simultaneously (Maynard Smith 1982, Partridge & Green 1985). However, to determine the mechanism(s) responsible for generating inter-individual differences, one must be able to assess the fitness accruing from each behaviour and, even more difficult, one must be able to determine the cause of any fitness difference associated with the alternative behaviours. Despite the difficulty in determining the mechanism underlying individual differences, most studies comparing foraging individuals within a population find considerable variation (Giraldeau & Lefebvre 1986, West 1988; see references in Heinrich 1976, 1979, Werner et al. 1981, Werner & Sherry 1987).

## **B) Direct Evidence for Skill Pool Formation**

Given the widespread documentation of individual foraging specializations and the evidence that joining is common, it is likely that skill pools can exist in nature. Giraldeau & Lefebvre (1986) provide experimental evidence for the formation of a skill pool. They explored individual foraging differences and the producing (finding a seed-containing patch) and joining system of a captive flock of 17 feral pigeons. The flock was exposed to three food patch types sequentially and the patch types each individual produced were noted. Individuals tended to specialize on producing a single type of patch. A bird's ability to produce one patch type was not an effective predictor of its ability at producing another type. In one part of the experiment, producers were removed in stages from the flock to determine whether producer-joiner relationships were fixed as a result of individual differences in learning ability. As producers were removed, birds which had previously discovered few or no food patches became producers. Producing and joining roles in the flock appeared to change depending on the patch type and flock composition. Although records of the joining frequency of each flock member were not kept, a bird that did not join at a patch type it did not search would have been extremely hungry since experiments involving a given patch type were run in a single series over several days. It is likely therefore that individuals benefited from the different producing skills of others in the flock. The experiment examined the potential for a skill pool under conditions analogous to temporal variation in food type because the three food patch types on which some individuals specialized were never presented simultaneously to the flock.

A skill pool, however, could also operate under conditions in which various food types are available simultaneously, such as those in Partridge's work with captive solitary great tits (*Parus major*, 1976), especially if the exploitation of each food type requires a relatively different behaviour. Different food source types are often available simultaneously under natural conditions (Rubenstein et al. 1977, Werner & Sherry 1987). Evidence for widespread joining and marked individual differences, taken with the experimental results of Giraldeau & Lefebvre (1987), suggest that the formation of skill pools within foraging groups is likely to be common. However, no published studies provide data demonstrating that skill pools can circumvent the jack-of-all-trades principle. Since Giraldeau & Lefebvre (1987) did not measure the foraging efficiency of their pigeons it remains unknown whether their birds would have achieved greater foraging success than generalist birds under the same conditions.

#### V. Objectives of the Present Study

The primary objective of this study is to test whether specialist foragers within a skill pool feed more efficiently than generalists in a group searching the same food types. To answer this question, I designed experiments with small captive flocks of spice finches (*Lonchura punctulata*). I ascertained the searching and joining patterns of individuals within both skill pools and generalist flocks. This allowed me to determine whether specialist and generalist individuals acted as expected by Giraldeau's (1984) skill pool hypothesis, and whether any subsequent difference in

foraging rates between the flocks were due to differences in the searching and joining patterns within flock types. Specifically, I investigated whether birds trained individually to be generalist searchers behaved as such in flocks and whether specialist searchers in the skill pool flock preferentially joined birds that searched patches of the type they could not search themselves.

Finally, I compared the foraging efficiencies of individuals in skill pool and generalist flocks. If the skill pool provides the advantage hypothesized by Giraldeau (1984), then skill pool finches should feed more quickly than generalist finches. An increased feeding rate, which is based on both searching and joining components and is thus a reflection of the food-discovering efficiency within the flock, should ensue because all specialists are searching patches more rapidly. As a result, both a forager's own searching efficiency and joining opportunities provided by others would be enhanced.

## Spice Finches

Spice finches, also known as the nutmeg mannikin, spotted munia, and rice-bird, belong to the Estrildidae. This is a large, recently derived, and very successful family within the Passeriformes (Immelmann 1982). Estrildids occur naturally in the old world only, with most of the 140 species inhabiting tropical or subtropical regions. Estrildids are good experimental subjects for study in captivity, as many species are commonly kept as cagebirds, notably the Java sparrow (*Lonchura oryzivora*), the spice finch (*L. punctulata*), the Bengalese finch (*L. striata*) and the zebra finch (*Taeniopygia guttata*) (Goodwin 1982).

Spice finches inhabit South-east Asia, the Philippines, and the Malay Peninsula. The species has been introduced to Singapore Island (Goodwin 1982), Mauritius, Reunion, the Seychelles, Hawaii, and Australia (Goodwin 1982, Immelmann 1982), and is so successful in towns where it has settled in northern Queensland, Australia that native species of grass-finches have been displaced (Immelmann 1982).

Spice finches exploit a wide range of habitats such as open or semi-open country with bushes or trees, secondary forest with grass patches, gardens and town parks, where they feed on the half-ripe and ripe seeds of grasses (Goodwin 1982). In common with the majority of estrildids, they pick seeds off the ground or hang from the plants themselves to obtain the seeds (Goodwin 1982). Though considered grass-seed specialists, they will feed on the seeds of herbaceous plants (Goodwin 1982,



Immelmann 1982), and there are records of occasional feeding on various kinds of human waste (Immelmann 1982), and even on dried remains of animals killed on the road in parts of Australia (Bell 1961). Seeds are husked before eaten and the crop is used as a storage organ. Laboratory studies (L.-E. Trudeau, unpubl. ms. Concordia University) have shown that the finches will fill their crops near the end of the photophase. Presumably, due to their small body mass (12-18g), this schedule provides them with energy to survive over the scotophase, when they cannot forage. Because the crop is used as a nightly food-storing organ, food deprivation before foraging experiments often requires up to 20h, without considerable loss of body mass.

Spice finches are typically found in monospecific flocks of up to several hundred birds (Immelmann 1982, Goodwin 1982), though small numbers have been observed joining flocks of other species of estrildids. They feed and sleep together and breed in dense colonies. Spice finches exhibit behaviour patterns typical of most Estrildids (Goodwin 1982). They build unwoven covered nests, with an extended side entrance, with pieces of grass. The males gather the nest material, but both sexes help build the nest. The female solicits copulation by quivering her tail, in contrast to the majority of non-estrildid passerines, in which wings are quivered (Immelmann 1982). It is not known whether spice finches are monogamous but it is likely, since most estrildids form stable pair bonds, stronger than the majority of passerines (Immelmann 1982). Both sexes incubate and brood the young. Characteristics not peculiar to spice finches or estrildids are that the males and females are

morphologically similar and that they appear to breed opportunistically in the wild, but most young are reared during or at the end of the rainy season. The rainy season occurs at various times of the year over their range. Their life-span in nature is unknown but I have kept non-breeding birds of unknown age for 5 years.

Spice finches are suitable subjects for my experiment for two main reasons. First, they are extremely social birds that forage in groups with little aggression, at least in the laboratory (Moynihan & Hall 1954) and do not form strong dominance hierarchies that affect access to a source of food (Giraldeau et al. 1990). Second, when Giraldeau et al. (1990) investigated the effect of divisible food patches on producing and joining payoffs, individuals did not consistently specialize in either producing or joining.

## Methods

Before observing flock-feeding behaviour I sexed the subjects, determined the amount of food to be used during trials, designed two patch types, trained individual birds to forage on either one of two experimental patch types (specialists) or both patch types (generalists), and measured the extent of any patch preference of generalists following their training. Once trained, the birds were combined to form either skill pools or generalist flocks and given the opportunity to forage from an environment offering both patch types simultaneously. Three measures of individual foraging efficiency within the flocks were compared.

### I. Subjects

Spice finches were obtained from a commercial supplier in August 1988 and May 1989 as mixtures of juveniles and adults. They were kept indoors in cages of 5-8 birds with a photoperiod of 8L:16D hours. Water, spray millet, and a seed mixture containing white millet, red millet, and canary seed were available to them *ad libitum*. Only adults were used as experimental subjects.

#### **A) Sexing the Birds**

It was important to sex the birds in order to control for any potential sexual differences in foraging behaviour. Because spice finches are sexually monomorphic, they were sexed behaviourally. Only males are known to "jingle", a vocalization accompanied by a distinctive display involving feather ruffling (Moynihan & Hall

1954, Immelmann 1982). The song occurs throughout the year and can either be given during courtship or solitarily. Females do not jingle, but exhibit distinctive copulation solicitation. Jingling was taken as evidence of maleness while solicitation and/or the absence of jingling was evidence of femaleness.

Birds were sexed in two steps. First, groups of variable size were observed *ad libitum* and any individual seen in the jingling display was removed and deemed male. Second, the remaining birds were observed for 20min daily on three consecutive days. Any birds that had not jingled or had solicited copulations during these observation periods were considered female. None of the birds deemed female were seen to jingle during the subsequent individual training or experimentation.

#### **B) Spice Finch Satiation Levels**

I performed an experiment to ascertain the quantity of seeds that a hungry spice finch would eat before ceasing to forage in order to calculate an appropriate patch-stocking density for the trials.

Eight adult spice finches of each sex were weighed and placed in cages in same-sex pairs. I recorded, from behind a one-way mirror, the number of seeds a bird that had been food-deprived for 16-20h ate from a pile of white millet seeds, until it no longer fed for three consecutive minutes. In total, two to three feeding bouts were recorded per bird.

There were no sex differences in satiation level. Therefore, the data for males and females were pooled. Spice finches ate  $123.0 \pm 11.6$  seeds ( $\bar{x} \pm SE$ ) before reaching satiation. In flock trials I wanted to minimize the effect of decreasing

hunger over trials during the same day, yet also wanted to avoid the weakening effects of prolonged food deprivation which, due to their small size and thus fast metabolism, could occur very quickly. Therefore, I chose a total seed number for food patches that was between 50 and 75% of the measured satiation level. These seeds were then evenly divided among the patches and among the three daily trials. Fourteen seeds/patch for eight patches corresponded, after three trials, to 68% of the satiation level, assuming all birds in a flock of four individuals shared seeds equally.

## II. Apparatus

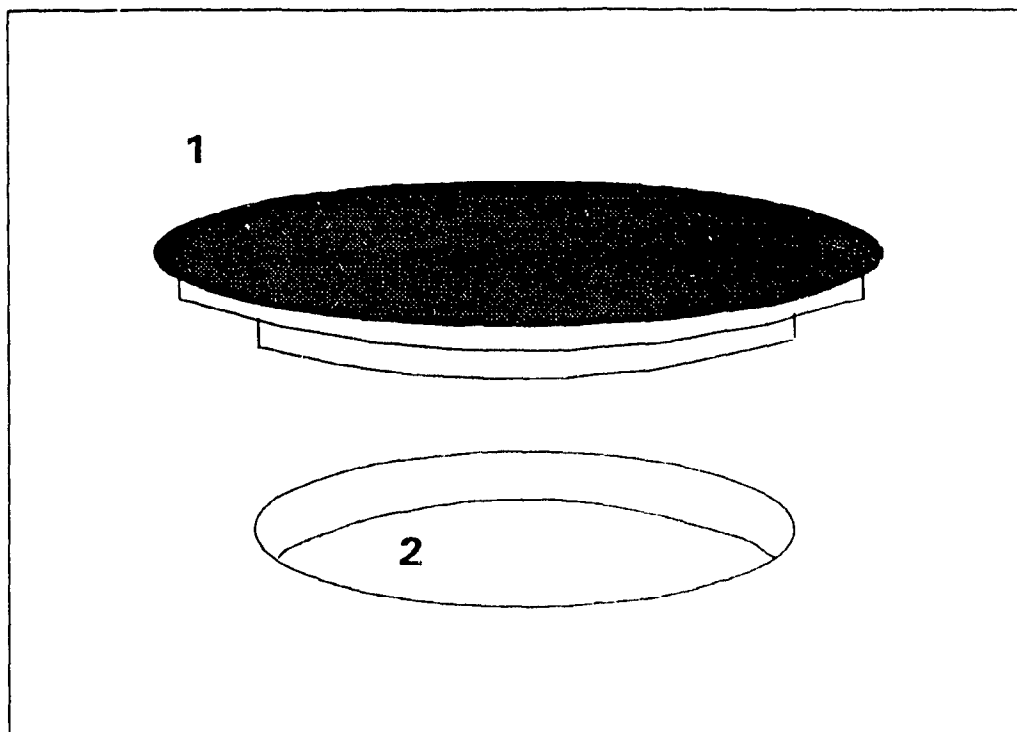
### **A) Food Patch Types**

Two types of food patches, wells (Fig. 1a) and stalks (Fig. 1b) were used. A well consisted of a circular depression in plywood, 1cm deep and 4cm in diameter. Wells were fitted with a plug made of a cardboard circle slightly less than 4cm in diameter so that it fit into the well. A circular 4.8cm diameter piece of cardboard was attached to the plug and prevented the birds from seeing the contents of the well before the plug was removed. A circular 5.4cm diameter piece of black cardboard topped the plug, providing the finches with a small lip that they could grab onto.

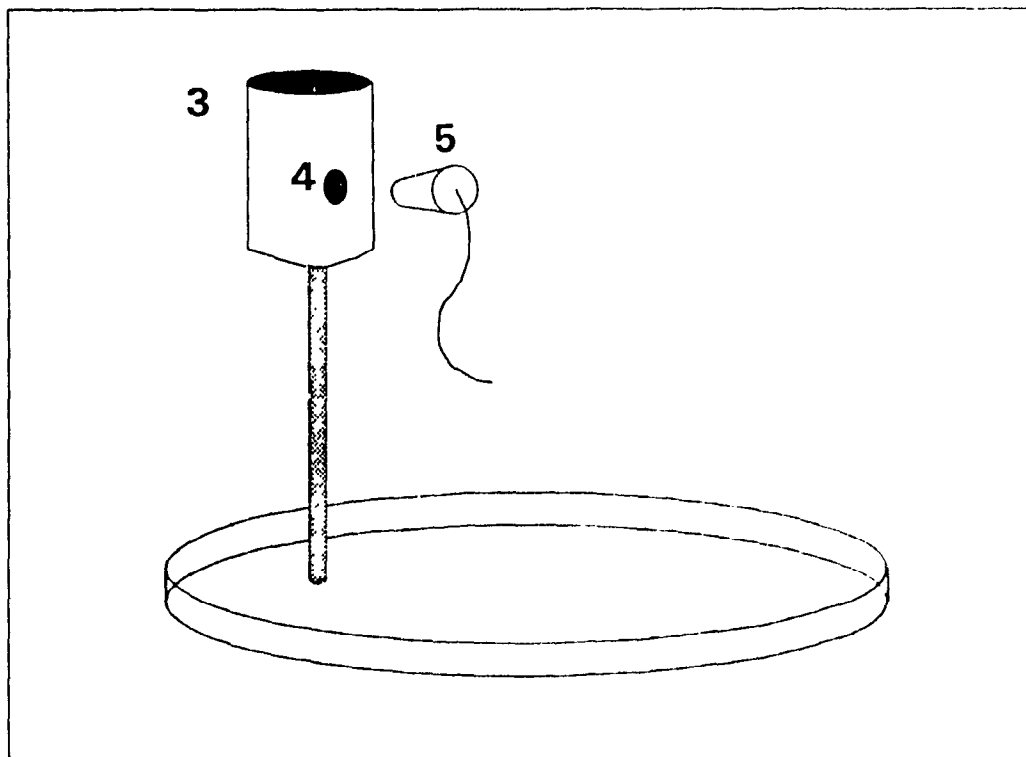
A stalk consisted of an elevated (10.0cm) seed holder that released seeds into a 8.5cm diameter plastic petri dish directly below. The seed holder consisted of a small (0.6cm) cylindrical seed chamber drilled diagonally into a 1.8 x 3.0cm piece of wooden dowelling. Seeds were prevented from falling out of the chamber by a small cork stopper fitted into its aperture. A 7.0cm string attached to the stopper allowed

Figure 1. Food patch types: a) well; 1 = cardboard plug, 2 = well, b) stalk; 3 = seed holder, 4 = seed chamber, 5 = cork stopper. Note that the diagrams are on different scales.

(a)



(b)



birds to pull the cork out, thus releasing the seeds from the chamber into the petri dish, which was lined with fabric to reduce the extent of dispersion of the seeds around the dish.

## **B) Foraging Grids**

Individual training and any individual assessment of patch opening proficiency was measured using a small training grid that could fit into individual holding cages. These square grids (24cm<sup>2</sup>), made of pieces of 1cm thick plywood, contained four equidistant patches, two of each type.

For flock feeding trials, I used a larger 82 x 71cm aviary grid. The aviary grid contained 21 wells and 21 stalks arranged in six rows of seven equidistant patches (10.5cm between centre points). Patch types were alternated between and within rows.

## III. Training the Birds as Specialists or Generalists

The objective of training was to produce three kinds of birds: stalk specialists, well specialists, and stalk-well generalists. The training consisted of three phases: 1) habituating the birds to feed on the training grid, 2) shaping the birds (rewarding progressively closer approximations of the desired behaviour) to search the patch type(s), and 3) ensuring that the birds would continue to search patches for the low reward ratio to be encountered in the flock-feeding trials.

1) Habituating to the training grid. As spice finches are very neophobic, the grid habituation sessions were conducted with flocks of six birds maintained in small



cages. These flocks were made up of four naive birds (two males, two females) that would be used in the flock-feeding experiment, plus two experienced companion birds. Birds were presented with the opportunity to feed *ad libitum* from the training grid placed on the bottom of their home cage. A seed mixture was placed in the uncovered wells and in the petri dishes below stalks.

After three to five days of habituation, when all four birds were seen to feed from the training grid, each bird was isolated in one half of a cage for individual training. A bird of matching sex, which had been used in previous experiments, was placed in the other section as a companion to reduce neophobia. Birds were allowed to habituate to the new situation for a minimum of 24h prior to the commencement of individual training.

The birds were food-deprived overnight and early morning (18-20h) prior to training sessions. Training commenced between 1100 and 1300h.

2) Shaping. Specialist birds were trained, via shaping, to remove covers from wells or to pull corks from the stalks. For stalk specialists, the lids were always on the wells of the training grid during training. Similarly, for well specialists all the stalks were present during training. This allowed specialist birds to habituate to the presence of both lids and stalks despite their specialist training. In all cases, only the patch type on which a bird was to specialize contained seeds.

Generalist birds were trained to remove covers from wells and pull corks from stalks. To ensure generalization, all birds were forced to alternate between patch types within every training day by having only one patch type available for

exploitation at any one time (i.e. the plug or cork was in place and that patch type contained seeds). Both patch types were available during the training of specialists, but the specialist birds opened the patch type on which they were specialized exclusively.

A specialist's training was considered complete when it had successfully opened eight consecutive patches. A generalist's training was considered complete once it had successfully opened eight consecutive patches of each type, presented in pairs in random order. Birds that failed to reach this criterion within seven days of all others were not used. This happened twice.

3) Once birds were trained, the proportion of full patches was reduced gradually until birds opened eight consecutive empty patches of the same type for specialists or four empty patches of each type for generalists. This approximated the average number of empty patches for each full patch that a bird would search in the flock-feeding experiment.

#### IV. Post-training Producing Ability and Bias

##### **A) Solo Feeding Rate**

It was important to detect any differences in foraging efficiency between food patches before flock trials, since they may indicate that patch types offered different foraging rates. Solo feeding rate was measured while subjects fed alone from the small training grid after having been food-deprived overnight and early morning (19-22h). Two patches of the appropriate type, containing six seeds each, were

simultaneously available on the grid. Landing on the grid, number of seeds eaten, and the time at which the bird lifted its head to husk each seed were recorded on an S&K Portable Event Recorder (to  $1.95 \times 10^{-2}$ s) from behind a one-way mirror. Feeding rate was defined as the mean number of seeds eaten per second over the solo trials.

Specialists' solo feeding rates were measured three times, on their appropriate patch type, on each of two consecutive days. Generalists' solo feeding rates were measured six times on each of two consecutive days, three times per day on each patch type. Each bird, whether specialist or generalist, therefore had the opportunity to forage from six wells and/or six stalks.

One-way ANOVAs, with two mean rates per bird treated as repeated measures, were employed to compare the solo feeding rate of generalists on wells and stalks. Hierarchical ANOVAs, with replicate flocks nested within specialist type, were utilized for comparisons between well and stalk specialists. Differences between the well and stalk solo feeding rates of individual generalists were assessed using paired t-tests for each bird (Zar 1984).

## **B) Patch Type Bias**

Generalist birds were unlikely to exploit both patch types equally. I therefore quantified the extent of any initial bias as the patch type that the birds opened first. To measure bias, I exposed birds to both patch types simultaneously on the training grid 10 times over two days. Each patch contained six seeds. I defined bias as the first patch type opened and the significance of patch bias was ascertained using the

chi-square test, assuming equal probability of opening a well or a stalk.

Specialist birds only opened one patch type and so naturally they had maximum bias. However, to compensate for the extra patch opening practice provided to generalists during bias assessment, each specialist was given 10 patch opening opportunities, over two days.

## V. Flock-feeding Experiment

### **A) Procedure**

Two skill pools and two generalist flocks were formed. The skill pools were composed of two stalk specialists (one male, one female) and two well specialists (one male, one female). Four generalist individuals formed each generalist flock (two males, two females). The birds in each flock had been caged together for at least one month prior to the start of training, unless a bird had been added as a replacement during the training. Only one flock was trained and tested at a time.

Birds were placed as a flock in the aviary for six days and fed *ad libitum*. On the sixth day the finches were allowed to feed *ad libitum* from the large aviary grid placed on the floor. During this habituation session, neither stalks nor well covers were present on the grid. Experimental trials began the following day.

Birds were food-deprived overnight and early morning (17.5-18.5h) before the start of daily trials. A trial started when the first bird landed on the grid and ended either when all the wells and stalks were uncovered, or when all the birds were off the grid for at least one minute after the start of a trial. Three trials were run per

day. Four randomly selected wells and stalks were supplied with 14 seeds each per trial. During the 30 min inter-trial intervals, the birds were food-deprived but had *ad libitum* access to water. Fifteen to 30 min after the last trial of the day the flocks were allowed to feed *ad libitum*.

Each flock was tested on the aviary grid until 30 complete trials were obtained. To ensure that all birds were motivated to forage and that the motivation was similar among trials, I only collected data from trials where every bird searched at least one patch and no more than eight patches (four of each type for the skill pool flocks) remained unexplored. Because the birds should have been hungrier during the first two trials of each day, data were collected during these trials only if no more than one seed-containing patch remained unexplored. If more than one seed-containing patch remained, I considered that the birds were not sufficiently hungry or that they were experiencing some outside disturbance and therefore foraging behaviour may have been adversely influenced. When this happened the birds were always highly motivated for the third trial. To reduce the effects of experience gained with the foraging conditions early in the experiment, all analyses were conducted only on the last 15 trials.

All trials were recorded on videotape and the following behaviour entered into the event recorder.

"Searching" - using the bill to pull at the string of a stalk to remove the cork or to remove the lid from any well such that once the lid came to rest, any part of the well could be seen. A bird was said to have "produced" only when it searched a

seed-containing patch.

"Searching attempts" - unsuccessful attempts to search an unopened patch.

Attempts are touching or pulling a stalk's string with the beak without removing the cork from the stalk, or touching or lifting the lid on a well without displacing it sufficiently to qualify as searching.

"Joining attempt" - moving the head to within 1.0cm of the edge of a produced well or close enough to a produced stalk that the beak overhung the edge of the petri dish. In all cases, at least one bird must already be at the patch or have been at the patch no more than 2.0s before the joiner bird's arrival. A bird could not be scored for producing and joining at the same patch.

## **B) Analysis**

### *i) Generalist and Specialist Searching and Joining Frequencies*

#### **a) Patch Searching Behaviour of Generalists**

I quantified the searching behaviour of each generalist bird during flock trials using two measures. For the first measure, I scored each trial as a plus or minus, according to whether the bird searched more wells or stalks, and used the sign test (Zar 1984) to determine whether the bird consistently searched more of one patch type in each trial than expected by chance.

The second measure examined the sequence of searching events of each bird within a trial. Since generalists could search both patch types, I counted the frequency with which well and stalk runs of each length occurred. A run was defined as a searching sequence of one or more identical patch types. For each generalist

bird, I compared the observed frequency distribution of run lengths with the distribution that could be expected by chance, using a chi-square goodness-of-fit test. The frequency distribution of run lengths expected by chance is best estimated by a geometric distribution (Derman et al. 1973). Each patch-type choice within this type of distribution is assumed to be independent, with the probability of searching each patch type based on the total number of patches of each type that were searched during the last 15 trials. This probability was not always 0.5, because corks sometimes fell out of the stalks when birds landed or flew off the grid and thus could not be counted as available to be searched. Occasionally, lids became stuck in a well and thus were not counted as available.

#### b) Joining Attempts

I compared the joining tendency among birds in skill pools and generalist flocks. Joining tendency was defined as the proportion of patches a bird attempted to join out of those available. Since a bird could not attempt to join a patch that it produced, the number of patches available to be joined by a bird was calculated by subtracting number of patches it produced from the total number of patches produced by the flock in the last 15 trials. The well and stalk joining tendencies of birds in the two flock types were compared with a two-way **ANOVA** using arcsine-square root transformed proportions. The well and stalk joining tendencies of a bird were treated as repeated measures and replicate flocks were nested within flock type (Zar 1984).

Joining preferences were assessed with a chi-square test, comparing the observed frequencies of joining attempts for each bird with the frequencies of patch-

type joining attempts expected if the birds were joining patch types in the same proportion as they were available on the grid.

*ii) Comparisons of Generalist and Specialist Foraging Efficiencies*

Three measures of individual performance during the flock trials were calculated from the event recorder records.

*a) Overall Feeding Rate*

I calculated the mean time required by each bird to obtain half of the seeds available to it, assuming that all birds ate equal shares (14 seeds). This mean time was converted to a mean overall feeding rate in seeds/s for each bird. Overall feeding rate includes seeds obtained via producing and joining and incorporates travel, patch handling, and eating times. Overall feeding rates of specialists and generalists were compared using a one-way ANOVA, with replicate flocks nested within flock type (Zar 1984). Since all types of birds were not, due to the nature of the experiment, present in each flock type, the particular comparison of the feeding rates of well specialists, stalk specialists and generalists required a one-way ANOVA, with three treatment levels.

*b) Patch Opening Ability*

Patch opening ability is a measure of a bird's efficiency at searching patches. Ability was defined as the number of searched patches per trial divided by the sum of of searching attempts and searched patches. Searching attempts were included to give an indirect indication of the energetic cost of producing for each bird, since unsuccessful attempts waste energy and time. Well opening and stalk opening ability



were compared between the flock types with two one-way ANOVAs on the arcsine-square-root-transformed proportions. Since generalists searched both patch types, these measures of opening ability were repeated measures, and since specialists searched only one patch type, comparisons of opening ability could not be combined in one analysis. Replicate flocks were nested within flock type (Zar 1984).

#### c) Patch Searching Rate

Patch searching rate measures a bird's patch handling time and the search or travel time between empty patches. However, because the patch types are alternated on the grid, the travel time between same patch types is necessarily longer than the travel times between different patch types. In order to standardize comparisons between specialist and generalist searching rates, I considered only instances where generalists searched two consecutive patches of the same type. Each bird's mean rate of searching was defined as the number of patches of one type produced per second, and was calculated from the time from the last bill contact with a stalk or well to the last bill contact with the subsequently searched stalk or well. In order to avoid biases due to patch depletion, events were excluded when they occurred after one of the patch types reached 50% depletion (11<sup>th</sup> patch cover touched), when the bird attempted to join at a patch in the interval, or when the bird produced a patch. Therefore, each bird's mean searching rate includes only travel time between empty patches and patch-cover handling time. As for patch opening ability, the mean well and stalk searching rates of generalist and specialist birds were compared using separate one-way ANOVAs, with replicate flocks nested within flock type (Zar 1984).

Overall feeding rate, opening ability, and searching rate were analyzed separately for correlation with the searching tendency of the generalists and with the joining tendencies of specialists and generalists using Spearman's rank correlation (Zar 1984). All statistical tests were conducted using SYSTAT statistical package (Wilkinson 1989) on a Packard Bell PC. Unless otherwise stated, all values in the text are means  $\pm$  standard error.

## Results

### I. Post-training Producing Ability and Bias

Both patch types presented similar levels of difficulty such that birds fed at similar rates on each. The solo feeding rates ( $\bar{x} \pm SE$ ) of well specialists ( $0.29 \pm 0.03$  seeds/s) and stalk specialists ( $0.26 \pm 0.04$  seeds/s) were not different ( $F_{1,4}=0.18$ , N.S.). Generalists had equal solo feeding rates on wells ( $0.35 \pm 0.04$  seeds/s) and on stalks ( $0.34 \pm 0.03$  seeds/s) ( $F_{1,6}=0.65$ , N.S.). Seven of the eight generalists showed no significant difference between their solo feeding rates on wells and stalks when tested before the onset of trials (Table I). Only one subject (G7) fed significantly more rapidly on stalks than on wells ( $t=5.02$ ,  $df=5$ ,  $P=0.004$ , two tailed).

Despite having equal feeding rates from each patch type, six of the eight generalists exhibited a significant preference for searching one of the two patch types first when tested alone (2 for wells, 4 for stalks; Table II). When re-tested after the flock trials, none of these biased generalists had changed their preference. Patch type bias before flock trials was significantly correlated with patch type bias after the flock trials (Spearman's  $r_s=0.88$ ,  $n=8$ ,  $P < 0.01$ ).

### II. Generalist and Specialist Searching and Joining Frequencies

#### **A) Patch Searching Behaviour**

Almost all (99.4%) seed-containing patches were produced during trials. Birds

Table I. Post-training solo feeding rate (seeds/s) of birds in generalist flocks.

Generalist		Wells	Stalks
Flock	Bird	( $\bar{x} \pm SE$ )	( $\bar{x} \pm SE$ )
1	G1	0.28 0.03	0.30 0.04
	G2	0.38 0.03	0.31 0.01
	G3	0.56 0.07	0.42 0.05
	G4	0.36 0.06	0.35 0.05
2	G5	0.51 0.04	0.47 0.03
	G6	0.29 0.05	0.28 0.02
	G7	0.26 0.01	** 0.40 0.02
	G8	0.35 0.05	0.27 0.03

\*\*  $P=0.004$

Table II. Generalists' post-training, flock, and post-trial bias for wells.

Values shown are the proportion of all patches searched that were wells.

Flock	Bird	Post-training	Flock	Post-trial
		solo		solo
1	G1	1.00 **	0.60	0.80 *
	G2	0.00 **	0.62 *	0.20 *
	G3	0.40	0.03 **	0.60
	G4	0.80 *	0.99 **	0.70
2	G5	0.50	0.73 **	0.40
	G6	0.00 **	0.56	0.10 *
	G7	0.10 *	0.40 *	0.10 *
	G8	0.00 **	0.13 **	0.00 **

\*  $P < 0.05$

\*\*  $P < 0.001$

trained to search as specialists remained exclusive specialists throughout the experiment. However, not all generalists searched equal numbers of stalks and wells during the flock trials, and some appeared to become strongly and consistently biased towards one patch type or the other over the course of the experiment (Fig.2). In the last 15 trials of the experiment, for instance, four of the eight generalists (G3, G4, G5, G8) searched more of one particular patch type in significantly more trials (Table III). Additionally, the number of trials in which one other subject (G7) searched more wells, reaches marginal levels of statistical significance (Table III). The generalists' bias during the last 15 flock trials did not correlate as well with the preferences noted during post-training and post-trial solo feeding tests ( $r_s=0.42$  and  $r_s=0.44$ ,  $n=8$ , both N.S. for post-training and post-trial, respectively).

Inspection of each generalist's searching sequences during the last 15 trials indicated that the four individuals that had significant searching preferences (G3, G4, G5, G8) also searched for their preferred patch type in a greater number of long runs than expected by chance (Fig.3; G3 on stalks  $df=1$ ,  $\chi^2=10.69$ ; G4 on wells  $df=1$ ,  $\chi^2=17.97$ ; G5 on wells  $df=3$ ,  $\chi^2=8.22$ ; G8 on stalks  $df=1$ ,  $\chi^2=11.01$ ). An additional subject (G6) was found to search wells in a significantly greater number of long runs ( $df=3$ ,  $\chi^2=9.01$ ). Therefore, only three of the eight generalists (G1, G2, G7) were searching patch types in run sequences that were either random or contained more short runs and thus more frequent alternation than expected by chance (Fig.3).

Figure 2. Searching by individual generalists over 30 trials. Each point is the proportion of the total patches searched that were wells and represents the mean of two trials. Zero indicates only stalks were searched.

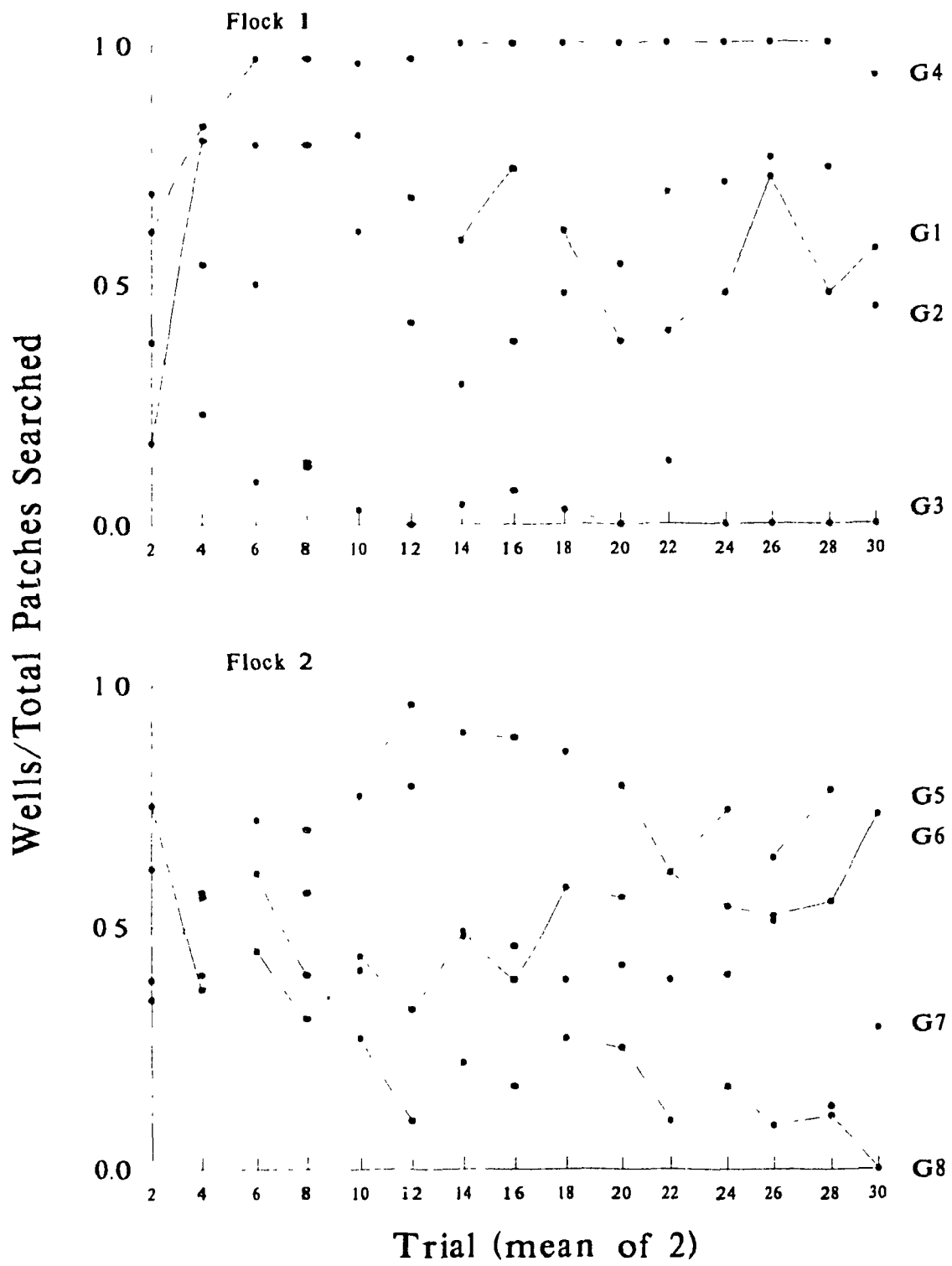
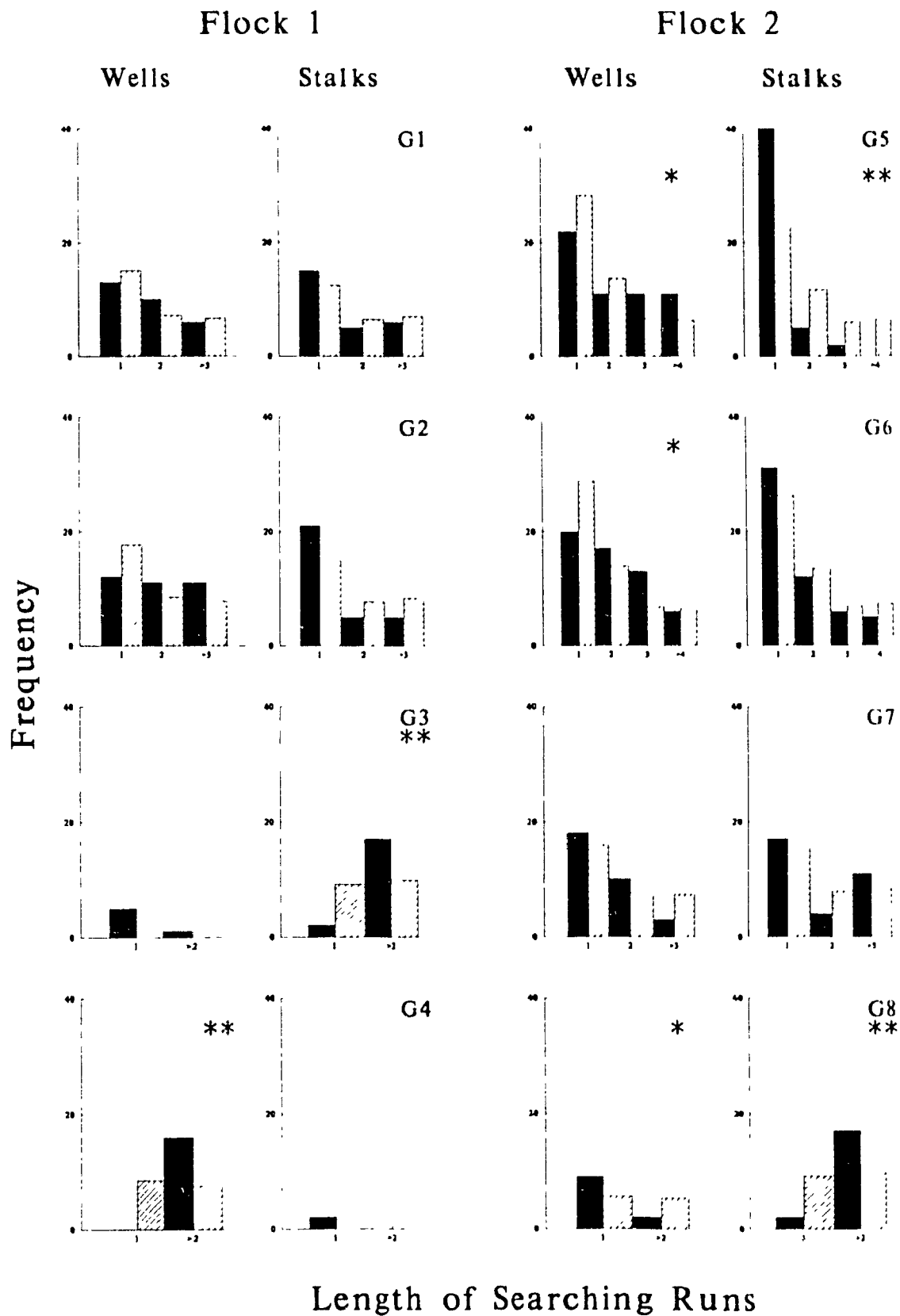




Table III. The number of trials in which each bird searched more wells. Significance levels are for sign tests.

Bird	Trials With More Wells	p (two-tailed)
G1	7/13	1.000
G2	10/14	0.180
G3	0/15	0.002
G4	15/15	0.002
G5	15/15	0.002
G6	10/15	0.302
G7	3/14	0.058
G8	0/14	0.002

Figure 3 Frequency distributions of the lengths of well and stalk searching runs of each of the generalists. Solid bars give the observed frequency of each searching run length, hatched bars give the expected frequency. Chi-square significant differences are indicated by  $*=P < 0.05$ ,  $**=P < 0.001$ .



## **B) Joining Attempts**

All subjects in both types of flocks attempted joining (Fig.4). The subjects' tendency to join at patches did not differ between flock types ( $F_{1,12}=0.002$ , N.S.; joining tendency, generalists= $0.45 \pm 0.09$  patches; specialists= $0.47 \pm 0.07$  patches). Within flock types there were no significant preferences for the type of patch joined at ( $F_{1,12}=2.70$ , N.S.) (generalists: joining tendency, wells= $0.49 \pm 0.09$ ; stalks= $0.46 \pm 0.08$ )(specialists: wells= $0.56 \pm 0.08$ ; stalks= $0.40 \pm 0.09$ ), though there was a trend for specialists to attempt to join at more wells than stalks (Fig.5). Only one generalist (G4) and one specialist (S3) showed significant joining preferences, and in both cases the subjects preferred to join at the same patch type (i.e. wells) they preferred to search (Table IV).

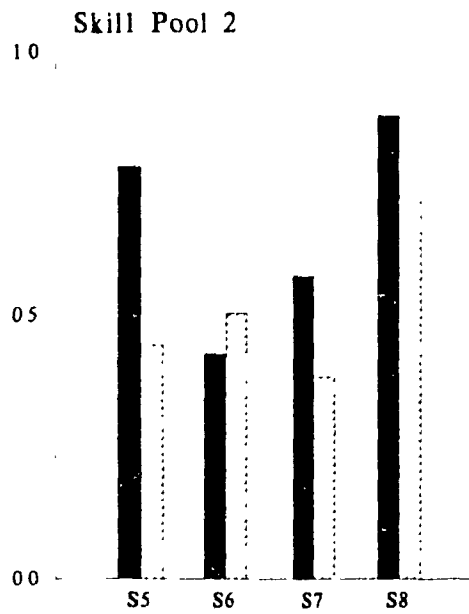
## **III. Comparisons of Generalist and Specialist Foraging Efficiencies**

### **A) Comparisons Between Flock Types**

Birds in skill pools achieved significantly higher feeding rates ( $0.29 \pm 0.02$  seeds/s) than birds in generalist flocks ( $0.25 \pm 0.01$  seeds/s)( $F_{1,12}=5.08$ ,  $P=0.04$ , Fig.6a).

The difference between skill pools and generalist flocks is not strongly related to differences in either patch opening ability or searching rate between specialist and generalist birds. Specialists tended to have greater stalk opening ability than generalists ( $F_{1,8}=5.07$ ,  $P=0.054$ ; Fig.6b). However, well

Figure 4. Joining tendency of each bird. Solid and hatched bars denote wells and stalks, respectively.



Bird

Figure 5. Mean well and stalk joining tendency of birds in skill pools and generalist flocks. ● = wells, ⊙ = stalks.

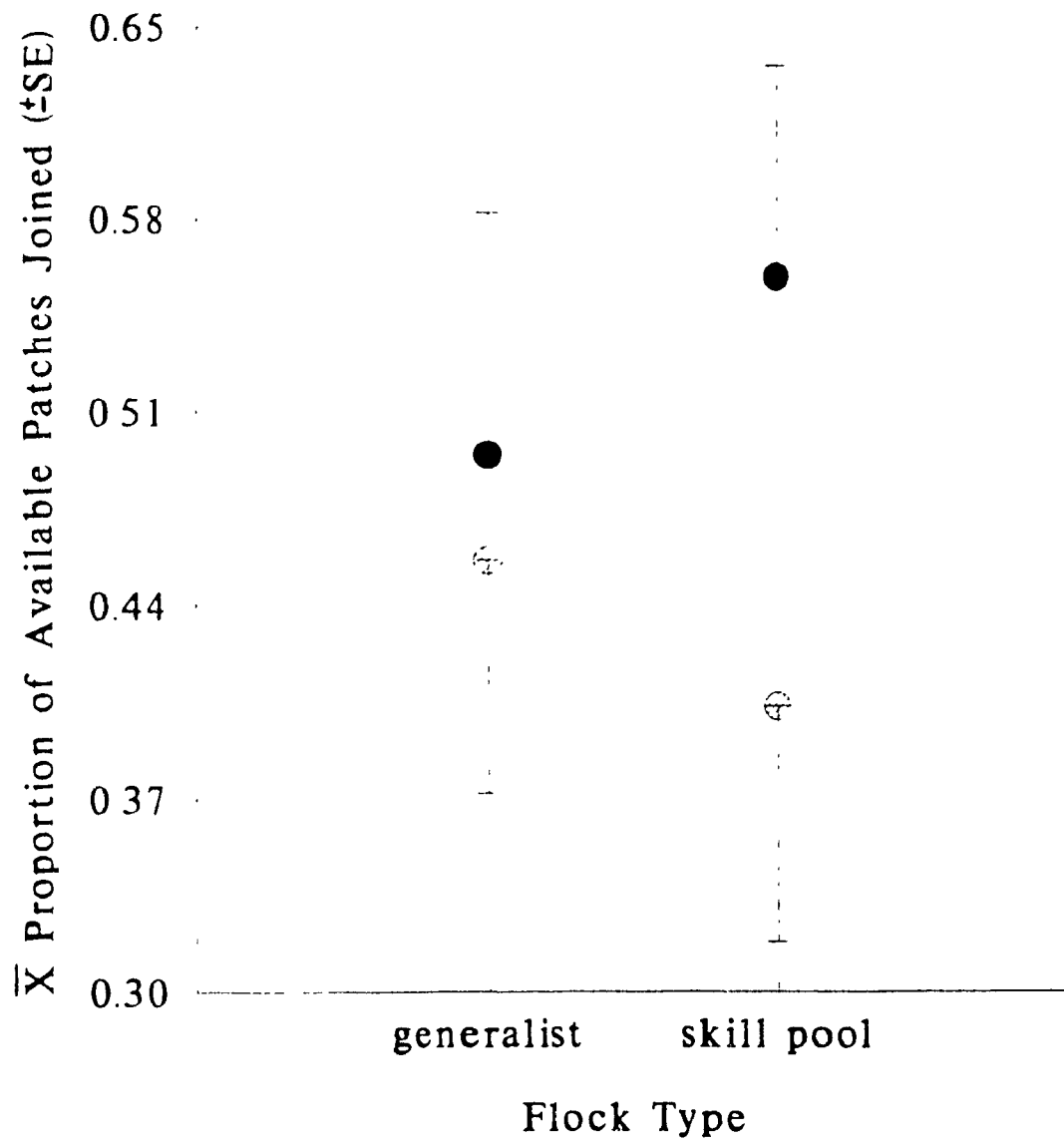




Table IV Contingency table of observed (obs) and expected (exp) total wells and stalks joined at in the last 15 trials.  $H_0$ : joining at wells and stalks was proportional to patch availability.

Bird(spec)	Wells		Stalks		$\chi^2$
	obs	exp	obs	exp	
G1 (-)	45	42.2	37	39.8	0.38
G2 (-)	25	25.9	28	27.1	0.06
G6 (-)	25	22.6	24	26.4	0.47
G7 (-)	12	14.4	15	12.6	0.86
G3 (s)	18	21.9	11	7.1	2.84
G8 (s)	41	37.3	22	25.7	0.90
G4 (w)	8	2.7	2	7.3	14.25**
G5 (w)	4	6.7	12	9.3	1.87
S1 (s)	24	23.9	10	10.1	0.001
S2 (s)	11	9.8	4	5.2	0.42
S5 (s)	46	38.7	15	22.3	3.77
S6 (s)	25	26.3	12	10.7	0.22
S3 (w)	19	6.5	0	12.5	36.54**
S4 (w)	15	17.1	34	31.9	0.40
S7 (w)	20	15.8	22	26.2	1.79
S8 (w)	21	18.5	42	44.5	0.48

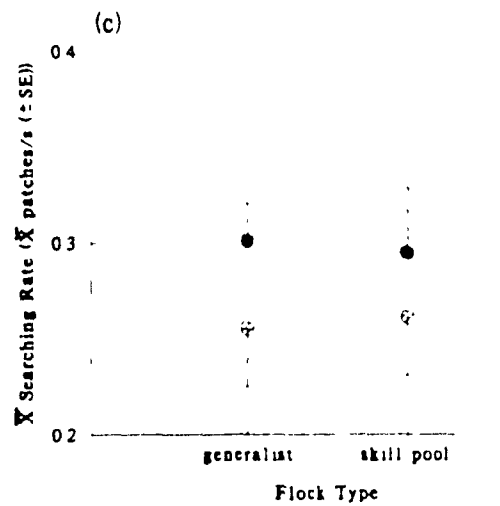
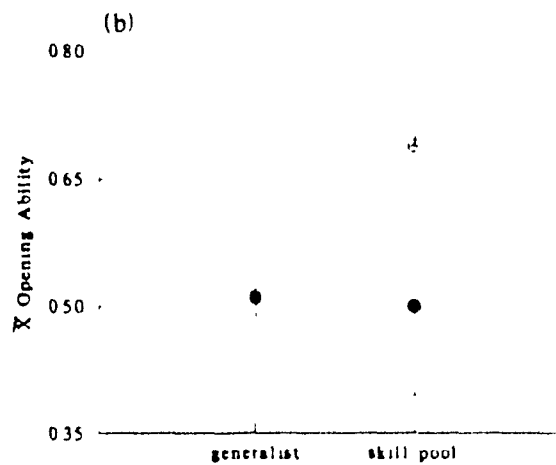
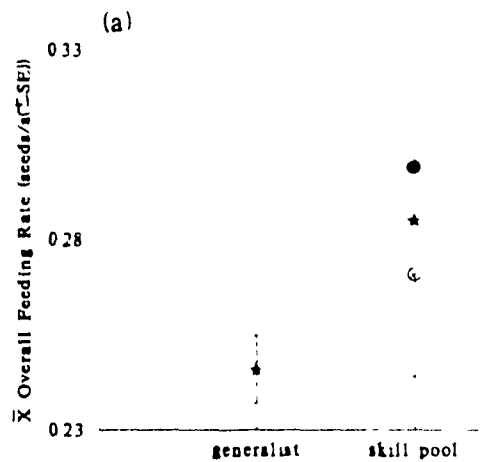
\*\*  $P < 0.001$

Figure 6. a) Means of each subject's mean overall feeding rate. Vertical lines indicate one SE. ★ = flock type means, ● = wells, ⊗ = stalks.

b) Means of each subject's mean patch opening ability in skill pools and generalist flocks. Note that for generalists well and stalk means are superimposed, the upper vertical bar gives one SE for stalks, the lower for wells.

c) Means of each subject's mean well and stalk searching rate.

● = wells, ⊗ = stalks.



specialists were not any better at opening wells than generalists ( $F_{1,8}=0.006$ , N.S.).

The lack of a significant difference between flock types in patch opening ability remained when the three most specialized generalists were removed from the analysis (stalks  $F_{1,5}=2.53$ , N.S.; wells  $F_{1,5}=2.58$ , N.S.).

The same conclusions hold for patch searching rates. Specialists were no faster than generalists at searching either type of food patch ( $F_{1,7}=0.09$ , N.S. for stalks;  $F_{1,6}=0.02$ , N.S. for wells; Fig.6c). The removal of the three most specialized generalists from these comparisons does not alter the conclusions.

#### **B) Comparisons Within Generalist Flocks**

Comparisons of foraging efficiencies among generalists with different degrees of searching specialization confirm that searching specialization had little effect on foraging success. Within the generalist flocks, for instance, there was no correlation between the extent to which an individual concentrated its searching on one particular patch type (i.e. specialized) and patch opening ability (stalk  $r_s=0.52$ ,  $n=8$ , N.S.; well  $r_s=0.33$ ,  $n=8$ , N.S.), its patch searching rates (stalk  $r_s=-0.36$ ,  $n=7$ , N.S.; well  $r_s=-0.32$ ,  $n=6$ , N.S.), or its overall rate of feeding ( $r_s=-0.24$ ,  $n=8$ , N.S.).

#### **IV. The Effect of Searching and Joining Tendency on Foraging Efficiency**

For generalists, the extent to which an individual tended to search for patches, whether wells or stalks, was not correlated with either its patch opening ability ( $r_s=0.01$ ,  $n=8$ , N.S.), its patch searching rate ( $r_s=0.16$ ,  $n=8$ , N.S.), nor with its overall feeding rate ( $r_s=0.17$ ,  $n=8$ , N.S.). For specialists, searching tendency was

more positively correlated with all three foraging efficiency measures (opening ability  $r_s=0.33$ ,  $n=8$ , N.S.; searching rate  $r_s=0.52$ ,  $n=8$ , N.S.; feeding rate  $r_s=0.33$ ,  $n=8$ , N.S.), but still none reached statistical significance.

For generalist flocks, an individual's joining tendency was not significantly correlated with either its mean patch opening ability ( $r_s=0.38$ ,  $n=8$ , N.S.) or its searching rate ( $r_s=-0.06$ ,  $n=8$ , N.S.). However, the generalists' overall feeding rate was significantly correlated with joining tendency ( $r_s=0.83$ ,  $n=8$ ,  $P=0.02$ ; Fig. 7). For skill pools, joining tendency appeared to have a much stronger effect on foraging efficiency. Joining tendency was not correlated with mean patch opening ability ( $r_s=0.41$ ,  $n=8$ , N.S.), but it was strongly and significantly correlated with mean searching rate ( $r_s=0.76$ ,  $n=8$ ,  $P<0.05$ ) and even more so with overall feeding rate ( $r_s=0.95$ ,  $n=8$ ,  $P=0.002$ ; Figs. 8a and b).

Figure 7. Joining tendency of generalists plotted against mean overall feeding rate.

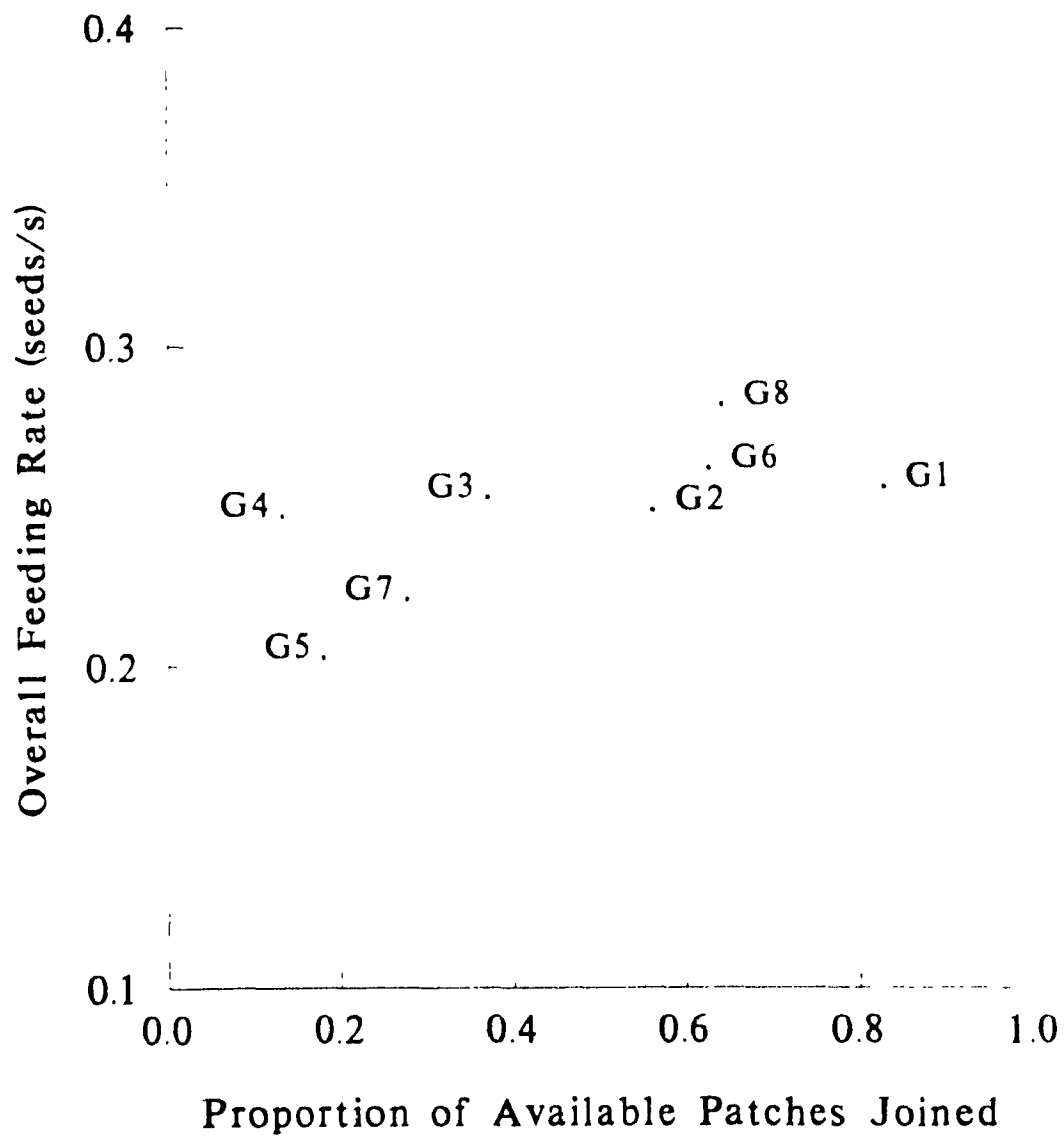
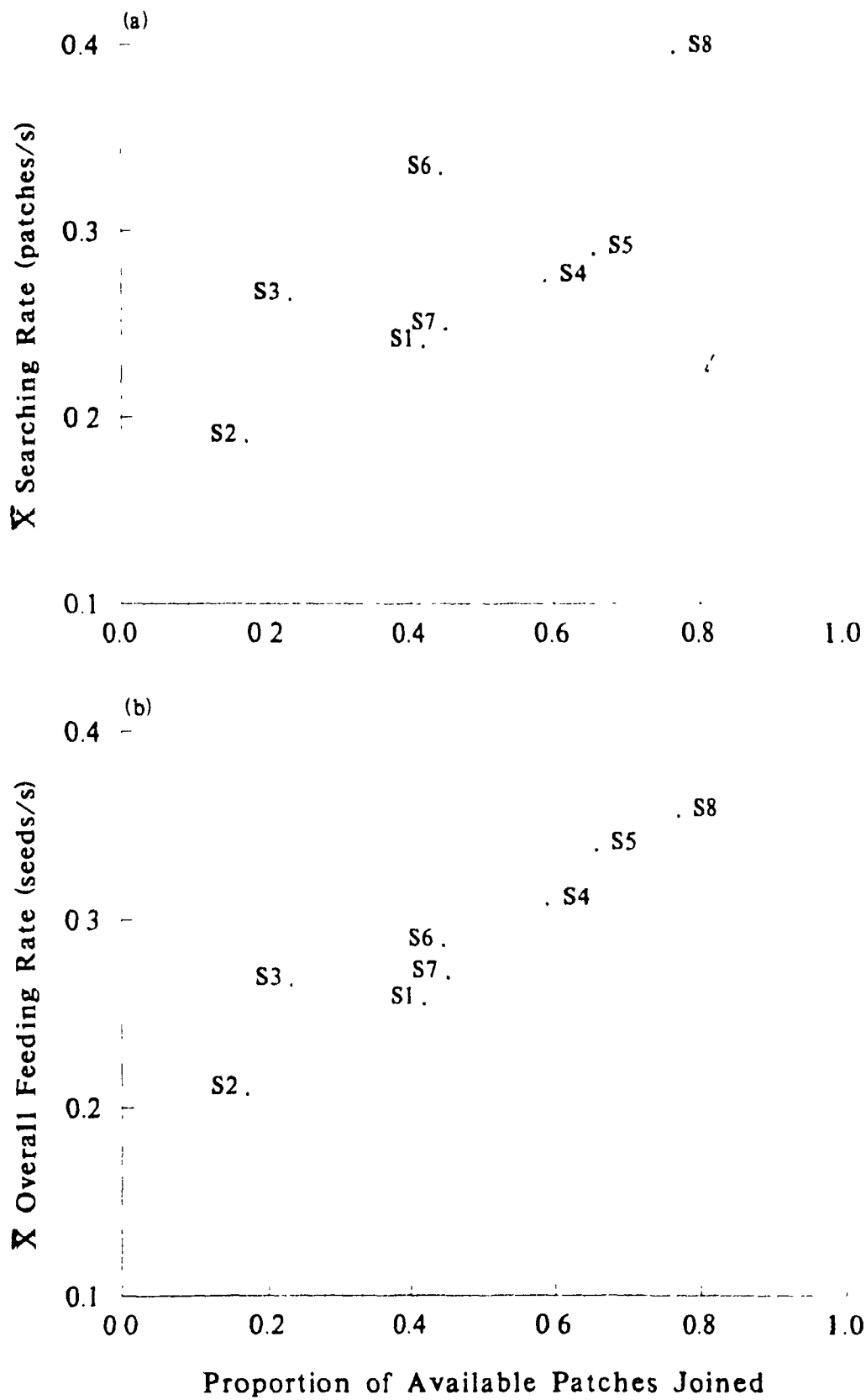


Figure 8. Joining tendency of specialists plotted against a) mean patch searching rate,  
b) mean overall feeding rate.





## Discussion

The skill pool birds achieved higher overall feeding rates than generalists. Giraldeau (1984) predicted that individuals foraging within a skill pool would achieve higher feeding rates, because the specialists would need fewer tries to open patches, and would search patches more quickly. However neither of these searching efficiency measures appeared to contribute greatly to the skill pool advantage observed in the current study. Thus, the formation of skill pools provided increased foraging rates, but apparently not through the operation of a jack-of-all-trades effect as Giraldeau (1984) had predicted. It is therefore important to determine whether a skill pool advantage in the absence of a jack-of-all-trades effect is due to problems with experimental design or whether it provides evidence of an important oversight of Giraldeau's (1984) skill pool hypothesis.

### I. Lack of Differences in Searching Efficiency Measures Due to Problems with Experimental Design?

It is possible that the generalist's foraging efficiency was enhanced by my experimental procedures in such a way that it became difficult to show any foraging advantage for specialization. Three aspects of my experimental procedure are potential candidates for inflating generalists' patch opening ability and searching rate. Firstly, during flock trials, my generalists may have been required to exploit too few patch types concurrently for any effect of the jack-of-all-trades principle to operate. Secondly, the food patch types were presented simultaneously, allowing generalists

the option to specialize on their preferred patch type. Thirdly, the pre-trial training and post-training assessment of individual feeding rate and patch bias may have artificially improved the generalist's foraging efficiency. I consider each of these points separately.

#### **A) Too Few Patch Types**

One could argue that the assumption of reduced generalist foraging efficiency on which the skill pool is based applies only when generalists are required to exploit more than two different food patch types. I feel this explanation is unlikely in the case of spice finches. Partridge & Green (1987) found a cost to generalist foraging in groups of jackdaws (*Corvus monedula*), even though they presented the jackdaws with only three different food types. Jackdaws are notoriously opportunistic foragers (Lockie 1956) who naturally forage on a wider variety of food types than spice finches. Spice finches, in comparison, have a narrower diet, exploiting grass seeds almost exclusively (Goodwin 1982, Immelmann 1982).

Contrary to the Partridge & Green (1987) study, my generalists had the opportunity to choose the types of patches they searched and, as a result, at least four of my eight generalists tended to specialize on one type spontaneously. This spontaneous specialization is consistent with the hypothesis that there may have been some cost to generalization. It is unlikely therefore, that the requirement of exploiting only two patch types was insufficient to prevent the jack-of-all-trades from operating in my experiment.

## **B) Simultaneous Availability of Patch Types**

The simultaneous presence of two food types allowed half of the generalist finches to specialize on a single patch type once in a flock foraging situation. Though opening ability and searching rate for the flock types were similar, the extent of specialization within the generalists did not lead to the same advantage in feeding rate documented in the skill pool flock. There are two reasons to believe that the selective foraging behaviour of my generalist finches was insufficient to have increased the similarity between the generalist and specialist flocks to any great extent. First, removal of the three most specialized generalist individuals from the analyses did not change conclusions. Naturally this is not strong support, since reducing sample sizes will reduce the chance of detecting significant differences. However the following second reason provides stronger support. The specialization of generalists did not seem to confer a foraging efficiency advantage to the generalist birds because there was no significant correlation between the degree of specialization of the generalists and any of the three efficiency measures.

## **C) Individual Training**

For the generalist jackdaws tested by Partridge & Green (1987), a daily alternation of patch types eliminated the efficiency differences between the generalists and the specialists for two of the three patch types used in their study. During post-training solo testing it was necessary to avoid providing generalist finches with an opportunity to form an extensive preference or bias for one of the two food types. Hence, the presentation of patch types was alternated at each feeding opportunity.

Additionally, the presentation of patch types during training trials was random, each bird being given the opportunity to search each patch type at least once during a training day. The frequency of patch type presentation in my experimental procedure, therefore, could have favoured increased generalist foraging efficiency. It is important to remember, however, that training and post-training efficiency assessment were conducted with solitary individuals and thus components of the birds' overall feeding rate concerned with joining activity would not be affected by this training.

Therefore, it is possible that the training and post-training assessment may have inflated the generalist's foraging efficiency, particularly their patch opening ability and searching rate. Nonetheless, specialists foraging within skill pools enjoyed a higher overall feeding rate than the generalists. Therefore, the mechanism through which the formation of skill pools provided foraging advantages is not likely related to the two components of patch searching efficiency.

## II. Differences in Overall Feeding Rate Due to Combination of Undetectable Differences in Searching Efficiency?

My results indicate that specialist searchers feeding in skill pools have higher overall feeding rates than generalist searchers in flocks of generalists. However, neither measure of searching efficiency was consistent with this finding. It is possible that moderate advantages in both measures of patch searching efficiency could have combined to yield improved overall feeding rates for the specialists. Yet, I feel that this is unlikely because between-flock differences were not consistent across the two

measures of patch searching efficiency (e.g. compare Figs.6b and c).

#### **A) Patch Opening Ability**

Some specialists showed greater patch opening ability than generalists. Stalk specialists exhibited greater opening ability than generalists, but among the specialists the differences were in inconsistent directions. In terms of feeding rates, well specialists tended to have higher feeding rates (Fig.6a). However, in terms of opening ability, stalk specialists were better (Fig.6b).

#### **B) Patch Searching Rate**

Patch searching rate measures not only the actual time required to handle a patch but also the time required to travel between patches. Specialists were no faster at searching patches than generalists (Fig.6c). Stalk specialists tended to search patches faster than generalists, but it was the well specialists that achieved the highest rates of feeding. In addition, even though the well specialists achieved the highest feeding rates, their own patch searching rates were slightly lower than those of the generalists (Fig.6c).

Given the inconsistent direction of differences between searching rates of specialists and generalists, it is therefore unlikely that small effects could have combined to generate the consistent differences I observed in feeding rates. These results suggest, therefore, that the foraging efficiency of a group forager may be independent of its ability to search patches.

### III. Differences in Overall Feeding Rate Due to Joining?

Overall feeding rate includes both producing and joining components of an individual's feeding. Given that the skill pool's advantage could not be related to an individual's patch opening ability nor its searching rate, and that overall feeding rate is not significantly correlated with an individual's searching tendency,

it seems that the searching efficiency is not the important component of overall feeding rate that Giraldeau (1984) anticipated. Instead, joining appears much more important, since joining tendency is significantly positively correlated with overall feeding rate (Figs.7 and 8b).

That joining is an important component of an individual's feeding rate makes intuitive sense. For instance, a generalist bird that foraged without any patch preference could obtain food in four ways in my experiment; producing wells, producing stalks, joining at wells, and joining at stalks. Therefore, joining could potentially constitute up to 50% of a generalist's type of feeding opportunities. For a specialist bird, joining would be even more important since it could obtain food in only three ways; producing the patch type it was specialized on, joining at wells, and joining at stalks. For this animal, joining could constitute up to 67% of its type of feeding opportunities. The fact that correlations between joining tendency and overall feeding rate were stronger for specialist than for generalist birds is consistent with this interpretation (Figs.7 and 8).

It thus appears that joining is an important determinant of an individual's foraging rate. However, unlike for searching where generalists are expected to be

less efficient because of the jack-of-all-trades principle, for joining there is no *a priori* reason to expect that individuals in skill pools should join more efficiently than those in flocks of generalists. My results raise the interesting possibility that specialization on one foraging component, namely patch type searched, influences the efficiency of another component, namely joining. Thus, specialized searching may not improve the efficiency of searching but instead the efficiency of joining. It remains to be determined what the important components of joining efficiency are.

#### IV. Implications for the Skill Pool Hypothesis

My study demonstrates that, in a group foraging context, specialization on searching one of two patches did not lead to increased searching efficiency, but instead may have allowed specialists to improve their joining efficiency. No study to date has ever investigated how specializing on producing one of two patch types could influence the efficiency of joining. If specializing at searching one patch type improves a subject's joining efficiency, then skill pool formation may provide an advantage through a mechanism that was not anticipated by Giraldeau (1984).

This study also suggests that individual foraging differences required for skill pool formation may develop in a way not anticipated by Giraldeau (1984). Giraldeau (1984) proposed that frequency-dependent effects constraining learning of foraging specializations would be a major contributor to strong intra-group differences. In groups individuals with differences in learning propensity or experience would, as a result of frequency-dependent learning, specialize on searching one or a few types of



food patches. The foraging skills that an animal learns should depend upon the number of and foraging behaviour of other searchers in the group.

In the present study, some generalists restricted their searching efforts while foraging in a flock (Figs.2 and 3). The mechanism of specialization could not be constrained by learning since the birds had previously been trained to search both patch types. In addition, specialization could not have resulted from individual preferences since the patch type bias of birds before and after trials was often different from the bias during flock trials. Five of the generalists either switched from one bias to another, from no bias to a bias, or from a bias to no bias while in the flock (Table II).

A more likely cause of specialization may have been random encounters with sequences of the same patch type. Dill (1983), in describing the effect of experience on prey preference in fish, noted that specialization often occurs simply from random sampling of a few prey types. A few consecutive encounters with a particular prey type may sufficiently reduce handling time or time elapsed between prey encounters to make specialization on that prey type the optimal strategy. In each trial, under the conditions of my experiment, the initial encounter rate with patch types was probably very similar. However, because of the group-foraging situation, once one bird, by chance or by choice, searched a sequence of the same patch type, the succeeding encounter rates of the two patch types would be dissimilar and the remaining flock members would be more likely to encounter more of one type and thus be encouraged to specialize on it. Hence, frequency-dependent effects on performance may have led

my birds to specialize. Although Giraldeau (1984) proposed that the skills an animal learns may be dependent on the behaviour of other group members, my study implies that the performance of skills previously acquired may lead groups of generalists to form skill pools. Group membership can constrain foraging behaviour so that even though individuals possess several foraging skills, the group limits the performance of these skills. Skill pools are thus likely to develop in a greater number of group foraging instances than has been previously anticipated (Giraldeau 1984, Giraldeau & LeFebvre 1986).

My results also suggest that the preferential joining assumption of the skill pool hypothesis may need modification. In the initial formulation of the skill pool hypothesis, Giraldeau (1984) assumed that skill pool individuals would join only at those food patch types they themselves could not discover. In this way birds would maximize their diet breadth because they gain access to food types they would not otherwise obtain if they were foraging alone. Preferential joining would suggest that joining is a cause of increased diet breadth. Indiscriminate joining would indicate that diet breadth is a consequence of joining. However, the fact that all my rewarded patches contained white millet eliminated the possibility that birds would develop a taste preference for a patch type. Moreover, a finch obtained the same type of food whether it joined at a well or at a stalk, and therefore there was no real increase in diet diversity to be gained from preferential joining. In this foraging situation maximum diversity did not require a bird to distinguish between the types of patches other birds searched. Hence, there was no benefit of preferential joining as far as

diet diversity is concerned. This could explain why the specialists did not join at the other patch type exclusively. Nevertheless, the results suggest that the original predictions of preferential joining in skill pools (Giraldeau 1984) only apply in a foraging environment where patch types contain different food types. Future studies should determine whether using different food types would promote preferential joining by the specialists.

#### V. Implications for the Jack-of-all-Trades Principle

My results suggest that the jack-of-all-trades principle may not affect group foragers to the same extent or in the same way as it does solitary foragers. The jack-of-all-trades principle has been formulated to account for interspecific differences in diet breadths. Consequently, the terms of "specialist" and "generalist" are most commonly applied to descriptions of the foraging characteristics of a species. The vast majority of cases in which the jack-of-all-trades principle has been documented has compared solitary foraging individuals of different species (eg. Scriber & Feeney 1979, Strickler 1979, Drummond 1983, Hassell & May 1986, Lavery & Plowright 1988). These comparisons have shown that specialist species acquired food faster when compared with generalist foragers in the same environment.

Although rarer, there is intraspecific evidence for the jack-of-all-trades principle (Partridge 1976, Pietrewicz & Kamil 1981, Werner et al. 1981, Persson 1985). Persson (1985), for example, presented individual perch (*Perca fluviatilis*) with the opportunity to hunt one prey species at a time and a mixture of two prey

types. The feeding efficiency (time/prey) of perch feeding on the mixture of prey types was reduced compared to that when feeding on either type of prey separately. However, all of the studies noted above deal with solitarily foraging animals.

Only one study compares the foraging efficiency of conspecific group foragers. Young jackdaws reared in the laboratory (Partridge & Green 1987) were trained as generalist or specialist foragers. One group of birds was trained to search three types of food patches (generalists) and each of three other groups were trained to search only one of the patch types (specialists). The generalist's efficiency on the various patch types, measured as duration of feeding attempt, which did not include travel or eating time, or as the proportion of feeding attempts that were unsuccessful, was compared with that of each of the respective patch-type specialists. The clearest results are that specialists were significantly more efficient than the generalists at the start of the testing, and that an increased rate of patch-type switching, or length of exposure to one patch type, eliminated the difference in efficiencies between specialists and generalists.

In summary, the quantitative evidence for the specialist efficiency assumption of the jack-of-all-trades principle from interspecific studies is strong but there is a need for better intraspecific studies, particularly for group foragers. The obvious difference between solitary and group foraging is the opportunity that is afforded to group foragers of joining at the food discoveries of others. Under my experimental conditions, joining seemed to be the key to the higher feeding rate enjoyed by the specialists. The foraging rate advantage of belonging to a skill pool probably lies in

the ability to join patches faster, and not in the ability to exploit patches more efficiently, which is what the jack-of-all-trades principle would suggest.

## VI. Conclusions

The present study has provided experimental evidence that the formation of skill pools can provide advantages in terms of overall feeding rates. The advantages, however, were quantitatively small and could not be attributed to the operation of the jack-of-all-trades principle. It is possible that the advantages provided by skill pool formation result from the potential for specialized searchers to join at patches more efficiently. This possibility, however, needs to be investigated experimentally.

The results also suggest that the jack-of-all-trades principle, as currently formulated, may not apply in group foraging situations. It is possible that group foraging offers conditions where specialization does not lead to increased efficiency of food finding. This possibility needs to be addressed by future studies.

Finally, the study suggests that formation of skill pools may occur even when individual members of a group have the acquired ability to generalize. The extent to which the generalist flocks behaved as skill pools was surprising, as they did not appear to gain any foraging advantage from their specialization, either due to the jack-of-all-trades principle or to joining more efficiently. However, the fact that anything short of absolute producing specialization failed to yield a skill pool advantage suggests that skill pool advantages only occur in highly specialized circumstances. The reasons why our generalist birds specialized therefore remains unclear. It is

possible that more accurate measurements of foraging advantages, coupled with larger sample sizes, will be necessary to resolve these questions more fully. Thus, although my results suggest that animals will form skill pools under a variety of circumstances, the skill pool will likely only result in foraging advantages when individuals are exclusively specialized on one food type.

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