# PATTERN LEARNING AND SPATIAL MEMORY IN RUFOUS HUMMINGBIRDS
## (*Selasphorus rufus*)

by

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# Abstract

In this study I examined spatial learning and memory in rufous hummingbirds. In laboratory experiments, hummingbirds rapidly learned 2-dimensional patterns of rewards. They used landmarks to find reward sites. Once birds were visiting most feeders in rewarding areas and avoiding most feeders in non-rewarding areas, they persisted in the same areas after their profitabilities were reversed. This is strong evidence for cognitive mapping. Persistence subsided rapidly once the birds' behaviour was no longer applicable, followed rapidly by learning the altered reward patterns. The types of landmark information I provided significantly influenced both the rate and persistence of learning. Hummingbirds learned more rapidly using edge landmarks than central landmarks. They also used colour information about reward quality embedded in both kinds of markers, although this was not a strong benefit to learning.

In one experiment, hummingbirds learned both spatial memory tasks and spatial associations. They learned spatial associations more rapidly than spatial memory tasks, achieving a high rate of performance after a very short time interval. Although spatial memory tasks required a slightly longer learning period, the birds' performance was eventually comparable to that on spatial association tasks.

The speed of forming spatial associations between cue and reward sites depended strongly on the distance between them, although hummingbirds eventually achieved comparable performance regardless of separation.

Birds were more resistant to change on spatial memory tasks than spatial association tasks. Greater separations between cue and reward resulted in more reliance on spatial memory and greater persistence of these memories in the face of change. Time spent foraging on rewarding patterns affected the birds' persistence when the pattern changed. After longer experience of successfully using a pattern of feeders, birds persisted longer in formerly rewarding behaviours. Time spent using a pattern of feeders influenced spatial memory tasks much more than spatial association ones.

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# Chapter 1.

## General Introduction

### Tactics of Survival

Animals must carry out a number of tasks in their everyday existence in order to ensure their survival and reproduction. These include finding food, shelter and mates and avoiding predators. For social animals, finding ways to coexist with their compatriots is another important task. Foraging has been extensively studied (see review by Schoener, 1987) perhaps because it is easy to quantify in an experimental setting.

### Learning

Learning is an important aid to survival. It is a change in an animal, as a result of experience, that can alter the animal's behaviour in given circumstances (Hintzman, 1978). Examples of learning range from nudibranchs learning to avoid electric shock to humans learning new languages. Generally, learning can be divided into two broad categories: non-associative and associative. Non-associative learning is the simple habituation or sensitization to a stimulus, such as in the nudibranch

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example (Raven and Johnson, 1989). Associative learning is the development of an association between two stimuli or between a stimulus and response. Most examples of complex learning such as language acquisition, spatial navigation, foraging and others are associative.

There are a number of theories about learning processes. Two dominant schools of thought are behaviourism and cognitivism. Behaviourists believe that learning should be discussed in terms of observable behaviours (Hintzman, 1978). Essentially, they treat animals as black boxes. The internal processes involved in learning a task are either considered unimportant, because they are unobservable, by some members of this group, or are considered mechanistically by other workers who take a similar approach to the behaviourists. A second school of thought considers behaviour in humanistic terms and treats the processes of animal learning as if they were equivalent to the thought processes found in humans. This group is interested in mental events like ideas, thoughts and purposes (Hintzman, 1978). In my view, neither approach offers the sole truth about learning and both offer valuable insights into the processes involved.

## Components of Learning

Perhaps the most basic idea in associative learning is the linkage between stimulus and response. An animal repeatedly presented with a stimulus, each time followed

closely by a reward on completion of a specific response, will link the items together into a stimulus-response association (Damianopoulos, 1989). One requirement for this association to be made is that the stimulus and reinforcer be closely linked in space and time. Either temporal or spatial separation between the reward and stimulus weaken the ability of the animal to associate the items (Gibbon *et al.*, 1988; Pinel *et al.*, 1986).

In a few cases, however, it has been possible to demonstrate learning in the absence of reinforcement. In some cases the mere contiguity of stimulus and response can create a learned association between the two (Hintzman, 1978). In most cases, though, reinforcement is an important element of formation of the stimulus-response association. This linking of stimulus and response is affected by the frequency and value of the reinforcement: Low value rewards, infrequent rewards or variable rewards can reduce the speed and degree of learning (Gibbon *et al.*, 1988; Morris and Capaldie, 1979). Cognitivists assume that animals carry out actions that yield rewards or avoid punishment due to internal motivation or the intrinsic value of the stimulus to the animal (Gleitman, 1974). Behaviourists attempt to deal only with observable behaviours, either ignoring motivation, or acknowledging its existence but treating it mechanistically.

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Another aspect that involves and affects motivation is the expectancy of an event occurring. This concept has been promoted by the cognitive school (Hintzman, 1978). These workers propose that animals develop expectations about rewards and future events based on past experience. None of these behavioural processes can occur, however, without the ability to use past experience through memory.

## Memory

"Memory" refers to processes through which experiences and learning are retained over time (Hintzman, 1978; Goelet *et al.*, 1986), and we are just beginning to understand them. At least three different types of memory have been suggested, based on durability of the memory. The least durable of these is working memory that is used during a task. Slightly more permanent is short term memory, that lasts beyond the task at hand but which is still measured in minutes or hours. Finally, long term memory can persist for days or throughout an animal's lifetime.

Working memory is used in the extreme short term. Generally, the difference between working memory and short term memory is not well understood. Some authors tend to doubt its existence as a separate form of memory from short term memory (van Luijtelaar *et al.*, 1989). The two may or may not be distinct processes with differing physiological bases, but workers agree the purpose of working memory is to retain only those elements of experience necessary to

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accomplish the immediate task at hand. These memories are "throwaways" (Maki, 1987) that are acquired quickly, used immediately and forgotten.

Short term memory includes those items which an animal may need to recall beyond the immediate task but which are not retained indefinitely. This form of memory seems to involve covalent modifications of existing proteins that regulate the activities of the neurons and their synapses (Barnes, 1988; Goelet *et al.*, 1986).

Long term memory includes everything retained indefinitely. These memories also involve proteins, but through modification of the expression of specific genes in neurons (Goelet *et al.*, 1986; Matthies, 1989; Thompson, 1986). If long term memory requires generation of new proteins, long term memories should develop more slowly than working or short term memory.

The difference between short and long term memory is in some ways analogous to the difference between hormone types. In this case, short term memory is stored in a fashion similar to protein based hormones such as adrenalin. Both provide immediate responses that are short lived. Long term memory is stored in a fashion similar to steroid hormones like testosterone. Here the effects take longer to develop but can survive indefinitely.

Wickelgren (1979) suggested that the hippocampal, limbic arousal system plays a key role in transferring items

from working memory to long term memory by isolating the altered neurons from continuing inputs while cellular structure shifts during creation of long term memories.

While some workers have suggested multiple forms of working memory, including a form used solely for remembrance of spatial relationships (Gallistel, 1990; Inui, 1988; Roberts, 1988), others suggest that there is no evidence for multiple forms of working memory, and that both spatial and non-spatial learning occur by similar processes in the very short term (Ennaceur and Meliani, 1992).

In the long term, however, there do seem to be differences. For example, Nadel and Willner (1980) suggested that some aspects of spatial memory can be used via short term or working memory but a cognitive map of an animal's surroundings is too large for short term storage and spatial reference to a cognitive map is fundamentally different from use of cues. It should be remembered, however, that animals attend to many senses at once, all of which involve at least slightly different sensors, pathways, neural processing mechanisms and storage sites, so that at least several overlapping brain areas will be involved in most learning tasks and memories are unlikely to be entirely isolated from each other in single locations in the brain (Squire, 1986). Many groups of advanced animals, including birds and humans, may share many of the same or similar neural structures and functions (Bingman *et al.*, 1989;

Griffin, 1976; MacPhail, 1982; Olton, 1985). Species differences may be important (MacPhail, 1982), such as lateralization of spatial memory in food storing birds (Clayton, 1993; Clayton and Krebs, 1993 and 1994) and possibly humans (de Renzio, 1982), or variation in relative hippocampal size coupled with variation in reliance on spatial memory (Sherry and Vaccarino, 1989; Sherry *et al.*, 1989), but there is general agreement that the basic principles are widely applicable.

## Spatial Memory

"Spatial memory" refers to the processes by which animals remember locations in their environment. Growing numbers of species are known to use spatial memory in various ways. Among vertebrates for instance, female bats use spatial memory to locate their young in colonies of several thousand pups (McCracken, 1993), monkeys use it to locate fruit in a three-dimensional jungle environment (Menzel, 1991), and fish locate nests and define territories with the help of spatial memory (Warburton, 1990). Among birds, spatial memory is used in both foraging and territoriality (Balda and Kamil, 1988; Gass and Montgomerie, 1981; Gass and Sutherland, 1985; Shettleworth, 1983), and is flexible enough to cope with rapidly changing conditions (Valone and Girardeau, 1993; Vander Wall, 1991; van Luijtelaar *et al.*, 1989; Wilkie, 1986b; Wilkie *et al.*, 1981; Wunderle and Martinez, 1987; Zentall *et al.*, 1990).

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Invertebrates also use spatial memory. Ants use a combination of spatial memory and olfactory cues to return to food sources or nest locations (Collett *et al.*, 1992; Haefner and Crist, 1994; Holldobler, 1980). Hoverflies use spatial memory to return to an unmarked location in mid-air (Collett and Land, 1975).

Spatial memory in honeybees is well documented and studied. For example, they use spatial memory to return to flower patches (Wellington and Cmiralova, 1979), to find the hive and to navigate within the hive (Dyer, 1991), and it is plastic enough to allow them to reorient to alterations of landmarks, such as may occur after swarming to a new nest location (Dyer, 1993).

The use of spatial memory affords distinct energetic and ecological advantages (Valone, 1991). Modelling studies suggest that using spatial memory to forage can provide greater than a five-fold energy advantage over completely random search and a three to five-fold advantage over systematic searching. (Armstrong *et al.*, 1987; Benhamou, 1994). Benhamou's studies also suggest that even animals with more limited learning abilities such as desert arthropods use spatial memory to gain these energetic advantages. Similar energetic advantages apply to different kinds of organisms performing similar ecological tasks such as territorial defense, nest building, and brood protection (Gallistel, 1990; Gould and Marler, 1987; Kramer and Weary,

1991; Wolf *et al.*, 1972). The physiological and ecological differences between species make the broad based nature of these advantages remarkable, and have provided one of the cornerstones of behavioural ecology (Gray, 1987; Schoener, 1987).

Learning enables animals to make more effective use of environments, although the advantages of spatial learning disappear if irregular temporal variability is too great (Bowers and Adams-Manson, 1993; Nishimura, 1994). Aside from the energetic and other physiological costs of storing memories, it becomes increasingly likely as temporal variability increases that the cost of foraging (or other ways of using memories) will be wasted.

## Role of Learning in Spatial Memory

If spatial memory is physiologically expensive, as most workers assume it to be, then simplifications of the process of remembering and using experience should be advantageous. Especially to the extent that animals can generalize what they learn about their environments across situations, they should be able to use their environments effectively with a minimum of stored information. For example, learning that all red tubular flowers of a certain shape are worth visiting should not be much more difficult than learning that a particular flower is rewarding, but clearly it is more useful.

Several studies have provided evidence that operant behaviours elicited in laboratory environments to demonstrate the use of spatial memory are equivalent to natural foraging activities (Dallery and Baum, 1991; Mellgren and Elsmore, 1991). Numerous studies have demonstrated that use of spatial memory in nature is a tool that increases foraging efficiency, to locate dens or hives or to find mates (Bowers and Adams-Manson, 1993; Haccou *et al.*, 1991; Kramer and Weary, 1991; Menzel, 1991; Robinson and Dyer, 1993).

The ability to learn spatial information is not universal; there are distinct species differences. Animals as closely related as blue tits and marsh tits, for example, have greatly different spatial memory abilities. The marsh tit, a food storing bird, has excellent spatial memory abilities, while the blue tit, which does not cache food, cannot perform similar learning tasks. A similar disparity exists between the closely related jay and jackdaw (Clayton and Krebs, 1994). Similar results have been found in other corvid and parid bird species (Balda and Kamil, 1989; Shettleworth and Krebs, 1986).

Even in spatially oriented species there is definite variation in the ability to use spatial memory. Insects such as bees, wasps and ants seem to rely most heavily on dead reckoning based on remembered landmarks, with a very limited ability to generalize and produce cognitive maps of

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their surroundings (Collett *et al.*, 1992; Collett *et al.*, 1993; Dyer, 1991; Dyer, 1993; Greggers and Menzel, 1993). Birds and mammals, on the other hand, often produce complex cognitive maps, as evidenced by their ability to find novel routes, avoid obstacles and vary their behaviour to respond to novel environmental changes (Bingman *et al.*, 1988; Collett, 1987; Ellen *et al.*, 1984; Etienne *et al.*, 1990; Gass and Sutherland, 1985; Menzel, 1973; Vander Wall, 1991).

While it may be possible for animals to remember dead reckoning paths (a series of movement vectors) between locations, there are ways to simplify spatial memory tasks by building up map-like images of the environment. Humans do this regularly (Giraudo and Perauch, 1988), and it seems likely, based on a range of studies, that animals do also (Aadland *et al.*, 1985; Gould, 1985; Maki *et al.*, 1979; Nadel and Willner, 1980; O'Keefe and Conway, 1980; Tolman, 1948).

## Cognitive Maps

A cognitive map is an internalized representation of an animal's environment including the geometric relationships between locations in that environment (Gallistel, 1989 and 1990; Gould, 1986c). The evidence for the use of cognitive maps in animals other than humans is circumstantial, but storing memories of the environment in such a fashion should be greatly advantageous. While animals with limited cognitive abilities such as ants are less behaviourally flexible, there is ample evidence that animals such as

mammals and birds go beyond inertial reckoning and simple repetitions of past activities (Tolman, 1948).

The concept of a cognitive map in any animal is still not universally accepted. In a fashion similar to the split between cognitivists and behaviourists there are two schools of thought on spatial navigation. One group, championed by authors such as Dyer (1991, 1993), have suggested that animals rely on dead reckoning, or movement along a set of remembered vectors, to navigate. Others, such as Gould (1986a and 1986c), argue that the ability to find novel paths and navigate with only a subset of previous cues and landmarks precludes the sole use of simplistic navigational tools as dead reckoning in many animals.

Cognitive maps of the environment provide numerous navigational advantages. Monkeys and chimps minimize the distance travelled to reward sources (MacDonald and Wilkie, 1990; Menzel, 1991; Menzel, 1973), gerbils orient themselves in novel locations with reference to objects they could only be remembering at the time (Thinus-Blanc and Ingles, 1985), and rats store multiple maps simultaneously, allowing for flexible exploitations of their environment (Maki *et al.*, 1979).

We understand poorly at best how animals develop maps of their environments. I believe that it is likely that the process begins with either random sampling forays or systematic sampling forays and that prior experience likely

biases use of these methods. Animals' search patterns are tied to their ecological needs (Root and Kareiva, 1984) and to abilities gained through evolution (Gould, 1986c). From the original trial and error investigation of the value of different portions of the terrain, an animal can begin to remember sets of rewarding and non-rewarding sites. Perhaps some animals cannot move beyond this stage.

In the case of birds such as hummingbirds, however, we know that they synthesize these sets of places into structures that incorporate spatial, geometric relationships among elements (Sutherland and Gass, in press; Sutherland, 1985; Thompson, 1994). These birds, along with groups such as primates, rodents and others, can apparently generate complex maps that allow highly flexible movement and exploitation of their environments (Bowers and Adams-Manson, 1993; Ellen *et al.*, 1984; Sholl, 1987).

## Cues and Landmarks

Part of the process of developing a map of the environment involves learning the positions of recognizable landmarks. Without cues or landmarks animals are presumably limited to dead reckoning as a means of navigation. Landmarks, by this definition, are any permanent or semi-permanent items that animals can sense and use as navigational aids. Typically, we think of a landmark as a physical item that an animal can easily see; however, it could be an area of specific wind currents or a site where

an odour, or any of a number of other sensory phenomena, is maximized. It must be consistent enough, however, for the animal to become conditioned to its presence and to learn to associate it with some specific reward or task in a particular place or area.

There is considerable overlap between this definition of a landmark and the definition of a reward cue. I will define a reward cue as an indicator of reward that is specifically linked to that reward in space and time (and in a 1:1 ratio: one cue, one reward), and a reward landmark as a navigational aid that indicates an area containing one or more reward sites.

The evidence hints that an animal deals with environmental information differently, depending on whether that information is a cue or a landmark. In practice, however, that difference is much more difficult to discern. It may be unimportant whether we label an item as a landmark or a reward cue and in many cases there will be considerable overlap between them. Differentiating between them is difficult short of invasive surgical techniques, such as work by D. Sherry (pers. comm., 1992) which suggests that landmarks register in areas of the brain used for long-term memory while cues are processed in short term memory. This memory storage difference makes sense if landmarks are part of an animal's continuing map of the world, while cues, although used for similar purposes and often permanent

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features of the landscape, are associated with a transient reward event.

### Cues

Previous studies of spatial memory and learning have differentiated several types of cue information. Cues may provide directional information, marking the site of a reward. This type of cue is common in many studies in which, for instance, a light comes on to mark the half of a screen that contains food (Suzuki *et al.*, 1980). Cues may also provide information about profitability. This same light provides the most basic information about reward quality, at the same time marking one side as offering a positive reward and the other as offering no reward. Other experiments have used cues to provide more detailed information such as the number of food items present at a site (Roberts, 1988), the quality of a nectar source (Bogdany, 1978; Collias and Collias, 1968; Dreisig, 1989; Greggers and Menzel, 1993), or the type of food present (Sherry, 1984).

The amount and kind of information that could be provided by a cue is highly flexible and depends as much on the experimenter as on the nature of cues themselves; whether the information is actually conveyed to the animal, of course, depends on the animal. Almost any information which an animal can be trained to detect or differentiate can be provided by a cue. This includes duration of reward

periods, reward variability, event sequences and many other forms of information (Colwill and Rescorla, 1985; Pepperberg, 1987; Rescorla, 1986; Roberts, 1988; Self and Gaffan, 1983).

**Landmarks**

Landmarks are navigational aids animals use to navigate through their environments. Studies of landmark use suggest that animals remember several characteristics of them. They distinguish landmarks on the basis of size, for example, and prefer to use large landmarks for navigation (Bennett, 1993). Shape, colour and other similar information about landmarks is remembered and used by animals in learning (Cheng *et al.*, 1987a; Vander Wall, 1991). Animals also remember the distance between landmarks and their accompanying sets of reward sites (Bennett, 1993; Cheng *et al.*, 1987b; Collet *et al.*, 1992), and this information is vital to navigation. Moving a landmark causes animals to miss the reward site by the same distance as the shift in landmark location (Cheng, 1986 and 1988; Tinbergen, 1932; Tinbergen and Kruyt, 1938; Vander Wall, 1982; Warburton, 1990). Angular direction to locations is also remembered and moving the landmarks used in triangulation may have a similar effect on assumed reward location (Cheng, 1989; Tengo *et al.*, 1990).

Cheng and others have suggested that animals use landmarks as navigational aids by calculating vectors

between the landmark and the reward site (Cheng, 1988). This hypothesis does not account for all the ways that animals use landmarks (Spetch *et al.*, 1992), but may still play a role in landmark navigation where landmarks and rewards are closely associated and there are few confounding objects.

## Role of Cues and Landmarks in Learning

Animals use landmark and cue information to develop cognitive maps of their surroundings, as first suggested by Tolman in 1948. Initial sampling forays provide information that the animal learns to associate with the rewards it obtains during these forays. Early navigation may consist of dead reckoning, but as an animal learns to identify landmarks, more flexible and effective approaches to the reward sites become possible and as it learns the cues there it can ignore non-rewarding or less rewarding sites altogether. Eventually, it may tie together information about individual reward locations into patterns that require less information storage and less time to locate and exploit repeatedly. This process of chunking or generalizing spatial information about their environments (cognitive mapping) is found in a number of vertebrate species and may be found in invertebrates as well (McNamara *et al.*, 1989; Olton, 1985; Shiffrin *et al.*, 1976).

## Outline of Studies

In this thesis I examine several aspects of spatial memory and its role in foraging using rufous hummingbirds (*Selasphorus rufus*). These birds have several advantages for learning and behavioural studies. One advantage is that their small size and space requirements allow them to be maintained without excessive space requirements. Their second advantage is that they have an extremely high metabolic rate, and require food often. This ensures that they are highly motivated to learn various foraging tasks. Their high feeding rates, compounded with their advanced learning abilities, allows the completion of complex learning experiments in a short period of time and with relatively short training requirements.

The first set of experiments examines the role of experience in spatial pattern learning, especially as a function of environmental instability. In my second set of experiments I study how visible cues and landmarks affect spatial pattern learning and the relative importance of different kinds of visual characteristics to learning. The final set of experiments examines the contrasting effects of spatial memory and spatial association memory.

# Chapter 2.


# Pattern Learning and Persistence of Spatial Memory in Rufous Hummingbirds


## Section I.  Introduction


## Learning

Learning aids effective use of available resources. Estes (1994) described an individual as actively sampling alternate courses of action, generating expectations and selecting those most likely to succeed.

In the laboratory, many learning experiments have dealt with simple environments, in which rats choose one arm of a maze, or pigeons learn a pecking protocol in order to receive a reward (Bolhuis *et al.*, 1987; Bond *et al.*, 1981; Colwill and Dickinson, 1980; Spetch *et al.*, 1992; Wilkie, 1986a).  In these experiments it is often the case not only that the environment is simplified but that the learning tasks required of the animal are straightforward.  This approach simplifies and controls the variables presented to the study animal in order to better understand some particular aspect of learning.

In natural environments, however, learning is seldom such a clean and straightforward affair. The characteristics of a refuge or foraging environment may change with the time of day, lighting conditions, and weather. Prey characteristics such as shape, activity and location vary in almost all cases (Dawkins, 1971a and 1971b; Dukas and Ellner, 1993; Dukas and Waser, 1994; Lawrence, 1989). Food sites for nectarivores such as hummingbirds change colour, size, shape and energetic profitability on a daily basis (Armstrong *et al.*, 1987; Gass and Sutherland, 1985; Wolf and Hainsworth, 1991). Food available from particular sources may be absent, richer or poorer on subsequent visits (Gass *et al.*, 1976; Weis, 1983; Wunderle and Martinez, 1987). Not only do things change, but they often change unpredictably in natural environments, and animals must tolerate this in their decision-making. As a consequence of these complexities, researchers must be careful in extrapolating results of simple laboratory studies to the behaviour of animals in the wild (Beecher and Stoddard, 1990).

**Advantages of Learning**

In many situations it benefits animals to learn the characteristics of their environments, especially those factors that most affect their fitness. These include such obvious things as the habits of predators, sites of refuge, and locations of food (Krebs and Davies, 1984). In stable

environments, individuals of a given species who learn are more fit (Benhamou, 1994; Valone, 1992).

### Disadvantages of Learning

The disadvantages of learning include the time and energy spent sampling the environment (Forkman, 1991; Valone, 1992) and processing information (Blough and Blough, 1990; M. Brown, 1992; Brown and Cook, 1986). One study found that foraging with no prior expectation (*i.e.* learning) to guide exploration was only 4 per cent effective (Vander Wall, 1991) so the exploration required for learning is expensive. Another disadvantage is the energetic cost of remembering (Bullock, 1993; Capelli *et al.*, 1986; Miller, 1956).

### Alternatives to learning

Animals presumably use learning due to its energetic advantages. Other foraging strategies may be preferred in resource poor or unstable environments, where this advantage is less prevalent. Similarly, learning need not be used if a simpler strategy will produce successful foraging. Such strategies include random foraging, or the use of simple rules of thumb to govern behaviour. Wolf and Hainsworth (1983 and 1991) found no evidence of memory use by hummingbirds foraging in resource limited environments. Under conditions of heavy competition, random behaviour that cannot be predicted by competitors may be advantageous (Bryant and Church, 1974). Bees taking nectar from flowers

often start at the bottom of the plant and give up when they encounter a poor blossom, demonstrating a simple systematic foraging pattern (Dreisig, 1989; Pyke, 1978; Pyke and Cartar, 1992). Parasitic wasp-like insects (*Torymus capite*) search for a host for a fixed time then give up (Weis, 1983). Such rules of thumb are the basis of the marginal value theorem, which states that animals should use their environments in ways that maximize their rates of return, including the use of prior knowledge (learning) when it is advantageous (Bond, 1980; Charnov, 1976; Krebs and Davies, 1984).

## Complex environments

Learning is advantageous for many animals in many situations. In perfectly stable environments animals need only learn once; however, learning consolidated over a period of time tends to be less flexible than newly learned tasks (Gould, 1986c). In extreme cases, long term exposure to a stable environment can lead to canalization or automation of behaviour (Gass, 1985; Tierney, 1986).

Learning can also be a response to rapidly changing, unpredictable environments (Tierney, 1986). Too much unpredictability, however, can negate the value of learning by reducing the effectiveness of memories (Bowers and Adams-Manson, 1993; Nishimura, 1994). Thus, the reliance of animals on learning and memory varies with the complexity of the environment (Bond *et al.*, 1981; Killeen and Fetterman,

1988; Warburton, 1990), and there is experimental evidence that animals prefer complex, changing environments (Denny, 1975). Learning seems to be enhanced in such complex environments (Gleitman, 1963), especially if the surroundings are familiar to the animal (Biederman *et al.*, 1973).

Despite the importance of understanding the effects of predictability on learning, our ability to study this important factor has been limited (Eisenberger, 1988; Papaj, 1988), partly because of the practical difficulties of creating precisely variable environments in the laboratory. Testing of some of these theories has concentrated on such changes as variations in reward levels or patch quality (Caraco, 1982; Dow and Lea, 1987; Kacelnik *et al.*. 1987; Regelmann, 1985). Other factors in unpredictability that have been examined in the laboratory include persistence in patches (Lima, 1983, 1984), responses to variance in the level of reward (Stephens and Paton, 1986) and scheduling of returns to cached food (Gill, 1988; Sherry, 1985).

**Mathematical modelling**

Mathematical modelling has been an important tool for developing theories about learning in complex, changing environments (Booth, 1986; Caraco and Lima, 1987; Colwell, 1974; Fagan and Young, 1978; Laming and Scheiwiller, 1985; McNamara, 1982; McNamara and Houston, 1985b, 1987). The use

of such models has allowed researchers to examine complex tasks that are difficult to duplicate in the laboratory (Cahoon, 1984; Cain, 1985; Haefner and Crist, 1994). These modelling exercises have provided us with insight into natural learning processes that can be applied in artificial intelligence systems to test the feasibility of our learning theories (Devi and Sarma, 1986; Faris and Maijer, 1988; Fuchs and Haken, 1988a and 1988b; Haken, 1988; Hobbs, 1986; Park, 1985; Selfridge and Nesser, 1960) or tested experimentally (Stephens and Paton, 1986).

One use of mathematical modelling has been to examine the internal processes of learning and memory. Based on a combination of modelling and experimentation, Kacelnik *et al.* (1987) suggested that animals store their memories of the environment by a means that can be modelled as an exponentially weighted moving memory window. Similarly, McNamara and Houston (1985b) suggested that a weighted moving memory window is an accurate model of learning. If memory window models are valid, then memory can be swamped or overcome by large inputs of new and varied experience. This theoretical expectation was corroborated experimentally by Nishimura (1994).

The ideas proposed in these memory window models suggest that experience of an environment (both time spent in an environment and number of experiences) contributes to what and how much an animal learns about its surroundings.

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Retention of a memory, then, should depend on both time since rewards were obtained (reinforcement) and intervening or intertrial experience. This expectation has been confirmed by several authors (Capaldie and Miller, 1988; Capaldie *et al.*, 1987a and 1987b; Hulse, 1978; Kamil and Mauldin, 1975). Increasing complexity could adversely affect the ability to learn and remember (Hochberg and McAlister, 1953; Laverty, 1994) since it provides more things to remember, swamping a memory window.

## **Perception of the environment**

The adaptive significance of learning has been examined under various but limited conditions (Damianopolous, 1989; Denning, 1989; Draulans, 1988; Dukas and Visscher, 1994; Dukas and Waser, 1994; Gleitman, 1963; Johannson *et al.*, 1980). When should an animal learn about its environment and when should it forage randomly or by some simple rule of thumb? If the environment is sufficiently predictable, learning the locations of individual food sources will save energy and foraging time (Bond, 1980; Vander Wall, 1982). Most food storing birds who rely on learning and memory to relocate food caches, for instance, are territorial and live in seasonal environments (Roberts, 1979). These birds experience change in their environments but many of the changes are irrelevant to their foraging and even when relevant, are often predictable and consistent. If consistent environments favour learning, the question can be

refined to ask how consistent environments must be for learning about them to be advantageous.

Discussions of energetic advantages often lead to considerations of optimal foraging, which has been a dominant theme in behavioural studies for about 30 years now (Charnov, 1976; McNamara and Houston, 1985a; Roberts, 1991; Tamm and Gass, 1986). It is apparent, however, that animals do things that are not easily explained by optimality concepts such as energy maximization (Forkman, 1991; Gass, 1985; Maier *et al.*, 1988; Roberts, 1991). They do not always optimize their efforts but instead adopt less efficient approaches which still meet their needs (Stephens, 1981).

It is important to place behaviours into the larger context of the animals' various activities when examining animal behaviour since animals must trade off benefits from one activity with its associated costs and its effects on other activities (Getty and Pulliam, 1993; Lima, 1984; Smith, 1974). Optimality cannot explain behaviour unless it is coupled with information-processing hypotheses (Bond, 1980; Todd and Kacelnik, 1993). Animals with knowledge of their environments are not limited to simple rules of thumb such as leaving a patch when food intake rates begin to drop. Learning in these situations allows for more sophisticated decision making.

What is optimal to do at any moment can depend on what an animal has done to learn about its environment, which often displays recognizable spatial structure. In turn, learning can be modified by perceptions of consistency. I intend to explore the role of predictability in spatial pattern learning, since the ability to return to food sources is a fundamental requirement for many animals' survival. The need to forage successfully, coupled with the advantages of learning, suggests that there is strong selection for the ability to learn patterns of food sites and spatial maps of the environment. Spatial memory has been studied in many animals and conditions, ranging from goldfish to honeybees to humans (Aadland *et al.*, 1985; Garber, 1988a and 1988b; Gould, 1987; Jue *et al.*, 1989; Shettleworth *et al.*, 1990; Spetch and Edwards, 1986; Woodard and Bitterman, 1973). Rufous hummingbirds, the species used in my study, can learn spatial patterns, as demonstrated by Sutherland and Gass (in press).

## Experimental protocols

Sutherland (1985) studied the ability of hummingbirds to learn patterns of rewarding feeders distributed in a two dimensional array. He allowed birds to learn a pattern of feeders over a series of 30 trials and then suddenly reversed the pattern, so that all rewarding feeders became non-rewarding and *vice versa*. Complete and sudden reversal of a learned pattern produced a significant drop in

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performance (successful feeder visitations dropped below chance). He repeated this procedure with four different patterns of feeders on the array, each providing a 50 per cent chance of reward with random feeder visitation. The patterns included "halves" where the rewarding feeders were all on either the left or right hand side of the array, "quarters" where the top left quarter and bottom right quarter of the array were rewarding (or *vice versa*), "checkerboard" where the array consisted of eight groups of four rewarding feeders arranged in squares alternated with eight groups of four unrewarding feeders arranged in squares, and "random" where rewarding feeders were located randomly on the array (although the random pattern presented at the start of the experimental run remained the same for all runs). From this study he concluded that the hummingbirds had learned the pattern of rewarding feeders and expected the pattern to persist.

### Current study

In order to examine the effect of experience on the persistence of behaviours that rely on spatial memory I performed similar experiments using the "quarters" pattern, but varying the number of trials birds were exposed to the pattern of feeders before a sudden and complete reversal of the pattern. If the strength of spatial memory or the strength of reliance on it develops with experience, in the sense that it persists longer in the face of no

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reinforcement, then as the pre-switch exposure increases the drop in performance after the switch should increase in magnitude or duration.

## Section II.  Materials and Methods

### Subjects

In this experiment I used 12 naive, adult rufous hummingbirds, (*Selasphorus rufus*):  4 males and 8 females. The birds were captured in the field (10 near Rosewall Creek, Vancouver Island, B.C., and 2 in the U.B.C. research forest north of Maple Ridge, B.C.) and maintained in individual 0.6 x 0.6 x 1.0 m fibreglass mesh cages for one to two months prior to testing.

Throughout the period of captivity the photoperiod was maintained at 14L:10D.  Excluding test periods, the birds were supplied with either Roudybush hummingbird diet or Nektar Plus hummingbird diet *ad libitum* on weekdays.  On weekends, birds were provided with 25% sucrose solution with added vitamins (Avitron avian vitamin supplement) and minerals (Avimin avian mineral supplement).  At all times outside of test periods, adult *Drosophila* were available.

### Experimental Environment

I conducted all training and experiments in a room 1.1 x 2.6 x 2.6m high with overhead full-spectrum fluorescent lights.  Walls and ceiling, except the feeder array, were a uniform light green colour and the floor was a uniform sand colour.  A single, stand-mounted, 1.7 m high perch was at

the centre of the room, fitted with a photocell to signal arrivals and departures to a computer monitoring the room.

On one end wall of the room a 1.0 x 1.0 m dark green metal panel extended from just below the ceiling. Inset into this panel were 64 feeders in a square 8 x 8 array spaced at 10.5 cm vertically and horizontally. Each feeder consisted of a 2.0 cm length of 1.67 mm I.D. Intramedic polyethylene tubing which had been flame heated and bent to form a terminal reservoir at one end. The resulting feeder tube resembled a small smoker's pipe, whose bowl was an open nectar reservoir and whose stem served as a floral corolla. The stem of the feeder extended through a photodarlington photodetector and a 4 mm hole drilled in the metal array panel and was flush with the front of the panel. Each hole was surrounded by an orange 19 mm Avery label punched with a 6 mm centre hole.

A computer recorded arrivals, departures, and visit durations for the perch and each individual feeder, using signals from the photocells. Recording was accurate to about 10 ms. Before each trial I supplied rewarding feeders with 2 µl of 22% sucrose solution (weight/weight) from a repeating dispenser (Hamilton PB-600-1). This volume is within the normal range of nectar volumes found in floral species used by rufous hummingbirds (Armstrong, 1986; Carpenter *et al.*, 1983; Gass and Roberts, 1992). Between trials the array was covered by a beige roller blind

operated from outside the experimental chamber by a pull cord.

## Training

Each bird was trained for three days immediately prior to testing. For the first two days birds lived in their cages but were fed maintenance food *ad libitum* from a feeder marked identically to those in the experimental chamber.

On the morning of the third day of training, birds and the training feeders from their home cages were moved to the experimental chamber (the feeder array was covered by the blind). The sole perch in the room was raised to a height of 2.4 m and the feeder was placed directly in front of this perch. As the bird became accustomed to using this perch its height was gradually decreased to 1.7 m, the height of the centre of the feeder array. After the bird was accustomed to the feeder and perch in this arrangement, the feeder was moved from its position near the ceiling to directly in front of the covered array until the bird again fed regularly. Next, all 64 array locations were provided with 2µl of 22% sucrose solution, the home cage feeder was removed, and the array was uncovered until the bird fed from several feeders. The array was then covered, the feeders refilled, and a new training trial was begun. Once the bird was consistently visiting the panel, and showed no or minimal levels of positional bias (based on informal estimation of any untrained preference for specific portions

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of the feeder array and if necessary enforced by temporarily covering areas of the array that the bird had not been foraging outside of until the blocking of preferred feeders caused foraging to become more widespread) it was put through a series of 10-20 sham trials with all feeder locations rewarding to accustom it to the 1 minute trial and 5 minute intertrial periods to be used during testing the following day.

## Experimental Procedures

On the day of testing each bird was presented with one of two mirror image quarters patterns of rewarding and non-rewarding feeders, selected randomly (Fig. 1). In both cases, rewarding feeders contained 2 µl of 22% sucrose solution (weight/weight) at the beginning of each trial, making 64 µl of nectar available each trial: approximately twice the preferred meal size of rufous hummingbirds under normal conditions (Diamond *et al.*, 1986). The treatment and bird used on any day was determined by a schedule that exposed each bird to one of the pre-switch exposure treatments. The order of the treatments was randomised, as was pattern orientation. In each treatment a bird was presented with its original pattern for a fixed number of trials. Then the pattern was suddenly switched (changed to its mirror image) between two trials, so that all previously rewarding array locations were now non-rewarding and *vice*
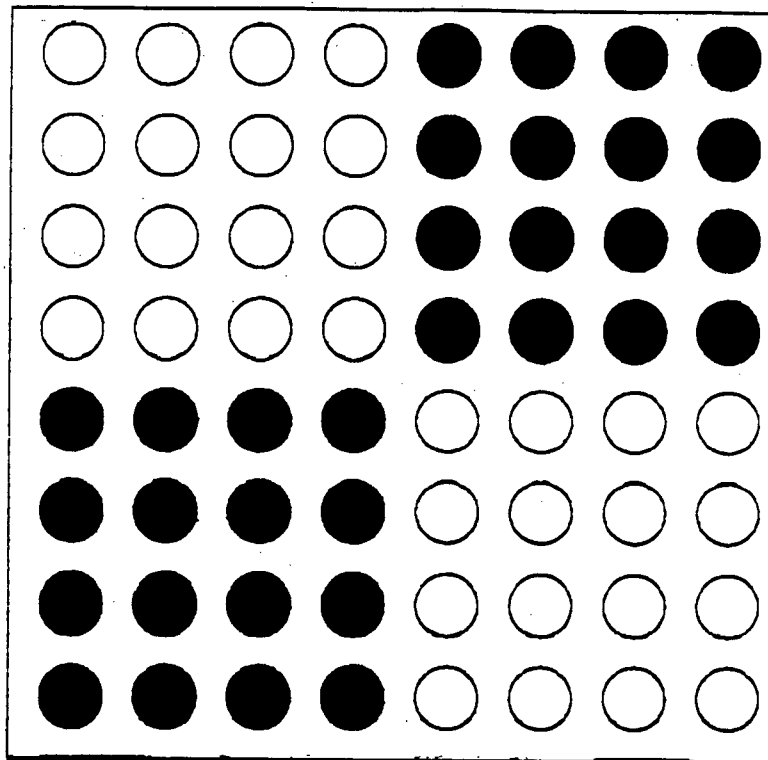
Figure 1. Stylized representation of one quarters pattern for the feeder array (not to scale). Each circle represents one feeder. Solid black circles represent rewarding feeders, and open circles are empty feeder locations.

*versa.* The four treatments consisted of pre-switch exposures of 10, 20, 30 and 40 trials.

The subject bird was fasted for 15-20 minutes immediately preceding the test period. Although trials lasted one minute, birds could stop feeding and return to the perch at any time. I ignored any trial in which the subject did not visit the feeder panel.

Previous studies (Sutherland, 1985) as well as pilot studies by myself have shown that hummingbirds remove all nectar from the feeders when a volume of 2µl is used. For this reason, I treated all second and subsequent visits to any feeder during a trial as non-rewarding. For analysis of results I treated only the first visits to rewarding feeders in each trial as correct visits. I treated first visits to non-rewarding feeders as incorrect visits and ignored revisits to feeders during any given trial for determining performance and foraging success.

At the end of each trial I covered the feeder array and refilled rewarding feeders which the bird had emptied during the trial. After an intertrial period of 5 minutes I uncovered the array and began the next trial. At the end of the initial exposure period, I covered the feeder array and emptied and flushed all feeders. I then filled the 32 newly rewarding feeders and carried out 40 more trials with this reversed feeder pattern. At the end of the experimental

run, the bird was returned to its home cage and all feeders were emptied and flushed.

## Section III. Results

### Initial Performance

Birds in all four treatments improved at similar rates (Fig. 2). Initially, their performance was near chance, then improved rapidly to 80% to 90% correct visitations by about 20 trials. These are decelerating monotonic curves.

I examined food consumption to test the applicability of two performance indicators and found that birds fed from the feeder array at a relatively constant rate during the day (Fig. 3). There is considerable variability in these curves; however, birds did not significantly change their feeding rate (amount of sucrose consumed every trial) in approximately half of the treatments (Table 1). Changes in feeding rates throughout the course of the experiments were poorly explained by the number of trials spent with a consistent pattern of rewarding feeders, as shown by the low $r^2$ values; this was true for all treatments.

| | Pre-switch Trials | | | Post-switch Trials | | | All Trials | | |
|---|---|---|---|---|---|---|---|---|---|
| | F | p | $r^2$ | F | p | $r^2$ | F | p | $r^2$ |
| Switch 10 | 4.317 | 0.071 | 0.350 | 3.287 | 0.078 | 0.079 | 8.450 | 0.006 | 0.150 |
| Switch 20 | 3.585 | 0.075 | 0.166 | 5.101 | 0.030 | 0.118 | 9.244 | 0.004 | 0.138 |
| Switch 30 | 9.688 | 0.004 | 0.257 | 9.832 | 0.003 | 0.205 | 2.253 | 0.138 | 0.036 |
| Switch 40 | 7.969 | 0.008 | 0.173 | 0.014 | 0.907 | 0.000 | 8.920 | 0.004 | 0.102 |

Table 1. Regression analysis of correct visits versus trial number (since the assumption is that the relationship will be linear and flat) for each of the treatments. Treatment names refer to the number of trials before reversal of the pattern of rewarding feeders.
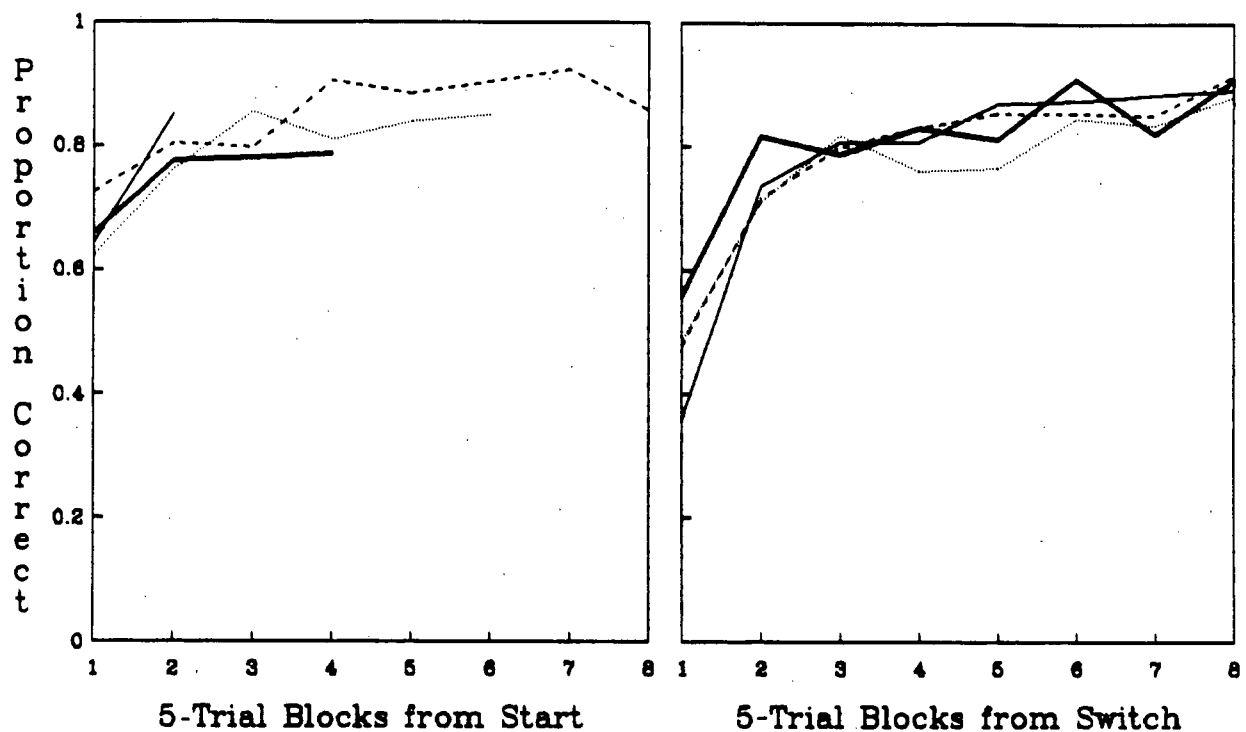
Figure 2. Proportion of first visits per trial that were
correct (rewarding) averaged over blocks of 5 trials and all
birds in each treatment for each of the 4 treatments.
Curves in the left panel are performance before the pattern
reversal and curves in the right panel are performance after
the reversal. Blocks of 5 trials after the pattern reversal
are numbered from 1 to standardize alignment of curves from
each treatment. The solid light line is the performance of
birds when the pattern was switched after 10 trials, the
solid bold line represents birds switched after 20 trials,
the dotted line is after 30 trials and the dashed line is
after 40 trials.
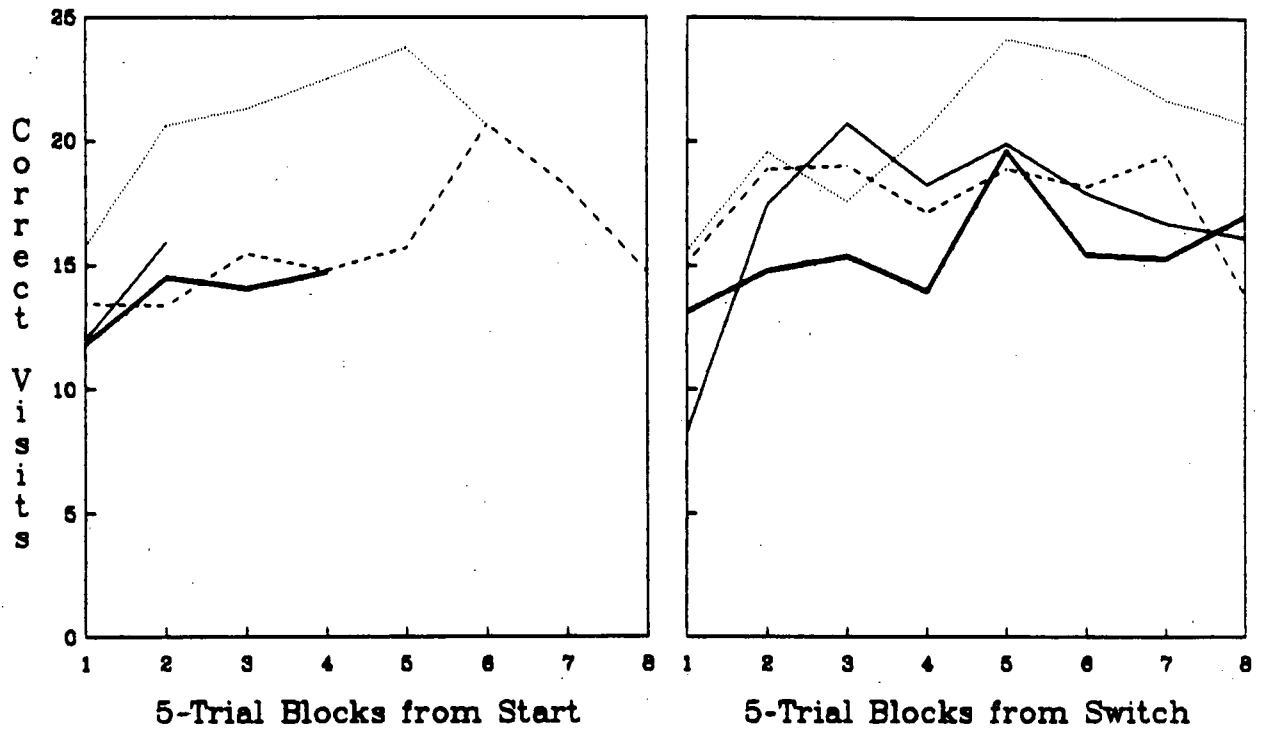
Figure 3. Number of correct visits per trial (averaged over
blocks of 5 trials and all birds in each treatment) for each
of the 4 treatments. Curves in the left panel are
performance before the pattern reversal and curves in the
right panel are performance after the reversal. Blocks of 5
trials after the pattern reversal are numbered from 1 to
standardize alignment of curves from each treatment. The
solid light line is the performance of birds when the
pattern was switched after 10 trials, the solid bold line
represents birds switched after 20 trials, the dotted line
is after 30 trials and the dashed line is after 40 trials.

Proportion correct is the most widely used indicator of performance (Fig. 2). Since the number of correct visits stayed relatively constant throughout the experimental runs, I was concerned that proportion correct may be a weaker test of performance than total incorrect (first) visits per trial. As a consequence, I have presented both values when there is a difference. The averages of the incorrect visits to the array by birds in each treatment are presented in Figure 4.

Birds improved significantly in performance during the initial learning period in all treatments (Table 2).

| Treatment | Proportion Correct | | Incorrect Visits | |
|---|---|---|---|---|
| | F value | probability | F value | probability |
| Switch 10 | 27.799 | 0.001 | 8.358 | 0.020 |
| Switch 20 | 8.356 | 0.010 | 2.108 | 0.164 |
| Switch 30 | 92.064 | 0.000 | 54.303 | 0.000 |
| Switch 40 | 8.393 | 0.006 | 37.589 | 0.000 |

Table 2. Regression analysis of initial performance versus natural log of trial (to improve linearity of regressions). Values for both performance indicators are given. Treatment names refer to the number of trials before the reversal of the pattern of rewarding feeders. Probabilities are the chance of no difference.

## Duration of Exposure and Pattern Reversals

Performance for all 4 treatments dropped sharply immediately after the quarters pattern of feeders was reversed. Performance was strongly significantly better in the 5 trials immediately before the switch than in the 5 trials immediately after (Table 3). As well, birds in
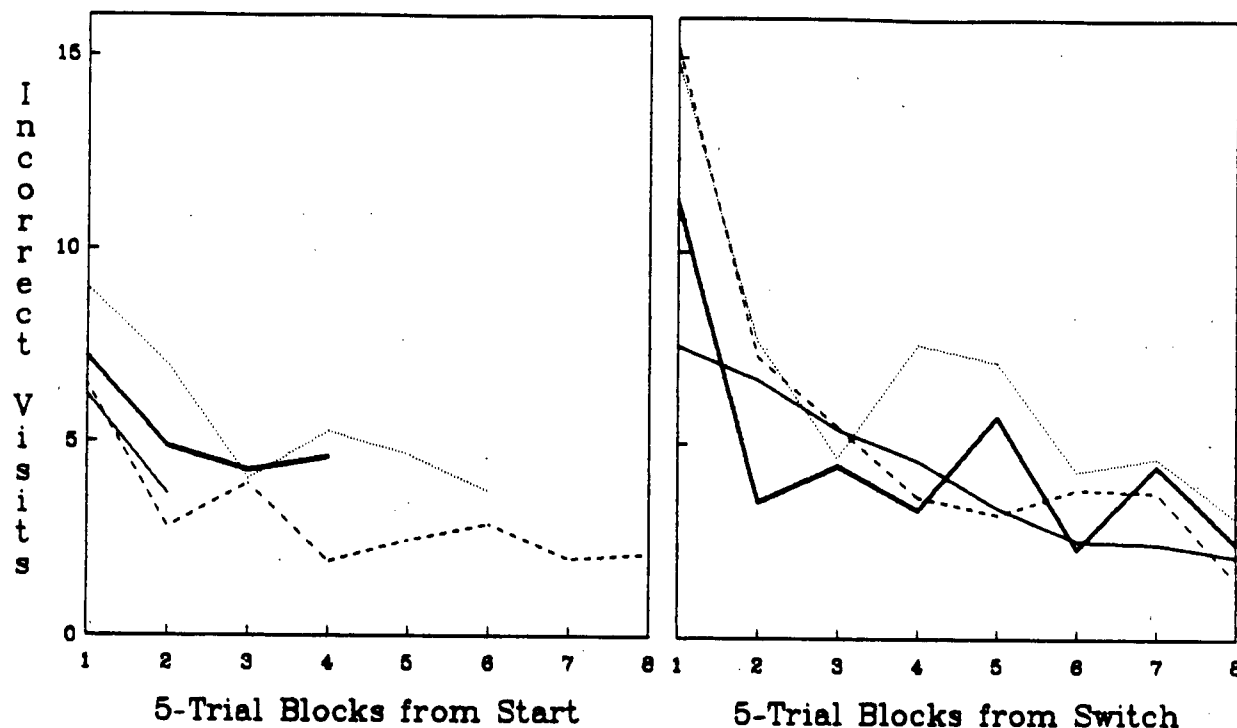
Figure 4. Average number of incorrect visits for each of the 4 exposure treatments. Curves in the left panel are performance before the pattern reversal and curves in the right panel are performance after the reversal. Blocks of 5 trials after the pattern reversal are numbered from 1 to standardize alignment of curves from each treatment. The solid light line is the performance of birds when the pattern was switched after 10 trials, the solid bold line represents birds switched after 20 trials, the dotted line is after 30 trials and the dashed line is after 40 trials.

treatments with greater numbers of trials before the switch (30 and 40 trial treatments) required more visits per trial to obtain the amount of nectar they required (Table 4), which remained relatively constant (Table 5).

| Treatment | t value | probability |
|-----------|---------|-------------|
| Switch 10 | 5.022 | 0.000 |
| Switch 20 | 4.102 | 0.001 |
| Switch 30 | 7.160 | 0.000 |
| Switch 40 | 6.208 | 0.000 |

Table 3. Comparison of performance before and after the switch. Figures are based on the average proportion correct for all birds in each treatment for the 5 trials immediately before and the 5 trials immediately after the reversal. Treatment names refer to the number of trials before the reversal of the pattern of rewarding feeders. Probabilities are the chance of no difference.

| Treatment | t value | probability |
|-----------|---------|-------------|
| Switch 10 | -1.522 | 0.203 |
| Switch 20 | 1.989 | 0.118 |
| Switch 30 | 3.595 | 0.023 |
| Switch 40 | 3.066 | 0.037 |

Table 4. Comparison of total visits before and after the switch. Figures are based on the average number of visits per trial for all birds in each treatment for the 5 trials before and the 5 trials after the reversal. Treatment names refer to the number of trials before the reversal of the pattern of rewarding feeders. Probabilities are the chance of no difference.

| Treatment | t value | probability |
|-----------|---------|-------------|
| Switch 10 | -5.573 | 0.005 |
| Switch 20 | -2.173 | 0.099 |
| Switch 30 | -2.166 | 0.096 |
| Switch 40 | 0.000 | 1.000 |

Table 5. Comparison of total correct visits before and after the switch. Figures are based on the average number of correct visits per trial for all birds in each treatment for the 5 trials immediately preceding the pattern reversal and the 5 trials immediately following the reversal. Treatment names refer to the number of trials before the reversal of the pattern of rewarding feeders. Probabilities are the chance of no difference.

Performance improved again over the next five to ten trials until it was at or near the level just before the pattern switch. Improvement following the switch was strongly significant in all cases using either performance measure, showing that birds in all treatments learned the new patterns of rewarding feeders during the 40 post-switch trials (Table 6).

| Treatment | Incorrect Visits | | Proportion Correct | |
|---|---|---|---|---|
| | F value | probability | F value | probability |
| Switch 10 | 56.698 | 0.000 | 55.550 | 0.000 |
| Switch 20 | 13.530 | 0.001 | 30.744 | 0.000 |
| Switch 30 | 38.850 | 0.000 | 53.234 | 0.000 |
| Switch 40 | 57.516 | 0.000 | 66.127 | 0.000 |

Table 6. Regression analysis of improvement in post-switch performance using both performance indicators (measured against the natural log of trial to improve linearity). Calculations are based on averages of the performance of all birds in a treatment. Treatment names refer to the number of trials before the reversal of the pattern of rewarding feeders.

As predicted, the intensity and duration of the performance drop was related to the duration of exposure to the pattern before the switch (Fig. 5). Drop in performance after the switch increased in magnitude as duration of exposure increased (positively sloped linear regression fitted to the 5 trial averages of total incorrect visits: $F = 42.280$, $r = 0.811$, residual df = 22, $p \approx 0.000$). Even excluding the zero point, the relationship between bird performance and exposure is strongly significant (positively sloped regression analysis excluding the zero point:
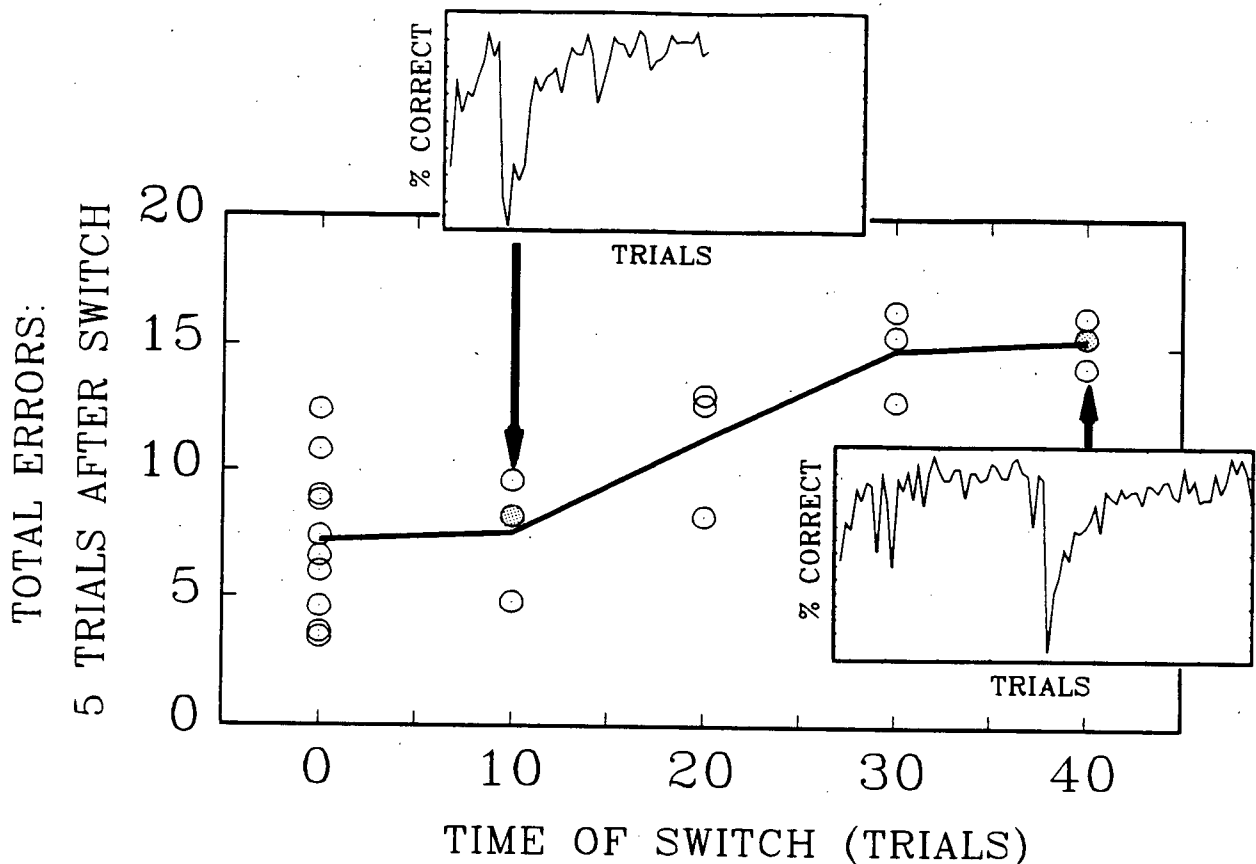
Figure 5. Average number of incorrect visits per trial by birds for each of the treatments in the 5 trials immediately following the pattern reversal (the maximum incorrect visits possible is 32). The X axis shows the number of trials birds experienced before the switch. The line passes through the average performance for each treatment. Individual points show the results for each bird (3 per treatment, and 12 for the zero point). The beginning of each experimental run exposes birds to a novel pattern with no previous exposure to a similar pattern, so it is equivalent to a switch after a zero trial exposure to the pattern, providing the fifth point. Insets show sample performances for birds in individual treatments (shaded circles surround these values).

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F = 23.914, r = 0.840, residual df = 10, p = 0.001). While the relationship does not appear linear, a non-linear fit to this line will be even stronger, since a straight line underestimates the strength of this relationship. This positive relationship between persistence of formerly rewarding behaviour and previous rewarding experience was not linear, but sigmoid; persistence increased little if any below 20 trials of initial experience and little beyond 30 trials, but increased markedly between 20 and 30 trials.

The greater drop in performance by birds with longer exposures to the pattern produced a range of errors between treatments that was initially large and was typically greatest between the 10 trial and 40 trial pre-switch treatments in the period immediately following the switch (Fig. 6). This difference in response by the birds to the pattern reversal (measured by incorrect visits) gradually decreases during the 40 post-switch trials until differences due to any remaining treatment effect are masked by random variation in performance among trials in each treatment.

## Visitation Patterns

Several potential sources of error could produce results similar to those I found. First, I needed to rule out the possibility of unplanned cues to rewarding feeders. There could conceivably be visual traces of nectar, marks on the array or any of a number of other possibilities. If such cues were available and birds knew how to use them,
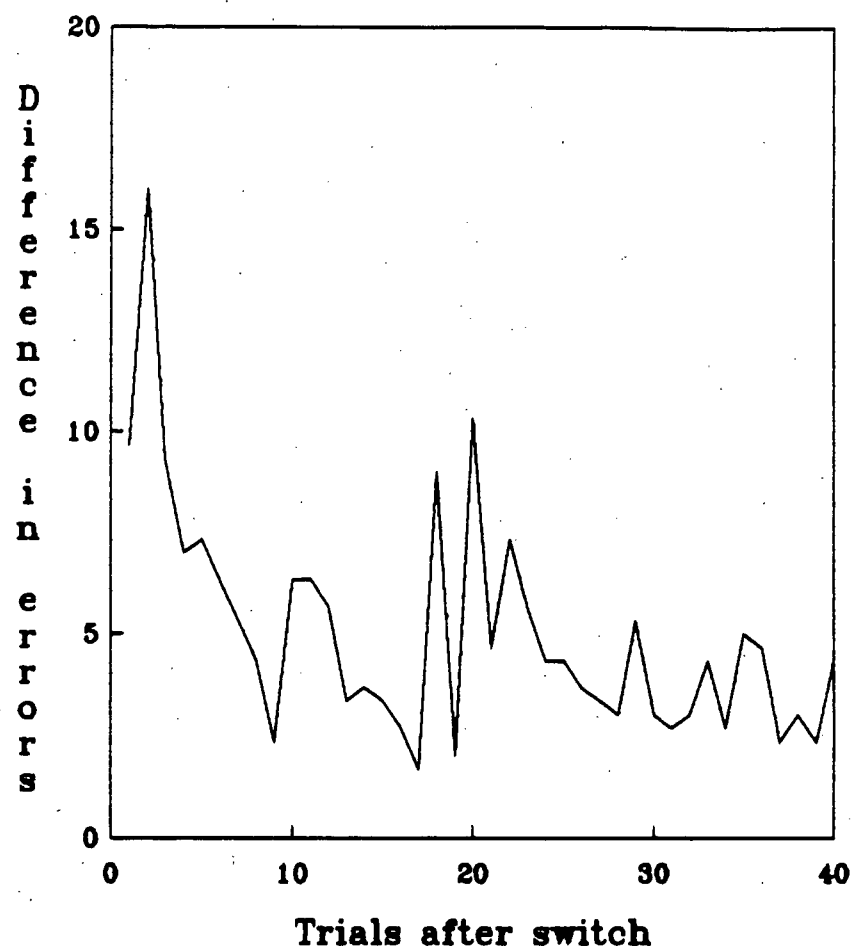
Figure 6. Differences in number of incorrect visits (errors) by birds in each of the treatments in the period following the pattern reversal. The line represents the maximum range of differences in the number of errors between the 4 treatments. This range is greatest immediately following the switch, and decreases throughout the course of the remaining trials.

they should visit more rewarding feeders than chance (50% correct) on the first trial, but the birds did not differ statistically from random visitation (t = 1.494, df = 11, mean difference = 0.066, p <= 0.163), providing no evidence for initial use of external cues.

Positional biases (which in some protocols could alter visitation patterns enough to affect performance measures) were not a major concern due to the diagonally symmetric nature of the quarters pattern and the randomised presentation of the two versions of the pattern in my protocol. These two factors (randomisation and a symmetric pattern), ensured that birds with horizontal or vertical biases would still encounter equal numbers of rewarding and non-rewarding feeders.

Birds did show some positional bias (Fig. 7). They significantly preferred feeders higher in the room (Kolmogorov-Smirnov test of observed visits versus a uniform distribution: Maximum difference = 0.391, p ≈ 0.000). There were both vertical and horizontal biases in visit patterns as well (K-S test of visits versus vertical uniformity: Maximum difference = 0.59, p = 0.004, K-S test of visits versus horizontal uniformity: Maximum difference = 0.63, p = 0.001). Birds were most heavily biased towards higher feeders during the first 10 trials (Fig. 8), although this bias did decrease over time as seen in Figure 7.
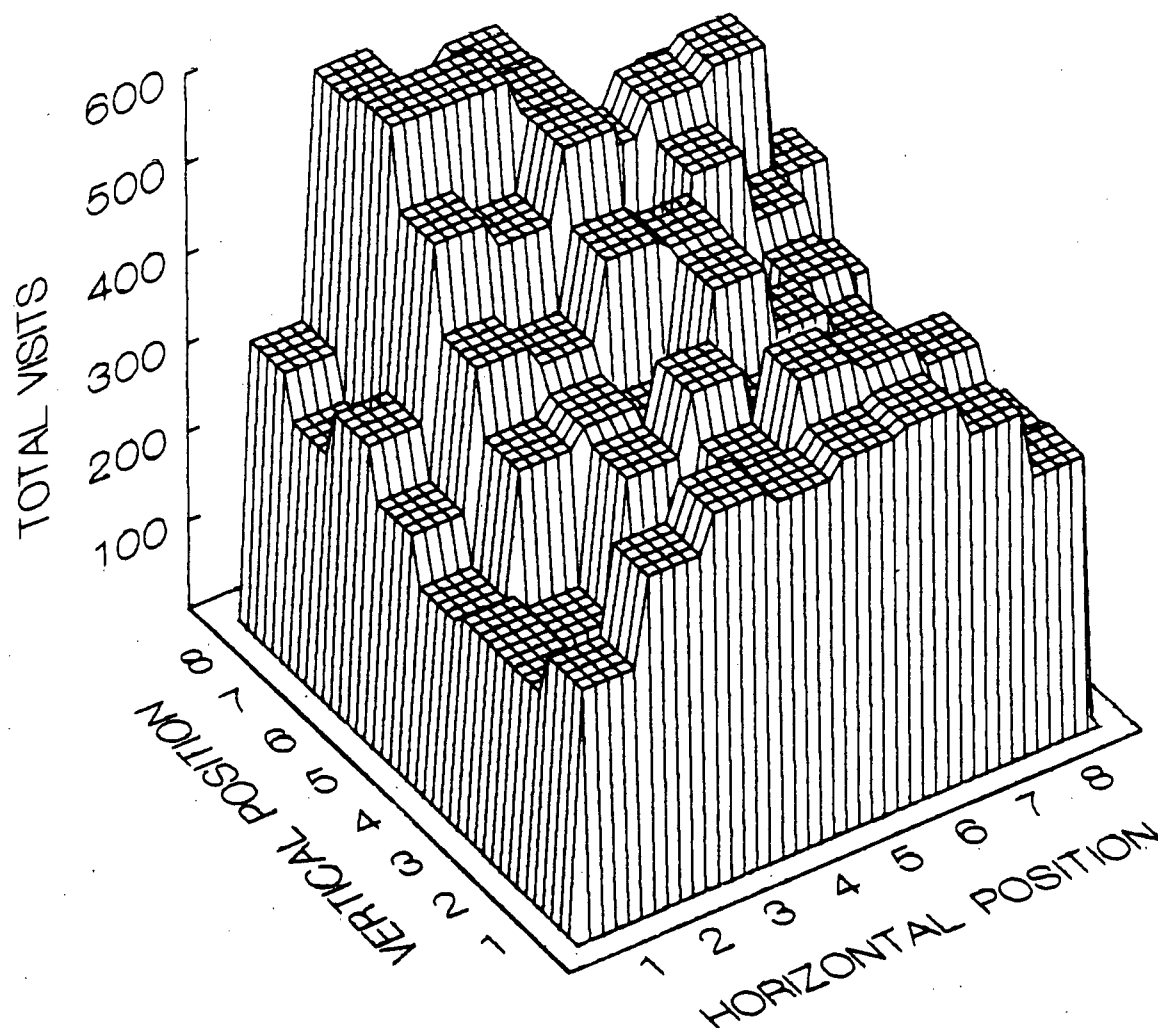
Figure 7. Total of all visits to each feeder (all birds on all treatments, before and after switch). If no positional bias occurred the height of the grid at each feeder location would be the same, producing a flat surface. This figure was produced using a step-smoothing algorithm. As a result, each feeder location is represented by 16 grid units.
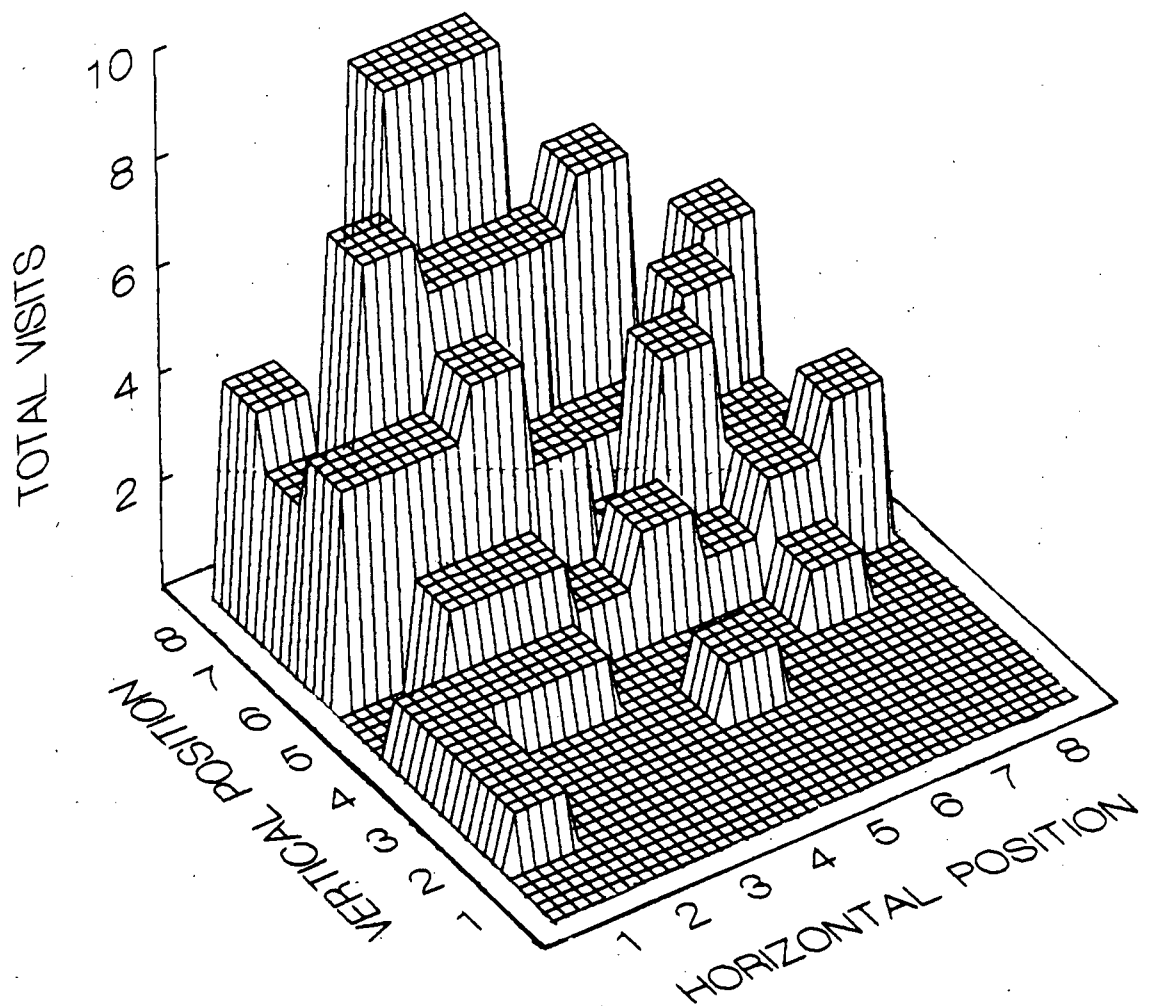
Figure 8. Total of all visits to each feeder in the first
10 trials (all birds on all treatments). If no positional
bias occurred the height of the grid at each feeder location
would be the same, producing a flat surface. This figure
was produced using a step-smoothing algorithm. As a result,
each feeder location is represented by 16 grid units.

While birds exhibited positional bias, their initial explorations of the array (on the first trial) were not predictable (Fig. 9), and did not appear to be systematic or ordered. Birds began to explore all areas of the array after their initial visits, but they showed no obvious systematic and consistent visitation patterns over time (Fig. 10).
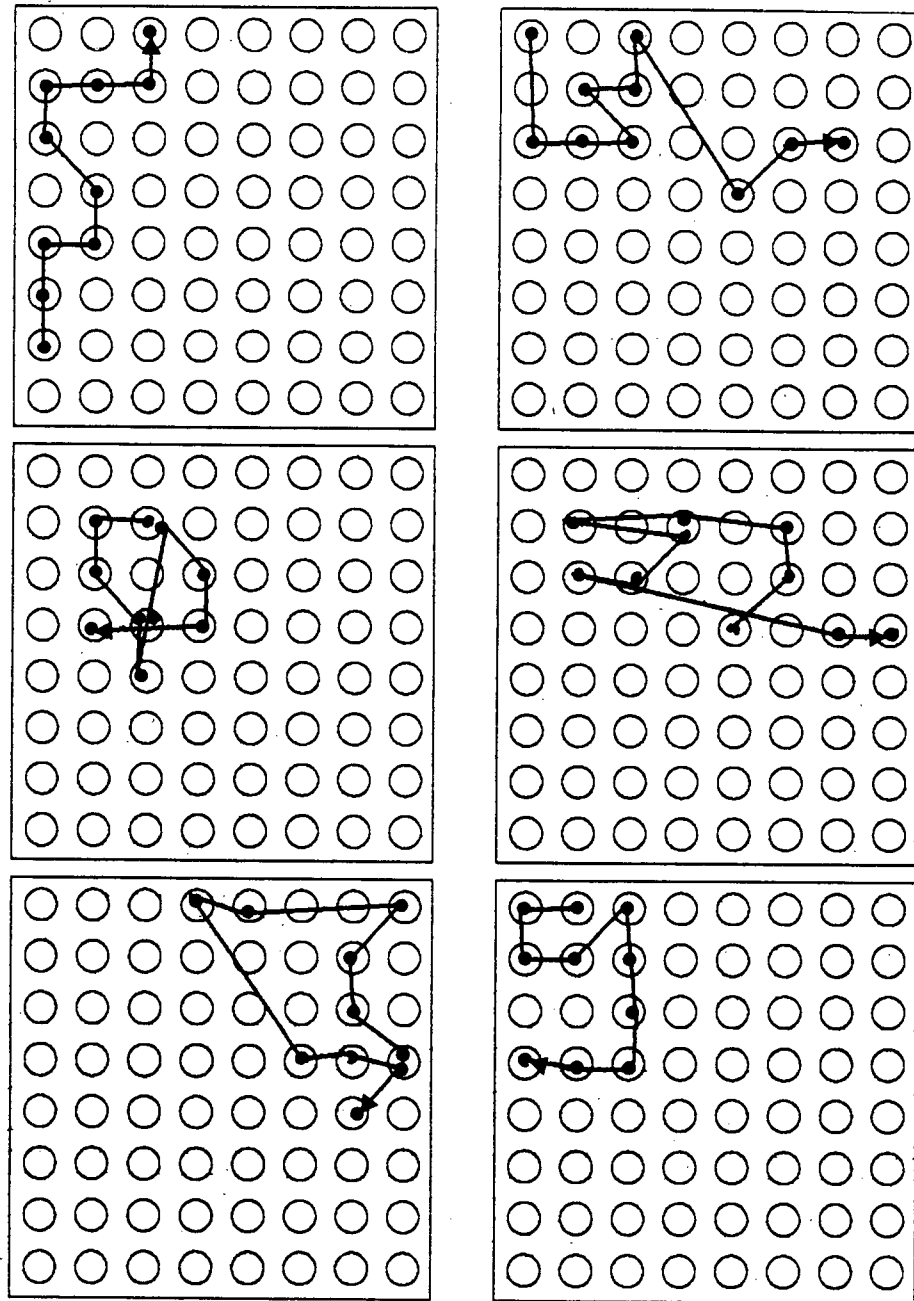
Figure 9. Sample visit trajectories of 6 different birds on their first 10 visits of Trial 1. Each box represents the feeder array and illustrates a different bird. In all cases shown, the top right and bottom left quarters of the array were rewarding. The solid line marking each array shows the visitation sequence during the trial. The arrow head represents the direction of travel and black dots represent feeders visited during the trial.

Figure 10. Sample trajectories for one bird on the first 10 visits of Trials 1 - 6. Each box represents the feeder array and illustrates a different trial. The top left and bottom right quarters of the array were rewarding. Trial numbers are to the left of each box. The solid line marking each array shows the visitation sequence during the trial. The arrow head represents the direction of travel and black dots represent feeders visited during the trial.

## Section IV.  Discussion

The birds in this experiment learned a simple pattern in a very short time, consistently achieving over 80% success after about ten trials.  Their rapidly improving performance suggests that in a novel environment they begin learning reward patterns right away, corroborating the results of Sutherland (1985).

### Advantages of Learning

Modelling studies indicate learning can reduce search times for hidden objects to at least one third of naive performance (Benhamou, 1994).  Since the rewarding feeders were uncued, learning the pattern provided a means to reduce energy spent on foraging.  In a predictable environment, learning is an efficient approach to foraging.  Learning through increased experience in a stable environment provides more efficient foraging because search time is reduced and food is located more rapidly (Gillingham and Bunnell, 1989).

### Factors Affecting Learning

#### Cues

Past studies have shown that global and distal cues beyond those presented intentionally can be an important source of information for foraging animals (Olton, 1990;

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Spetch and Edwards, 1988; Suzuki *et al.*, 1980; van Luijtelaar *et al.*, 1989). There was no evidence here that birds used such things as odours or small visible traces of nectar to initially locate rewarding feeders, but their bias towards high feeders indicates that cues outside of the array (such as the arrangement of ceiling and walls, echoes, or even gravity) play some role in their spatial explorations.

Since profitability was uncued, the arrangement of feeders on the array, combined with distal cues such as position in the room, should have played a primary role in learning. Using distal cues to locate rewards without specific local cues is harder than using local cues (Spetch and Edwards, 1988). In my experiment, feeder position was cued (by a surrounding orange ring) but not feeder quality.

### Search Techniques

In learning feeder quality, the birds used trial and error exploration during initial trials. Early feeding flight trajectories (Figs. 8 and 10) suggest that initial exploration was not random, but I could find no evidence for systematic search (stereotyped series of visits with predictable rules about direction, number of visits or other characteristics of the visit) to their explorations. In a study on hummingbird foraging in the wild (Wolf and Hainsworth, 1991), hummingbirds used random but area restricted search; that is, they showed no predictable

sequence of movements yet still remained within a restricted area of a patch on a given bout rather than moving freely throughout the entire patch. In my experiments, once birds located rewarding feeders they tended to return to those locations within and between bouts and sample areas around those sites. When these searches were not rewarding, birds might search nearby areas to see if more distant places might be better. Trial and error combined with area restricted search has also been seen in species such as badgers (Mellgren and Roper, 1986) and Japanese monkeys (Menzel, 1991) and in models simulating efficient foraging tactics (Ollason, 1983). Systematic search patterns have also been seen, especially in insects such as bumblebees and honeybees (Dreisig, 1989; Menzel, 1985). It appears that search techniques are tied to the unique needs of each species and to the situation (Root and Kareiva, 1984).

Some times my birds quickly found one rewarding quarter of the array but were extremely slow to locate the other one. I selected intertrial periods and reward amounts so birds could easily maintain their weight throughout the day, that may have reduced their motivation to feed. Using longer intertrial periods (e.g. Sutherland, 1985) or decreasing the amount or quality of rewards could have forced greater exploration of the array, but I chose to minimize risk to the animals, since I was already concerned about their overall health.

**Stability**

Learning is most effective in stable environments (Nishimura, 1994). Caching birds such as Clark's Nutcrackers have surroundings that retain similar characteristics for long periods of time. These birds can learn and remember food caches for at least 6 months (Balda, 1980; Balda and Kamil, 1992). Chickadees, who also cache food, can retain cache memory for at least 4 weeks (Hitchcock and Sherry, 1990).

Spatial learning abilities are a consequence of the normal distribution of resources for species (Bond *et al.*, 1981). Animals discount the value of unpredictable resources (Bowers and Adams-Manson, 1993). As a broad generalization, animals in stable environments appear to have better abilities to learn and remember tasks dealing with stable items than animals who must deal with continual and unpredictable change in similar items. Thus, while caching species remember stored food locations for long periods, the continual depletion and renewal of hummingbird nectar sources over days to months in the same location biases them not to remember individual flower qualities during feeding bouts. When they do show evidence of foraging memory within bouts in a patch they usually exhibit win-shift behaviour, avoiding previously successful locations (Cole *et al.*, 1982). Similar results have been seen in other nectarivorous species such as bananaquits

(Wunderle and Martinez, 1987). This does not mean that nectar feeding animals have inferior spatial memory or learning abilities but that they learn and remember items that are liable to remain stable such as characteristics of rewarding flower types. Their spatial memories are also evident at coarser spatial scales, as they clearly remember the quality of patches of flowers (Armstrong *et al.*, 1987; Cole *et al.*, 1982; Gass and Sutherland, 1985; Mitchell, 1989; Valone, 1992), and whole foraging habitats (Armstrong, 19?.; Gass, 1978b; Sutherland *et al.*, 1992; Tamm, 1987).

## Costs of Learning

### Sampling

Once the birds learned the general pattern of rewarding feeders, the number of incorrect visits dropped to a small but continuing amount. While most of these incorrect choices were probably errors, some were probably ongoing sampling of the environment by the bird in an attempt to detect changes in reward location, as seen in other animals (Draulans, 1988; Gass, 1985; Kramer and Weary, 1991; Tamm, 1987; Wilkie *et al.*, 1981). Sampling and mistakes cannot be distinguished in most protocols, including mine.

Sampling is a way for an animal to continue exploring its environment and test for change, as in exploration of novel items by rats to improve their knowledge of their surroundings (Pinel *et al.*, 1986); however, if uncertainty increases greatly, animals explore less and spend more time

exploiting known resources instead of searching for additional ones (Forkman, 1991).

**Change**

Learning can be a disadvantage in the face of major changes in an animal's surroundings, such as the sudden and complete reversal of the pattern in this experiment. Performance dropped strongly and significantly after the reversal of the feeder pattern; it dropped below chance for the first few trials after the switch (typically 3 - 5 trials). During this short period of poor performance after the switch, birds incurred a cost that directly reflected their persistence with what they had learned before the switch instead of immediately changing their behaviour to explore the new pattern. While the number of correct visits remained relatively constant, reflecting hummingbirds' tendencies to forage in ways that provide constant energy intakes (Tooze and Gass, 1984), birds who experienced more trials before the switch required more visits per trial to obtain the same amount of nectar after the switch.

Before the switch, learning was advantageous because it reduced foraging effort during the period of pattern stability. In an extremely variable environment in which the pattern of profitability changed often and unpredictably, reliance on spatial learning would continue to incur costs with each change. Both resource poor environments and highly variable environments can overcome

the value of learning (Nishimura, 1994). Similar persistence in the face of change with similar associated costs was seen in rufous hummingbirds by Sutherland (1985) and in Anna's hummingbirds by Collias and Collias (1968). A drop in performance and increase in exploration was also seen in goldfish (Warburton, 1990) and chipmunks (Kramer and Weary, 1991).

### Expectations and Persistence

As experience with the stable pattern increased, performance following the pattern reversal dropped more. Animals use past experience to gauge future returns (Bowers and Adams-Manson, 1983). Until the pattern was reversed there was no reason for the birds to discount the value of using their spatial memory of the pattern to guide foraging bouts. Given my experimental design, the birds had no way to expect the unexpected and reduce their persistence with learned behaviours; however, my result strongly suggests that hummingbirds weight their past experience increasingly heavily as their experience in stable environments increases.

Animals act as if their most recent experience is the most important for the purposes of guiding future choices (Haccou *et al.*, 1991; Haefner and Crist, 1994; Todd and Kacelnik, 1993), and discount less recent events as a function of the time since they were learned and the number of intervening experiences (McHose and Peters, 1975;

McNamara *et al.*, 1989). These concepts were incorporated into the memory window models suggested by several sets of authors (Kacelnik *et al.*, 1987; McNamara and Houston, 1985b), but are distinct from the primacy effect, a preference for information acquired early in training (MacPhail, 1982), and the recency effect, a preference for information acquired most recently (Crystal and Shettleworth, 1994; Gaffan, 1992; Gaffan, 1994; Kesner *et al.*, 1994; Olton, 1985; Reed, 1994; Wright, 1994). Other models of spatial memory also incorporate the idea that time since learning affects memory guided behaviours (Spetch, 1990; Wilkie and Kennedy, 1987; Wilkie *et al.*, 1990).

The sigmoid shape of the curve seen in this experiment (Fig. 5) implies that by ten trials, birds had already begun to exhibit persistence in the face of changes in the profitability of rewarding feeders. Over the next thirty trials their persistence increased to a maximum.

The maximum change in bird performance after the switch may correspond to a duration of exposure at which the birds treated the learned patterns as if they had always existed. This point may correspond roughly to the size of the memory window for this kind of learning task for these birds. In this interpretation, longer durations of exposure to consistent patterns could not produce a larger surprise effect because they had exceeded the size of the working memory windows of the animals. Further, the initial level

portion of the curve would correspond to a period when, for the animals, the patterns of rewarding feeders were still new and had not been fully learned. The rapidly increasing persistence near the inflection point of the curve may represent a period of rapidly increasing expectations about stability of the pattern.

This general strategy of rapidly learning to rely on past experience, strong but ephemeral resistance to change, and more rapid abandonment of newly learned responses makes sense for animals in a natural environment. An animal in a novel situation, if it realizes that its situation is new, will be unlikely to risk wasting energy by stereotyping its foraging before it is certain of the location, abundance, and predictability of food sources. Alternatively, it is unlikely to abandon its perception of its environment in a familiar situation when it experiences minor variations in its foraging success; that is, the persistence of learned behaviours, or behavioural inertia, makes ecological sense. Generally, behaviours based on short term experiences tend to be more flexible, while consolidated memories and experiences are less flexible (Gould, 1986c). Hull (1943) applied a similar principle when he described habit strength (the strength of an association between stimulus and response) which he believed increased with increasing reinforcement.

These same principles should apply to the memory window hypothesis. In a variable habitat, older information is less likely to remain valid due to ongoing environmental change, and we know that reliance on spatial memory varies with the temporal and spatial complexity of the environment (Warburton, 1990). In a complex environment, too much information can overload memory capacity (Nishimura, 1994). In the case of a hummingbird foraging, this complexity could be generated by territorial raids by intruder birds (Ewald and Bransfield, 1987; Ewald and Carpenter, 1978; Ewald and Orians, 1983; Gill and Wolf, 1979), new nectar production (George, 1980), maturation of new flowers and deterioration of old blooms (Gass *et al.*, 1976), changes in the quality of whole patches of flowers (Gass and Sutherland, 1985), or a myriad of other items. Given a limited ability to remember past events, more recent items should also be given higher weighting to reduce the impact of memory fading over time, which is a common problem (Aronsohn *et al.*, 1978) that can lead to increasing errors in spatial tasks (Bolhuis *et al.*, 1987; Spetch, 1990; Strijkstra and Bolhuis, 1987).

**Relearning After a Change**

The reduction in foraging success induced by the pattern reversal eventually led to the birds changing their foraging behaviour, visiting previously unrewarding feeders which they had been avoiding. This change took a short time, occurring over five to ten trials (or 30 to 60 minutes

of actual time). During this period, some birds did not visit the feeder array, visited one or two formerly good feeders and then gave up, or fed repeatedly at non-rewarding feeders, but none of them immediately began intensive exploration of the array for changes in profitability of formerly non-rewarding feeders. Over the course of five to ten trials after the switch, the birds learned the new feeder pattern, eventually returning to performance levels above 80% correct.

## Conclusions

These experiments have corroborated earlier findings that hummingbirds learn 2-dimensional patterns quickly (Sutherland, 1985). More importantly, they demonstrate persistence of learned patterns in the face of sudden change as a function of experience of stability before the change. This persistence dissipates rapidly, however (in this case under the pressure of severely reduced foraging profitability), and the birds soon learn the altered reward pattern. Hummingbirds seem disposed to a strategy of rapid learning in spite of or perhaps because of the problems imposed by unpredictability.

# Chapter 3.

## Landmark Forms and Spatial Memory in Rufous Hummingbirds.

### Section I.  Introduction

### Spatial Memory

Spatial memory is the process by which animals remember locations in their environment.  Among bird species, spatial memory is used for tasks such as navigating, foraging and defending territories (Balda and Kamil, 1988; Gass and Montgomerie, 1981; Shettleworth, 1983).

Spatial memory affords distinct energetic and ecological advantages (Valone, 1991).  Modelling studies suggest that using spatial memory to forage can provide greater than a five-fold energy advantage over completely random search and a three to five-fold advantage over systematic searching (Armstrong *et al.*, 1987; Benhamou, 1994).

### Cues and Landmarks

One component of developing a map of the environment is to learn the positions of recognizable landmarks and cues to

associate items in the environment with expected results. I will define a reward cue (hereinafter termed "cue") as an indicator of reward that is associated with that reward in space and time (and in a 1:1 ratio), and a reward landmark (hereinafter termed "landmark") as a navigational aid that indicates an area containing reward sites.

In many foraging cases there will be considerable overlap between these two aids to locating food, because the difference between areas and specific locations may be unclear; for example an area may contain only one potential site. Differentiating between these ways of relating to the environment is difficult not only in practice, but in principle. It may be unimportant whether to label a given object as a landmark or a cue. For my purposes, I will generally use the term landmark to describe the features I used in my experimental arrays, because I intended them to delimit groups of feeders, not individual feeders. These features do, however, contain information that could be considered to be cue information.

### Cues

There are several categories of cues. Distal cues are separated by some variable distance from the reward site (Brown, 1994; Brown and Gass, 1993; Schenk, 1987; Sutherland *et al.*, 1987). Local cues are near the reward site (Spetch and Edwards, 1988), contiguous cues adjoin the reward site (Brown and Gass, 1993; Pinel *et al.*, 1986), and global cues

have a more tenuous relationship with a specific reward site (Spetch and Edwards, 1988). Global cues (and in some cases distal cues) include many items that other authors would call landmarks. Examples of global cues in a laboratory setting include positions of the walls, overhead lights and doors.

### Landmarks

I have defined landmarks as navigational aids animals use to locate reward sites (food is only one kind of reward). This definition suggests at least two ways to use these aids. I defined landmarks in the middle of foraging patches as centre landmarks. In nature, this could be a tree surrounded by nectar-producing berry bushes, the central stalk of a flowering plant, or a rock in the middle of a territory. A second type of landmark defines the edge of an item. A stream at the edge of a territory or a fence surrounding a vegetable garden could both serve as edge landmarks.

## Role of Cues and Landmarks in Learning

Animals use landmark and cue information to develop cognitive maps of their surroundings (Tolman, 1948), and this requires the use of spatial memory. The ability to use spatial learning is not universal; there are distinct species differences in skill levels. Various studies have suggested that animals, including primates, have difficulty learning tasks in which there is a spatial separation

between reward sites and reward cues (Pinel *et al.*, 1986); hummingbirds, however, regularly use landmarks and cues to navigate towards reward sites that are separated from reward cues, and this behaviour can be duplicated in a laboratory environment (Brown and Gass, 1993).

## Current Study

The ability of hummingbirds to use spatial information has been demonstrated in laboratory and field experiments (G. Brown, 1992; Cole *et al.*, 1982; Collias and Collias, 1968; Gass, 1978a and 1978b; Gass and Sutherland, 1985; Gass *et al.*, 1976; Miller and Gass, 1985; Miller *et al.*, 1984; Thompson, 1994). One recent study failed to find evidence of spatial memory use by foraging hummingbirds, but the authors suggested possible methodological reasons for the failure (Wolf and Hainsworth, 1991).

In this experiment I examine how rufous hummingbirds use edge and centre landmarks in a spatial memory task. I expect birds to learn faster with edge landmarks than centre landmarks. Both types of landmark provide navigational information to find profitable feeders, but edge landmarks also delimit groups of rewarding feeders and can be used for triangulation due to the shape of the lines I use for edge landmarks.

Of special interest is the information provided by these landmarks that helps animals to locate potential food sources and assess their quality. In some treatments I

provide cues to profitability in the landmarks and expect these cues to further speed learning.

Chapter 2 demonstrated that hummingbird learning and use of spatial memory are sensitive to environmental changes. By changing the environment, we can estimate the degree of reliance on memory. Here I again suddenly change the profitability of distributions of feeders to probe learning and memory. In one treatment I move cues to feeder profitability simultaneously with the change in profitability to assess the use of these cues by the birds. I expect birds to be less surprised by this treatment and recover more rapidly from this reversal than from uncued reversals.

## Section II.  Materials and Methods

### Subjects

In this experiment I used 6 adult, female rufous hummingbirds, (*Selasphorus rufus*) captured in the field near the Rosewall Creek salmon hatchery, Vancouver Island, B.C. in May 1991 and maintained in individual 0.6 x 0.6 x 0.6 m wire mesh cages for several months prior to testing, during which time they were used in other learning experiments. Due to poor health, one bird was replaced during the course of the treatment sequence, bringing the total number of birds to seven (all female).

Throughout the period of captivity the photoperiod was maintained on a schedule that mimicked seasonal variation under conditions in the wild. Excluding test periods, the birds were supplied with either Roudybush hummingbird diet or Nektar Plus hummingbird diet *ad libitum* on weekdays. On weekends, they had 25% sucrose solution with added vitamins (Avitron avian vitamin supplement) and minerals (Avimin avian mineral supplement).

### Experimental Environment

I conducted all training and experiments in two rooms, each of which was 1.1 x 2.6 x 2.6 m high with overhead full-spectrum fluorescent lights. Walls and ceiling, except the

feeder array, were a uniform light green colour and the floor was a uniform sand colour. A single, stand-mounted, 1.7 m high perch was located at the centre of each room. Each perch was fitted with a photocell to signal arrivals and departures.

On one end wall of each room a 1.0 x 1.0 m dark green, metal panel extended from just below the ceiling. Inset into this panel were 64 feeders in a square 8 x 8 array spaced at 10.5 cm vertically and horizontally. Each feeder consisted of a 2.0 cm length of 1.67 mm I.D. Intramedic polyethylene tubing which had been flame heated and bent to form a terminal reservoir at one end. The resulting feeder tube resembled a small smoker's pipe, whose bowl was an open nectar reservoir and whose stem served as a floral corolla. The stem of the feeder extended through a photodarlington photodetector which bridged a 4mm hole drilled in the metal array panel. The tip of the feeder was flush with the front of the panel. Each hole was surrounded by an orange 19 mm Avery label punched with a 6 mm centre hole.

Perch and feeder array photocells led to a computer which recorded arrivals, departures, and visit durations, accurate to about 10 ms. Before each trial I supplied each rewarding feeder with 2 µl of 22% sucrose (weight/weight) from a Hamilton PB-600-1 repeating dispenser. This volume is within the normal range of nectar volumes found in floral species used by rufous hummingbirds (Armstrong 1986;

Carpenter *et al.*, 1983; Gass and Roberts, 1992). Non-rewarding feeders were left empty, as a previous study showed that birds behaved the same if feeders were empty or filled with water (Sutherland and Gass, in press). Between trials the array was covered by a beige roller blind operated from outside the experimental chamber by a pull cord.

In several cases, an 8 mm videocamera, its tripod and control cables were also present in the chamber to allow me to videotape the session and obtain anecdotal information about performance.

**Experimental Design**

Treatments were designed to compare the utility of edge and centre landmarks in spatial pattern learning and to evaluate the additional utility of providing information in these landmarks about the energetic quality of groups of feeders. Landmarks were patterns of lines (edge landmarks) or coloured disks (centres), and they were either coloured differently in rewarding and non-rewarding sectors of the array or were a uniform colour throughout the array. Two treatments combined edge and centre landmarks but provided quality information only in one of the two. Finally, in one treatment that provided information about quality, I examined the effects of moving landmarks along with profitable feeders.
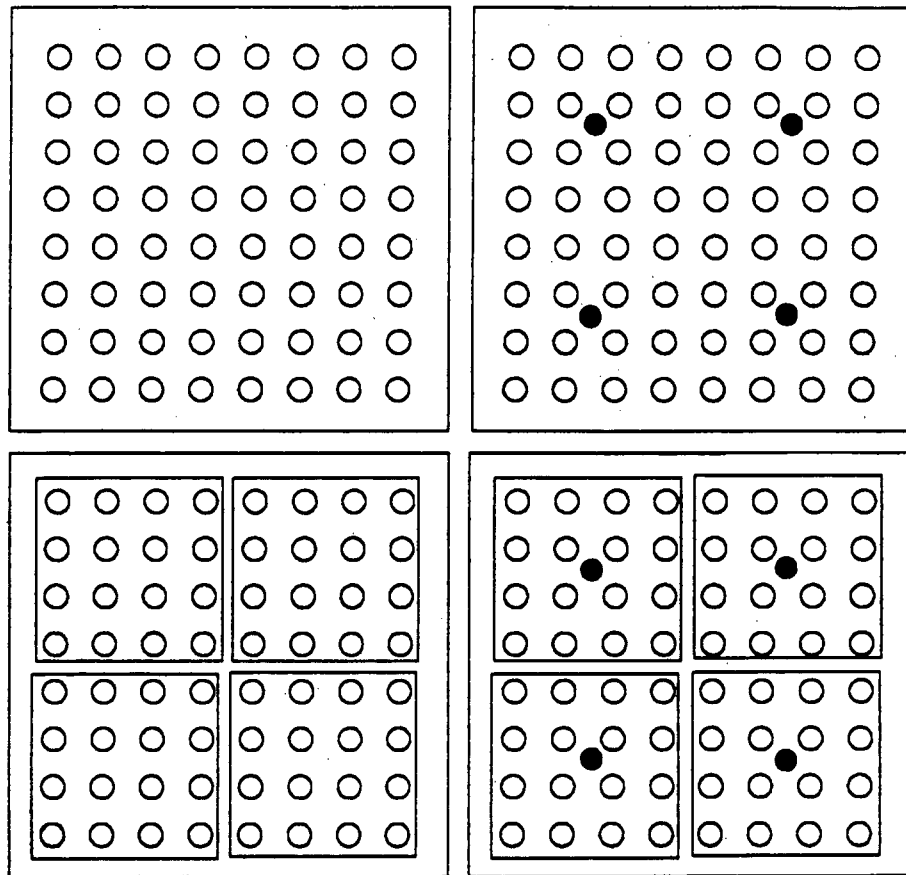
Figure 11. Stylized representations of the array markers used for the eight treatments described in the text (not to scale). In each diagram the unfilled circles represent feeder locations marked by orange labels. Top left: Plain array. Top right: Centre landmarks. Bottom left: Edge landmarks. Bottom right: Both edge and centre landmarks.

The basic forms for these treatments are shown in stylized representations in Figure 11. I use the acronyms listed below to represent the treatments in the graphs and tables of the results section. The eight treatments for this experiment were (in expected order of increasing performance over sixty trials):

1.  Plain. A plain array in which all feeders were marked only with the orange feeder stickers that were present in all treatments (top left diagram in Fig. 11).

2.  Plain Centres (Plctr). A 1 inch circular Avery label in the centre of each of the four quadrants of the array. All four labels were the same colour (Fig. 11, top right).

3.  Coloured Centres (Clctr). Same as Plctr, but the labels in rewarding sectors were a different colour than those in non-rewarding sectors (Fig. 11, top right).

4.  Plain Lines (Pline). Lines of 6 mm drafting tape surrounding the four sectors of the array. All four squares were of one colour (Fig. 11, bottom left).

5.  Coloured Lines (Cline). Same as Pline but rewarding sectors were marked with a different colour than non-rewarding sectors (Fig. 11, bottom left).

6.   Plain Lines with Coloured Centres (Plcct).  Squares of one colour surrounding the four sectors, with labels of two colours marking rewarding and non-rewarding quarters (Fig. 11, bottom right).

7.   Coloured Lines with Plain Centres (Clpct).  Labels of one colour in each quarter with squares of different colours differentiating rewarding and non-rewarding quarters (Fig. 11, bottom right).

8.   Coloured Line Switch (Clnsw).  Differently coloured squares marking the rewarding and non-rewarding quarters (Fig. 11, bottom left).  When I reversed the profitability of feeders, I also reversed the landmark pattern so that the coloured squares that had previously been associated with rewarding feeders maintained this association.

Global landmarks such as walls, floor and other room paraphernalia cannot be eliminated from the experiment, even in a control situation, and to the extent that birds attend to them, they will always add some underlying noise to measures of performance.  Since these features remained constant across all experimental treatments (differences between experimental rooms should have been cancelled out by randomisation of room use across treatments), I ignored them in my analysis, assuming that any systematic effects would cancel out.

In each treatment the original reward and landmark pattern continued for 50 trials, then the reward pattern was switched to its mirror image for 10 more trials so that all previously rewarding array locations were now non-rewarding and *vice versa*. The ten trial period after the reversal of the pattern of rewarding feeders indicates differences in the persistence with which birds used previously learned knowledge and their resistance to new learning.

Each bird in the experiment was exposed to each of the eight treatments. The order of these treatments was randomized for each bird as was the arrangement of pre- and post-switch patterns, the experimental room used, and the landmark colours seen.

## Training

Each bird was trained for three days immediately prior to testing. For the first two days a bird lived in its cage but was fed *ad libitum* from a standard commercial unlimited volume feeder marked identically to those in the experimental chambers.

On the morning of the third day of training, the bird was moved to an experimental chamber with the training feeder from its home cage (the experimental feeder array was covered by the blind). The sole perch in the room was raised to a height of 2.4 m and the feeder was placed directly in front of this perch. When the bird was using this perch normally, it was gradually lowered to 1.7 m,

level with the centre of the covered feeding array. When the bird was using both feeder and perch, the feeder was moved directly in front of the centre of the covered array. Once the bird was again feeding regularly, all 64 array locations were provided with 2 µl of 22% sucrose solution, the home cage feeder was removed, and the array was uncovered until the bird had fed from several feeders. The array was then covered, the feeders refilled, and a new training trial was begun. Once the bird was consistently visiting the panel, and showed minimal or no positional bias (based on informal estimation of any untrained preference for specific portions of the feeder array and if necessary enforced by temporarily covering areas of the array that the bird had not been foraging outside of until the blocking of preferred feeders caused foraging to become more widespread) it was put through a series of 10-20 sham trials with all feeder locations profitable in order to accustom it to the 1 minute trial and 5 minute intertrial periods to be used during testing the following day.

**Experimental Procedures**

On the day of testing each bird was presented with one of two randomly selected mirror image patterns of rewarding and non-rewarding feeders (Figure 1 in Chapter 1) with one of the sets of markings described in Experimental Design (Figure 11). In each case, feeders in the rewarding portions of the array were filled with 2 µl of 22%

(weight/weight) sucrose solution at the beginning of each trial. This provided a potential for 64 µl of nectar to be taken in each trial and exceeded the preferred meal size of rufous hummingbirds under normal conditions (Diamond *et al.*, 1986) to minimize stress to the birds.

Lime green and light blue landmarks were used for all treatments; both contrasted well with the dark green panel. In treatments using only one colour, green or blue was randomly assigned. When both colours were present, the one associated with rewarding sectors for the first 50 trials was assigned randomly.

Each experimental run consisted of sixty one minute trials with five minute intertrial periods. This was intended to allow the birds to maintain their weight throughout the experimental run. Although trials were one minute in length, birds could stop feeding and return to the perch at any time. During the intertrial period, the feeder array was covered by a blind so that trials offered the only opportunity to see the array and any array markings as well as the only opportunity to feed. Emptied rewarding feeders were refilled during the intertrial period. Immediately preceding the first trial, the subject was fasted for 15-20 minutes, or 2 to 3 normal meals.

I ignored any trial in which the subject did not visit the feeder panel, imposed the normal intertrial interval and continued as before. Previous studies by Sutherland (1985)

and myself have shown that hummingbirds remove all nectar from the feeders when a volume of 2µl is used. For this reason, I treated all second and subsequent visits to feeders during trials as non-rewarding.

At the end of fifty trials, I temporarily halted the experiment, emptied, flushed and dried all rewarding feeders and filled all previously non-rewarding feeders. In all but one treatment I left array markings unchanged. In Treatment 8 (the coloured line switch treatment), I changed the landmark lines so that the colour formerly associated with rewarding feeders was still associated with rewarding feeders but in the opposite quarters of the array to the period of the previous 50 trials. Once I had completed the appropriate changes I restarted the experiment; this usually took 5 to 10 minutes.

After these changes, I continued for an additional ten trials using the same procedures as in the first fifty trials. After the last trial, I returned the bird to its home cage, flushed all feeders, and removed the array markings.

## Section III.  Results

### Performance Indicators

I measured learning by the proportion of correct first visits in each trial out of the total visits to filled feeders and by the total incorrect first visits to feeders. In Chapter 2 I emphasized that total incorrect visits was a stronger indicator than proportion correct when birds can satiate themselves during trials.  In this experiment, however, birds could not always obtain sufficient food to maintain their weight throughout sixty trials.  Birds increased their feeding (total correct first visits) over the course of the experimental runs in six out of eight treatments (Fig. 12); this was significant for four of the eight treatments (see Table 7 for summary statistics).

### Initial Learning

As in Chapter 2, learning proceeded for all treatments as decelerating monotonic curves (Figs. 13 and 14).  The differences between treatments lie in the rate of learning (initial slope) and in peak performance.  Since the learning rates were not constant, I tested the significance of the learning by linear regression of the appropriate performance indicator on the natural log of the trial number.
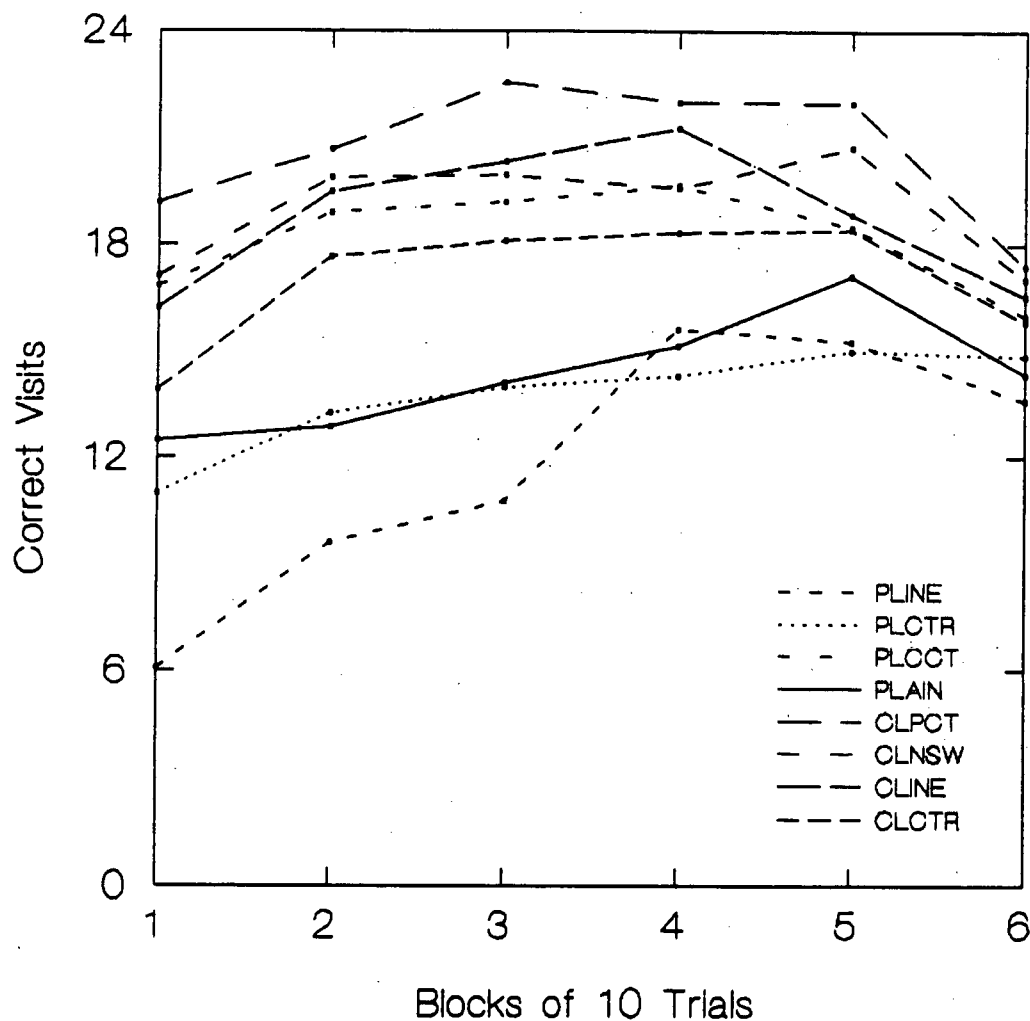
Figure 12. Total correct visits per trial (averaged across
all birds in each treatment and across blocks of 10 trials)
for all treatments. The X axis is divided into blocks of 10
trials. The pattern was reversed after block 5 (trial 50).
Acronyms in the legend correspond to the descriptions of
treatments in Methods. Pline = plain lines. Plctr = plain
centres. Plcct = plain lines and coloured centres. Plain =
plain array. Clpct = coloured lines and plain centres.
Clnsw = coloured line markers switched after the pattern
reversal. Cline = coloured lines. Clctr = coloured
centres.
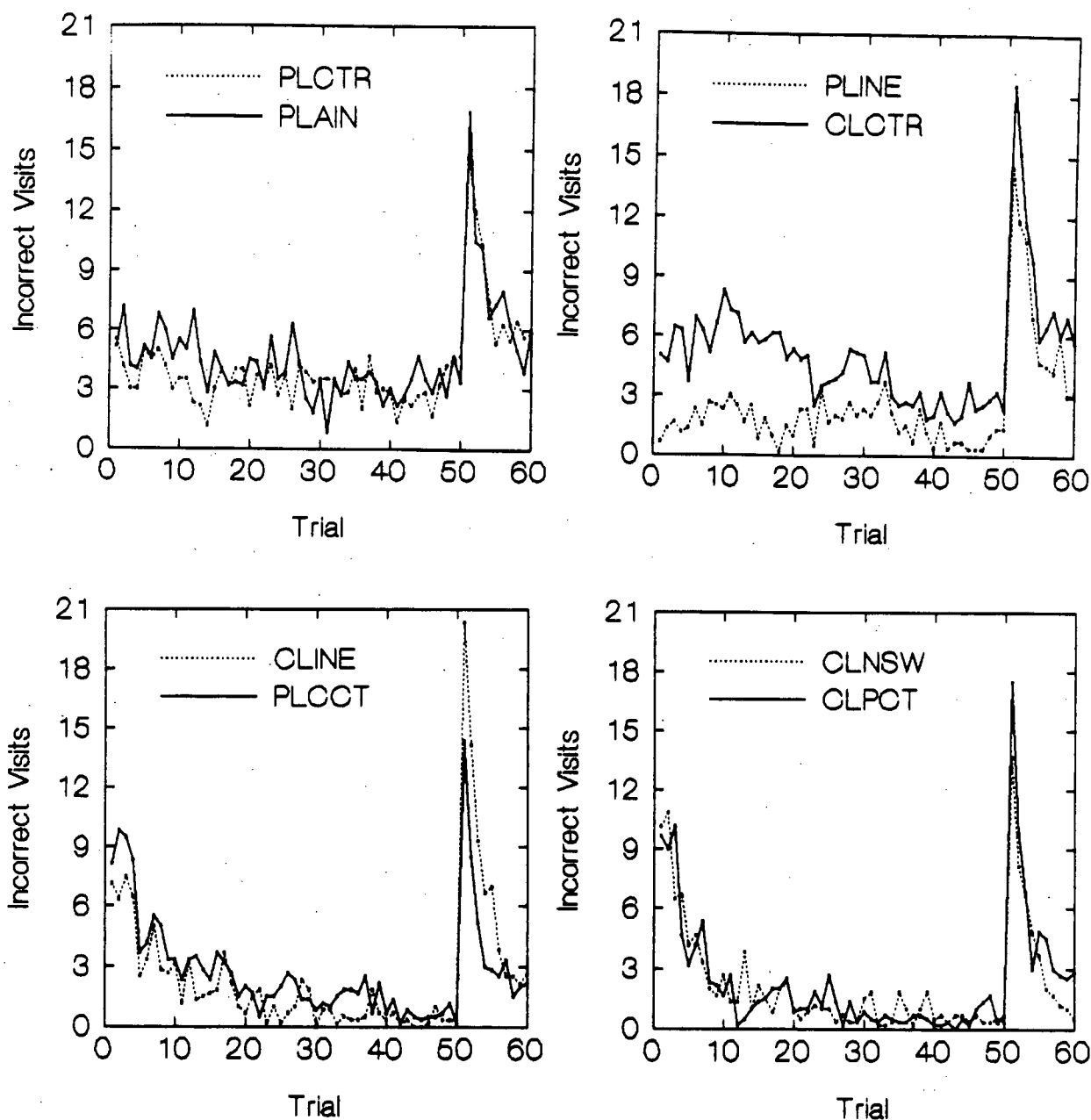
Figure 13. Number of incorrect first visits per trial averaged for all birds in each of the 8 treatments. Two treatments are shown in each panel. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.
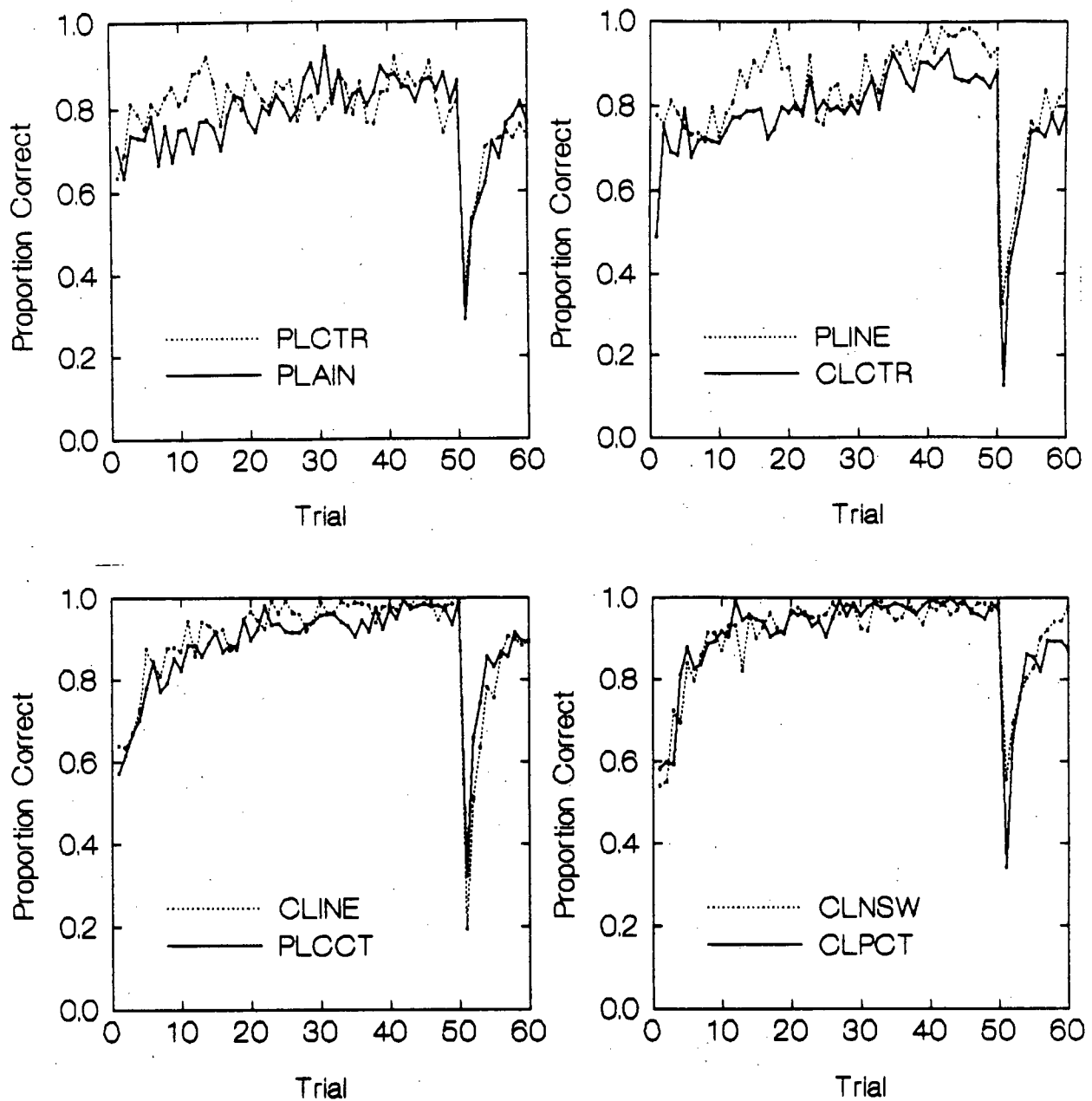
Figure 14. Proportion of first visits per trial that were
to rewarding feeders, averaged for all birds in each of the
8 treatments. Two treatments are shown in each panel.
Acronyms for treatments are fully described in the methods
section. Clnsw = coloured line markers switched after the
pattern reversal. Clpct = coloured lines and plain centres.
Cline = coloured lines. Plcct = plain lines and coloured
centres. Pline = plain lines. Clctr = coloured centres.
Plctr = plain centres. Plain = plain array.

| Treatment | F value | Probability | Y intercept | Slope |
|-----------|---------|-------------|-------------|-------|
| 1. Plain | 17.899 | 0.000 | 12.142 | 0.072 |
| 2. Plctr | 35.107 | 0.000 | 11.387 | 0.076 |
| 3. Clctr | 4.302 | 0.043 | 15.699 | 0.044 |
| 4. Pline | 102.399 | 0.000 | 6.52 | 0.174 |
| 5. Plcct | 0.206 | 0.652 | 18.422 | 0.000 |
| 6. Cline | 0.190 | 0.664 | 18.452 | 0.01 |
| 7. Clpct | 0.096 | 0.758 | 20.853 | -0.007 |
| 8. Clnsw | 0.476 | 0.493 | 18.612 | 0.014 |

Table 7. Linear regressions (since the relationship is assumed to be linear and flat) of total correct first visits on trial number for the first 50 trials. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.

Improvement in performance was strongly significant for all 8 treatments using proportion correct for the first 50 trials. Measuring performance by total incorrect indicated significant improvement for birds in 7 out of 8 treatments, with birds in the plain line treatment showing the lone insignificant improvement (Tables 8 and 9).

## Differences Between Treatments

Birds learned the patterns differently in the 8 treatments (Fig. 13 and 14); repeated measures ANOVA of proportion correct using 5 trial blocks as the repeated measures was strongly significant: $F(7,40 \text{ df}) = 13.875$, $p \approx 0.000$. Differences in total incorrect first visits were similarly highly significant (repeated measures ANOVA of the first 50 trials for 5 trial blocks: $F(7,40 \text{ df}) = 5.289$, $p \approx 0.000$).

| Treatment | F value | Probability | Y intercept | Slope |
|-----------|---------|-------------|-------------|-------|
| 1. Plain | 68.599 | 0.000 | 0.628 | 0.058 |
| 2. Plctr | 13.215 | 0.001 | 0.738 | 0.028 |
| 3. Clctr | 134.565 | 0.000 | 0.573 | 0.078 |
| 4. Pline | 42.581 | 0.000 | 0.676 | 0.064 |
| 5. Plcct | 463.101 | 0.000 | 0.596 | 0.101 |
| 6. Cline | 279.550 | 0.000 | 0.644 | 0.094 |
| 7. Clpct | 170.072 | 0.000 | 0.642 | 0.096 |
| 8. Clnsw | 199.572 | 0.000 | 0.618 | 0.102 |

Table 8. Linear regressions of proportion of correct first visits on natural log of trial number for the first 50 trials. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.

| Treatment | F value | Probability | Y intercept | Slope |
|-----------|---------|-------------|-------------|-------|
| 1. Plain | 21.736 | 0.000 | 6.453 | -0.835 |
| 2. Plctr | 6.894 | 0.012 | 4.468 | -0.387 |
| 3. Clctr | 32.463 | 0.000 | 8.030 | -1.229 |
| 4. Pline | 0.749 | 0.391 | 1.961 | -0.120 |
| 5. Plcct | 245.653 | 0.000 | 9.502 | -2.358 |
| 6. Cline | 198.277 | 0.000 | 7.428 | -1.926 |
| 7. Clpct | 143.252 | 0.000 | 8.487 | -2.256 |
| 8. Clnsw | 182.978 | 0.000 | 8.733 | -2.326 |

Table 9. Linear regressions of total incorrect first visits on natural log of trial number for the first 50 trials. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.

Since the ANOVAs showed significant differences in performance between treatments I conducted Tukey honestly significant difference analyses to contrast pairs of individual differences in both measures (Figs. 15 and 16).

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In general, there were few significant differences in performance (based on treatment means) in early trials, but increasing differences throughout the period leading up to the pattern switch after trial 50. Differences between treatments reached a maximum in trials 30 - 40. From trial 40 - 50, the Tukey tests show that performance was significantly better on arrays marked with lines than on plain arrays or those marked only with centres. Immediately after the switch there were again few significant differences in performance, but the differences reappeared more rapidly during this period of relearning than they appeared in the initial learning phase. Performance from trial 56 to trial 60 reveals a number of significantly different responses to the pattern switch.

Tukey analyses show 2-tailed differences only. I compared sets of these pairwise differences to indicate the order of difficulty of the treatments (Table 10). In most cases the resulting ranks correspond closely with my predictions. For the first 50 trials, I expected that performance would increase in the order: plain, plain centres, coloured centres, plain lines, plain lines with coloured centres, coloured lines and coloured line switch (tied), with the best performance from birds visiting an array marked with coloured lines and plain centres. The observed rankings differ only in the poor performance of the birds on the coloured centres pattern.
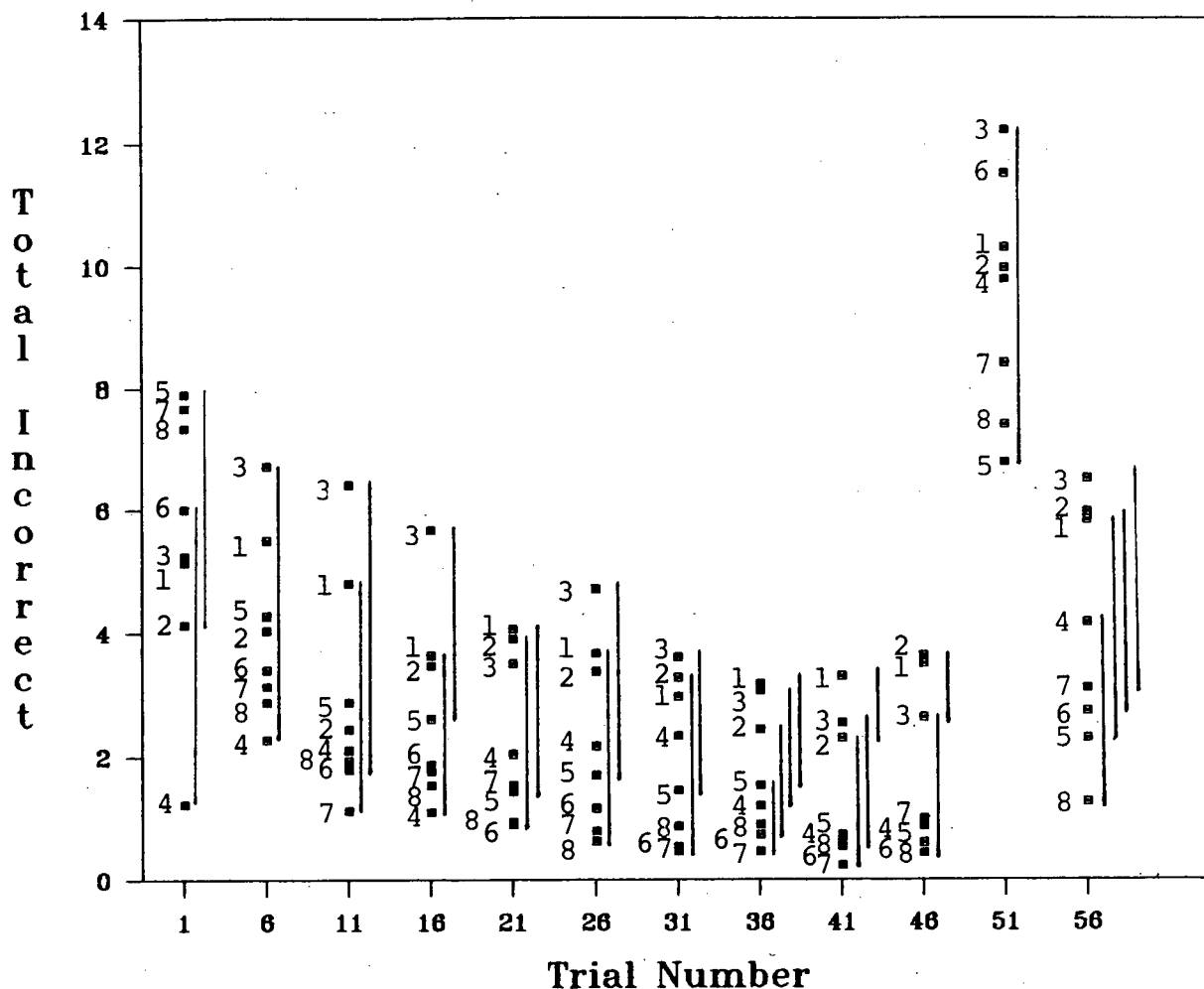
Figure 15. Summary of Tukey analysis of total incorrect
first visits per trial averaged for all birds in each of the
8 treatments. Results along the x axis are grouped into
blocks of 5 trials, with axis numbers indicating which trial
begins the 5 trial block. The switch occurred immediately
before trial 51. Lines connecting treatments indicate that
there was not a significant difference in performance for
the birds in these treatments during the indicated block.
Numbers refer to the different treatments: 1 = plain array,
2 = plain centres, 3 = coloured centres, 4 = plain lines, 5
= plain lines and coloured centres, 6 = coloured lines, 7 =
coloured lines and plain centres, 8 = coloured line markers
switched after the pattern reversal.

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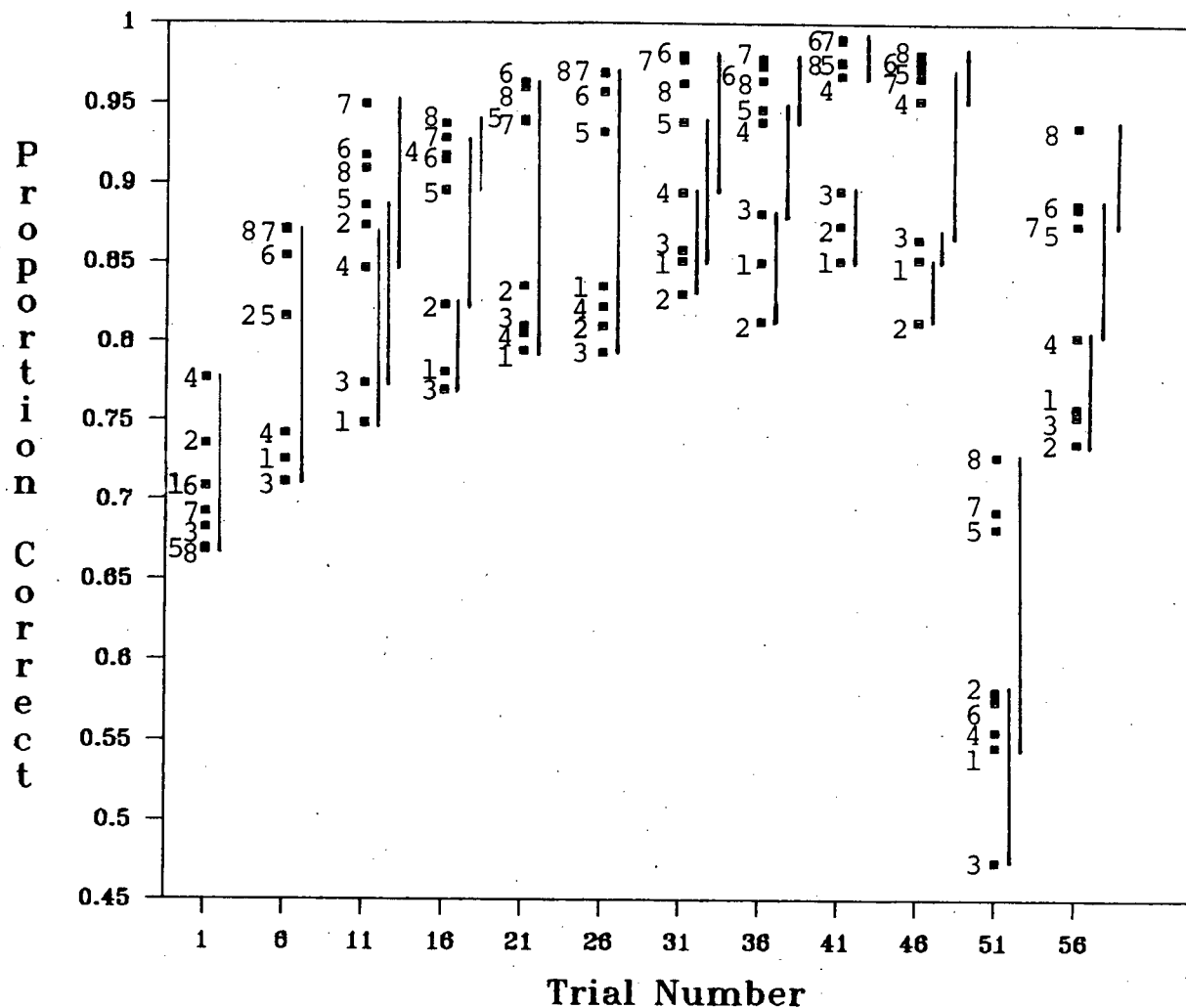
Figure 16. Summary of Tukey analysis of proportion of first visits per trial that were correct, averaged for all birds in each of the 8 treatments. Results along the x axis are grouped into blocks of 5 trials, with axis numbers indicating which trial begins the 5 trial block. The switch occurred immediately before trial 51. Lines connecting treatments indicate that there was not a significant difference in performance for the birds in these treatments during the indicated group of trials. Numbers refer to the different treatments: 1 = plain array, 2 = plain centres, 3 = coloured centres, 4 = plain lines, 5 = plain lines and coloured centres, 6 = coloured lines, 7 = coloured lines and plain centres, 8 = coloured line markers switched after the pattern reversal.

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| Treatment | Pre-Switch Only | | | Post-Switch Only | | | Complete Run | | |
|---|---|---|---|---|---|---|---|---|---|
| | Prop Corr | Tot Inc | Comb Rank | Prop Corr | Tot Inc | Comb Rank | Prop Corr | Tot Inc | Comb Rank |
| 1. Plain | 2 | 1 | 1.5 | 2.5 | 2 | 2 | 2 | 2 | 2 |
| 2. Plctr | 3 | 3 | 3 | 2.5 | 3 | 3 | 3 | 3 | 3 |
| 3. Clctr | 1 | 2 | 1.5 | 1 | 1 | 1 | 1 | 1 | 1 |
| 4. Pline | 5 | 4 | 4 | 5 | 4 | 4 | 5 | 4 | 4.5 |
| 5. Plcct | 4 | 5 | 5 | 7.5 | 5.5 | 6.5 | 4 | 5 | 4.5 |
| 6. Cline | 7.5 | 7 | 6.5 | 4 | 5.5 | 5 | 6.5 | 6 | 6 |
| 7. Clpct | 6 | 8 | 8 | 6 | 7 | 6.5 | 6.5 | 8 | 7 |
| 8. Clnsw | 7.5 | 6 | 6.5 | 7.5 | 8 | 8 | 8 | 7 | 8 |

Table 10. Ranked means of treatments from Tukey analysis. In this table a rank of 8 indicates that birds in this treatment performed better than birds in any other treatment, while a rank of 1 indicates the worst performance of any group of birds. Prop. Corr. = rankings based on proportion correct. Tot. Inc. = rankings based on total incorrect first visits. Comb. Rank = Average of the two ranks. Numbers in the pre-switch only column are averages of the ranks for the first 50 trials. The post-switch only column shows averages from trials 51 - 60. Complete run data are averages across all 60 trials. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.

After the pattern reversal I expected a similar order of performance as in the first 50 trials, but with birds in the coloured line switch pattern outperforming those in any other treatment. Again, the observed rankings corresponded well with these expectations. Birds in the coloured centres treatment performed surprisingly poorly again, while those with plain lines and coloured centres showed surprisingly good recovery from the pattern reversal.

Overall, I expected the order of performance to be plain, plain centres, coloured centres, plain lines, plain lines with coloured centres, coloured lines, coloured lines with plain centres and coloured line switch. The observed rankings followed these predictions with the exception of birds using the array marked with coloured centres, on which performance was poorest.

## Switch Effect

Birds in the 8 treatments responded differently to a pattern reversal as shown graphically (Figs. 13 and 14) and by Tukey analysis (Table 10; Figs. 15 and 16). Rankings of bird performance after the pattern reversal were different than before the reversal. Birds using arrays with both lines and centres performed relatively more poorly after the switch (compared to other treatments) than before.

The most obvious difference in responses to pattern reversals was between coloured line and the coloured line switch treatments, which I used specifically to test the effect of pattern reversals on learning. I moved the rewarding colours with the rewarding feeders in the coloured line switch treatment but not in the coloured line treatment. When the coloured indicator of profitability followed the movement of profitable feeders, birds made markedly fewer errors after the switch (compared to the same pattern when feeders were switched but landmark patterns stayed the same).

Birds in all treatments learned the new pattern of rewarding feeders as shown by the significant linear regressions of performance on the natural log of trial number (Tables 11 and 12).

| Treatment | F value | Probability | Y intercept | Slope |
|-----------|---------|-------------|-------------|-------|
| 1. Plain | 89.780 | 0.002 | 240.096 | -57.790 |
| 2. Plctr | 20.590 | 0.002 | 210.157 | -50.358 |
| 3. Clctr | 24.413 | 0.001 | 292.914 | -70.625 |
| 4. Pline | 36.071 | 0.000 | 274.380 | -66.603 |
| 5. Plcct | 14.579 | 0.005 | 240.830 | -58.853 |
| 6. Cline | 34.356 | 0.000 | 406.061 | -99.362 |
| 7. Clpct | 14.569 | 0.005 | 285.390 | -69.648 |
| 8. Clnsw | 44.806 | 0.000 | 286.374 | -70.246 |

Table 11. Linear regressions of total incorrect first visits on natural log of trial number for the 10 trials after the switch. Acronyms for treatments are fully described in the methods section. Clnsw = coloured line markers switched after the pattern reversal. Clpct = coloured lines and plain centres. Cline = coloured lines. Plcct = plain lines and coloured centres. Pline = plain lines. Clctr = coloured centres. Plctr = plain centres. Plain = plain array.

## Visitation Patterns

When birds had gained considerable experience with the pattern of rewarding feeders (trials 46 - 50), they made most errors to non-rewarding feeders bordering the groups of rewarding feeders (Fig. 17). Birds visited non-rewarding feeders beside rewarding feeders four times more often, on average, than they visited other non-rewarding locations (0.096 versus 0.025 times per trial, respectively).

| Treatment | F value | Probability | Y intercept | Slope |
|-----------|---------|-------------|-------------|-------|
| 1. Plain | 33.616 | 0.000 | -9.740 | 2.588 |
| 2. Plctr | 17.391 | 0.003 | -7.129 | 1.940 |
| 3. Clctr | 24.826 | 0.001 | -12.989 | 3.388 |
| 4. Pline | 41.334 | 0.000 | -11.212 | 2.962 |
| 5. Plcct | 13.752 | 0.006 | -9.722 | 2.616 |
| 6. Cline | 24.297 | 0.001 | -13.897 | 3.643 |
| 7. Clpct | 11.946 | 0.009 | -9.046 | 2.448 |
| 8. Clnsw | 81.525 | 0.000 | -8.513 | 2.327 |

Table 12.   Linear regressions of proportion correct on natural log of trial number for the 10 trials after the switch.  Acronyms for treatments are fully described in the methods section.  Clnsw = coloured line markers switched after the pattern reversal.  Clpct = coloured lines and plain centres.  Cline = coloured lines.  Plcct = plain lines and coloured centres.  Pline = plain lines.  Clctr = coloured centres.  Plctr = plain centres.  Plain = plain array.

Birds can remember rewarding locations, as demonstrated by their high performance on first visits, but they continued to revisit unrewarding feeders during a trial. Even in the final 5 trials before the switch, birds revisited feeders regularly, averaging 4.84 revisits per rewarding location per trial.  Thus, only about 20% of "correct" visits were rewarding.
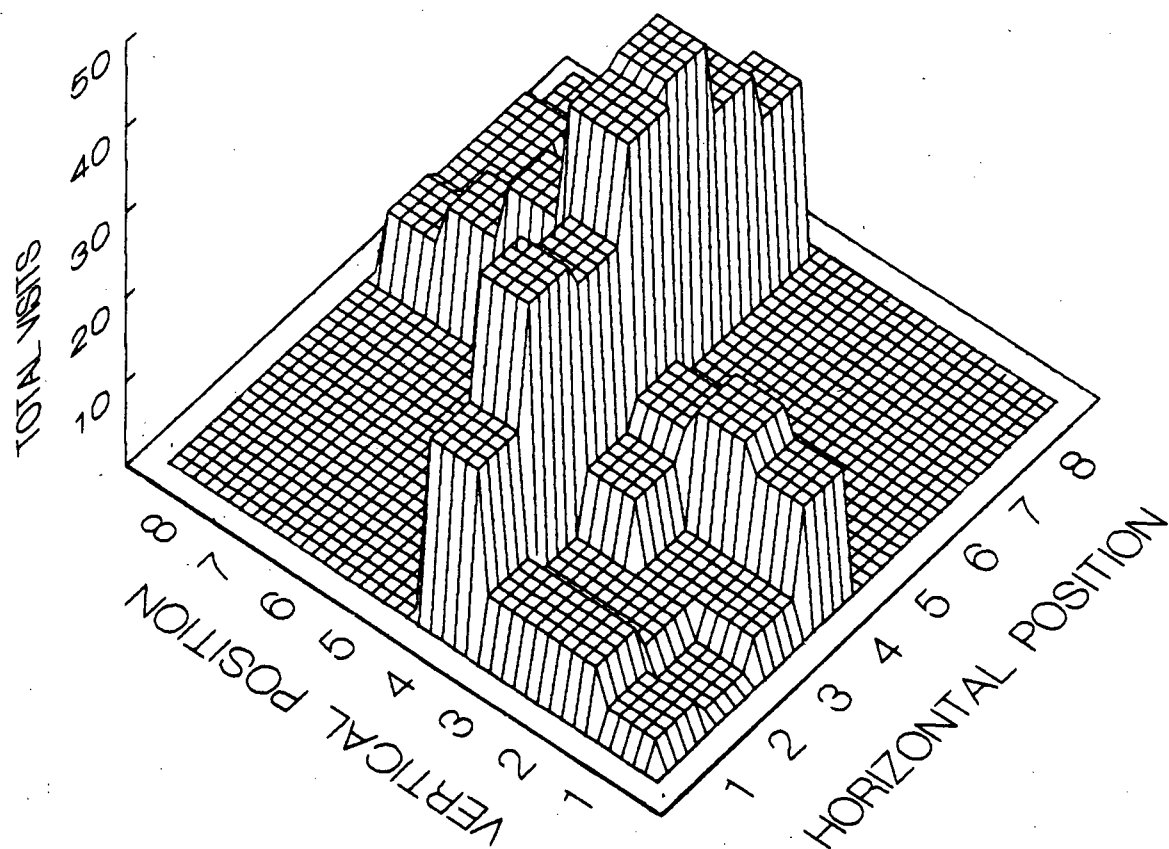
Figure 17. Total visits by all birds to non-rewarding
locations in trials 46 - 50 of all treatments. Visits to
rewarding locations are not shown. This figure was produced
using a step smoothing algorithm. As a result, each feeder
location is represented by 16 grid units.

## Section IV.  Discussion

### Use of Array Markers

The hummingbirds learned the distribution of rewarding feeders under all sets of experimental conditions.  The similar shapes of the initial performance curves for all 8 treatments suggests that the birds used similar processes to learn all of the treatments.  Given this, the significant differences between the curves represent the relative usefulness of visual aids in locating rewarding feeders. Adding markers to the plain array sped up learning the array; birds more rapidly approached asymptotic performance with markers, and achieved a higher asymptote.  The rankings of the different treatments indicate that edge markers are more useful locators of patches than centre marks and that providing a colour indicator to profitability in the landmarks provides some learning benefits to the birds.

### Lines versus Centres

The strongest and most obvious difference between these treatments is that lines were much more effective aids to learning than central marks, which were little better than a plain array.  Among several possible reasons for the superiority of lines, the most feasible is that for hummingbirds, perhaps because of how they move during foraging, information delimiting the edges of patches is

more useful than information indicating their centres. Geometry is an important aspect of landmark use (Cheng, 1986; Cheng and Gallistel, 1984; Gallistel, 1989 and 1990). My edge landmarks were arranged into 4 squares surrounding feeders that were all either rewarding or non-rewarding. Birds could have used these edge landmarks to develop spatial rules of thumb about profitability based on either left-right and up-down movement in relation to a set of lines, or in-out orientations in relation to the squares. Birds using arrays marked only with centre landmarks could form rules about near and far feeders in relation to the landmarks. Alternatively, they could use vector orientation from either type of landmark to find profitable feeders, in a fashion similar to that suggested by Cheng (1989 and 1990). This vector sum model of orientation has some flaws though, especially in relation to diagonal vectors, which animals seem to have more difficulty using.

Another possible explanation for the difference between edge and centre landmarks is that the differences in the total amount of colour added to the array (centres = 20.3 cm$^2$, lines = 566.4 cm$^2$) was sufficient to make the lines more useful. There may be some truth to this second possibility. In general, animals prefer to use large landmarks near their rewards over others (Bennett, 1993; Cheng, 1989). The line form of array mark may provide a

large landmark that is more useful to a foraging hummingbird than the smaller central place mark.

### Lines versus Colours

There was a strong difference between the usefulness of both kinds of landmarks, *per se*, and landmarks with reward information. There was a much stronger difference between forms (lines versus centres) than there was between presence or absence of reward information (contrasting or same coloured markers). Adding colour as an indicator of profitability did not significantly increase performance but the interaction of colour and form did provide a benefit to learning. The significant interaction effect could have several possible meanings. Various authors have demonstrated that animals can attend to several types of stimuli at once (Clayton and Krebs, 1994; Gass and Montgomerie, 1981; Giraudo and Perauch, 1988; Gleitman, 1963; Gould and Marler, 1987; Olton, 1990; Rescorla, 1986; Roberts *et al.*, 1988; Sattath and Tversky, 1987; Sherry, 1984; Spetch and Edwards, 1988; Vallortigara and Zanforlin, 1989). The birds in this experiment also attended to two types of information at once; they performed better when provided with the combination of landmarks and information about profitability than with uniform array markers.

What do these differences in usefulness mean ecologically? Various authors have demonstrated the importance of colour in hummingbird foraging. Collias and

Collias (1968) used simple preference tests in outdoor feeders to show that Anna's hummingbirds use colour cues in choosing feeders of different quality. Miller *et al.* (1984) and Wheeler (1980) also demonstrated that colour is an important visual cue for hummingbirds. All of these studies, however, demonstrated that colour is less important than positional cues. The effect of colour was also overshadowed in my study, in this case by the type of marker.

## Cognitive Maps

I believe that birds will use these differing landmark forms as an integral part of a cognitive map of their environments. Edge landmarks may help birds delimit patch boundaries, especially during a period of area restricted search after a reward site has been located and exploited by techniques such as random search. The larger overall area of the edge landmarks may also have facilitated learning. Information about the quality of food locations is presumably another component necessary for a successful cognitive map.

The cognitive map concept has been challenged repeatedly in the literature (M. Brown, 1992; Collett *et al.*, 1986; Collett *et al.*, 1993; Dyer, 1991 and 1993; Restle, 1957) but has gained wide acceptance by many authors (de Renzio, 1982; Ellen, 1980; Gallistel, 1989; Giraudo and Perauch, 1988; Gould and Marler, 1987; Nadel and Willner,

1980; Okaichi, 1987; O'Keefe and Conway, 1980; Olton, 1990; Sholl, 1987; Spetch and Honig, 1988; Srinivasan *et al.*, 1989; Sutherland and Dyck, 1984; Thinus-Blanc and Ingle, 1985). Skeptics suggest that at least some groups of animals, especially invertebrates, rely on dead reckoning to navigate rather than a remembered representation of the environment and argue that the evidence for cognitive mapping is weak (Collett *et al.*, 1993; Dyer, 1991). Another alternative to cognitive mapping is the maintenance of a list of specific locations with no reference to the geometric organization of these locations with respect to each other (M. Brown, 1992).

Map-using animals should be capable of more adaptable movement patterns than those using dead reckoning or those checking lists, including finding a goal site from a novel environmental position (Ellen *et al.*, 1984; Gallistel, 1989; Gould and Marler, 1987; Menzel, 1991; Nadel and Willner, 1980; Schenk, 1987; Sutherland and Dyck, 1984; Thinus-Blanc and Ingle, 1985) or navigating without using local landmarks in a stereotyped fashion (Gould, 1986c; Kramer and Weary, 1991; Morris, 1981; Olton, 1990). The birds in my experiment were not constrained to approach the feeder array from a novel position, (navigation through a known landscape from a novel position is a common test for mapping), but there was no evidence for repeated, stereotyped or

systematic movements within the array (an indication of the use of dead reckoning).

## Chunking

Learning a pattern of feeders is an important step in the development of an overall cognitive map. If birds learn a spatial pattern of rewarding feeders rather than learning a set of individual rewarding locations, they could gain the advantage of reduced information stored in memory. This process involves grouping items such as environmental characteristics into units in memory; this is known as chunking. Humans do this (Fisk and Lloyd, 1988; Hemenway and Palmer, 1978; Shiffrin *et al.*, 1976), and it has also been described in several animal species (Olton, 1985; Suzuki *et al.*, 1980; Vallortigara and Zanforlin, 1987 and 1989). The process of learning a group of spatially distributed components as an overall pattern was demonstrated in hummingbirds by Sutherland and Gass (in press).

Tolman, who suggested the concept of cognitive maps in 1948, believed that broadly applicable and inclusive maps were the norm, and that narrowly defined maps or sets of instructions were the result of inadequate cues, restricted training, or strong motivations. If this is true, a map in this experiment might include not only the pattern of feeders, but also the location and distance from the perch to the array, and the location of walls, lights and doors in

the experimental chamber. Several studies have suggested the importance of such global cues in spatial learning (Bennett, 1993; Spetch and Edwards, 1988; Spetch and Honig, 1988; Suzuki *et al.*, 1980).

## Environmental Change, Complexity and the Switch Effect

Information about temporal changes in reward sites is an important aspect of cognitive mapping and effective foraging in general (Biebach *et al.*, 1989; Gallistel, 1989); however, the scale of temporal change is important in examining its effects (Gass, 1985; Gass and Montgomerie, 1981; Gass and Roberts, 1992). Hummingbirds in my experiments did not learn to avoid depleted feeders during the course of a trial, but learned to avoid empty feeders across a series of trials.

The tendency to explore or sample the surrounding environment is strongly affected both by the actual quality of the environment and the animal's memories and perceptions of it. For instance, animals change their foraging strategies more rapidly in response to temporal variations in reward when they possess information about several or many foraging sites than if they know only one food source (Mitchell, 1989). Animals with such restricted information rapidly change their behaviour only if there is an environmental change and they possess sufficient information about the environment.

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The switch in this experiment demonstrated that hummingbird spatial memory is resistant to sudden change. As Chapter 2 demonstrated, this resistance is related to the number of trials in which a bird has experienced stability in its environment. The results from this experiment into array markings also suggest (although not strongly) that when birds learn more about their environment and have more visual cues providing unchanging information, they are less likely to change their behaviour in the face of sudden and unpredictable change, as shown by the comparatively poorer performance of birds in treatments with both edge and centre landmarks.

If the cues in their environment change, however (as demonstrated in the movement of coloured lines after the switch in one treatment), they are less resistant to change (Roberts *et al.*, 1988). Performance by birds in the treatment where array markers (coloured lines) moved with the rewarding feeders showed that the birds are able to track changes in the array markers. The performance of birds on this pattern after the switch was better than any other. This result indicates that the birds learned to associate the colour of array markers with feeder quality and followed the colour cues instead of relying on spatial memory of feeder locations. The association between colour and reward, which was "portable", was balanced against the spatial memory of past reward locations. The birds in this

treatment showed a small drop in performance after the switch but recovered more rapidly than birds in any other treatment. Their use of spatial memory was flexible enough to rapidly adapt to rearrangement of groups of feeders.

Responses to the switch reveal no simple patterns that apply to all treatments. The type of array markings had little effect on the level to which performance dropped after the switch. Immediately after the switch, birds in all treatments (excepting the treatment where profitability indicators followed the switch in feeder profitability) performed similarly, dropping to levels of foraging success which were statistically indistinguishable from each other. By the second block of 5 trials after the switch, however, birds returned to the pre-switch order of performance, with birds using arrays with edge landmarks performing better than those with plain arrays or centre landmarks only.

In a review of the timing of behaviour, Killeen and Fetterman (1988) suggested that the richness or complexity of the environment affects animals' foraging. Studies with various animals have shown a similar link between environmental richness and foraging. Chipmunks vary their exploratory behaviour based on the predictability and richness of the environment (Kramer and Weary, 1991). Rats use systematic linear foraging when food is easily visible, but become selective in their search when the food is hidden (Ilersich *et al.*, 1988). Gerbils reduce exploration and

become short term energy maximizers when unpredictability increases (Forkman, 1991). Bee foraging is adapted to the temporal and spatial patterns of their natural food sources (Laverty and Plowright, 1988; Menzel, 1985).

Nor is this variability in search limited to foraging. Birds in fragmented forests appear to locate new breeding sites by random search for suitable sites (Haila *et al.*, 1993). Chipmunks may adjust their search techniques to temporal and environmental conditions both in foraging and other tasks such as searching for a mate (Kramer and Weary, 1991), as may other species (Gibb, 1961; Guilford and Dawkins, 1987; Warren and Warren, 1973). Heller (1980) suggests that animals begin foraging in a patch by using limited criteria for food sources, then broadening their criteria as time in a patch increases.

Various forms of search are likely an initial step in a naive exploration of an animal's environment. Once a rewarding site has been found and exploited (perhaps by random search for a limited set of foraging criteria), the forager may restrict itself to search around that site (Wolf and Hainsworth, 1991), although this step is variable and depends on the animal's knowledge of the surrounding environment (Mitchell, 1989), its motivation (Forkman, 1991), the variability of the environment (Kramer and Weary, 1991) and a number of other factors (Weiss, 1983). If random search helps locate new food sources, area restricted

search is an effective way to define the boundaries of food sources. The birds in my experiments may be treating one sector of the array in a similar fashion to a compound inflorescence or a bush or some other form of restricted patch. Once birds had experienced a number of trials they made most errors (first visits to non-rewarding feeders) at feeders adjoining the rewarding feeders. This may be due to uncertainty about the edges of the rewarding patch or may be sampling of areas around the rewarding patch to detect changes in profitability.

Eventually the animal will learn the reward sites and values of the rewards in its environment. The locations and values of the rewards should be a major portion of its cognitive map. In order to return to the known reward sites, however, the animal must use information from landmarks and cues to navigate through its environment (Cheng, 1986; Gallistel, 1989 and 1990; Shettleworth and Krebs, 1986). The markers provided on the array presumably provided information to assist in this step in map formation.

## Conclusions

This experiment demonstrates that hummingbirds use landmarks to locate reward sites. The form of these landmarks is important, and hummingbirds learn patterns of rewarding feeders more rapidly and better using edge landmarks than with central landmarks. They also use

information about reward quality conveyed by the colour of these markers, although the effect of reward information does not provide a very strong benefit to learning.

Once birds have learned their surroundings, they persist in using this knowledge until they have sufficient evidence that their memories are no longer a valuable source of information in foraging. The strength of this persistence may be related to the success they have achieved in their environment before a change. Persistence of use of spatial memories can be reduced by providing information indicating that a change has occurred.

# Chapter 4.

## Spatial Association and Spatial Memory in Rufous Hummingbirds

### Section I.  Introduction

In this experiment I examined the contrasting effects of spatial association and spatial memory by varying the period of exposure to a pattern of rewarding feeders and the spatial separation between a cue to profitability of a feeder and that feeder.  This study was also intended to tie together some of the aspects of spatial learning discussed in Chapters 2 and 3.

### Spatial Association Learning

Simple associative learning is the process of associating a contiguous cue and response site.  Typical examples of simple associative learning include a rat pressing the correct bar in a group of bars to obtain a reward or associating movement to the correct arm of a maze with a food reward (Bond *et al.*, 1981; Colwill, 1985; Hoffmann and Maki, 1986; Mackintosh, 1983; Maki, 1979).  In these situations, the animal learns to respond at the same location as the stimulus.  In other situations, however,

there may be a displacement in space between the stimulus and the response or reward sites (Rumbaugh *et al.*, 1989). In such cases, many animals have difficulty learning the task without special training protocols and lengthy training periods (Davis, 1974; Pinel *et al.*, 1986; Schrier *et al.*, 1963; Stollnitz and Schrier, 1962). For the purposes of this study I define spatial association learning as the process of associating a spatially separated cue and reward (Bowe, 1984; Brown and Gass, 1993). Simple associative learning, in which the reward and cue are contiguous, is a much simpler task for animals to learn in both natural and laboratory environments and has been heavily documented (for instance Aadland *et al.*, 1985; Balda *et al.*, 1986; Bond *et al.*, 1981; Bruce and Herman, 1987; Clayton and Krebs, 1993 and 1994; Cole *et al.*, 1982; Colwill, 1985; Dallery and Baum, 1991; Dawkins, 1971a and 1971b; Gallistel, 1989; Gillingham and Bunnell, 1989; Fuchs and Haken, 1988a).

In nature, however, there are various examples of animals learning to associate a separated cue and response or reward site. The use of marks on banner petals to assess nectar quality of flowers by bees (Gori, 1989), and the use of circling vultures by predators to locate prey (Houston, 1983; Rabenold, 1983 and 1987) are both examples of spatial association learning. Brown and Gass (1993) demonstrated the ability of hummingbirds to carry out spatial association

learning tasks in a laboratory environment after a short and simple training period.

## Spatial Memory

Similarly, facility with spatial memory tasks has been demonstrated for varied tasks and species (Gleitman, 1963; Gould, 1986a and 1986b; Grigoryan and Stolberg, 1989; Healy and Krebs, 1992; Hermer and Spelke, 1994). Spatial memory is simply the use of remembered information about location to navigate through the environment. Previously visited sites may be found only by dead reckoning (moving between two fixed points along a series of remembered vectors) in some primitive animals (Collett *et al.*, 1993; Dyer, 1993) but there is considerable evidence for cognitive maps of the environment in most higher animals (Gould, 1986a; Menzel, 1973; O'Keefe and Conway, 1980; Olton, 1990). Spatial memory may be used for almost any ecological function, from foraging for food (Hitchcock and Sherry, 1990; Kamil and Roitblat, 1985; MacDonald and Wilkie, 1990; McQuade *et al.*, 1986), to finding the way home (Holldobler, 1980; Robinson and Dyer, 1993) or to some other location (Morris, 1981; Schenk, 1987; Shettleworth, 1983), to finding mates (Kramer and Weary, 1991) or finding offspring (McCracken, 1993).

## Learning Processes

Why would animals easily remember locations (on their own or locations directly associated with response sites)

but have difficulty learning to associate cues that are displaced from response sites with the response sites? This difference suggests that there may be some underlying physiological difference in how these learning processes occur and that these differences may affect which form of learning is more advantageous in specific instances. The best we can say about this is that the neural bases for these forms of learning are still speculative. We do have strong evidence that spatial memory is a form of long term memory stored at least partly in the hippocampus (Ellen, 1980; Kesner, 1980; Okaichi, 1987; O'Keefe and Conway, 1980; Olton, 1990). Species with superior spatial memories have a large hippocampus (Sherry *et al.*, 1989), and place cells in the hippocampus may in fact correspond to elements of an animal's cognitive map of its surroundings (Speakman and O'Keefe, 1989).

The hippocampus has been implicated in various other functions as well. It is involved in forming associations between stimuli and in discounting cues when they are no longer valuable or when better predictors of reward become available (Moore and Stickney, 1980). As well, the hippocampus is involved in non-mapping types of spatial behaviour, temporal mapping, and non-spatial learning (Kesner, 1980; Olton, 1990; Speakman and O'Keefe, 1989). The hippocampus may be involved in monitoring speed and direction vectors along with the visual, motor and parietal

cortex (Olton, 1990). Spatial working memory may also be stored in the hippocampus (Olton *et al.*, 1980).

While long term memories (items stored for an indefinite period) seem to involve actual changes in which genes are expressed by a neuron, short term memory (items stored for a short period only) seems to involve covalent modifications of pre-existing cellular proteins (Barnes, 1988; Goelet *et al.*, 1986; Matthies, 1989; Thompson, 1986). Some authors suggest a third form of memory, working memory, which is used only while tasks are ongoing. It is essentially non-associative and is discarded at the end of the current task (Barnes, 1988; Maki, 1987). The hippocampus plays a key role in transferring items from working memory to long term memory (Wickelgren, 1979). Most aspects of spatial memory are long term memory tasks (Nadel and Willner, 1980). It appears that these neural processes are similar across a wide variety of species of birds, mammals and possibly other advanced groups of animals (Bingman *et al.*, 1989; Olton, 1985).

### Differences in Learning

In simple associative learning, spatial association learning and spatial memory, the initial learning processes may occur similarly as part of working memory. If there is a processing difference, it probably occurs at the point of transfer to short term or long term memory. Work by various authors suggests that many cue (associative) tasks

are limited to short term memory while landmark (spatial memory) tasks are transferred directly to long term memory (Barnes, 1988; Kamil and Mauldin, 1975; Kesner, 1980; Nadel and Willner, 1980; Sherry, pers. comm.).

### Advantages and Disadvantages

These differences, if real, suggest that the development of spatial memory takes longer and is more involved than direct associative learning. Spatial association learning should fall somewhere between the two since it involves both associative and spatial learning, but generally will still be quicker than reliance solely on spatial memory. In a situation in which either spatial or associative learning would be possible and effective, simplicity dictates that associative learning should predominate. These physiological differences between associative tasks and spatial memory tasks should result in differences in biases towards particular types of learning.

Another advantage to simple associative learning is that animals using it need learn only one thing: the association between cue and response. Spatial memory, on the other hand, requires the development of a set of memories about landmarks, cues, reward sites and their interrelationships. This suggests that simple associative learning should be preferred to spatial memory when either is sufficient to complete the task. Again, spatial association learning should fall between simple association

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and pure spatial memory in difficulty, since spatial associations require animals to remember only the spatial relationship between cue and reward in addition to the fact that they are associated.

**Uncertainty and Perception**

An animal's perception of its environment should also influence whether it uses spatial memory or association in a given situation. If the environment is stable, the long term development of maps of spatially structured information should be advantageous as they allow efficient and flexible exploration and use of the environment. On the other hand, spatial mapping would be a waste of time and energy in a highly variable environment, because the spatial structure of the environment could change enough before they are used sufficiently to balance the cost of learning them. In this case, short term associative learning would be more of an advantage because it involves remembering rules that are not affected by changes in the environment as long as the association remains intact. Associations between stimuli and responses are "portable" and can be applied in various locations and times. For example, if a hummingbird learns the association between red flowers and nectar production, it can apply that association to any red nectar producing flowers. If, however, it uses spatial memory to learn the spatial location of a particular set of red flowers, the

memory is useful for only the nectar producing lifespan of those flowers.

There is an important difference between the actual temporal variability of an animal's environment and the animal's perception of it. While there will generally be a strong similarity between perception and actuality, it is not absolute. Animals normally develop perceptions of their environments based on current sensory input and memory of past experiences (Church and Miller, 1991; Valone and Girardeau, 1993). In Chapter 2 I presented evidence of the effects of experience on persistence of spatial memories. Perceived variability results when expectations do not correspond to sensory evidence. In this case, animals will tend to reduce planned foraging and rely on exploration and sampling of the environment (Valone, 1992).

In gauging the value of past experience, animals tend to value the most recent experience most highly (Todd and Kacelnik, 1993). This phenomenon may be the reason for the recency effect, or improved performance for recently learned tasks (Sherry, 1984). Animals not only discount past experience based on the elapsed time since they obtained a reward, but also based on the amount and perceived variability of the reward (Bowers and Adams-Manson, 1993; Gibbon *et al.*, 1988). Variable rewards increase the amount of information required to retrieve them. Since animals have a limited ability to remember past experiences, at some

point they will reach their capacity for stored memory, based on a combination of elapsed time, individual experience and environmental complexity, each of which increases the amount of information to be processed (Nishimura, 1994).

## Current Study

This study had two primary purposes. First, it provided an opportunity to contrast the roles of experience with a simple pattern of rewarding feeders and cue characteristics (in this case, cue distance). In chapter 2 I studied the effect of experience (measured in terms of number of trials with a stable pattern of feeders) on persistence of visitations to formerly rewarding feeders. In chapter 3 I looked at how differing perceptual information assisted spatial learning. In this study I examine how these factors interact.

A second reason to do this study was the potential to contrast the roles of spatial association learning and spatial memory in hummingbird foraging. In previous studies with rufous hummingbirds, Brown and Thompson both found that cue separation from the response site hampered learning (G. Brown, 1992; Thompson, 1994). This study provides a contrast between the spatial association learning examined by Brown and Thompson and the spatial memory examined by myself and Sutherland (Sutherland, 1985).

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This study also continues my exploration of the role of environmental instability in hummingbird learning. As in chapter 2, where I found that persistence with a pattern of feeders increased with increasing experience with that pattern, I provide the animals with a stable foraging environment for differing periods of time followed by a sudden change in the pattern of rewarding feeders to probe the extent and persistence of their previous learning.

There are nine different treatments in this set of experiments, consisting of exposures of three different durations (30 minutes, 90 minutes and 300 minutes of free access to a pattern of rewarding and non-rewarding feeders) and three different cue conditions (close cues: LEDs cueing rewarding feeders at distances of 1 cm; far cues: LEDs at 12 cm; and uncued: no LEDs at all). For each duration, the exposure is tied not only to the clock but to the number of feeding bouts by the hummingbirds. I expect that shorter durations will tend to favour the use of associated cues, while longer time periods will favour the development of spatial memory. Uncued treatments will require spatial memory, and close cues will favour the association aspects of spatial association learning over a given duration. Far cues should fall somewhere between these two extremes, but will also involve spatial association learning. The combination of these two factors should allow me to explore

how the interactions between time and cue distance will bias
birds towards use of either type of learning.

## Section II.  Materials and Methods

### Subjects

The subjects of these experiments were 12 adult rufous hummingbirds (*Selasphorus rufus*):  1 male and 11 females. The birds were collected in the wild in May 1991 from the vicinity of the Rosewall Creek salmon hatchery, Vancouver Island, British Columbia, and the University of British Columbia research forest in Maple Ridge, British Columbia and had been used in previous learning experiments.  Due to excessive weight loss two of the females could not complete all treatments and were each replaced for their final run by different birds (both female), bringing the total number to 14.  The animals were maintained in individual 0.6 x 0.6 x 0.6 m wire mesh cages for several months prior to testing.

Photoperiod mimicked seasonal variation in the wild. Excluding test periods, the birds were supplied with either Roudybush hummingbird diet or Nektar Plus hummingbird diet supplemented with isolated soy protein (3% w/w) *ad libitum* from standard commercial unlimited volume feeders on weekdays.  On weekends, they had 25% sucrose solution with added vitamins (Avitron avian vitamin supplement) and minerals (Avimin avian mineral supplement).  The birds

participated in several foraging experiments prior to this study.

## Experimental Environment

I conducted all training and experiments in 3 experimental rooms, each 1.3 x 2.5 x 2.5 m high with 2 overhead 40 watt incandescent light bulbs. Walls and ceiling, except the feeder array, were a uniform light green colour. The floor was a uniform sand colour. A single, stand-mounted, 1.5 m high perch was located at the centre of each room and fitted with a photocell to signal arrivals and departures.

A feeder array covering part of one end wall consisted of a metal panel (107 cm wide x 61 cm high) painted a flat dark green colour with a horizontal array of eight evenly spaced feeders. Each feeder was marked by a round 19 mm diameter fluorescent orange Avery label with a 3 mm diameter central hole. Behind each feeder was an infrared photocell which detected the presence of a hummingbird's bill. A small food reservoir consisting of the plastic fitting of a disposable 21 gauge hypodermic needle was also positioned behind each feeder. Each syringe was connected by flexible plastic tubing to a computer controlled, miniature solenoid valve (General Valve Corporation, series 3). If the feeder was designated as rewarding during a particular time period, the valve released 2 $\mu$l of 20% sucrose solution (mass/mass)

into the reservoir immediately when the bird probed the feeder. If the feeder was non-rewarding, the bird received no food from that feeder.

There were three variations on this basic panel design, with one variation in each experimental room. In one, feeders were unmarked except as noted above. In another, a small red light (4 mm diameter LED) protruded through the panel 1 cm directly above each feeder. In the third panel design, the lights were 12 cm above the feeders. These three panels represented the three treatments: uncued, close cues and far cues. When the light above a feeder was turned on by the controlling computer at the start of a test period, it signalled that the feeder was rewarding. In all 3 cases, a buzzer also indicated the start of a test, so even birds using the plain panel were given a signal that a rewarding feeder was present somewhere in the array.

Hummingbirds were allowed free access to the array and all areas of the room during experiments, but they could feed successfully only from one rewarding feeder during each exposure period.

## Training

On the day before testing, the feeder in each bird's home cage was modified to resemble the feeders in the experimental arrays. Birds quickly learned to use these feeders and they and their feeders were moved to the experimental rooms in the late afternoon. These feeders

were hung directly in front of the centres of the experimental arrays, which were covered.

The following morning, the commercial feeders were removed and one array feeder was uncovered in each room and birds were allowed access to the array until they were feeding regularly. This took about 2 hours in total. The array was then recovered for a short period (about 20 minutes) until testing began.

## Experimental Procedures

Each bird experienced nine different experimental conditions (excepting the two birds removed from the experiment and their substitutes). The order of presentation of these conditions and the birds used on any given test day were randomized.

The conditions consisted of exposure to each of the 3 experimental arrays (uncued, close cue and far cue) for 3 differing exposure periods before the rewarding feeder was switched. The 3 exposure times to the original pattern of feeders were short (30 minutes or 3 successful feeds if the birds had not met this requirement in the 30 minute exposure period), medium (90 minutes or 9 successful feeds), and long (300 minutes or 30 successful feeds). A successful feed was any rewarding visit to the array followed by a return to the perch.

One of the feeders in the 8 feeder array was rewarding for the entire exposure period and the others were not.

Rewarding feeders were randomly assigned for all experimental runs, although neither end feeder was ever rewarding. End feeders were left empty to prevent birds from using a simple rule of thumb such as visiting the feeder nearest the wall, as seen in previous studies (Miller *et al.*, 1984). A soft buzzer sounded for 0.5 s to indicate the beginning of test periods. In the close and far cue treatments, the cue above the rewarding feeder was lit during test periods to indicate that it was rewarding. During the experiment, the rewarding feeder provided 2μl per probe. Each visit to the array followed by a return to the perch was considered to be a single feeding bout no matter how many times the bird probed feeders.

The rewarding feeder was changed randomly to a new location in the array after the initial exposure period (at least 30, 90 or 300 minutes). As in the initial exposure period, the two end feeders were never rewarding. The experimental run continued for a minimum of thirty minutes longer, or until the bird made three successful foraging bouts. At the end of the run, the bird was returned to its home cage and the equipment was cleaned and flushed.

## Section III.   Results

### Initial Learning

In all cases the birds performed significantly better than chance within the first 10 minutes of the test (Table 13).   In this case, chance performance was 12.5% correct probes.   During this initial period, the birds showed the poorest performance with the uncued panel (Fig. 18); even so, they averaged over 60% correct visits in the first 30 minutes.   Performance in the medium and long exposure treatments showed continual improvement, reaching nearly perfect performance in the close cue treatments and exceeding 90% correct performance in all treatments by the end of the long, 300 minute exposure period.

| Exposure Time | | Cue Distance | | |
|---|---|---|---|---|
| | | Close | Far | Uncued |
| Short | t value | 9.593 | 4.605 | 3.238 |
| | probability | 0.000 | 0.001 | 0.008 |
| Medium | t value | 16.787 | 10.196 | 3.336 |
| | probability | 0.000 | 0.000 | 0.007 |
| Long | t value | 6.855 | 15.973 | 4.291 |
| | probability | 0.000 | 0.000 | 0.001 |

Table 13.   Differences between average proportion correct and random visitation for all treatments in the first 10 minutes of experimental runs.   Analysis is based on a one sample t test against a random performance level of 0.125 (one chance out of 8).   Terms for cue distance and exposure time are explained in the methods section. Probabilities indicate the likelihood that performance did not differ from success due solely to random chance.

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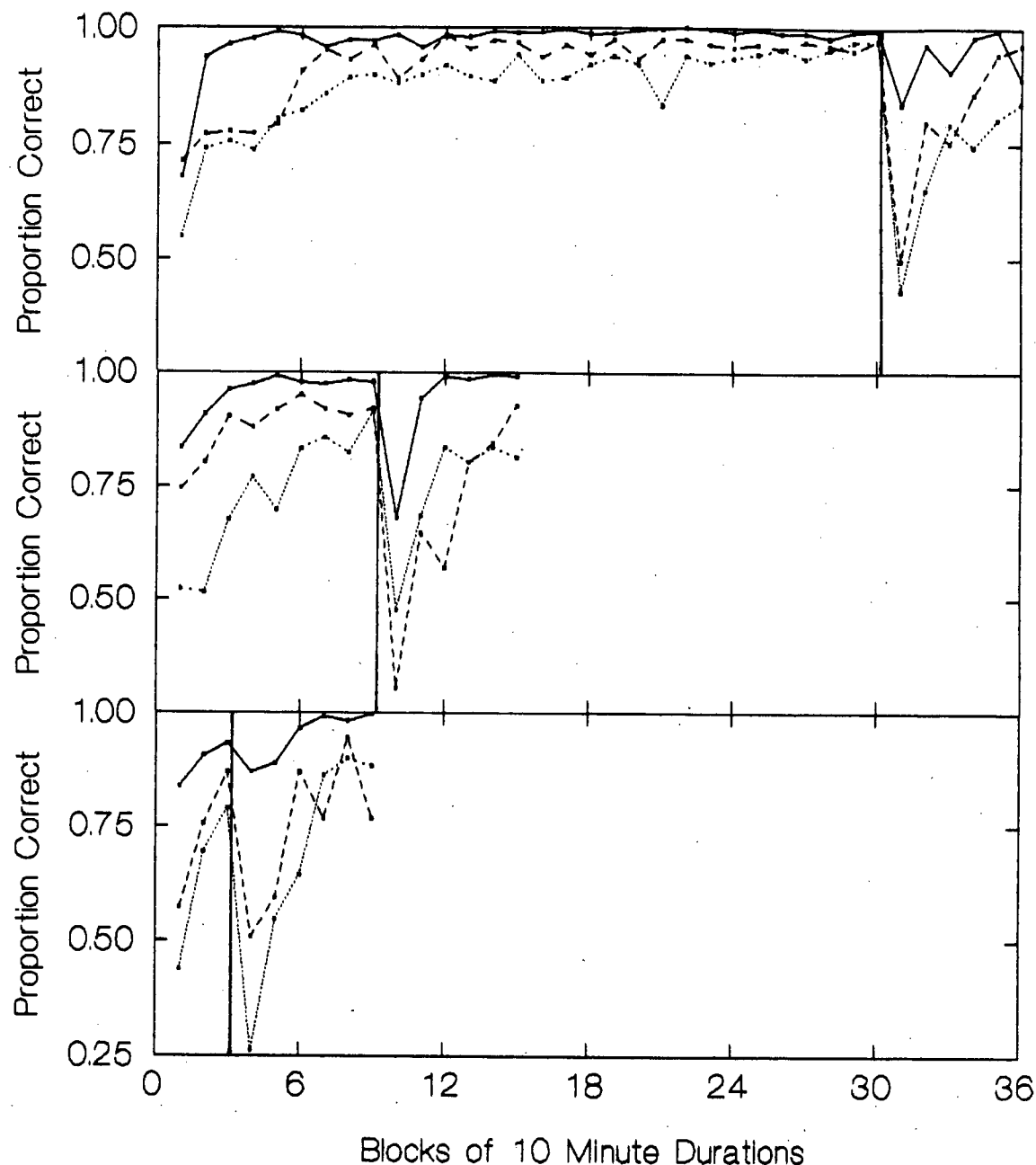
Figure 18. Proportion of visits that were to the correct feeder for each of the 9 treatments. Each line represents the average of the 12 birds from each treatment. The X axis is divided into blocks of 10 minute durations. The top panel shows the 3 long (300 minute) treatments, the middle panel contains the 3 medium (90 minute) treatments and the bottom panel has the 3 short (30 minute) exposure treatments. The feeder switch is indicated by the vertical line through the graphs on the 3 panels. On all 3 panels, the solid line shows the close cue treatment, the dashed line is the far cue treatment and the dotted line is the uncued treatment.

Performance followed the predicted order for all three exposure times.  Birds using close cues performed best, followed by birds using far cues, who in turn performed better than birds using the uncued panel (Fig. 18).

## Switch Effect

Performance in the period after the switch also followed the predicted order.  Birds in uncued treatments persisted longest in visits to the previously rewarding feeder after the switch, followed by birds with far cues and finally birds with close cues (Fig. 19).  Birds with long pre-switch exposure times persisted longest, followed by birds with medium exposures and finally those with a short exposure to the initial feeder positions.

### Time, Distance, and the Interaction Effect

Two way analysis of variance of the effect of cue distance and exposure time shows that both factors significantly affect post-switch feeding behaviour.  This is most apparent in the persistence of the birds in returning to the formerly good feeder.  Using this criterion, distance to the cue ($F = 19.953$, $df = 2,99$, $p \approx 0.000$) and time ($F = 8.622$, $df = 2,99$, $p \approx 0.000$) are both highly significant, but distance is a stronger effect than time of exposure.  This comparison is most clear for the proportion of correct visits in the 30 minute period after the feeder switch.  In this case, distance to the cue is still a highly
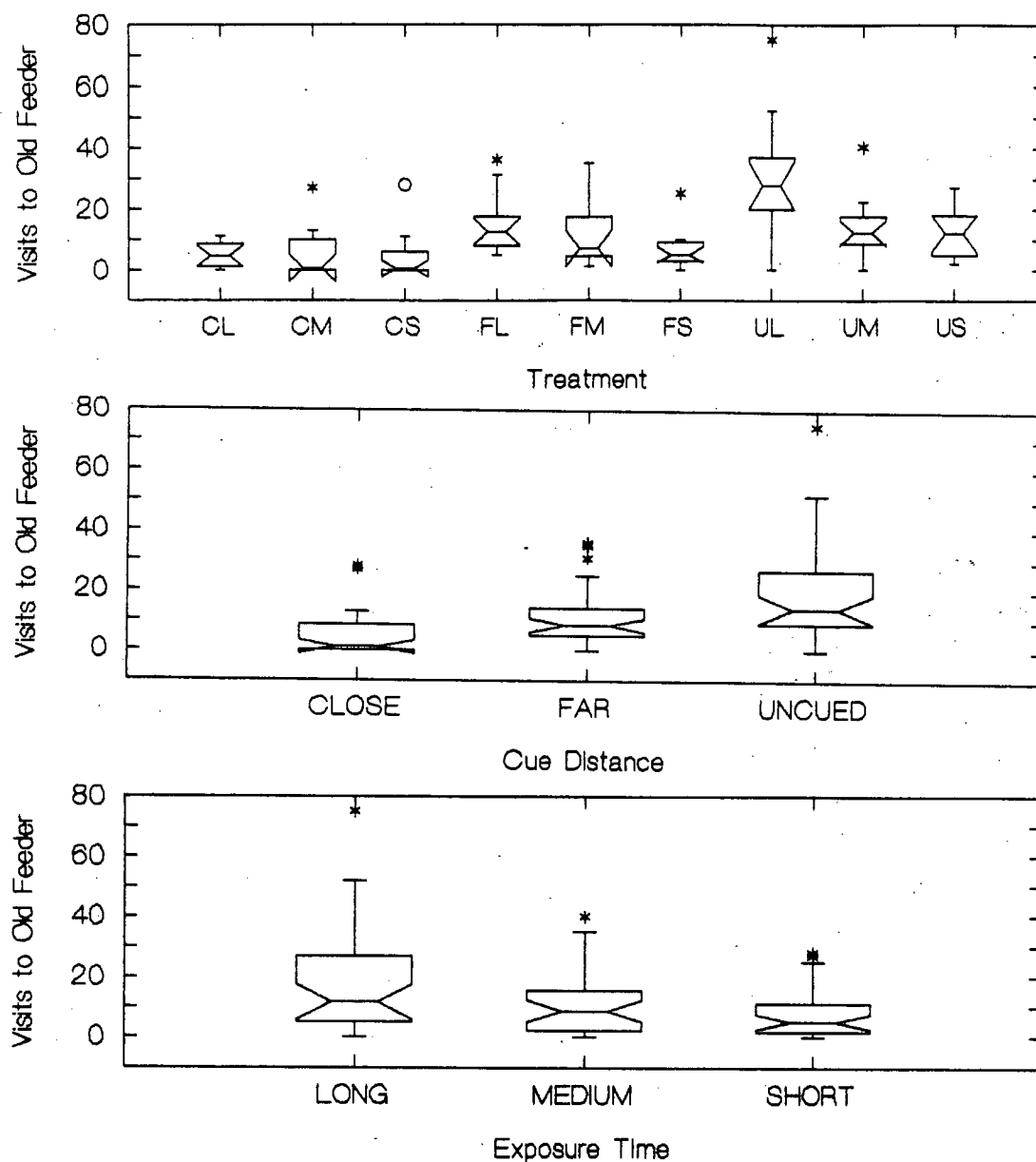
Figure 19. Box plots of number of visits by birds to the formerly good feeder after the feeder switch. The top panel shows each treatment, the middle panel is birds grouped by cue distance and the bottom panel is grouped by duration of exposure. In each box plot the central horizontal line is the median, the upper and lower box edges are the first and third quartiles (the difference between these quartiles is known as the fourth spread), the vertical whiskers extend out to 1.5 times the fourth spread, asterisks indicate mild outliers (more than 1.5 times the fourth spread), the empty circle is an extreme outlier (more than 3 times the fourth spread), and the notches in the vertical edges of the boxes represent 95% confidence intervals (which may extend beyond the fourth spread causing a folded edge to the box). Treatment acronyms in the top panel are based on cue distance (C = close, F = far and U = uncued) and duration of exposure (S = short, M = medium and L = long).

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significant effect on bird performance (F = 41.472, df = 2,99, p ≈ 0.000) but the effect of time on post-switch performance is no longer significant (F = 0.214, df = 2,99, p = 0.808).

## Differences in Persistence

Analyses of variance for the effects of changing the rewarding feeders show that individual treatments differ significantly in the performance birds achieved. These highly significant differences can be seen in the number of feeding bouts required for birds to first find the new good feeder (F = 3.803, df = 8,99. p = 0.001), the number of bouts until birds visited the new good feeder as the first visit of a feeding bout (F = 4.683, df = 8,99. p ≈ 0.000), and the number of bouts until the third time the bird visited the good feeder as its first visit of a feeding bout (F = 6.664, df = 8,99. p ≈ 0.000).

| Treatment | New Good Feeder | | | Old Good Feeder | | | Neither | | |
|-----------|-------|-----|--------|-------|-----|--------|-------|-----|--------|
|           | Close | Far | Uncued | Close | Far | Uncued | Close | Far | Uncued |
| Short     | 7     | 3   | 1      | 2     | 5   | 4      | 3     | 4   | 7      |
| Medium    | 6     | 1   | 0      | 4     | 5   | 4      | 2     | 8   | 8      |
| Long      | 4     | 0   | 0      | 5     | 9   | 7      | 3     | 3   | 5      |

Table 14. Post-switch performance of birds in the different treatments. Figures for new good feeder are the number of birds who went directly to the new rewarding feeder immediately following the feeder switch. Old good feeder shows the number of birds who went immediately to the formerly rewarding feeder after the switch, while neither is the number of birds who went to neither the new or old rewarding feeder.

Birds' behaviour differed dramatically among treatments (Table 14). This table suggests that persistence was greatest in the uncued array, that switching occurred most rapidly in the close cue array and birds in the uncued treatments were more likely, on their first visit after the feeder switch, to choose feeders that had never been rewarding. The only significant difference, however, was that fewer birds switched immediately to the new rewarding feeder at greater cue distances ($\chi^2$ = 19.736, df = 2, p ≈ 0.000). Analysis of the pairwise differences is also not clear. Based on a Tukey analysis, the order of the treatments is indicative of the predicted order, but many of the differences are not significant (Fig. 20).

CL
CS CM FS UM  FL      FM US          UL

Find New Feeder

CS            UM
CM CL  FS           FL    FM  US          UL

Correct First Visit

CS CL CM          FS              UM FM FL    US   UL

3 Correct First Visits

0  1  2  3  4  5  6  7  8  9  10 11 12 13 14 15 16 17 18 19 20

# Number of Bouts to Criterion
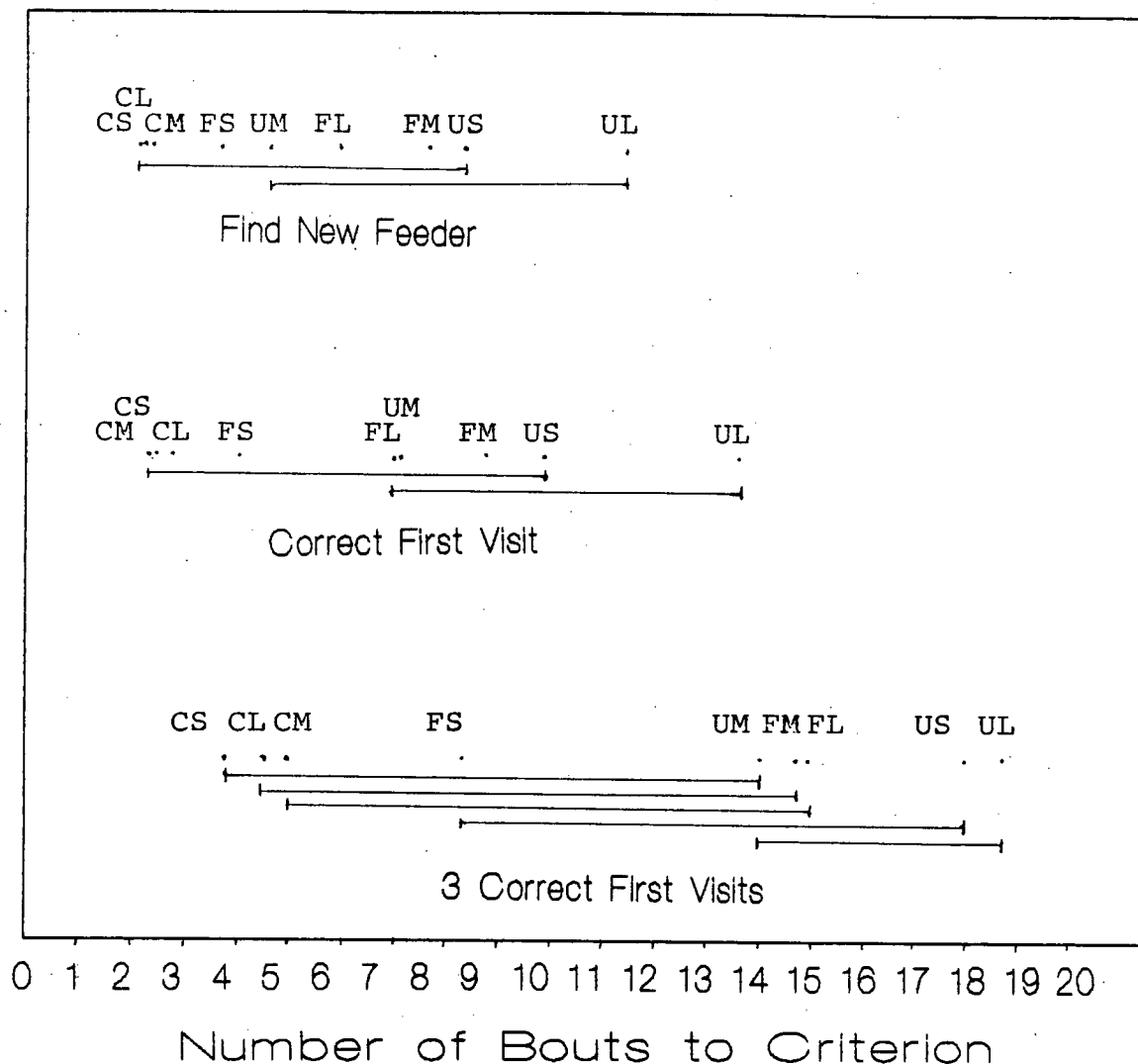
Figure 20.   Tukey honestly significant difference analysis
of differences in mean post-switch foraging success.   Lines
connecting   treatments   indicate   that   there   was   not   a
significant difference in performance for the birds in these
treatments.    3 increasingly demanding criteria to measure
new learning by the birds are shown.    The top group of
differences is measured by the number of bouts until birds
found the new rewarding feeder.    The middle set of figures
shows   the   number   of   bouts   until   birds   visited   the   new
rewarding feeder as the first visit of a feeding bout.    The
bottom group shows the number of bouts until the third time
birds visited the new rewarding feeder as the first feeder
in a feeding bout.    Treatment acronyms are compounded of cue
distance (C = close, F = far and U = uncued) and duration of
exposure before the feeder switch (S = short, M = medium and
L = long).

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## Section IV. Discussion

These experiments provide further evidence that hummingbirds easily learn spatial associations accurately even when cues are displaced from feeders (Brown, 1994; Brown and Gass, 1993). Hummingbirds learn spatial associations more slowly and less well as the distance between cue site and reward site increases, corroborating Brown's findings. This is similar to the results of other studies (Milner *et al.*, 1979; Pinel *et al.*, 1986; Stollnitz and Schrier, 1962).

The birds responded similarly to all treatments but their speed of learning and peak performance varied between treatments. The birds in all treatments showed gradual and continual improvement in performance until they reached an asymptote that was less than perfect. While some of this lack of perfection was due to errors, birds also may have been sampling to detect changes in the environment and to search for survival requirements beyond pure calories, as documented by several authors (Brown and Cook, 1986; Carroll and Moore, 1993; Collias and Collias, 1968; Draulans, 1988; Forkman, 1991; Gass, 1985; Kramer and Weary, 1991; Smith, 1974; Wilkie and Spetch, 1980; Wilkie *et al.*, 1981).

Treatments differed strongly in birds' responses to a switch in feeder profitability. While both duration of experience of static patterns and distance between cues and

feeders produced significant effects, separations between cues and feeders affected behavioural persistence more strongly. This distance relationship is consistent with the increasing learning difficulty other authors have seen for increasing separation between cues and reward sites (Brown, 1994; Davis, 1974; Pinel *et al.*, 1986; Schrier *et al.*, 1963; Stollnitz and Schrier, 1962). The relationship between experience and persistence of previously successful behaviour is consistent with the results of Chapter 2.

## Association, Spatial Association and Spatial Memory

The hummingbirds learned faster with close cues, which encouraged standard associative learning most strongly, although this treatment still required the use of spatial memory to orient from cues to their associated rewarding feeders. Previous studies have suggested that animals learn associative tasks rapidly by using trial unique working memory of cue and response position (memories that are quickly laid down and discarded at the end of the task) to increase speed and efficiency in their tasks (Barnes, 1988; Kamil and Mauldin, 1975). Spatial memory tasks seem to require the use of long term memory (Goelet *et al.*, 1986; Nadel and Willner, 1980).

### Cue Distance

The uncued treatments most closely correspond to a pure spatial memory task. It seems likely that birds in the near and far cue treatments are learning both an associative task

and a spatial memory one. Birds learned the spatial memory task (uncued treatment) slower than a task biased towards the associative learning component of the task (close cue treatment). Performance in the far cue treatment fell between these two extremes; while there were cues to help locate the rewarding feeder, their greater distance from the rewards made them more difficult to use and probably biased the birds to rely more on spatial memory. This may account for the intermediate level of performance on this set of treatments.

How animals use cues or landmarks (in this case the lit LED, which also acts as a cue to the profitability of its associated feeder) to locate objects is still not clear. There is a definite geometric component to the use of landmarks (Cheng, 1986 and 1989; Cheng and Gallistel, 1984; Hermer and Spelke, 1994), although it appears that a simple arithmetic model of vector addition of distances from landmarks to their related locations does not apply (Cheng, 1990; Spetch *et al.*, 1992). If the birds learn to use the LEDs to point to the direction of the rewarding feeder, the simplest rule to learn might be to go to the feeder nearest to the lit LED. Thompson (1994) showed that hummingbirds will use this strategy. Several studies show that animals prefer to use near landmarks over almost any other landmark option in navigation (Bennett, 1993; Cheng, 1989; Cheng *et al.*, 1987b; Vander Wall, 1982). The distance between landmark and reward site may be calculated metrically

(Cheng, 1990; Gallistel, 1989) or by the size of the landmark's retinal image (Collett *et al.*, 1992; Gould, 1987; Srinivasan *et al.*, 1989) although the latter measure seems to apply in limited cases (Cheng *et al.*, 1987b), and primarily in invertebrates such as honeybees.

The more complex task of developing a vector relationship (distance and direction) between a landmark and reward site is possible, but may not be necessary in this case, where a simple rule of thumb such as going to the feeder nearest the cue will suffice. Certainly, if a more complex relationship than the one in this experiment occurs, hummingbirds can learn it. G. Brown (1992) showed that hummingbirds can learn to go to a feeder other than the one closest to the lit LED. Similarly, in Thompson's (1994) experiments, hummingbirds used geometric relationships among cues and response sites to obtain a reward.

Birds persisted longer in visiting the formerly good feeder (after a switch of both profitability and cue) if the cue was further from the feeder. This suggests animals relying more on spatial memory respond less rapidly to change than those relying more on the associative components of spatial association learning (Roberts *et al.*, 1988). Although birds using the close cue panel had visible indicators of a change, those using spatial memory with the uncued panel had to rely totally on trial and error to learn the new location of the rewarding feeder. Birds on the cued panels simply had to transfer their spatial association to

the new cue position instead of modifying a cognitive map, and they did this more quickly when cues were close to feeders.

### Duration of Exposure

As birds gained experience over time with a stable feeder position, their performance improved in all treatments. By the end of the 300 minute exposure time, birds were performing well above ninety percent accuracy, on average, on all 3 panels. This suggests that in a stable environment, birds perform as well using spatial memory as with spatial association learning, but only after they have gained sufficient experience in utilizing their surroundings. It should be noted, of course, that 5 hours of exposure to an environment is not a long time. Even though spatial memory developed more slowly than spatial association, the effort required to learn a spatial memory task paid dividends in a relatively short time in this experiment.

### Advantages and Disadvantages

Spatial memory use corresponds to slower learning and longer intervals before responding after encountering a stimulus (Brown and Cook, 1986), while associations, especially those using working memory, can increase the speed of learning a task (Kamil and Mauldin, 1975). The advantage of learning a simple, contiguous association rather than a spatial relationship seems especially

important in short term tasks or variable environments. In a long term task or a stable environment, performance relying on spatial memory can approach that relying on associative learning. A similar relationship should exist for spatial association learning, which combines association learning with spatial memory, so that all three modes of learning should yield high levels of performance in stable environments.

Associations between cues and rewards need not be tied to particular points in space. As a result, birds who learned an association between cue and reward could apply this relationship when both cue and profitable feeder moved. This portability of either contiguous associations or the spatial associations in my experiment provides a strong learning advantage in environments with the kind of redundancy that makes portability of associations valuable. In tasks that allow associative learning, the bird needs to learn only this association, and is not required to learn the various geometric relationships and other items necessary for spatial mapping. In spatial association learning, smaller separations between cue and response site improve performance, perhaps because the spatial relationship between the two is easier to define than for more distant pairings of cue and response site. This idea is consistent with Gestalt principles of spatial proximity, which suggest that objects will be perceived as sets if they are closer to each other than to other neighbouring stimuli .

(Pomerantz, 1981; Wertheimer, 1950). Animals prefer to use near landmarks to navigate (Bennett, 1993; Cheng, 1989; Cheng *et al.*, 1987b; Vander Wall, 1982), perhaps for similar reasons.

If speed of learning and portability are advantages of associative learning, one of its disadvantages is its susceptibility to interference, perhaps due to its reliance on working memory to speed up learning (Barnes, 1988). Several studies have documented the effects of interference on associative learning in rats and other animals (Olton, 1985; Zentall *et al.*, 1990). As well, associative learning is susceptible to decay when there is a significant delay between the stimulus and the response, between initial training and testing, or merely between periods when the animal can respond (Kamil and Mauldin, 1975). Long intertrial periods may be sufficient to reduce performance in laboratory environments. One possibility is that animals are not always able to discriminate between trial and intertrial periods, so that the learned association may be extinguished during non-rewarding intertrials (Hoffman and Maki, 1986; Maki, 1979).

In contrast to associative learning, spatial memory seems resistant, if not immune, to these forms of interference, presumably due to the storage of spatial relationships in long term memory (Maki *et al.*, 1979). This immunity to interference may also provide a way to distinguish between the use of cognitive maps by animals and

lists of separate locations. Lists are subject to interference, as demonstrated with black-capped chickadees (Crystal and Shettleworth, 1994). This shortcoming of spatial lists suggests an advantage of cognitive maps over spatial lists. As a result of the resistance to interference, animals using spatial memory are able to learn conflicting tasks in different contexts and perform well in all of them (Beatty and Shavalia, 1980; Maki *et al.*, 1979).

In previous studies of spatial association (G. Brown, 1992; Brown, 1994; Brown and Gass, 1993; Thompson, 1994), birds showed no appreciable decline in performance overnight in multi-day experiments. Perhaps spatial association tasks suffer less from temporal declines in performance than simple associative learning, although it may be that hummingbirds are resistant to any form of forgetting over this time frame.

Spatial memories can be maintained for long periods of time. Storing birds can remember cache sites for the duration of a winter or longer (Balda, 1980; Balda and Kamil, 1989 and 1992; Healy and Krebs, 1992; Sherry, 1984; Shettleworth, 1983). Non-storing animals also seem to retain spatial information for a long time (Balda and Kamil, 1992; Healy and Krebs, 1992; Hitchcock and Sherry, 1990; Menzel, 1991). In the laboratory, rats have performed spatial tasks ten months after training and testing (Bierley *et al.*, 1987). Hummingbirds and other species return to the

same breeding and feeding sites annually (Cole *et al.*, 1982; Colwell, 1974; Gass, 1985; Roberts, 1979).

One of the main disadvantages of spatial memory is also due to its long term nature. Due to their storage in long term memory, spatial maps are resistant to change and may result in inappropriate behaviour in the face of change. There are various examples of animals dodging barriers that are no longer present or searching for food or nests in places that are no longer correct (Collett *et al.*, 1986 and 1993; Gallistel, 1989; Kamil and Balda, 1985; Speakman and O'Keefe, 1989; Spetch *et al.*, 1992; Sutherland and Gass, in press).

The persistence of birds in visiting incorrect feeders seen in my experiments is an example of how spatial memories can rapidly become inappropriate. While animals relying purely on cue associations are subject to interference and loss of recall after even short delays (Kamil and Mauldin, 1975), the portability of their association allows them to respond rapidly to changes in their environment, as long as those changes don't affect the relationship between cue and reward. All of the treatments in my experiments required spatial memory, although the increasing importance of the associative component of the task in the far and close cue treatments decreased persistence at formerly rewarding feeders since birds could use the same learned association between cue and reward for the new feeder location.

Change can cause problems for animals using spatial memory, but some animals respond to regular environmental change by remembering the pattern of temporal changes. These temporal maps have been documented for daily fluctuations in the environment (Biebach *et al.*, 1989; Krebs and Biebach, 1989; Olton, 1990). Perhaps animals can also develop temporal maps for seasonal change, such as migratory species encounter.

The differing advantages and disadvantages of associative and spatial learning does not mean that they cannot work in concert with each other, as spatial association demonstrates they can do. In fact, there is evidence that in a stable environment, a working map of the surroundings may benefit associative learning as well as functioning in spatial memory (Spetch and Honig, 1988). There are many natural examples of the interaction of spatial and association learning including use of marks on banner petals to assess nectar quality of flowers by bees (Gori, 1989), and the use of circling vultures by predators to locate prey (Houston, 1983; Rabenold, 1983 and 1987). G. Brown (1992) lists other examples including social transmission of foraging information.

### Memory Load

Maintaining both spatial and temporal maps places a heavy load on the memory capacity of animals. Energy models of hummingbird foraging suggest that in some cases the costs

of long term memory of foraging environments may outweigh the benefits (Armstrong *et al.*, 1987). In my experiments (and others, for instance Sutherland, 1985) continuing revisits to emptied feeders suggests that the birds neglected to use working memory to remember visits to individual locations. Roberts (1988), also found little evidence that pigeons retained a working memory of visitations within patches, and suggested that rats have similar deficiencies. Revisitations during bouts of foraging in given patches may in fact be evidence that an animal has learned the patch boundaries rather than the individual components of the patch (Mellgren and Roper, 1986). This would then suggest that the animals are reducing memory load by chunking.

Chunking is another way to reduce the memory load imposed by cognitive mapping (Capelli *et al.*, 1986). This process of generalizing the features of the environment may be what leads to high revisitation rates under some experimental protocols. The experimental animal stores only the overall features of the environment rather than the fine grained details (Gass, 1985).

Nishimura (1994) suggested that the advantages of learning are tightly tied to the memory capacity of the animal. If the animal has a limited capacity, the advantages of learning are soon lost. This is especially true when resources are depressed, so that the animal must remember more information for each potential reward. Memory

load seems to be a significant problem for animals in some situations, so that they modify their memory use throughout a prolonged task in response to this load (Cook *et al.*, 1985).

## Conclusions

These experiments have demonstrated that hummingbirds can learn both spatial memory tasks and spatial associations, for which I believe the latter requires a combination of spatial memory and associative learning. Hummingbirds learn spatial association tasks more rapidly than tasks that rely solely on spatial memory, achieving high levels of performance after a very short time interval. While the spatial memory tasks I used required a slightly longer learning period, the birds eventually achieved performance levels comparable to those for spatial association tasks.

The amount of experience with a specific rewarding pattern affects the persistence of the birds' behaviour once the pattern has changed. Generally, the longer the period of stability before a pattern switch, the longer the animal will resist changing its previously successful foraging behaviour. The effect of exposure time appears to have less influence on spatial association tasks than spatial memory ones.

The difficulty of forming a spatial association between a cue and reward site is strongly dependent on the spatial

separation of the two sites. Greater separations slow the speed of learning, and tend to result in more reliance on spatial memory and greater persistence in the face of change.

Greater separations between cue and reward and longer periods of exposure favour the use of spatial memory over spatial association, while the opposite is true for cues close to the reward and short periods of exposure.

# Chapter 5.

## General Discussion

Various questions arise out of studies like mine, but Rescorla and Holland (1982) narrowed them down to three basic ones: What conditions produce learning? How is learning revealed in performance? What is learned? All three questions deal with external factors and their role in learning. I will address the first two questions briefly, then expand the third to ask: What do animals learn about their environments and how do they learn it?

### What Conditions Produce Learning?

In these studies, the birds learned spatial relationships among features of their foraging environments under a variety of conditions. Learning was promoted by the use of visual and auditory cues and landmarks and by the motivation of the birds to feed. In all experiments the birds were provided with visual cues to feeder locations in the form of orange rings surrounding the feeders that revealed nothing about their profitability. In the experiments described in chapter 2, feeders offered only this information, so birds had to learn the pattern of rewarding and non-rewarding feeders using position only, as

in the experiments described in Sutherland and Gass (in press). Most treatments described in chapter 3 provided additional information in the form of landmarks. In some cases these landmarks also included information about the profitability of feeders. In 6 of the 9 treatments of the experiment described in chapter 4 they could use spatially separated LED cues to rewarding feeders.

Aside from the various cues, landmarks and arrays of feeders, the main condition that led to learning was motivation of the birds to feed frequently and their expectancy of reward from array feeders. I will deal with the importance of each of these factors as part of my consideration of what is learned.

## How is Learning Revealed in Performance?

In these experiments the birds demonstrated learning through their improving performance over time. I reported this performance only through two measures of first visits to feeders in trials because birds continued to revisit locations even after depleting them. Their failure to learn to avoid revisiting depleted feeders suggests that they learned rewarding regions of the array rather than learning individual rewarding feeder locations. Indicated by their first visits to locations in trials, the birds showed rapid progression to rates of feeding well above chance, revealing that they had begun to learn the locations of rewarding feeders within five minutes of exposure to the arrays (five

trials).  Five minutes of exposure here refers to actual foraging opportunities and excludes intertrial periods when they were unable to see or visit the array but could integrate information from previous visits.

The birds also provided evidence of learning when their performance dropped after pattern reversals.  In this case, decreased performance demonstrated their persistence in visiting feeders which had been but were no longer rewarding.  The magnitude of their drop in performance, as measured by the number of incorrect visits they made in the trials immediately following the reversal, was positively related to the duration of exposure to the pattern before the switch.

## What is Learned about their Environments and How?

### Pattern Learning

These experiments reinforced earlier conclusions that hummingbirds rapidly learn both one and two dimensional patterns of feeders.  While this work was based primarily on a two dimensional array of feeders divided simply into 4 quarters, hummingbirds learned more complex patterns in past work (Sutherland and Gass, in press).  In my studies, not only did the birds learn the patterns of rewarding feeders, but also several kinds of landmarks and cues that signalled the location of rewarding feeders or demarcated patches of feeders.  They did this using both spatial memory and memory of spatial associations.

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**Chunking**

If the birds learned the pattern of feeders rather than individual locations, they were exhibiting chunking, which is the process of grouping stimuli together into a single mental unit (Olton, 1985). Chunking has been demonstrated in studies with humans and laboratory animals (Capaldie *et al.*, 1984 and 1986; Miller, 1956), although it is difficult to substantiate because remembering all of the stimuli separately could produce results very similar to chunking them into units (Sutherland and Gass, in press). If an animal loses the ability to distinguish individual items in a group while still demonstrating knowledge of the grouped structure this may provide evidence for chunking of the separate items into an overall pattern (Olton *et al.*, 1980).

Animals appear to chunk items together based on their perception of relationships of various kinds between them. Hummingbirds may be chunking individual feeders into an overall pattern in my array studies. Their tendency to revisit individual feeders, to make most errors on the edges of feeder groups and to perform better when rewarding feeders are marked with edge landmarks, all argue that they are learning a pattern of rewarding feeders (chunking) rather than learning the individual feeders. This evidence is indirect and still inconclusive, although birds demonstrated it consistently.

One of the more prominent results from these studies was that the birds did not learn to avoid revisiting emptied feeder locations. While they effectively learned the overall pattern of feeders, they showed no improvement in revisitation rates during experiments. Sutherland (1985) also observed a high rate of feeder revisitation and no improvement in his work on pattern learning with this same species in similar arrays, Shettleworth and Krebs (1982) found continuing revisitation to emptied cache sites in marsh tits, and Roberts (1988) found no evidence for use of working spatial memory to avoid within patch revisitation by pigeons.

In a modelling study, Armstrong *et al.* (1987) predicted a different result than this, suggesting that use of short term memory by hummingbirds to avoid flower revisits during foraging bouts in patches would be energetically beneficial. Brown (1987) found that pigeons could integrate a group of elements into a unified pattern if they were trained on the separate elements, but if they were trained with a compound group of items, they were unable to dissociate the grouped items to use the separate elements. One possible explanation for continuing revisitation in my study and Sutherland's, despite the theoretical energy benefits suggested by Armstrong *et al.*'s models, is that once the birds chunked feeders into patterns they were unable to dissociate individual feeders.

## Spatial Memory

In chapter 4, I demonstrated that hummingbirds learn locations of rewarding feeders faster when the profitability of the individual feeders is cued. In the uncued treatments birds had to rely only on spatial memory alone rather than using a spatial association between feeder and reward cues. Since birds learned more slowly in the uncued treatments, this may suggest that spatial memory requires a longer learning period than spatial association. At the same time, however, spatial memory is resistant to interference learning or distractions (Maki *et al.*, 1979). Thus, it seems that items stored in spatial memory by birds are those to be remembered in the long term, and the experiment described in chapter 2 suggests the time course over which hummingbirds commit spatial patterns to long term memory. The importance of long term memory to spatial learning has been noted in several studies (Beatty and Shavalia, 1980; Kesner, 1980; Nadel and Willner, 1980).

## Cognitive Maps

The evidence that hummingbirds used cognitive maps in these experiments is based on visitation patterns and the evidence for chunking discussed above. If the birds were dead reckoning, they should show stereotyped approaches to the array and regimented sequences of visits once they began feeding. Such systematic patterns of feeding have been seen in insects such as bumblebees, euglossine bees and hawkmoths

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(Dreisig, 1989; Pyke and Cartar, 1992) as well as more advanced animals such as nectar-feeding birds and bats (Kamil, 1978; Pyke, 1978) and in previous studies with hummingbirds using more complex patterns of feeders (Sutherland, 1985). I found no evidence of systematic foraging in any of the experiments I conducted. Scholl (1987) suggested that the ability of animals to access all sites in a cognitive map with equal ease was one of its main advantages over dead reckoning, where the need to follow a series of memorized vectors makes some sites more difficult to access.

### Landmarks and Cues

In the experiments of chapter 3, the birds demonstrated that they can use landmarks to enhance their learning of spatial patterns. Edge landmarks that differentiated rewarding and non-rewarding areas of the array were more useful than circular disks marking the centres of these areas. Since lines have a directional component that circles lack, perhaps the birds used this additional information to help navigate to rewarding feeders. The lines that marked edges of rewarding groups of feeders were joined into squares, so aside from the possible left-right or up-down directions birds could derive from them, they could learn that inside two of the squares was rewarding, while outside them (inside the other two squares) was non-rewarding.

The birds in all of my experiments used cues to locate the feeders. In all the array treatments they had surrounding orange rings as cues to feeder locations that they may or may not have used as information. In the chapter 4 experiments they used spatially separated LEDs to identify rewarding feeders. In the studies of chapter 3, they used colour to identify rewarding groups of feeders on the array. This provided some benefits to learning, but the incremental value was not large. The benefits of providing cues to profitability were more apparent in the experiments of chapter 4. In these studies, the addition of reward cues significantly improved performance. Performance was higher when cues were closer to the rewarding feeder, which was also found in previous studies that have suggested that increasing separation between cue and reward increases the learning difficulty (G. Brown, 1992; Brown and Gass, 1993; Pinel *et al.*, 1986; Stollnitz and Schrier, 1962).

In my experiments birds may also have used cues external to the array. I have no direct evidence that the birds oriented themselves via external visual cues such as distance to the walls and lights but I believe that they used these global cues when they were first developing cognitive maps to exploit the array. Distal cues are an important aspect in the development of cognitive maps (Ellen, 1980; Ellen *et al.*, 1984; Gallistel, 1989; Mellgren and Roper, 1986; Miller *et al.*, 1984; Morris, 1981; Spetch

and Edwards, 1988; Spetch and Honig, 1988; Sutherland and Dyck, 1984; Suzuki *et al.*, 1980). Even an author who did not accept the idea of cognitive mapping suggested that spatial learning was a conditioned response to distal cues (Restle, 1957).

### Expectancy and Persistence

By showing that birds persist in formerly profitable patterns of foraging in the face of sudden environmental shifts that make this behaviour unprofitable, all of my experiments demonstrated that birds' expectations about the distribution of rewarding feeders was affected by the amount of time they spent using that pattern. As exposure to a pattern increased, so did the birds' persistence in feeding at the formerly rewarding feeders after the switch. In laboratory studies, it appears that the expectancy of reward is directly tied to the past frequency and magnitude of reward (Mellgren *et al.*, 1973). Expectancy is also an increasing function of the number of rewarding trials (Morris and Capaldie, 1979). Chapter 2 shows that persistent visitation to formerly profitable feeders increased only slightly with the change from 10 to 20 exposure trials, presumably because birds' success with the distribution of rewarding feeders was too limited in time to induce a large degree of persistence after the switch. Persistence at unprofitable feeders then increased rapidly over intermediate numbers of trials before plateauing after

an exposure period of about 40 trials. Possibly persistence stopped increasing because there is a limit to the amount of experience that is stored in a bird's memory. This type of result was predicted by several authors, who developed the hypothesis of a limited and weighted memory window to explain limitations on animal learning and memory (Kacelnik *et al.*, 1987; McNamara and Houston, 1987; McNamara *et al.*, 1989).

The birds in all of my experiments relearned patterns of rewarding feeders after the pattern had been reversed. Although I introduced a complete and sudden reversal of the pattern of rewarding feeders, this was still a one time change in the distribution of feeders. Perhaps subsequent and repeated reversals would have produced enough temporal variability to make learning unprofitable. In field studies with black-chinned hummingbirds, Valone (1992) found that birds in stable environments relied on prior experience to find food. In variable environments some birds adopted a sampling approach, but birds using memory were more successful foragers. Learning is more effective in conservative environments where change is less likely to reduce the profitability of behaviour based on memory (Nishimura, 1994).

Animals respond to unpredictable variation by discounting the value of highly unpredictable resources (Bowers and Adams-Manson, 1993). Temporal variability plays

an important role in foraging choices for many species (Caraco, 1982; Caraco and Lima, 1987; Gibbon *et al.*, 1988; Stephens, 1981). Animals as diverse as honeybees and tamarins, for instance, respond to both the mean and variance of food sources and adjust their foraging choices based on changing energy requirements (Cartar, 1991; Garber, 1988a; Stephens and Paton, 1986). As environmental instability increases, animals reduce extraneous behaviours and focus on maximizing their short term gains (Forkman, 1991). At some point of increasing environmental instability and unpredictability, individuals should abandon a strategy dependent on learning and memory because it will lose its energetic advantage.

## Future Studies

My studies have left several avenues open that need further exploration. The evidence that hummingbirds synthesize the distribution of rewarding feeders into a single pattern rather than learning individual feeder locations is strongly suggestive but still not conclusive. Better ways to discriminate between these two possibilities are needed.

Work by Brown (1987) might provide an approach to this problem. He suggested that animals who grouped a set of elements into a single unit or pattern could not transfer that learning back to the individual elements; in the case of hummingbird spatial memory this would mean that once they

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have learned a pattern they essentially throw away the memory of individual locations. If hummingbirds were trained to use an array with a simple but large pattern of rewarding and non-rewarding feeders, and if they learn a cohesive pattern and not just individual locations, they should not change visit patterns to a small number of reward locations that are changed without warning to non-rewarding, but are still surrounded by rewarding feeders.

The removal of small pieces of a pattern of rewarding feeders (by making feeders non-rewarding) could be continued to the point where there was a significant and growing drop in rewards available from the profitable group of feeders. At some point in the continuing deterioration of the pattern, birds should abandon their expectations and reliance on memory of reward based on the pattern of feeders and change to exploitation of the array based either on memory of individual locations (if they could) or without reference to memory of past visits.

The role of the stability of environments could also be investigated by carrying out multiple pattern reversals. In my experiments, birds relearned reversed patterns, but this might change if the reversals happened more than once. As the number or frequency of pattern reversals increased, this experimental protocol would begin to resemble the constant shifts in reward sites seen in many psychological experiments where animals learn the association between

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stimulus and response and apply that association irrespective of spatial position. In this spatial memory experiment, however, animals would lack a simple associative rule which they could apply.

Another area that needs further investigation is visitation patterns in natural habitats to contrast random, systematic and area restricted search methods. The work that has been done so far in this regard (Kamil, 1978; Wolf and Hainsworth, 1983; Wolf and Hainsworth, 1991), is intriguing and seems to be compatible with laboratory studies but many questions remain unanswered. One item that needs detailed investigation is the degree and effect of revisitation to nectar sources by nectar-feeding animals. Modelling studies (Armstrong *et al.*, 1987) seem to contradict the results seen in laboratory studies such as mine. The reasons behind this difference need to be examined. If the energetic arguments raised by the models are accurate, why do animals in the laboratory show continuing revisitation? Is revisitation due to integration of feeder locations into a non-dissociable pattern? Is this behaviour also seen in foraging behaviour in the wild?

Finally, one of the drawbacks to working with rufous hummingbirds is that they are highly territorial and antisocial. As a result, observational learning and social communication are difficult to explore, especially in a laboratory environment, which reduces the general

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applicability of the results from hummingbird studies to date. These two forms of learning play a significant role in foraging by more social animals (Bryant and Church, 1974; Galef, 1976; Haefner and Crist, 1994; Rabenold, 1983) and by food-storing birds such as nutcrackers, jays and others (Baker *et al.*, 1988; Roberts, 1979; Sasvari, 1979; Shettleworth and Krebs, 1986; Vander Wall, 1982). Observational learning and communication are important adjuncts to spatial memory and visual cues in social species (Valone and Girardeau, 1993) and their ameliorating effects on dealing with environmental uncertainty and instability deserve investigation.

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